

THE QUARTZ FIELDS OF SOUTHERN AFRICA

flora, phytogeography, vegetation, and habitat ecology



Inaugural-Dissertation

zur

Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Universität zu Köln

vorgelegt von
Ute Schmiedel

aus Helsinki / Finnland

Köln 2002

Berichterstatter:

1. Referent: Prof. Dr. Norbert Jürgens,
2. Referent: Prof. Dr. Michael Melkonian
3. Referent: Prof. Dr. Burkhard Büdel

Tag der mündlichen Prüfung:

16.05.2002

CONTENTS

I	INTRODUCTION	13
I.1	The southern African quartz fields	13
I.2	Objectives	14
I.3	Previous research conducted on quartz fields or related issues	14
I.4	Definition of quartz fields	15
I.5	Definition of the obligate quartz-field flora	15
I.6	Geographical distribution of the quartz fields	16
I.7	Geomorphology of the quartz fields	18
II	MATERIAL AND METHODS	20
II.1	Field campaigns	20
II.2	Floristic data	20
II.2.1	Floristic and growth-form composition	20
II.2.2	Nomenclature	21
II.2.3	Source of floristic data	21
II.2.4	Phytogeographical analysis	21
II.3	Sampling	22
II.3.1	Vegetation data	22
II.3.2	Identification of the plant species	23
II.3.3	Nomenclature	24
II.3.4	Vouchers	24
II.3.5	Soil and habitat data determined in the field	24
II.4	Soil analysis	24
II.5	Vegetation analysis	26
II.5.1	Vegetation table	26
II.5.2	Gradient analyses	26
II.6	Climatic and microclimatic measurements	28
III	RESULTS	30
III.1	The phytogeographical subdivision of the quartz-field flora	30
III.1.1	Phytogeographical subdivision on species level	30
III.1.2	Phytogeographical patterns on regional scale: subdivision of the Knersvlakte Phytochorion	35
III.1.3	Phytogeographical subdivision on genus level	38
III.2	Comparison of the structural and floral features of the phytochoria	42
III.2.1	Growth-form spectra	42
III.2.2	Morphological and phenological features	48
III.3	Floral similarities between the phytochoria	51

III.3.1	Major taxonomic groups	51
III.3.2	Family spectra	54
III.3.3	Spectrum of genera	61
III.3.4	Species inventories of the phytochoria	66
III.3.5	Species-to-genera ratio	72
III.4	Patterns of diversity within the phytochoria	73
III.4.1	Centres of diversity of the obligate QFF	73
III.4.2	Species richness and size of the phytochoria	79
III.4.3	Relationship between growth-form diversity and species richness	80
III.5	Endemism in the obligate quartz-field flora	81
III.5.1	Growth-form spectra	82
III.5.2	Morphological and phenological features	83
III.5.3	Family spectra and major taxonomic groups	84
III.5.4	Spectra of widespread genera and species	86
III.6	Vegetation classification	88
III.6.1	Main groups within the vegetation	88
III.6.2	Little Karoo and adjacent areas	90
III.6.3	Knersvlakte	93
III.6.4	Riethuis-Wallekraal area	101
III.6.5	Richtersveld	102
III.6.6	Bushmanland-Warmbad area	102
III.7	Environmental variables controlling the species composition	103
III.7.1	Little Karoo	103
III.7.2	Knersvlakte	113
III.7.3	Riethuis-Wallekraal area	125
III.7.4	Richtersveld	128
III.7.5	Bushmanland-Warmbad area	133
III.8	Growth-form composition of the vegetation	136
III.8.1	Growth-form composition inside and outside the quartz fields of different phytochoria	136
III.8.2	Environmental variables controlling the growth-form composition of the vegetation	138
III.8.3	Distribution of growth forms along gradients of increasing quartz cover and salinity	149
III.9	Microclimatic conditions	152
III.9.1	Radiation	152
III.9.2	Air temperature near the ground	153
III.9.3	Soil-surface temperature	154
III.9.4	Leaf-surface temperature	158
III.9.5	Surface temperatures of a quartz stone	159
IV	DISCUSSION	161
IV.1	The floral composition of the obligate quartz-field flora	161
IV.1.1	Major taxonomic groups	161
IV.1.2	Family spectrum	162
IV.1.3	State of taxonomy within Mesembryanthema and its implication for the floral analysis	164
IV.1.4	Outliers in the phytogeographical analysis	164
IV.2	Indications for the age and the history of the quartz-field flora	165
IV.2.1	The formation of stone pavements	166
IV.2.2	Age of the stone pavements	167
IV.2.3	Palaeo-environmental conditions in South Africa	167
IV.2.4	Correspondence between the phytochoria	169
IV.2.5	Hypothetical trends in the floral history of the QFF	174
IV.2.6	Difference in diversity between the phytochoria	176
IV.2.7	Hypotheses on the floral history of the Knersvlakte	179

IV.3	The ecological background of the quartz-field flora	184
IV.4	Vegetation classification.....	185
IV.4.1	Little Karoo	185
IV.4.2	Knersvlakte	188
IV.4.3	Riethuis-Wallekraal area.....	189
IV.4.4	Richtersveld	189
IV.4.5	Bushmanland-Warmbad area.....	189
IV.5	Monodominance in the quartz-field vegetation	190
IV.6	Vegetation ecology of the quartz fields.....	191
IV.6.1	Little Karoo and adjacent areas	191
IV.6.2	Knersvlakte area	193
IV.6.3	Riethuis-Wallekraal area.....	196
IV.6.4	Richtersveld	197
IV.6.5	Bushmanland-Warmbad area.....	198
IV.6.6	Summary and conclusions.....	199
IV.7	Soil conditions of the quartz fields	201
IV.8	Structural composition of flora and vegetation.....	202
IV.8.1	The selection of functional traits	202
IV.8.2	The growth-form composition the quartz-field flora	204
IV.8.3	Correspondence in growth forms between the phytochoria	204
IV.8.4	The dominance of leaf-succulence	206
IV.8.5	The occurrence of leaf-deciduous plants.....	208
IV.8.6	Correspondence between growth-form and species richness.....	208
IV.8.7	Edaphic control of the growth-form composition of the quartz-field vegetation.....	209
IV.9	Microclimatic conditions of quartz fields	210
IV.9.1	Radiation	211
IV.9.2	Thermal regime on quartz fields	212
IV.9.3	Water supply	213
IV.9.4	The possible impact of the microclimate on the vegetation of the quartz fields	213
IV.10	Synthesis and prospects	214
V	ACKNOWLEDGEMENTS	217
VI	REFERENCES	219
VII	SUMMARY	237
VIII	ZUSAMMENFASSUNG	238
IX	APPENDICES	241
IX.1	Description of the plant communities	250
IX.1.1	Communities of the Little Karoo and adjacent areas.....	250
IX.1.2	Communities of the Knersvlakte outside quartz fields.....	260
IX.1.3	Communities of the Knersvlakte inside the quartz fields	278
IX.1.4	Communities of the Riethuis-Wallekraal area.....	290
IX.1.5	Communities of the Richtersveld	294
IX.1.6	Communities of the Bushmanland-Warmbad area.....	298
IX.2	Tables and figures	302

Content of Tables

Table 1. Field work conducted for this study in the southern Africa.....	20
Table 2. Growth forms sensu Raunkiaer (1937), modified by Ellenberg & Mueller-Dombois (1966) and Jürgens (1986).....	21
Table 3. Number per area of relevés inside and outside the quartz fields sampled by the author.....	23
Table 4. Identification of plant taxa: taxonomic groups and consulted specialist.....	23
Table 5. Units used for description of the vegetation and habitats.....	25
Table 6. Number of relevés per area employed for the CCA ordinations.....	27
Table 7. Numbers of taxa and level of endemism for the defined phytochoria.....	32
Table 8. Species number and level of endemism of the defined phytochoria of the obligate QFF.....	32
Table 9. Presence/absence per quarter-degree square of the quartz-field taxa showing the phytogeographical subdivision of the obligate QFF of the Knersvlakte.....	35
Table 10. Genera of the obligate QFF sorted according to their occurrence (from right to left) in the scatter diagram of the genera (Figure 10).....	41
Table 11. Number of taxa and percentage of particular morphological and phenological features within the southern African obligate QFF.....	49
Table 12. Morphological and phenological features of the species / subspecies of the regional obligate QFFs. First figure = number of species / subspecies; second figure in brackets = percentage within the regional obligate QFFs.....	50
Table 13. The floral composition of the obligate QFF in terms of numbers of families, genera, taxa (species/subspecies) of the major taxonomic groups (Monocotyledonae, Dicotyledonae) and (<i>in brackets</i>) the percentage within the flora.....	52
Table 14. The percentage [%] of the major groups in terms of numbers of families, genera, and species/subspecies within the quartz field flora (QFF), in comparison with the Succulent Karoo flora (SKF). Data for the SKF from Hilton-Taylor 1996a.....	52
Table 15. Monocotyledonae / dicotyledonae ratio of the QFF (QFF) and the Succulent Karoo flora (SKF) at different taxonomic ranks.....	52
Table 16. Percentage of monocotyledonae and dicotyledonae taxa in the regional obligate QFFs of southern Africa.....	53
Table 17. Comparison of the percentage of monocotyledonae and dicotyledonae within the obligate QFFs and general floras of the phytochoria.....	54
Table 18. Family spectrum of the flora of the southern African quartz fields (QFF). Percentages refer to importance of the families in terms of numbers of species and subspecies within the flora.....	55
Table 19. Numbers of genera per family represented in the QFF and their percentage in terms of numbers of genera.....	55
Table 20. Families that are under- or over-represented in the quartz-field flora (QFF) in terms of numbers of species/subspecies compared to the general Succulent Karoo flora (SKF).....	57
Table 21. Family spectra of the obligate QFF of the defined phytochoria) Numbers of species / subspecies per family.....	60
Table 22. Number of families, diversity index and evenness on family level of the regional obligate QFFs.....	61
Table 23. Fourteen most species-rich genera within the obligate quartz-field flora (QFF) and the total number of taxa (species and subspecies) per genus.....	62
Table 24. Genera that were largely or completely restricted to the southern African quartz fields.....	63
Table 25. Quartz-field species/subspecies of <i>Crassula</i> their sections and distribution.....	64
Table 26. Quartz-field species that are endemic to the Little Karoo.....	66
Table 27. Quartz-field species of the Knersvlakte.....	66
Table 28. Quartz-field species of the Riethuis-Wallekraal Phytochorion.....	68
Table 29. Quartz-field species of the Southern Richtersveld Phytochorion.....	69
Table 30. Quartz-field species of the Northern Richtersveld Phytochorion.....	70
Table 31. Quartz-field species of the Bushmanland-Warmbad Phytochorion.....	71
Table 32. The species/ genera ratio of the regional obligate QFFs.....	72
Table 33. Density of obligate quartz-field taxa within the defined phytochoria.....	79

Table 34. Number of growth-form groups (including 4 nano-chamaephyteous subgroups), Shannon-Wiener diversity index, and evenness value on growth-form level of the regional QFFs (QFF)	81
Table 35. Number of growth-form groups, Shannon-Wiener diversity index and evenness value on growth-form level of the entire obligate QFF, endemic and non-endemic quartz-field species.....	83
Table 36. Number of species (above) and percentages (below) of particular morphological and phenological features of the regional endemic, non-endemic and entire flora of the quartz fields.....	84
Table 37. Comparison of the percentage of the families within the endemic and the non-endemic obligate QFF	85
Table 38. Percentage of non-endemic compared to their occurrence within the entire quartz field taxa of the plant families	86
Table 39. Shannon-Wiener diversity index and evenness value for the family spectra of the entire, endemic and non-endemic QFF.	86
Table 40. Genera that contribute more than one species / subspecies to the non-endemic obligate QFF. Number of taxa within the non-endemic and the entire obligate QFF and the percentage of non-endemic taxa within the entire obligate QFF	87
Table 41. Quartz-field species that occur in more than one phytochorion.....	87
Table 42. Plant cover and number of species for the communities # 1-16 of the Little Karoo and adjacent areas (mean, minimum, maximum).....	93
Table 43. Major habitat unites of the Knersvlakte and their geographical subsections.....	94
Table 44. Vegetation communities and sub-communities of the Knersvlakte (without quartz-field vegetation) and their association with Major Habitat Units.	100
Table 45. Summary statistics of the CA of species data of the quartz-field and related habitats of the Little Karoo and adjacent areas.....	104
Table 46. Correlation matrix of the supplementary environmental variables and CA axes of species data of the Little Karoo and adjacent areas.....	104
Table 47. Summary statistics of the CA ordination of species and environmental variable data of quartz fields and related habitats of the Little Karoo and adjacent areas.	105
Table 48. Correlation matrix of the supplementary environmental variables and CA axes of species data of the Little Karoo and adjacent areas.....	105
Table 49. Summary statistics of the CCA ordination of species and environmental variable data of quartz fields and related habitats of the Little Karoo and adjacent areas.	106
Table 50. Summary statistics for the CA of species data of the quartz-field relevés from the Knersvlakte.	115
Table 51. Summary statistics for the CA of species data of the quartz-field relevés from the Knersvlakte without <i>Oophytum oviforme</i> Community (# 29).....	115
Table 52. Summary statistics for the CA analysis (Figure 50) of the species data of saline quartz fields of the Knersvlakte with subsequently included environmental variables.....	116
Table 53. Summary statistics of the CCA ordination of the species and environmental variable data from quartz fields of the Knersvlakte.....	118
Table 54. Summary statistics of the CCA ordination of species and environmental variable data from the saline quartz fields of the Knersvlakte (without <i>Oophytum oviforme</i> Community # 29).....	120
Table 55. Summary statistics of the CA ordination of species data and subsequently added environmental variables of quartz-field and adjacent relevés of the Riethuis-Wallekraal area.	125
Table 56. Summary statistics of the CCA ordination of species and environmental variable data of quartz-field and adjacent relevés of the Riethuis-Wallekraal area.	127
Table 57. Summary statistics for the CA of species data from quartz fields and surroundings in the Richtersveld...	129
Table 58. Summary statistics for the CCA of species and environmental data from quartz fields and surrounding habitats in the Richtersveld	131
Table 59. Summary statistics for the CA ordination of species data and subsequently added environmental variables from quartz-field habitats in the Bushmanland-Warmbad area.	133
Table 60. Summary statistics for the CCA ordination of species and environmental variable data from quartz-field and surrounding habitats in the Bushmanland-Warmbad area.	135
Table 61. Weighted means (above) and weighted standard deviation (below, in brackets) of environmental variable data employed for ordinations for the different areas.	135
Table 62. Average canopy cover (mean values) of quartz-field and zonal vegetation in five different areas with frequent occurrence with quartz fields.	136

Table 63. Summary statistics for the CCA analysis of growth-form and environmental variable data from quartz fields in the Little Karoo and adjacent regions.....	138
Table 64. Summary statistics for the CCA of growth-form and environmental variable data from quartz fields and surrounding sites in the Knersvlakte.....	140
Table 65. Summary statistics of CCA analysis of growth-form and environmental variables of quartz-field and adjacent relevés in the Riethuis-Wallekraal area.....	143
Table 66. Summary statistics of CCA analysis of growth-form and environmental variable data of quartz fields and adjacent habitats of the Richtersveld.....	145
Table 67. Summary statistics of the CCA analyses of the growth-form and environmental variable data of relevés from the Bushmanland-Warmbad area.....	147
Table 68. Characteristic range of edaphic variables for the two main groups of quartz fields in the Little Karoo, Knersvlakte, Riethuis-Wallekraal, Richtersveld.....	199

Content of Figures

Figure 1. Geographical distribution of areas with frequent occurrence of quartz fields in southern Africa.....	16
Figure 2. Climate diagrams for selected weather stations in the study area. In comparison: Pretoria.....	18
Figure 3. DCA ordination of half-degree squares (HDS) of the southern African obligate QFF.....	30
Figure 4. DCA ordination of quarter-degree squares (QDS) of the western areas with respect to their inventories of quartz-field taxa (species/subspecies).....	31
Figure 5. Sørensen's quotient (C_s) of similarity for the species/ subspecies inventories of the six regional QFFs. Figures in brackets below the quotient show the shared taxa.....	33
Figure 6. Geographical distribution of the six phytochoria of the southern African obligate QFF.....	34
Figure 7. Phytogeographical subdivision of the obligate QFF of the Knersvlakte. The bold figures below the show the numbers of quartz-field species in each square.....	36
Figure 8. Phytogeographical subdivision of the obligate QFFs on genus level: DCA scatter diagram of the QDSs.....	38
Figure 9. Phytogeographical subdivision of the obligate QFFs on genus level. Scatter diagram of the genera.....	39
Figure 10. Growth-form spectrum of the QFF of Southern Africa (1).....	42
Figure 11. Growth-form spectrum of the southern African QFF (2) with special reference to the nano-chamaephyteous subgroups.....	43
Figure 12. Growth-form spectra (percentage) of the six regional obligate QFFs.....	43
Figure 13. Growth-form spectra (percentage) of the six phytochoria of the obligate QFF. The nano-chamaephytes are subdivided into subgroups.....	46
Figure 14. Comparison of the growth-form spectrum of the obligate quartz-field flora (QFF) and of the Succulent Karoo.....	47
Figure 15. Comparison of the growth-form spectra (percentage of the species /subspecies) of the six regional QFFs and the general Succulent Karoo Flora (SKF).....	48
Figure 16. Percentage of taxa with particular morphological and phenological features within the regional obligate QFFs.....	49
Figure 17. Dendrogram of a cluster analysis (using Ward Method) of the six regional obligate QFFs based the percentage of 17 structural features (9 growth-form groups, 8 morphological and phenological features).	51
Figure 18. Percentage of families in terms of numbers of species / subspecies within the obligate quartz-field flora (QFF) and the Succulent Karoo Flora (SKF).....	56
Figure 19. Percentage of families in terms of numbers of genera within the obligate quartz-field flora (QFF) and the Succulent Karoo Flora (SKF).	57
Figure 20. Family spectrum of the main regional obligate QFFs of southern Africa.....	59
Figure 21. Relationship between number of quartz-field taxa (species and subspecies) and species-to-genera ratio of the regional obligate QFFs.....	73
Figure 22. Quartz-field species / subspecies per QDS within the main phytochoria.....	74
Figure 23. Numbers of genera of the obligate QFF per QDS within the main phytochoria.....	75
Figure 24. Numbers of families of the obligate QFF per QDS.....	76
Figure 25. Number of growth-form groups within the obligate QFF per QDS.....	77
Figure 26. Relationship between richness of species / subspecies and growth forms per QDS in the six main phytochoria of the obligate QFF.....	78

Figure 27. Relationship between richness of species / subspecies and growth forms in the Knersvlakte: QDS with low species richness only.	78
Figure 28. Relation between size of the quartz-field phytochoria and number of quartz-field taxa and regional endemics of the obligate QFF.	80
Figure 29. Relationship between number of quartz-field taxa and number of growth forms per phytochorion.	81
Figure 30. Percentage of different growth-form groups in terms of numbers of taxa (species and subspecies) of the entire flora, the endemic, and non-endemic species within the obligate QFF.	82
Figure 31. Percentage of morphological and phenological features of the entire obligate QFF as well as the endemic and non-endemic taxa.	83
Figure 32. Family spectrum of the non-endemic compared to the entire and the endemic obligate QFF. Percentage of plant families in terms of numbers of species and subspecies.	85
Figure 33. CA ordination of all quartz-field relevés of the study area. Scatter diagram of relevés.	88
Figure 34. CA ordination of species of quartz-field relevés of all phytochoria.	89
Figure 35. CA ordination of quartz-field relevés of the Namaqualand and Bushmanland-Warmbad Phytochorion. Joint plot of relevés and species.	89
Figure 36. CA ordination of the data matrix of the synoptic table.	91
Figure 37. Hierarchical cladogram of the plant communities, Little Karoo.	92
Figure 38. Box-Whisker plots of total cover values and species numbers of communities # 1-16 of the Little Karoo and adjacent areas.	93
Figure 39. Spatial distribution precipitation in the Knersvlakte and surroundings on a resolution of 5 x 5 km.	95
Figure 40. Distribution and delimitation of the Major Habitat Units of the Knersvlakte.	98
Figure 41. CA ordination of species data of quartz fields and related habitats of the Little Karoo and adjacent areas. Communities # 1-16.	104
Figure 42. CA ordination of species data of quartz fields and related habitats of the Little Karoo and adjacent areas. Without the <i>G. angulipes</i> Community (# 3).	105
Figure 43. Joint plot of the unconstrained relevé scores of the CCA ordination of the Communities # 1-16 and eight edaphic variables of the Little Karoo and adjacent areas.	107
Figure 44. Details of the central part (extract) of Figure 43.	108
Figure 45. Joint plot of the constrained relevé scores of the CCA ordination of the communities # 1-16 and eight edaphic variables of the Little Karoo and adjacent areas.	109
Figure 46. Box-Whisker-plots showing the range of the environmental variables within community # 1-16 of the Little Karoo and adjacent areas.	111
Figure 47. Absolute (above, in meq/kg) and relative (below) composition of cations and anions of selected relevés of the communities (# 1-15) in the Little Karoo and adjacent areas.	112
Figure 48. CA ordination of species data of all quartz-field relevés of the Knersvlakte.	114
Figure 49. CA ordination of species data of the quartz fields of the Knersvlakte calculated without <i>Oophytum oviforme</i> Community (# 29).	115
Figure 50. CA ordination of species data of saline quartz fields of the Knersvlakte. Arrows indicate the direction of strongest variance of the environmental variables.	117
Figure 51. Joint plot of the unconstrained relevé scores of the CCA ordination with species data and environmental variables of the saline quartz fields of the Knersvlakte (without <i>Oophytum oviforme</i> Community # 29).	117
Figure 52. Joint plot of the constrained relevé scores of the CCA ordination of the species and environmental variable data from all quartz-field relevés of the Knersvlakte.	118
Figure 53. Joint plot of the unconstrained relevé scores of the CCA ordination of the species and environmental variable data from the saline quartz fields of the Knersvlakte (without <i>Oophytum oviforme</i> Community # 29).	121
Figure 54. Joint plot of the constrained relevé scores of the CCA ordination of the species and environmental variable data from the saline quartz fields of the Knersvlakte (without the <i>Oophytum oviforme</i> Community # 29).	122
Figure 55. Absolute content of ions (given in meq/kg) of selected relevés of the communities of saline quartz fields (Communities # 21-30, top), non-saline acid quartz fields (Communities # 31-49, middle), and outside the quartz fields (Communities # 1-20, bottom) of the Knersvlakte.	123
Figure 56. Relative composition of ions of selected relevés of the communities of saline quartz fields (Communities # 21-30, top), non-saline acid quartz fields (Communities # 31-49, middle), and outside the quartz fields (Communities # 1-20, bottom) of the Knersvlakte.	124

Figure 57. CA ordination of species and subsequently added environmental variable data of the quartz fields and adjacent relevés of the Riethuis-Wallekraal area.....	125
Figure 58. Joint plot of the unconstrained relevé scores and environmental variables of the CCA ordination of the quartz-field and adjacent relevés of the quartz fields in the Riethuis-Wallekraal area.....	126
Figure 59. Joint plot of the constrained relevé scores and environmental variables of the CCA ordination of the quartz-field and adjacent relevés of the quartz fields in the Riethuis-Wallekraal area.....	127
Figure 60. CA ordination of species and subsequently added environmental variable data of quartz-field and adjacent habitats of the Richtersveld. Seven communities and two sub-communities were distinguished.....	128
Figure 61. Joint plot of unconstrained relevés scores of the species and environmental variable data from the quartz-field and adjacent habitats of the Richtersveld.....	129
Figure 62. Joint plot of constrained relevé scores of the CCA ordination of quartz-field and adjacent habitats of the Richtersveld.....	130
Figure 63. Absolute (above, values given in meq/kg) and relative (below) composition of cations and anions of selected relevés of the communities in the Riethuis-Wallekraal area (# 40-45) and the Richtersveld (# 48-51).....	132
Figure 64. CA ordination of species data and subsequently added environmental variables of quartz-field habitats in the Bushmanland-Warmbad area.....	133
Figure 65. Joint plot of unconstrained relevé scores of quartz-field habitats of the Bushmanland-Warmbad area ...	134
Figure 66. Joint plot of constrained relevé scores of quartz-field habitats of the Bushmanland-Warmbad area (Community 1-4 B-W).....	134
Figure 67. Mean canopy cover [%] of the growth forms on relevés with quartz cover (white columns) and without quartz cover (black columns) of five geographical regions.....	137
Figure 68. CCA ordination of growth-form and environmental variable data of quartz-field and related habitats in the Little Karoo and adjacent areas. For the analysis species names were replaced by the species' growth form..	139
Figure 69: CCA ordination of data from the Knersvlakte. For the analysis species names were replaced by the species' growth form.....	142
Figure 70. CCA ordination of growth-form and environmental variables of quartz-field and adjacent relevés from the Riethuis-Wallekraal area. For the analysis species names were replaced by the species' growth form.....	144
Figure 71. CCA ordination of growth-form and environmental variable data of quartz-field and adjacent relevés from the Richtersveld. For the analysis, species names were replaced by the species' growth from type.....	146
Figure 72. CCA analysis of growth-form and environmental variable data of quartz fields and adjacent relevés of the Bushmanland-Warmbad area.....	148
Figure 73. Distribution of growth forms (average cover values per growth form) along a gradient of increasing density (0-100 %) of quartz cover in different regions.....	150
Figure 74. Distribution of growth forms (average cover values per growth form) along a gradient of increasing salinity in soil (> 0.0 - > 10 mS/cm) for the vegetation of different regions.....	151
Figure 75. Above: incoming global solar radiation (300-3000nm) (black line), net radiation on soils with (blue line) and without (red line) quartz cover. Below: difference between reflected solar radiation (300-3000nm) by quartz fields and soils without quartz cover (quartz fields — soils without quartz cover). Knersvlakte, September to October 1996.....	152
Figure 76. Air temperature 10 mm above soil surface on soils with (continuous line) and without quartz cover (dotted line) compared to air temperature in 2 m height (grey line) under winter (W) and summer (S) conditions in the Knersvlakte.....	153
Figure 77. Daily maximum temperatures on soils with (dotted line) and without (continuous line) quartz cover (right column) and net differences of temperatures (with quartz — without quartz) (left column). Knersvlakte 1997-1998.....	154
Figure 78. Surface temperature of soils with (dotted line) and without (continuous line) quartz cover compared to air temperature in 2 m height (grey line) under winter (W) and summer (S) conditions in the Knersvlakte.....	156
Figure 79. Surface temperature 3 mm underneath the soil surface of soils with (dotted line) and without quartz cover (continuous line) compared to air temperature in 2 m height (grey line) under winter (W) and summer (S) conditions in the Knersvlakte.....	157
Figure 80. Leaf surface temperatures (median) of four <i>Argyroderma</i> spp. plants growing inside (blue line) and outside (red line) quartz fields compared to air temperature in 2 m height (black line) under winter (W) and summer (S) conditions in the Knersvlakte.....	158
Figure 81. Left: leaf surface temperatures (median) of four <i>Gibbaeum cryptopodium</i> plants growing inside (blue) and outside (red) quartz fields. Right: differences. Little Karoo, March 1998.....	159

Figure 82. In situ surface temperatures of a quartz stone (dark blue line), temperatures (light blue line) and dew-point temperature (black line) of the ambient air.	160
Figure 83. In situ surface temperatures of a quartz stone (dark blue line), temperatures (light blue line) and dew-point temperature (black line) near the ground of the quartz-field compared to a piece of shale (red line).....	160
Figure 84. Map of the Knersvlakte showing the major drainage systems and hypothetical migration of the QFF of the Knersvlakte	182
Figure 85. Namaqualand <i>sensu lato</i> : Knersvlakte, Riethuis-Wallekraal, Richtersveld.....	260

Content of tables and figures in the Appendices

Appendix 1. Check list of the taxa of the obligate quartz-field flora.....	241
Appendix 2. Non-endemic taxa of the obligate QFF listed according to the number of QDS they were recorded for.	249
Appendix 3. Species names, family and Raunkiaer's growth form of the species in the phytosociological table (Phytosociological Table I, Fehler! Ungültiger Eigenverweis auf Textmarke.) of the relevés from the Little Karoo and adjacent area.	302
Appendix 4. Synoptic table I. Vegetation of the quartz fields and related habitats in the Little Karoo and adjacent areas	306
Appendix 5. Phytosociological Table I: Vegetation of the Little Karoo and adjacent areas see separate folder.....	308
Appendix 6. Distribution of Community # 1-8 of the vegetation of quartz fields and related habitats of the Little Karoo and adjacent areas.....	309
Appendix 7. Distribution of Community # 9-16 of the vegetation of quartz fields and related habitats of the Little Karoo and adjacent areas.....	310
Appendix 8. Header data of the Phytosociological Table I: Vegetation of the Little Karoo and adjacent areas	311
Appendix 9. Synoptic Table II: Vegetation of the Knersvlakte and the quartz fields vegetation of the Namaqualand see separate folder.	315
Appendix 10. Phytosociological Table II: Vegetation of the Knersvlakte and the quartz fields vegetation of the Namaqualand see separate folder.	315
Appendix 11. Names and author of the diagnostic species recorded for the quartz-field communities in the Bushmanland-Warmbad area	315
Appendix 12. Phytosociological Table III. Quartz-field communities of the Bushmanland-Warmbad area	316
Appendix 13. Habitat data and median values for the quartz-field communities of the Bushmanland-Warmbad area.	317

Abbreviations

assim	= Assimilating (referring to plant growth forms)
CA	= Correspondence Analysis
CCA	= Canonical Correspondence Analysis
Ch	= Chamaephyte
co	= Compact (referring to plant growth forms)
DCA	= Detrended Correspondence Analysis
decid	= Deciduous (referring to phenology of plants)
G	= Geophyte
H	= Hemicryptophyte
HBG	= Herbarium Hamburgense
HDS	= Half-degree square (30'x30', referring to a geographical grid)
LP	= Living Plant, lodged with the Living Plant Collection of the University of Hamburg
nCh	= Nano-chamaephyte
non-succ	= Not succulent (referring to plant growth forms)
MHU	= Major Habitat Unit (referring to the Knersvlakte)
meCh	= Mega-chamaephyte
meCh	= Micro-chamaephyte
P	= Phanerophyte
QDS	= Quarter-degree square (15'x15', referring to a geographical grid)
QFF	= Quartz-field flora (exclusively related to the obligate quartz-field flora as defined in Chapter I.4)
SKF	= Succulent Karoo Flora (referring to the entire flora of the Succulent Karoo Biome)
sg	= Sub-globose (referring to plant growth forms)
SG	= Species group (referring to the diagnostic groups in the synoptic and phytosociological tables)
st	= Subterraneous (referring to plant growth forms)
succ	= Succulent (referring to plant growth forms)
T	= Therophyte

I INTRODUCTION

I.1 The southern African quartz fields

Quartz fields represent an unusual habitat type of the Succulent and Nama Karoo Biomes in the arid parts of southern Africa (Figure 1). The fields are characterised by a dense layer of white, angular quartz stones on soil surface. The vegetation of these quartz fields differs considerably from its surroundings by low height, low cover values, a particular species composition, and the dominance of dwarf and ground level growth forms.

The characteristic features of the quartz fields are their restricted size and distinct boundaries. Sharp borders, together with the low vegetation density and height, make the quartz fields conspicuous, giving them an island-like appearance. Even the vegetation within the quartz fields shows a clear pattern of small scale mosaics of vegetation units which are typically dominated by a single taxon (monodominant vegetation units) (Schmiedel 1994).

Whereas the general vegetation of the Succulent Karoo shows a variety of growth forms typically comprising fruticose, well-branched chamaephytes and nano-phanerophytes the vegetation of the quartz fields is dominated by dwarf growth forms. Short internodes which result in stunted axes, low branching and low number of leaf pairs per axis are common. The majority of the taxa have leaf pairs which are highly connate and form spheroid bodies (so called *Korpuskeln*, Ihlenfeldt 1978). Some plants even grow submerged below the soil surface, receiving light only through chlorenchyma-free windows of the leaf tips (window plants). The majority of the plants are leaf succulent, as is typical for the Succulent Karoo vegetation, but in comparison to the general flora of the Succulent Karoo, they tend to have fewer leaves which are larger in size. The quartz-field vegetation seems to present an extreme and highly derived form of the Succulent Karoo vegetation.

Although quartz fields are dominant and frequent in the Succulent Karoo, they are not restricted to that biome but also occur in the Bushmanland and Warmbad regions, both belonging to the Nama Karoo biome (Figure 1). The Nama Karoo receives mainly summer rainfall and the vegetation is dominated by non-succulent shrubs and grasses (Palmer & Hoffman 1997). However, the quartz-field vegetation in the Nama Karoo is dominated by succulents and comprises the same growth-form composition as in the Succulent Karoo. Each area where quartz fields occur has a quartz-field flora of its own, comprising a high percentage of endemics. The high similarity in growth-form composition in various regions supplied by taxa of different lineages has been already interpreted as a result of convergent evolution (Jürgens 1986, Schmiedel & Jürgens 1999).

Numerous plant species are entirely restricted to this habitat type, representing a flora of its own and providing a high proportion of the regional endemic flora. For example, in the Knersvlakte around 40 % of the app. 150 endemic species are restricted to quartz fields (Hilton-Taylor 1994).

Regarding the growth-form particularities of their vegetation and flora and their convergence in different biomes, quartz fields obviously represent an ecologically special habitat.

I.2 Objectives

The present study aims to

- understand the composition, distribution, and phylogenetic pattern of the quartz-field flora in order to get insight into its origin, history, and age.
- get insight into the vegetation ecology of the quartz fields, the environmental control of the vegetation structure, species composition, diversity, and distribution.
- understand the microclimatic impact of the quartz cover on soil surface on the habitat conditions on quartz fields.
- provide understanding of the ecology and evolution of the Succulent Karoo vegetation in general.
- to supply relevant data for applied conservation purposes.

For this purpose, three main strings were followed up:

- 1) **Floristic and phytogeographical analyses of the obligate flora of the quartz field were conducted in order to gain insight into its floristic composition and geographical patterns as well as to derive hypotheses on the origin and age of the flora.** These analyses comprise the floristic and growth-form composition, the phylogenetic relationship of the taxa as well as the distribution and the phytogeographical subdivision of the QFF (Chapter III.1).
- 2) **Gradient analyses of the vegetation and of those variables that were most likely to be responsible for the special habitat conditions were employed, i.e.,** physical and chemical soil properties and microclimatic conditions (Chapter III.6 and III.8).
- 3) **An hierarchical classification and formal description of the vegetation and characteristic habitat conditions of quartz fields and neighbouring sites was supplied in order to improve the understanding of the vegetation of the quartz fields and also to facilitate future research.** As a contribution to the New Vegetation Map of South Africa as well as to permit a delimitation the quartz-field vegetation from the zonal vegetation, a map and formal description of the vegetation of the Knersvlakte has been supplied. The Knersvlakte represents the centre of highest diversity of the quartz fields (Chapters IX.1.2 and IX.1.3).

I.3 Previous research conducted on quartz fields or related issues

Although the quartz fields of southern Africa represent an extraordinary azonal habitat of great ecological significance and conservation value (Desmet *et al.* 1999, Hilton-Taylor 1994, Hilton-Taylor & Le Roux 1989, Le Roux *et al.* 1995) they have been the focus of surprisingly little research (Hilton-Taylor 1994). However, some pilot studies had been conducted on various aspects of quartz-field ecology (Eller 1982, Jürgens 1986; von Willert *et al.* 1992; Schmiedel 1994).

Jürgens (1986) analysed the relationship between growth forms and edaphic features on the Knersvlakte quartz fields. His study showed that abrupt change in floristic and growth-form composition across quartz field boundaries is associated with a corresponding increase in soil conductivity and decline in soil pH. Jürgens (1986) also mentions identical sequences of similar growth-form types along quartz-related soil catenas in the Knersvlakte and Little Karoo, which

he interpreted as a result of multiple events of convergent evolution. Schmiedel (1994) conducted a vegetation ecological study on the quartz fields of the Knersvlakte which resulted in a preliminary classification and first hypothesis on its habitat ecology.

Von Willert *et al.* (1992) showed that the reflectivity of solar radiation of quartz was considerably lower than in brown shale and red soil environments and that this was correlated with differences of leaf temperatures of plants growing inside and outside the quartz fields. Eller (1982) investigated the solar radiation absorbed by *Argyroderma pearsonii* (N. E. Brown) Schwantes (Mesembryanthema), a species restricted to the quartz fields of the Knersvlakte. He found that the solar energy absorbed by an *Argyroderma pearsonii* plant increases less than the increase of the direct solar radiation. This reduction in absorbed radiation energy was considered to be important for the plant to avoid critical temperatures during hot summer days.

Very little is known about the geomorphology and age of the southern African quartz fields. No particular study on the geomorphology of the quartz fields has yet been published and the more general literature about the geology and geomorphology of the southern African subcontinent (King 1978, Partridge & Maud 1987, Partridge 1997, Meadows & Watkeys 1999) does not give any indication of their origin and age.

I.4 Definition of quartz fields

Quartz fields, as defined here, are geomorphologic features of southern Africa's arid lands (Schmiedel 1994, Schmiedel & Jürgens 1999). They have a surface layer of white, angular quartz stones (0.2 - 6 cm in diameter) which originates from weathered quartz veins (see Chapter I.7). The long axis of a single quartz field ranges between 1 m and more than 100 m. The size of the quartz fields depends on their position at the topographical sequence. The most extensive quartz fields are found along drainage lines (rivier). The quartz fields that lie on top and around the quartz veins are typically smaller in size and are found on upper slopes and hilltops. Quartz fields are typically "island-like", showing abrupt transitions in both soil conditions and vegetation.

In contrast to quartz outcrops, quartz fields provide a certain layer of fine material between the surface layer of quartz stones and the bedrock, whereas outcrops provide only small pockets of fine material. However, there is a gradual transition between quartz fields and quartz outcrops. Numerous taxa that are typically found on outcrops (*Crassula* spp. in particular) are often found on quartz fields as well.

I.5 Definition of the obligate quartz-field flora

There are about 800 plant species that have been recorded on relevés sampled on southern African quartz fields during this study. Although the most of them are characteristic for the vegetation of the quartz fields, the majority of these species are also found outside the quartz fields at other rocky or shallow-soil habitats. But 150 plant taxa (species and subspecies) seem to be restricted to quartz fields¹. Taxa were assigned as "restricted to quartz fields" if the main and

¹ According to the present state of knowledge which is based on own observations, personal communications, and literature, 150 plant taxa are to be addressed as quartz-field taxa. The question whether a taxon has species or subspecies rank is often contradictory within the literature anyway (one author's species may be another author's subspecies). In particular for the phytogeographical analyses the subspecies will be considered equivalent to species because they are generally defined by their disjunct geographical distribution.

preferred habitats of the taxa are quartz fields. Outside the quartz fields, these taxa occur (if ever) as single individuals only. In the following, these taxa will be addressed as "obligate quartz-field taxa" or "obligate quartz-field flora" (obligate QFF), respectively.

I.6 Geographical distribution of the quartz fields

Quartz fields as defined above are found in the arid areas in the west of southern Africa (Figure 1). Their distribution area covers both winter and summer rainfall zones as well as the transition zone. The Richtersveld, Riethuis-Wallekraal area, Knersvlakte, and the Little Karoo fall within the Succulent Karoo Region *sensu* Jürgens (1991) of the Greater Cape Flora. The Greater Cape Flora is defined botanically by a high number of species of Mesembryanthema (Aizoaceae *sensu* Bittrich & Hartmann 1988) and a strong dominance of leaf-succulent, fruticose growth forms (Low & Rebelo 1996). The overwhelming dominance of leaf-succulence is a world-wide unique phenomenon and is, presumably, an adaptation to the mild and highly predictable winter rainfall climate of the Region. The climatic conditions of the Succulent Karoo Region promote a plant species diversity on local and regional level which is unparalleled in arid regions world-wide (Cowling *et al.* 1989, Cowling & Hilton-Taylor 1999) and also result in an extremely low structural diversity (Esler *et al.* 1999). The Succulent Karoo Region is ecologically characterised by a relative mild temperature regime and low (most areas receive less than 150 mm) but highly predictable winter rainfall (Hoffman & Cowling 1987, Cowling *et al.* 1999b). Hot, desiccating so-called Berg Winds occur throughout the year and have a profound effect on plant life (von Willert *et al.* 1992).

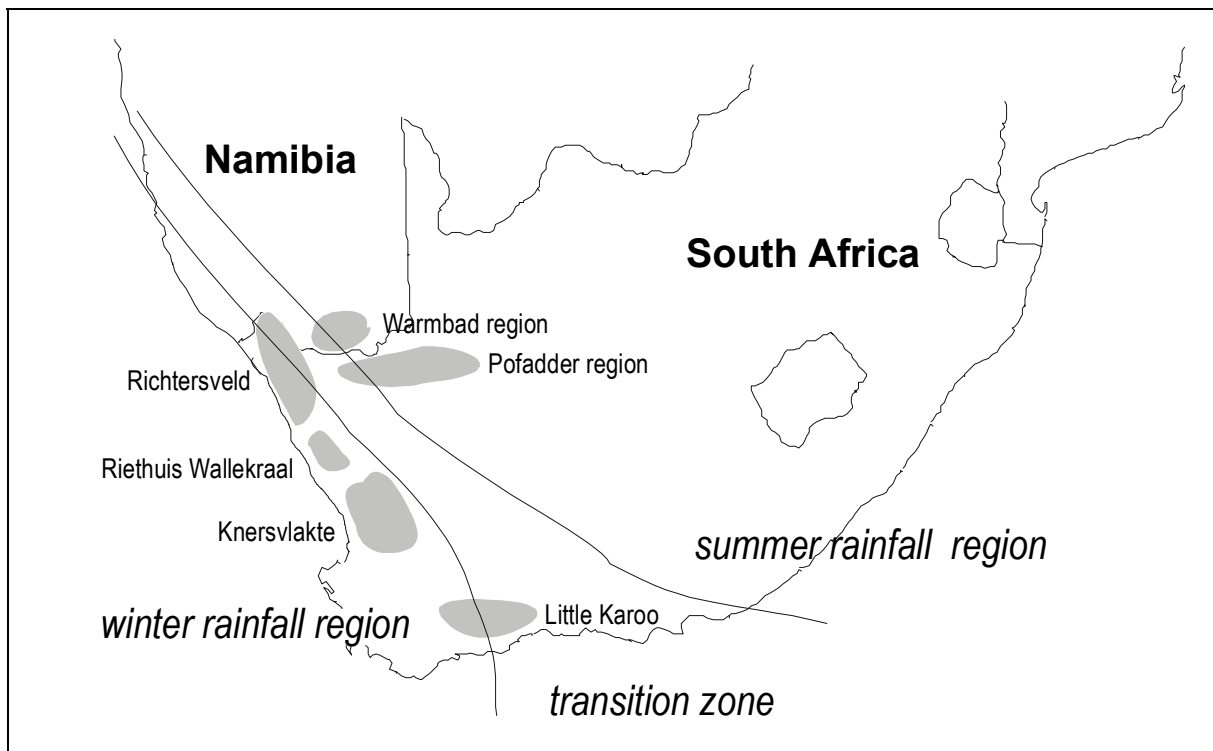


Figure 1. Geographical distribution of areas with frequent occurrence of quartz fields in southern Africa

In four species, only some subspecies are restricted to quartz fields whereas the other subspecies are found outside the quartz fields. In this cases, the species were only partly included into the QFF. This is true for *Conophytum lithopsoides* (only *C. l.* ssp. *lithopsoides*, and *C. l.* ssp. *koubergense* are restricted to quartz fields), *Conophytum obscurum* (only *C. o.* ssp. *vitreopapillum* is restricted to quartz fields), *Crassula congesta* (only *C. c.* ssp. *laticephala* is restricted to quartz fields), and *Lithops divergens* (only *L. d.* ssp. *divergens* is restricted to quartz fields).

The area that comprises the Knersvlakte, Riethuis-Wallekraal area, and the Richtersveld is called the Namaqualand (Cowling *et al.* 1999b), which forms part of the Succulent Karoo Biome. In addition to the low but predictable winter rainfall which is generally typical for the Succulent Karoo, highly predictable coastal fog supplements the meagre rainfall along the coastal margin and in the foothills of the escarpment. Owing to high humidity and relatively cool nocturnal temperatures, copious dewfalls are widespread (Desmet & Cowling 1999b) even in summer months (von Willert *et al.* 1992).

The Richtersveld (28°00'-29°15'S, 16°30'-17°30'E) in the northern Namaqualand (Cowling *et al.* 1999b) is very mountainous in the north and moderately undulating to flat in the south. The area is bordered by the Orange River in the north and the Atlantic Ocean in the west. The mountainous part comprises a varied sequence of pre-Gondwana rocks (about 2.5 billion years old) that were extensively intruded at least a billion years ago by granite and gneiss of the Namaqua Metamorphic Province (Cowling *et al.* 1999b, Meadows & Watkeys 1999). The parent rock comprises quartzites, shales, and granite-gneiss. The mean annual rainfall is between 46 mm at the coast (Alexanderbay, Orange River mouth) and 71.5 mm app. 30 km inland in the southern part of the Richtersveld (Lekkersing) (Weather Bureau 1988). Depending on the altitude the vegetation is classified as Lowland or Upland Succulent Karoo (Hoffman 1996a,b).

The Riethuis-Wallekraal area (30°05'-25'S, 17°15'-35'E) in the coastal lowlands of the central Namaqualand is a moderately undulating plain at the border to the Namaqualand uplands. The area lies at the interface between the coastal sands and the granitic-gneiss uplands (Namaqualand Rocky Hills) of the Namaqua Metamorphic Province (Meadows & Watkey 1999). The soils are underlain by shales and gneiss-granitic bed rock. The dominant vegetation type is Lowland Succulent Karoo (Hoffman 1996a).

The Knersvlakte (30°45'-31°40'S, 18°15'-19°00'E) in southern Namaqualand is a moderately undulating coastal plain bordered by the Atlantic Ocean in the west, the Olifants River Valley in the south, the steep scarp of the Cape Folded Belt (quartzitic sandstones of the Cape Supergroup) in the east, and the granitic-gneiss uplands (Hardeveld) of the Namaqua Metamorphic Province in the north (Meadows & Watkey 1999). The area is underlain by shales, phyllites, and limestones of the Nama Group and is streaked by numerous quartz veins. The Knersvlakte receives a reliable winter rainfall (May-August) of between 100 and 175 mm (Weather Bureau 1988). Like the Riethuis-Wallekraal area, the vegetation is classified as Lowland Succulent Karoo (Hoffman 1996a)

The Little Karoo (33°25'-55'S, 20°10'-22°30'E) consists of a series of intermontane valleys, bounded on all sides by the east-west trending anticlines of the Cape Folded Belt. These mountains impede the penetration of both winter frontal rains as well as post-frontal rains derived from the warm Indian Ocean to the south (Desmet & Cowling 1999b). The predominant bottomland rocks are Bokkeveld group shales, softer sediments within the Cape Supergroup. Quartz veins and associated quartz patches are concentrated in the western part. Annual rainfall in the western part of the Little Karoo is app. 200 mm (Weather Bureau 1988) and seasonality is less pronounced than in the Knersvlakte - the rainy season extends from March until October. The eastern part of the Little Karoo receives a considerable amount of summer rainfall and is floristically and with respect to growth from structure a transition between Succulent and Nama Karoo (Cowling & Hilton-Taylor 1999). However, the majority of the Little Karoo form part of Jürgens' (1991) Southern Karoo Domain of the Succulent Karoo Region.

The Warmbad area (28°30'-50'S, 18°00'-19°30'E) in Namibia and the area around Pofadder (29°7'S, 19°24'E) in South Africa are located on both sides of the Orange River, in its hot and arid drainage basin. The geology is ancient basement granites and gneisses of the Namaqualand Mobile Belt on the south edge of the Richtersveld Craton. The dominating soils are yellow

apedal, freely draining, young soils of low soil depth (Hoffman 1996b). These areas are part of the Nama-Karoo Region of the Palaeotropis (Jürgens 1991) and are located in the subtropical summer rainfall zone (rainfall peak occurs in February to April, i.e., late summer to autumn). The average annual rainfall is 100 mm (Pofadder) and 90 mm (Warmbad). There is a distinct peak of rainfall in late summer from February to April. The dominating vegetation type is Orange River Nama Karoo which is characterised by tree and bush forming species (*Boscia albitrunca*, *B. foetida*, *Euphorbia gregaria*, *Acacia mellifera*, and *Rhigozum trichotomum*) as well as grasses in the herb layer (e.g., *Stipagrostis uniplumis*). Succulents dwarf shrubs are rare and play a subordinate role in the vegetation.

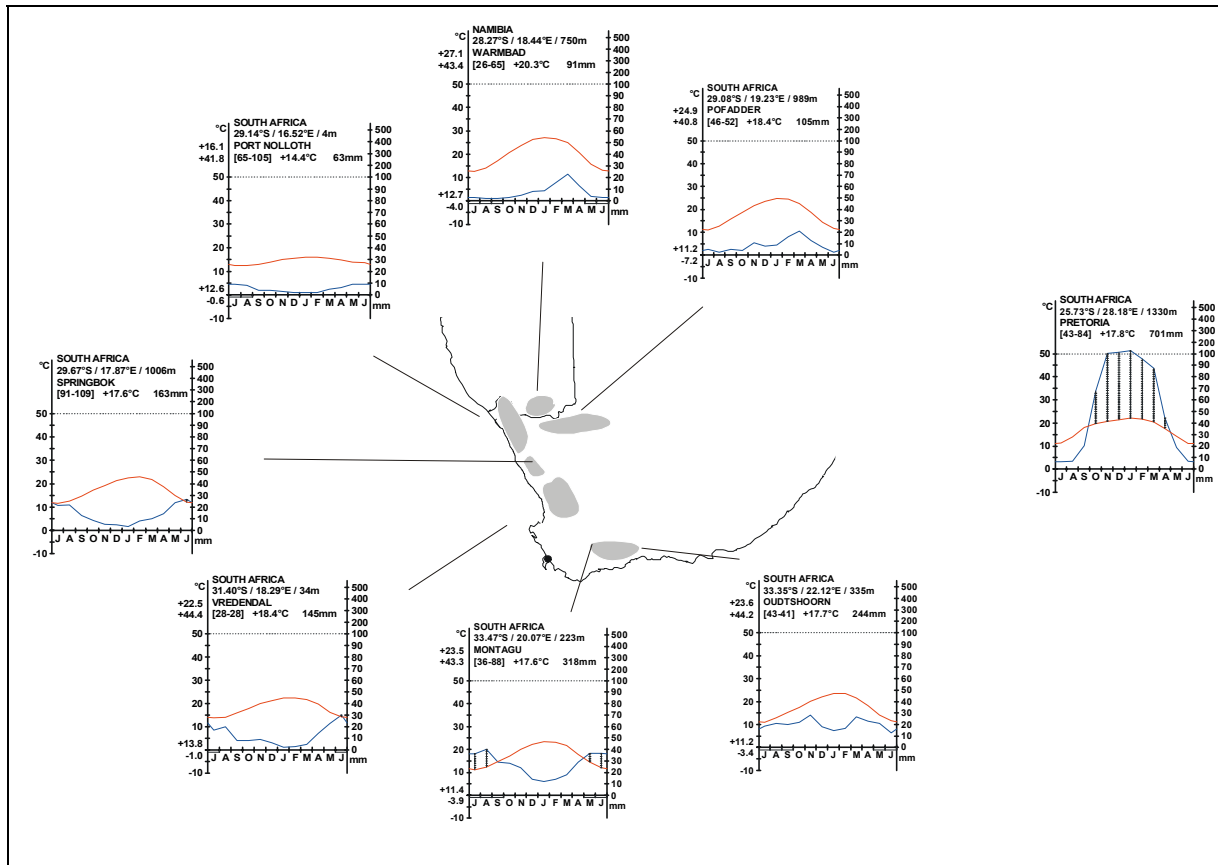


Figure 2. Climate diagrams for selected weather stations in the study area. In comparison: Pretoria.

I.7 Geomorphology of the quartz fields

Botanists often referred to quartz fields as quartz pebble fields or, in German literature, “*Quarzkieselflächen*”. Pebbles (or “*Kiesel*”), however, are particles which are rounded by fluvial transport (AG Boden 1994) which does not apply to the quartz stones of the quartz fields as defined above (Chapter I.4). Geomorphologically, the quartz stones are debris, which are defined as particles that commonly originate from flaking, spalling, or splitting of rock outcrops (Cooke & Warren 1973). On quartz fields quartz sometimes covers up to 100 % of the ground surface.

Very little is known about the geomorphology and age of the southern African quartz fields. No particular study on the geomorphology of the quartz fields has yet been published and the more general literature about the geology and geomorphology of the south African subcontinent (King 1978, Partridge & Maud 1987, Partridge 1997, Meadows & Watkeys 1999) does not give any indication of their origin and age. However, personal observations reveal that the quartz stones originated from weathering quartz veins which are embedded in softer bedrock (shale, phyllite).

The softer bedrock weathers faster than the hard quartz, exposing the quartz as veins (see also Jürgens 1986, Schmiedel & Jürgens 1999). In several areas the quartz veins have disintegrated so completely that the source of the quartz cover can hardly be found anymore. This is particularly true for some quartz fields in the Little Karoo, the Knersvlakte and the Warmbad area.

II MATERIAL AND METHODS

II.1 Field campaigns

For the study, field work was conducted on the quartz fields of Southern Africa (South Africa and Namibia). The field trips were carried out during the vegetation period, i.e., during or shortly after the rainy season. For the winter rainfall zone that is between June and October and for the summer rainfall zone and the region without seasonal precipitation between March and April (Table 1).

Table 1. Field work conducted for this study in the southern Africa.

Number	Period	Areas where field work was conducted
1	August to October 1995	Little Karoo, Knersvlakte, Riethuis area, Richtersveld
2	August to October 1996	Little Karoo, Knersvlakte, Riethuis area, Richtersveld, Pofadder area, Warmbad area
3	June to September 1997	Little Karoo, Knersvlakte, Riethuis area, Richtersveld
4	March to April 1998	Little Karoo, Knersvlakte, Pofadder area, Warmbad area
5	August to October 1998	Little Karoo and Swellendam area, Knersvlakte, Richtersveld, Pofadder area, Warmbad area
6	August to September 1999	Little Karoo, Knersvlakte

The field work comprised the sampling of vegetation relevés and soils, the collection of herbarium and life plant specimens as vouchers, for identification purposes, as well as phylogenetic studies and microclimatic measurements on the quartz fields.

II.2 Floristic data

II.2.1 Floristic and growth-form composition

In keeping with the aim of this study, each species was classified into a growth-form category, which was based on the species' life form *sensu* Raunkiaer (Raunkiaer 1934, elaborated by Ellenberg & Mueller-Dombois 1966) using additional subdivisions of chamaephytes comprising mega-chamaephytes (15-50 cm, meCh), micro-chamaephytes (5-15 cm, miCh), and nano-chamaephytes (0-5 cm, naCh) (Jürgens 1986).

Owing to the overwhelming dominance of the quartz patch flora by nano-chamaephytes the nano-chamaephyteous growth forms were subdivided into following subgroups (compare also Table 2):

- long-leaved nano-chamaephytes with short, non-visible internodes (i.e., naCh comp = compact), e.g., *Argyroderma fissum* (Haworth) L. Bolus, *Gibbaeum pubescens* (Haworth) N. E. Brown, both Mesembryanthea
- nano-chamaephytes with leaves forming a more or less spherical, aerial body (i.e., naCh subglob = subglobose), e.g., *Argyroderma pearsonii* (N. E. Brown) Schwantes and *Gibbaeum album* N. E. Brown, Mesembryanthea

- nano-chamaephytes sunken below the soil surface (i.e., naCh subterr = subterranean), e.g., *Argyroderma delaetii* Maass or *Gibbaeum cryptopodium* (Kensit) L. Bolus, both Mesembryanthema
- nano-chamaephytes that do not fit any of the categories above (i.e., naCh others) e.g., *Anacampseros papyracea*, Portulacaceae

Table 2. Growth forms sensu Raunkiaer (1937), modified by Ellenberg & Mueller-Dombois (1966) and Jürgens (1986)

Definition for the subgroups of chamaephyteous and phanerophyteous growth forms after Raunkiaer (1937), Ellenberg & Mueller-Dombois (1966) and Jürgens (1986)
Chamaephyte Dwarf Shrub < 50 cm in height
Nano-chamaephyte: Dwarf shrub 0-5 cm in height
Compact Nano-chamaephytes: long-leaved nano-chamaephytes with short, non-visible internodes
Nano-chamaephytes with leaves forming a more or spherical aerial body
Nano-chamaephytes sunken below soil surface in height
Micro-chamaephyte: Dwarf shrub 5-15 cm in height
Mega-chamaephyte: Dwarf Shrub 15-50 cm in height
Phanerophyte: Shrub or tree > 50 cm in height

II.2.2 Nomenclature

The nomenclature for the scientific names of the Mesembryanthema is derived from the latest taxonomic revisions. The nomenclature of the remaining taxa (except Mesembryanthema) follows the species data base of the Turbowin programme, Version 1.93e (Hennekens 1996, latest update of species list June 2000).

II.2.3 Source of floristic data

The information on the habitat preferences and distribution of the species which were used for the phytogeographical analysis of the flora of the quartz fields was derived from various taxonomic monographs (Hammer: *Conophytum*, Cole: *Lithops*, Gerbaulet: *Anacampseros*, *Phyllobolus*, Tölken: *Crassula*, Hartmann: *Argyroderma*, *Cephalophyllum*, *Ihlenfeldtia*, Ihlenfeldt: *Oophytum*, *Monilaria*) and regional floras (Le Roux & C. Boucher, in prep: Flora of the Namaqualand) as well as personal communications with P. Bruyns, M. Gerbaulet, S. Hammer, H.E.K. Hartmann, H.-D. Ihlenfeldt, B. Nordenstam, and U. Meve. The distribution data on quarter-degree square (QDS) level of each quartz-field taxon were compiled in a data base. At a longitude of about 30° a QDS is about 25x25km in size. A QDS is the common reference for herbaria and botanists. In order to analyse phytogeographical subdivisions within main phytochoria, a finer scale would have been desirable but not practical due to the data available.

II.2.4 Phytogeographical analysis

For the analysis of the patterns of distribution of the QFF, Detrended Correspondence Analysis (DCA) of the CANOCO 4.0 computer program (ter Braak & Smilauer 1998), a multivariate statistic program for vegetation analysis was applied. The distribution data were used as presence

/ absence of the taxa per each square. The analysis was conducted on two different scales: the entire data set was first analysed on a broader scale employing half-degree squares (HDS). For this analysis the taxa were employed on species level only. Subspecies were taken into account when merely parts of the subspecies within a species were restricted to quartz fields. A finer scale, employing quarter-degree squares (QDS), was applied when in a second step geographical subsets of the data set were analysed separately. Here all subspecies were employed as separate taxa.

The analyses resulted in ordination diagrams that show the relative similarity or dissimilarity between the squares. The higher the similarity between the squares, the closer they are plotted to each other in the diagram. Distinct clusters of half or quarter degree squares indicate high overlap of their species inventories and consequently high floristic similarity. Squares that were plotted within a distinct cluster were defined as phytochoria.

The distribution of seven quartz-field taxa deviate entirely from those of the majority of the other quartz-field taxa. Hence, the corresponding grids (HDS) were outliers in the ordination and were therefore omitted from the DCA: *Schwantesia borchersii* (2820A), *Glottiphyllum oligocarpum*, *Pleiospilos nelii* from the Eastern Cape area (3222D, 3223C, 3322B, 3323A,B, 3324A,B), *Diplosoma retroversum* (3218A,B) from the Swartland, and *Acrodon quarcicola*, *Gibbaeum esterhuyseniae*, *Gibbaeum haagei* from the Swellendam area (3419B, 3420A,B,C). Due to their occurrence outside the six phytochoria of the obligate QFF, the outliers were omitted from the floristic analysis of the regional floras. However, they were included into the floristic analysis of the entire QFF and of the floral analysis of the endemic and non-endemic quartz-field taxa (Chapter III.4).

The degree of relationship between two phytochoria was calculated by employing **Sørensen's quotient of similarity** (Sørensen 1948, Schaefer 1992), calculated as follows:

$C_s = [2 (\text{number of shared taxa}) / (\text{number of taxa of Phytochorion } x) + (\text{number of taxa of Phytochorion } y)]$. The C_s -value lies between 0 and +1.

II.3 Sampling

II.3.1 Vegetation data

In order to investigate the vegetation of the southern African quartz fields, 926 vegetation relevés and soils were sampled in 7 different areas (i.e., Littler Karoo, Knersvlakte, Pofadder area, Richtersveld, Riethuis area, Warmbad area, Swellendam area) inside and outside the quartz fields (see Table 3). In addition, data that I collected earlier (Schmiedel 1994) was included, i.e., 145 relevés from the Knersvlakte and 12 relevés from the Richtersveld. For the vegetation map of the Knersvlakte, 48 vegetation relevés sampled by Anja Schulte in 1993 in the Knersvlakte (Schulte 1994), were partly included into the analysis (not included in the figures given in Table 3).

In the Little Karoo and Swellendam area, *Gibbaeum* species (Aizoaceae) play a major role in the flora and vegetation of the quartz fields. The genus comprises the majority of obligate quartz-field taxa within the area but is not completely restricted to quartz fields. Several *Gibbaeum* species were also found on special habitats without quartz cover, such as shale bands, soils with sandstone gravel etc. In order to get insight into the habitat ecology and phytogeography within the *Gibbaeum*, the sampling of vegetation relevés comprised nearly all *Gibbaeum* species inside and outside the quartz-field habitats. Only two very rare species were not taken into consideration, i.e., *G. esterhuyseniae* L. Bolus, which has been defined as extinct (Anonymus 1998; Hilton-Taylor 1996b) but rediscovered recently for a single location (P. V. Brunys, pers. comm.) as well as the recently discovered *G. johnstonii* Van Jaarsveld & Hammer.

The relevés are based on a modified Braun-Blanquet method: the projected canopy cover (%) of each plant species was estimated in 5x5 m plots. Due to the typically low vegetation cover on the quartz fields, values down to 0.01 % were differentiated. Owing to small-scale mosaic patterns of the vegetation units, such a small relevé size was appropriate. For the mapping of the zonal vegetation of the Knersvlakte, the canopy cover was estimated in 10x10 m plots.

Table 3. Number per area of relevés inside and outside the quartz fields sampled by the author

Area	Total number of relevés with soil samples	Relevés inside quartz fields	Relevés outside quartz fields	Additional relevés without soil samples
Knersvlakte	585	275	310	135
Little Karoo	240	154	86	9
Richtersveld	101	68	33	12
Riethuis area and other parts of the central Namaqualand	54	46	8	12
Warmbad area	33	33	0	1
Pofadder area	16	13	3	5
Swellendam area	10	10	0	0
Total	1039	599	440	174

II.3.2 Identification of the plant species

Most of the specimens of the Mesembryanthema group were identified by specialists (see Table 4) or by comparison with the type specimens at the Bolus Herbarium / University of Cape Town by myself. The remaining taxa (besides the Mesembryanthema) were identified at the Compton Herbarium / National Botanical Institute, NBI, in Kirstenbosch. Where necessary, specialists were consulted as well (see Table 4).

Table 4. Identification of plant taxa: taxonomic groups and consulted specialist

Taxon	Consulted specialist
Anacampseros (Portulacaceae)	M. Gerbaulet (Hitzacker / Germany)
Asclepiadaceae	P.V. Bruyns (Cape Town / South Africa)
Asteraceae (mainly succulent Senecio and Othonna)	B. Nordenstam (Stockholm / Sweden)
Argyroderma (Mesembryanthema)	H.E.K. Hartmann (Hamburg / Germany)
Cephalophyllum (Mesembryanthema)	H.E.K. Hartmann (Hamburg / Germany)
Conophytum (Mesembryanthema)	S. Hammer (Vista / California)
Crassulaceae	P.V. Bruyns (Cape Town / South Africa)
Dicrocaulon (Mesembryanthema)	H.-D. Ihlenfeldt (Hamburg / Germany)
Drosanthemum (Mesembryanthema)	C. Bruckmann & B. Hansen (Hamburg / Germany)
Euphorbiaceae	P.V. Bruyns (Cape Town / South Africa)
Mesembryanthemoideae (Mesembryanthema)	M. Gerbaulet (Hitzacker / Germany)
Monocotyledoneae	J. Manning (Kirstenbosch / South Africa)
Pelargonaceae	U. Meve (Bayreuth / Germany)
Phyllobolus (Mesembryanthema)	M. Gerbaulet (Hitzacker / Germany)
Psilocaulon (Mesembryanthema)	C. Klak (Cape Town / South Africa)
Lachenalia (Hyacinthaceae)	G. Duncan (Kirstenbosch / South Africa)
Spiny Mesembryanthema	D. Stüber (Hamburg / Germany)

- In addition, the following keys were used:
- A preliminary version of the "Flora of Namaqualand" edited by Le Roux and Boucher (version from 1993, Le Roux & Boucher, unpublished)
- Müller (1985): Gräser Südwestafrika/Namibias
- Gibbs Russel *et al.* (1990): Grasses of Southern Africa
- Leistner (eds.): Flora of South Africa (various volumes)
- Monographs on various taxa

II.3.3 Nomenclature

See Flora (Chapter II.2.2).

II.3.4 Vouchers

For each species, herbarium or living plant specimens were collected. The vouchers were lodged at the Herbarium Hamburgense of the University of Hamburg (HBG), at the Bolus Herbarium at the University of Cape Town / South Africa or at the McGregor Herbarium in Kimberley/ South Africa. The live plants are lodged at the living plant collection of the Botanical Garden of the University of Hamburg.

II.3.5 Soil and habitat data determined in the field

The following soil and habitat data were collected per relevé (see Table 5 for synoptic presentation of the units and abbreviations):

- Inclination of slope (in percent), determined with an inclinometer (SUUNTO)
- Exposition of slope (in degree), determined with a compass
- Soil depth (in centimetre) by digging soil profiles to the bedrock or crusts
- Cover values of small to mediate-sized quartz fractions (2 mm-60 mmØ) on soil surface (estimated in %)
- Cover values of coarse quartz fractions (estimated in %) on soil surface (estimated in %)
- Cover values of stone of other lithology than quartz on soil surface (estimated in %)

II.4 Soil analysis

For 1039 vegetation relevés, the following soil data were collected (compare Table 5 for synoptic presentation of the units and abbreviations):

- Stone content in soil quantified as the proportional weight of stones (> 2 mm in diameter) in the soil profile
- Soil texture by employing the standardised finger test outlined in the *Bodenkartieranleitung* (AG Boden 1994).
- The thickness of the fine material above the bed rock or crust in centimetres.
- Limiting layer of the horizon (bed rock, different sorts of crusts).

- Each of these 1039 relevés were sampled in the following way: a) 1 sample at the soil surface (0-1 cm) and 1 sample between 1-10 cm. In addition, for several relevés further samples from deeper layers and mixed samples from the whole soil profile were taken.
- Carbonate content (semi-quantitative) by employing the standardised HCl-test outlined in *Bodenkartieranleitung* (AG Boden 1994)
- Electrical conductivity determined in a 1:5 suspension of air-dry fine material and aqua bidest, employing the WTW LF 91' instrument.
- Soil pH in a 1:2.5 suspension of air-dry fine material and 0.01M CaCl₂. After one hour time the suspensions were measured by using a WTW Digital pH meter.

Table 5. Units used for description of the vegetation and habitats

Parameter	Method	Unit	Symbol
Cover values of vegetation	Projected from the top on the ground, estimated (0.01-100)	Percentage	%
Species richness	Species per relevés of 5 x 5 = 25 m ²	spp. / relevé	-
Cover values of stones	Percentage of coverage of the total soil surface, estimated (1-100 %)	Percentage	%
Inclination	Handheld inclinometer	Percentage	%
Exposition	Compass (0-360°)	Degree	°
Soil depth	Soil profiles	Centimetre	cm
Stone content	Related to the entire soil profile	Percentage of weight	%
Soil texture	Finger test	-	S / s = sand / sandy U / u = silt / silty T / t = clay / clayey L / l = loam / loamy Sl = loamy sand Su = silty sand Lt = clayey loam etc. f = fine fractions (of sand) g = coarse fractions (of sand)
Salinity	Electrical conductivity meter	mS/cm	EC
pH	pH-metre		pH

Carbonate content	HCl test (estimate), according to the (AG Boden 1994)	carbonate in % of weight	c0 = 0 % c1 < 0.5 % c2 = 0.5-2 % c3.2 = 2-4 % c3.3 = 4-7 % c3.4 = 7-10 % c4 = 10-25 % c5 = 25-50 % c6 > 50 %
-------------------	-------------------------------------------------------	--------------------------	--------------------------------------------------------------------------------------------------------------------------------------

For 183 relevés from quartz fields and neighbouring sites (i.e., 107 relevés from the Knersvlakte, 19 from the Riethuis-Wallekraal area, seven relevés from the Richtersveld, and 50 from the Little Karoo) the content and composition of soluble salts were determined in the soil lab of the Institute of Soil Science of the University of Hamburg. The determination was restricted to the most relevant ions for plants. The following cations were determined: chloride, nitrate, sulphate. Due to technical implications, carbonate and phosphate could not be included. However, previous studies of the area (Schmiedel 1994, Bartels 1994) and HCl-tests conducted within this study revealed that carbonate occurred with very low frequency on quartz fields. For the anions calcium, magnesium, sodium, and potassium for the cations were determined. For the analysis, a suspension of 30g air-dry fine material ($\varnothing < 2$ mm) and 30 ml aqua bides was used. The suspensions were shaken for 1h, centrifuged at 3000 U/min for 20 min and filtered through a cellulose-acetone filter. The anions were determined in watery extracts by employing an ion-chromatography instrument (Metrohm). The cations were determined in water extracts by employing a (flame) Atom Absorption Spectrometer (PE 1100B). For conservation purposes, the watery extracts were acidified by adding nitric acid (ca. 10 μ l of 1:1 nitric acid-water solution per 1 ml water extract) immediately after extraction. Calcium and magnesium were determined with an addition of 2000 ppm of Lanthanum. Sodium was determined with an addition of 2000 ppm of potassium and potassium without any addition. The measurements of sodium and potassium were carried out by employing the emission mode whereas sodium and the potassium were measured by employing the absorption mode.

II.5 Vegetation analysis

II.5.1 Vegetation table

The vegetation was classified in the soft ware programme MEGATAB by employing the TWINSpan algorithm and subsequent manual refining of the table in MEGATAB. For the hierarchical order of the vegetation the synoptic tables were classified (on association level) using the TWINSpan algorithm employing presence data only.

II.5.2 Gradient analyses

To analyse the major dissimilarities within the data sets and interpret them in terms of gradients of environmental variables responsible for the dissimilarities, indirect (Correspondence Analysis = CA) and direct gradient analysis (Canonical Correspondence Analysis = CCA) were applied

(Gauch 1982, Jongman *et al.* 1995, Okland 1996). The ordinations were run using the programme CANOCO 4.0 (ter Braak & Smilauer 1998). CA ordination methods aim at ordering samples and/or species along axes that represent the main compositional gradients in the data set, using abundance data for the species in the sample plots. CCA is a multivariate direct gradient analysis (ter Braak & Smilauer 1998) by which, in a two-dimensional space, the relevés are scattered in relation to gradients in selected variables. For the CCA both possible options were selected: unconstrained (the final site/samples scores are weighted averages from the species scores) and constrained relevé scores (i.e., the final site/sample scores are linear combinations of environmental variables) (McCune 1997b).

The indirect gradient analysis reveals dissimilarities within the data set which can be interpreted by relating the axis to supplied environmental variables as has been done in the present study. The unconstrained scores of the relevés of the CCA ordination were applied parallel since the unconstrained relevé scores best present the community structure and are less sensitive to noise in the environmental data whereas only in the constrained ordination the relevés are linear combination of the environmental variables and thus only the constrained ordination presents a direct gradient analysis *sensu stricto* (McCune 1997b, Kovach, pers. comm.).

The number of relevés per area employed for the analysis differed. The number of relevés and corresponding soil data which were available per area depended on the size and heterogeneity of the quartz fields of the area (Table 6).

Table 6. Number of relevés per area employed for the CCA ordinations

Areas	Number of relevés included into the CCA
Bushmanland	46
Richtersveld	82
Riethuis-Wallekraal	46
Knersvlakte	217
Little Karoo	239

The following environmental variables were employed:

Inclination, percentage of total quartz cover on soil surface, percentage of coarse fragments of quartz on soil surface (20-63 mm in diameter = *Grobgrus* according to the German standard, AG Boden 1994), percentage of cover of other stones (e.g., shale, phyllite, sand stone), soil depth, stone content in soil, electrical conductivity, H⁺ concentration in soil, and carbonate (see Chapter IV.7). For the CCA the soil pH values were transformed into H⁺ concentration in order to receive a linear scale.

Canonical correspondence analysis of the growth-form composition of the vegetation of different areas

- For the vegetation analysis the same growth-form categories were used as for the analysis of the growth-form spectrum of the obligate QFF (see Chapter III.1.4). However, the four nano-chamaephyteous subgroups were extended by three additional types that do not play a role in the obligate QFF:
- nano-chamaephytes with creeping axis with adventitious roots (i.e., naCh rept = reptant) e.g., *Cephalophyllum framesii*, Mesembryanthea
- nano-chamaephytes prostrate, non-rooting axis (i.e., naCh pros = prostrate) e.g., *Dicrocaulon prostratum* spec. nov., Mesembryanthea

- nano-chamaephytes with upright stem-like, non-assimilating axis (naCh stem) e.g., *Tylecodon pygmaeus*, Crassulaceae
- Moreover, monocotyledoneous and dicotyledoneous geophytes and hemicryptophytes were distinguished (G mon, G dic, H dic, H mon) as well as graminoid hemicryptophytes designated as a separate group (H gram). Succulent therophytes (T succ) were distinguished from the others (T).
- For the CCA the species names were replaced by the species' growth form as described above and the cover values of each species summed up for cover values per growth-form group. A list of all obligate quartz-field species and their designated growth forms is given in Appendix 1.

The CCA were run using the same programme as for the CCA on species level (CANOCO 4.0 (ter Braak & Smilauer 1998). The results were depicted visually by plotting on the two-dimensional ordination space (constrained relevé scores only), the relative canopy cover of selected growth-form groups.

For each area, the same array of environmental variables was employed and the same groups of growth forms were designated.

II.6 Climatic and microclimatic measurements

In 1995 and 1996 preliminary measurements of weather and microclimatic conditions were conducted in the Knersvlakte (Quaggas Kop) and the Little Karoo (Eyerpoort). From October 1997 to September 2000 weather and microclimatic data were collected continuously in the Knersvlakte:

- from October 1997 to September 1999 on the farm Wolvenes (31°22' S, 18°35' E)
- from September 1999 to September 2000 on the farm Kaap se Drif (31°28' S, 18°46' E)

In spring (August to October) 1996, measurements of incoming global solar radiation (300-3000nm) and reflected radiation above soils with and without quartz cover were conducted in the Knersvlakte (Quaggas Kop, 31°24' S, 18°38' E).

Measurements of leaf surface temperatures of *Argyroderma* spp. were conducted intermittently on the farm Quaggas Kop from 1997 to 1999 and continuously on the farm Kaap se Drif from September 1999 to September 2000. In the Little Karoo leaf surface temperatures were measured in March 1998 on *Gibbaeum cryptopodium* plants on the farm Eyerpoort (33°39' S, 20°33' E).

The automatic weather station (ecoTech, Bonn) gathered the following variables:

- Temperature (PT1000 sensors) and relative humidity (capacitive sensor) of air in 2 m height
- Wind direction in 2 m height
- Wind speed (m/s) in 2 m height
- Precipitation (tipping scale)
- The data recording interval was 30 min, the actual values were determined.

The microclimatic measurements were conducted on level, adjacent sites with and without quartz cover. They comprised:

- Air temperature (PT1000 sensors) and relative humidity (capacitive sensor) at 10 mm above soil surface (same sensors as for the air temperature in 2 m height)
- The measurement of relative humidity of the air close to the soil surface is technically problematic; due to the impact of dust and salt the reliability of the values decreased after several weeks in the fields and tend to be too high and unstable. These values were therefore only used for the period just after their calibration.

- Soil temperature on soil surface (PT100 sensors)
- Soil temperature at 3 mm below soil surface (PT100 sensors)
- Temperature of leaf surface of *Argyroderma pearsonii* (N.E.Brown) Schwantes, *A. delaetii* C.A. Maass and *Gibbaeum cryptopodium* (Kensit) Bolus (all Aizoaceae) inside and outside of quartz fields (thermocouples type K: nickel-chromium/nickel-aluminium)
- The actual values were recorded by a data logger in 20 or 30 minutes intervals.

Two *Argyroderma* species and *Gibbaeum beathii* were chosen for the temperature measurements on plant surfaces. They represent two different types of dwarf growth forms, i.e., submerged (*A. delaetii*, *G. cryptopodium*) and subglobose dwarf shrubs with few, almost spheroid leaves (*A. pearsonii*) (Schmiedel & Jürgens 1999). The species were selected because of their flat leaf-tips which enable a vertical application of the sensors on a horizontal surface and thus differences in temperature caused by different exposure to the sun have been avoided. Four plants were measured per each habitat type.

Measurements of surface temperatures of a quartz and a shale stone (Ø app. 40 mm) at Eyerpoort / Little Karoo as well as a quartz stone at Quaggas Kop / Knersvlakte has been conducted intermittently by employing thermocouples type K (nickel-chromium/nickel-aluminium).

Due to the immense amount of data (measuring period of several years) only some extracts of the data can be shown here. To understand the habitat ecology of quartz fields, main focus was put on the differences of summer and winter temperatures, as two extremes of climatic conditions.

III RESULTS

III.1 The phytogeographical subdivision of the quartz-field flora

III.1.1 Phytogeographical subdivision on species level

The obligate quartz-field flora (Chapter I.5) comprises 150 plant taxa (species and subspecies) and 142 taxa on species level. Only a few of them were found at quartz-fields of all areas but inhabit a very restricted range size of distribution. An analysis of the phytogeographical subdivision of the obligate quartz-field flora shall indicate the pattern of distribution and centres of diversity and endemism of the flora. A subsequent comparison of the regional quartz-field floras regarding taxonomic and growth-form composition will reveal the similarity and differences between the regional quartz-field floras.

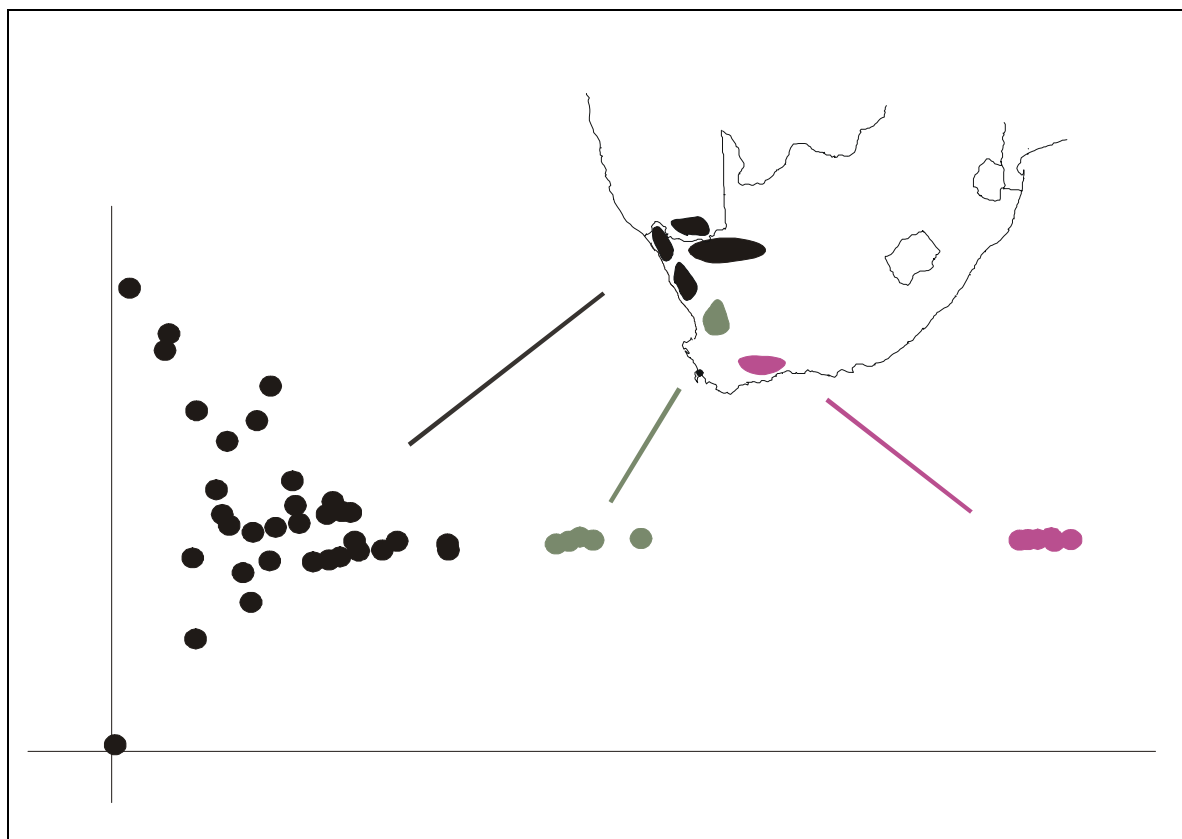


Figure 3. DCA ordination of half-degree squares (HDS) of the southern African obligate QFF.

For the DCA ordination based on the presence / absence of the quartz-field taxa per half-degree square (HDS) following eight taxa had to be omitted as outliers from the ordination, which were all *Mesembryanthema* (*Aizoaceae*):

Schwantesia borcherdsii (*Mesembryanthema*) is presently only known from a restricted area near Augrabies Falls (Zimmermann & Hartmann 1995).

Diplosoma retroversum occurs on isolated quartz fields far south-east of the Knersvlakte, between Het Kruis and Eendekuul (32° 30'-45'S, 18° 45'-19° 00'E; Ihlenfeldt 1988).

Glottiphyllum oligocarpum, *Glottiphyllum peersii*, and *Pleisopilos nelii* are the only obligate quartz-field dwellers between the Little Karoo in the west and the Steytlerville Karoo in the east.

Acrodon quaricola, *Gibbaeum esterhuyseniae*, and *Gibbaeum haagei* which are restricted to the Swellendam area south of Langeberge which forms the southern border of the Little Karoo.

The resulting DCA ordination (Figure 3) showed a clear separation of the entire flora into three main divisions. The HDS of the Little Karoo (3220C, 3221D, 3319B,D, 3320A,B,C,D, 3321A,B,C,D, 3322C) were scattered on the right-hand side of the diagram. The HDS of the Knersvlakte (3017D, 3117B, 3018C, 3118A,B,C,D) formed a distinct cluster in the centre of the diagram. The HDS of the remaining areas in the northwest (central Namaqualand to the Richtersveld and Bushmanland) were plotted together on the left-hand side of the diagram. This clear separation indicates little overlap between the inventories of quartz-field taxa. Least overlap was shown between the obligate QFF in the Little Karoo on the one hand and those of the other areas on the other. The obligate QFF of the Knersvlakte showed a closer relationship with Namaqualand, Bushmanland and the Warmbad area, than with the Little Karoo.

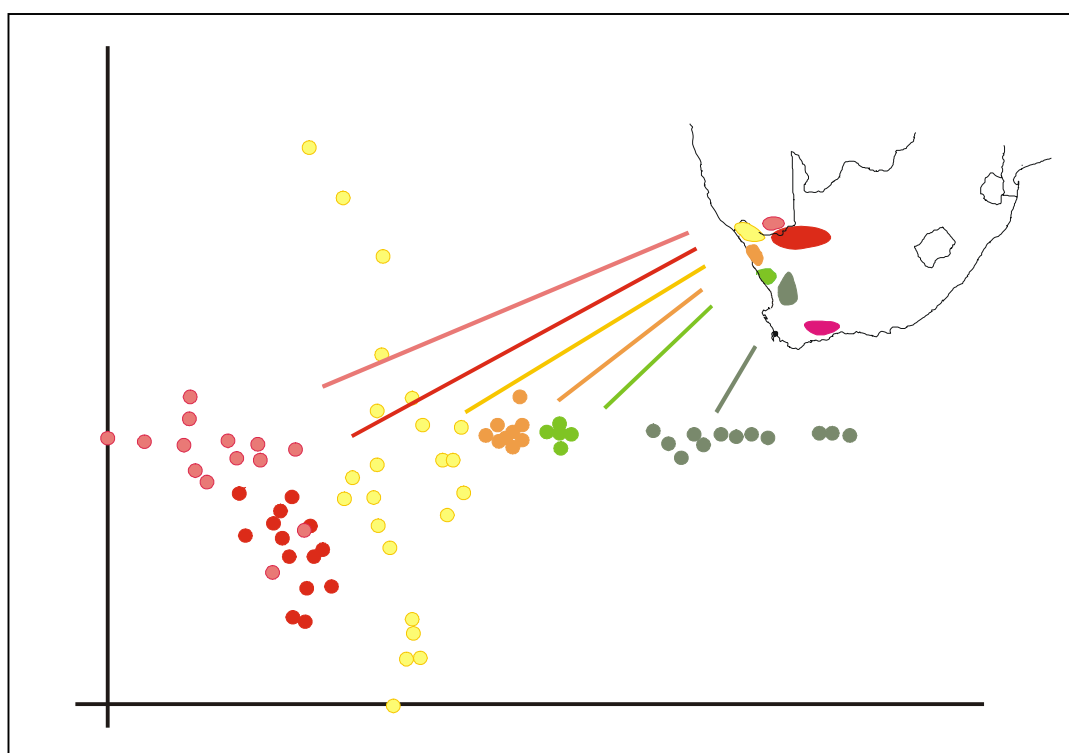


Figure 4. DCA ordination of quarter-degree squares (QDS) of the western areas with respect to their inventories of quartz-field taxa (species/subspecies)

To analyse the phytogeographical patterns of the obligate QFF of the western areas in more detail, a separate analysis omitting the squares of the Little Karoo Phytochorion was performed. For a separate analysis of the western areas (i.e., without the Little Karoo) the grids were divided into quarter-degree squares (QDS). In addition, for nine species *Anacampseros papyracea*, *Argyroderma framesii*, *Conophytum calculus*, *Conophytum maughanii*, *Crassula columnaris*, *Dinteranthus*

microspermus, *Dinteranthus wilmotianus*, *Monilaria scutata*, and *Phyllobolus digitatus*) the subspecies were considered separately because of their differing geographical distributions.

The resulting ordination diagram (Figure 4) showed five clusters of differing distinctiveness. Again, the Knersvlakte was clearly separated from the rest, The QDS of this area were plotted in an isolated dense cluster. The Riethuis-Wallekraal Phytochorion formed a bridge between the cluster of the Phytochoria of the Knersvlakte and the Southern Richtersveld. The QDS of the Northern Richtersveld Phytochorion were plotted next to the squares of the Southern Richtersveld. The cluster of squares on the left-hand side of the diagram represents the Warmbad and Bushmanland area; these areas were largely plotted together.

Table 7 showed the numbers of taxa and level of endemism for the six phytochoria of the obligate QFF as they resulted from the analyses described above. Altogether, there were 150 taxa (species and subspecies) in the entire obligate QFF of which 130 taxa (86.7 %) were endemic to one of the six phytochoria. If only species (not subspecies) were taken into account, there were 142 quartz-field species in total of which 115 species (81 %) were endemic to one of the defined phytochoria. The Swellendam and the Eastern Cape region (Steytlerville) each housing three endemic species, lay outside the defined phytochoria.

Table 7. Numbers of taxa and level of endemism for the defined phytochoria

Taxonomic level	Quartz-field taxa in total	Quartz-field taxa endemic to the six defined phytochoria	Relative share [%]
Species only	142	115	80.98
Species and subspecies	150	121	80.66

The highest number of taxa restricted to quartz fields occurred in the Knersvlakte (Table 8). Here 63 taxa are exclusively found on quartz, of which 94 % were endemic to the Knersvlakte. The next highest number of quartz-field taxa and a high level of endemism were found in the Northern Richtersveld Phytochorion with 39 quartz taxa of which 22 are restricted to the area. The Northern Richtersveld Phytochorion is followed by the Bushmanland-Warmbad Phytochorion, the Southern Richtersveld Phytochorion, and the Riethuis-Wallekraal Phytochorion. The lowest number of taxa within the regional obligate QFF is found in the Little Karoo Phytochorion but this area has a very high level of endemism (81.8 %) in the obligate QFF.

Table 8. Species number and level of endemism of the defined phytochoria of the obligate QFF

Phytochoria of the obligate QFF	Obligate quartz-field taxa occurring per phytochorion	Number of obligate quartz-field taxa endemic to the phytochorion	Relative share of obligate quartz-field taxa endemic to the phytochorion
Knersvlakte	67	63	94.0
Northern Namaqualand	39	22	56.1
Bushmanland-Warmbad	24	16	66.6
Southern Namaqualand	19	6	31.6
Riethuis-Wallekraal	17	7	41.2
Little Karoo	11	9	81.8

The degree of relationship between two phytochoria was calculated by employing **Sørensen's quotient of similarity** (Sørensen 1948, Schaefer 1992), calculated as follows

$$C_s = [2 (\text{number of shared taxa}) / (\text{number of taxa of Phytochorion } x) + (\text{number of taxa of Phytochorion } y)]$$

The C_s -value lies between 0 and +1. A high quotient indicates a high level of similarity in terms of species inventories between the two respective phytochoria.

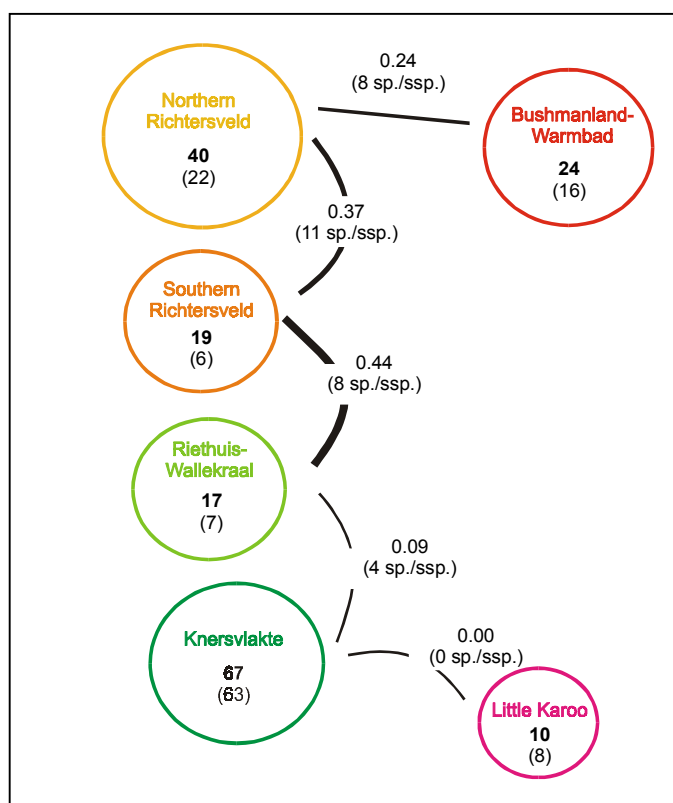


Figure 5. Sørensen's quotient (C_s) of similarity for the species/ subspecies inventories of the six regional QFFs. Figures in brackets below the quotient show the shared taxa. The figures in the circles represent the total number of obligate quartz-field taxa (above) and the number of endemics (in brackets below).

The regional obligate QFFs showed different levels of similarities in terms of species/subspecies inventories (Figure 5). The most isolated obligate QFF was found in the Little Karoo (C_s between Little Karoo and Knersvlakte = 0). The second lowest quotient of similarity between neighbouring phytochoria was found between the obligate QFFs of the Knersvlakte and of the Riethuis-Wallekraal Phytochorion ($C_s = 0.09$). The obligate QFF of the Knersvlakte has a very high level of endemism, it shares only four species/subspecies with other phytochoria. All of them also occur in the neighbouring Riethuis-Wallekraal Phytochorion. Two of these non-endemic quartz-field taxa (*Crassula columnaris* ssp. *prolifera* and *Senecio aloides*) have a wide distribution which stretches to the Southern Richtersveld and Northern Richtersveld Phytochoria and, in the case *C. c.* ssp. *prolifera* into the Bushmanland-Warmbad Phytochorion.

The highest quotient of similarity was found between the obligate QFF of the Riethuis-Wallekraal Phytochorion and the Southern Richtersveld Phytochorion ($C_s = 0.44$). Both

phytochoria contain a relatively low number of quartz-field taxa and a low level of endemism. The next highest quotients are found between the Northern and the Southern Richtersveld Phytochorion ($C_s = 0.35$) as well as between the Northern Richtersveld and the Bushmanland-Warmbad Phytochorion ($C_s = 0.22$). The Southern and the Northern Richtersveld Phytochorion have taxa in common than the Southern Richtersveld and the Riethuis-Wallekraal Phytochorion. But in contrast to the latter, the Northern Richtersveld Phytochorion comprises a high number of quartz-field taxa and endemic taxa. The Sørensen's quotient between the Northern Richtersveld and the Bushmanland-Warmbad Phytochorion is four times higher than the quotient between the Southern Richtersveld and the Bushmanland-Warmbad Phytochorion indicating a close relationship between the obligate QFFs of the two northernmost phytochoria.

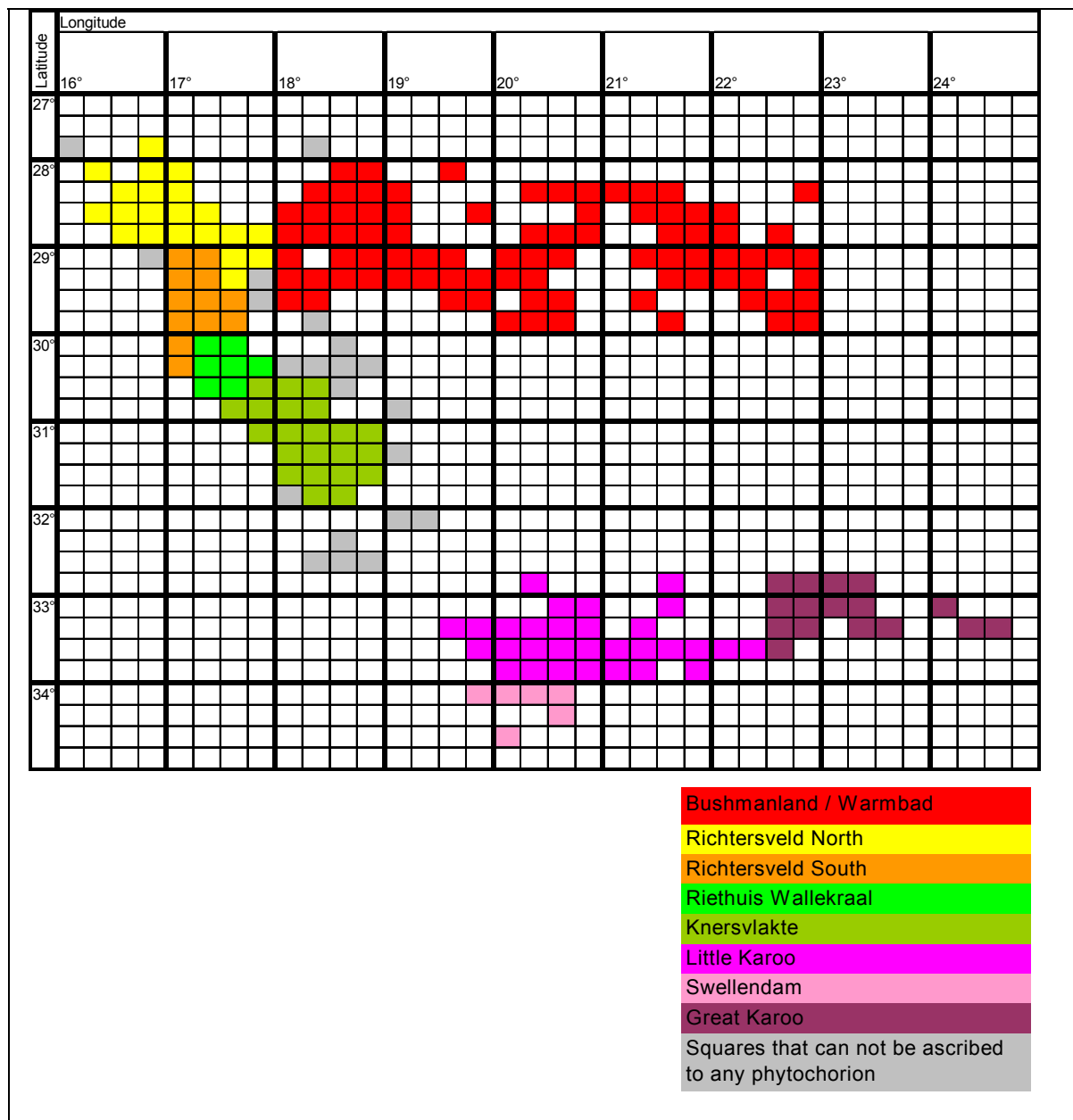


Figure 6. Geographical distribution of the six phytochoria of the southern African obligate QFF.

40. <i>Argyrodema testiculare</i>	x				x					
41. <i>Lachenalia patula</i>	x					x				
42. <i>Tylecodon peculiaris</i>	x						x			
43. <i>Conophytum subfenestratum</i>	x	x					x		x	
44. <i>Eriospermum titanopsoides</i>		x				x				
45. <i>Tylecodon pygmaeus</i>	x	x	x	x	x	x	x			
46. <i>Othonna intermedia</i>	x	x	x	x	x	x	x			
47. <i>Oophytum nanum</i>	x	x					x	x		
48. <i>Dicrocaulon nodosum</i>	x	x		x	x					
49. <i>Leucoptera subcarnosa</i>		x		x	x				x	
50. <i>Monilaria chrysoleuca</i>	x	x								x
51. <i>Argyrodema delaetii</i>	x	x								x
52. <i>Cephalophyllum caespitosum</i>	x	x	x							x
53. <i>Phyllobolus herbertii</i>	x	x								x
54. <i>Diplosoma luckhoffii</i>	x		x	x	x					x
55. <i>Tylecodon occultans</i>	x	x		x	x					x
56. <i>Crassula columnaris</i> ssp. <i>prolifera</i>	x	x	x	x	x	x				x
57. <i>Senecio aloides</i>	x	x	x		x	x				x
58. <i>Monilaria moniliformis</i>	x	x	x	x						x
59. <i>Argyrodema crateriforme</i>	x	x	x		x	x				x
60. <i>Conophytum calculus</i> ssp.	x	x	x		x	x				x
61. <i>Phyllobolus tenuiflorus</i>	x				x	x				x
62. <i>Dicrocaulon microstigma</i>										x
63. <i>Crassula multiceps</i>				x		x				
64. <i>Crassula barklyi</i>	x		x			x				
65. <i>Argyrodema ringens</i>										x
66. <i>Bulbine diphylla</i>										x
67. <i>Dicrocaulon longifolium</i>						x	x			x

Latitudes	Longitudes					
	17°30'		18°			19°
30°30'		3017DB 1	3018CA 1	3018CB 3	3018DA 1	
	3017DC 1	3017DD 6	3018CC 2	3018CD 19		3019CC 1
31°		3117BB 11	3118AA 11	3118AB 24	3118BA 22	3118BB 1
			3118AC 2	3118AD 33	3118BC 38	3118BD 17
				3118CB 20	3118DA 8	3118DB 3
				3118CD 1	3118DC 5	

Figure 7. Phytogeographical subdivision of the obligate QFF of the Knersvlakte. The bold figures below show the numbers of quartz-field species that occur in each square. Pink: Central Knersvlakte; red: Northern Knersvlakte; green: Western Knersvlakte.

According to the table, five geographically defined groups of species and subspecies was distinguished. The first group of taxa (# 1-27) was largely restricted to the southern and central part of the Knersvlakte, i.e., the triangle between Klaver in the south, Goedehoop in the north and Deelwater in the east (3118AD, BC, BD, CB). Due to its central position within the Knersvlakte in total, this zone will be addressed as Central Knersvlakte in the following. Merely four species covered the entire quartz-field area of the Knersvlakte (# 1-4) whereas the other had been recorded for parts of it only. The second group (# 28-33) was largely restricted to the northeastern corner of the Knersvlakte, to the area south-east of Nuwerus to northwest of Bitterfontein (3018CD, 3118AB, BA). This zone will be addressed as Northern Knersvlakte. The quartz-field species of the third group (# 34-39) were restricted to the western out-layers of the Knersvlakte between Komkans and Kotzesrus (3117BB, 3118AA). The fourth group (# 40-61) comprise those obligate quartz-field taxa that are broadly distributed in all three zones of the Knersvlakte. The area covered by this species group (surrounded by a blue line in Figure 7) can be addressed as the main distribution area of the obligate QFF of the Knersvlakte. The remaining quartz-field species (# 62-67) occurred roughly to the same extent inside and outside the floral centre.

The **Central Knersvlakte** is the largest and most species-rich area. It stretches from Moedgewin in the north-west (3118AD) to the escarpment in the east (3118BD). In the south-west it also includes the quartz fields between Kokenaap and Vredendal (3118CB). The most species-rich QDS lies between Luiperskop and Saggiesberg station (3118BC).

The **Northern Knersvlakte** borders on the first in the north. It covers the area from Bitterfontein in the west to the Flaminkvlakte in the east (3118AB and 3118BA) and to Stofkraal in the north (3119CD). The QDS around Nuwerus and Bitterfontein (3118AB) comprises the highest number of quartz-field species.

The **Western Knersvlakte** covers the smallest area which is also the poorest in terms of quartz-field species and subspecies. It stretches from Meerhofkasteel in the east (3118AA) to the Kotzesrus area in the west (3117BB). The Western Knersvlakte comprises the lowest number of quartz-field species and subspecies.

Table 9 makes emerge that the three sub-units show different levels of species overlap. The highest correspondence was found between the Central and the Northern Knersvlakte. The two sub-units share 11 quartz field taxa which show no preference to any of the two sub-units. Eight taxa occur in all three sub-units. Merely one species (*Pentstemon peduncularis*, Asteraceae) is restricted to the Western and Northern Knersvlakte sub-unit and is absent in the Central Knersvlakte. All other quartz-field taxa in the list that are centred in the three sub-units (no. 1 to 61) are either restricted to the Western or to the Northern Knersvlakte sub-unit. The remaining six quartz-field taxa (no. 62 - 67) do not fit into the common patterns of distribution as described above.

By far the highest numbers of quartz-field taxa were found in the squares 3118BC (38 species/subspecies) and 3118AD (33 species/subspecies) of the Central Knersvlakte (Figure 7, pink). Also the other squares of the Central and Northern Knersvlakte showed a considerably high number of quartz-field taxa. In contrast, the numbers of quartz-field species in the western zone (3117BB, 3118AA) was comparatively low with 11 species each.

The remaining QDSs of the Knersvlakte area harbour comparatively little quartz-field species / subspecies only (up to 8) and could not be clearly ascribed to any of the floral sub-units. They are located in a fringe around the three sub-units. They were shown in black in Figure 7.

III.1.3 Phytogeographical subdivision on genus level

Figure 8 is based on a DCA ordination employing the obligate QFF inventory per QDS on genus level with simple present-absent data. For the analysis the same methods were applied as for the phytogeographical subdivision on species level (Figure 3). Four genera were omitted as outliers (*Acrodon*, *Glottiphyllum*, *Pleiospilos*, and *Schwantesia*) since the occurrence of their intraspecific quartz-field taxa did not overlap with that of any of the other genera. *Crassula*, a very widespread genus that occurs in all phytochoria and in almost all QDSs was also omitted from the ordination in order to achieve a better resolution. The QDS were marked according their association with one of the six regional obligate QFFs as they were defined above.

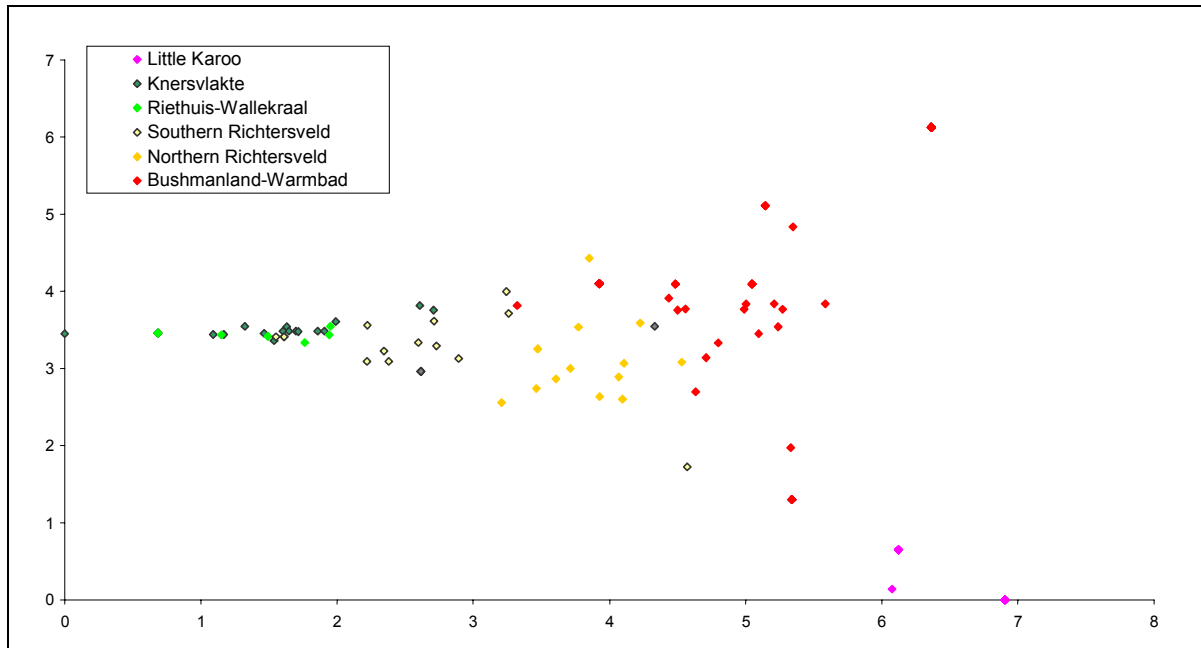


Figure 8. Phytogeographical subdivision of the obligate QFFs on genus level: DCA scatter diagram of the QDSs.

The distribution of the QDS in the ordination (Figure 8) corresponded largely with that of the ordinations on species / subspecies level (Figure 3). In correspondence with the latter, the Little Karoo Phytochorion was clearly separated from the remaining five obligate QFFs which were largely arranged (from left to right) along a south-north gradient according to their geographical distribution. The QDS of the Knersvlakte Phytochorion were plotted on the left hand side of the diagram in a dense cluster. Within this cluster also QDS of the Riethuis-Wallekraal Phytochorion were plotted. The two phytochoria formed one unit on genus level. The next group to the right mainly comprised QDS of the Southern Richtersveld Phytochorion. Only two QDS of the Knersvlakte Phytochorion were plotted among them. The QDSs of the Northern Richtersveld Phytochorion were plotted next to those of the Southern Richtersveld, forming a bridge between the QDSs of the Southern Richtersveld Phytochorion and of the Bushmanland-Warmbad Phytochorion. The QDSs of the Little Karoo Phytochorion were located at the lower fringe of the diagram.

From the left (QDSs of the Knersvlakte Phytochorion) to the right (QDSs of the Bushmanland-Warmbad Phytochorion) the density of the QDSs decreased significantly.

The scatter plot of the genera (Figure 9) formed a very dense cloud on the left side (formed by the genera occurring in the Knersvlakte and Riethuis-Wallekraal Phytochorion) and a more sparse

cloud in the centre of the diagram (formed by the genera of the Southern and Northern Richtersveld Phytochoria and the Bushmanland-Warmbad Phytochorion).

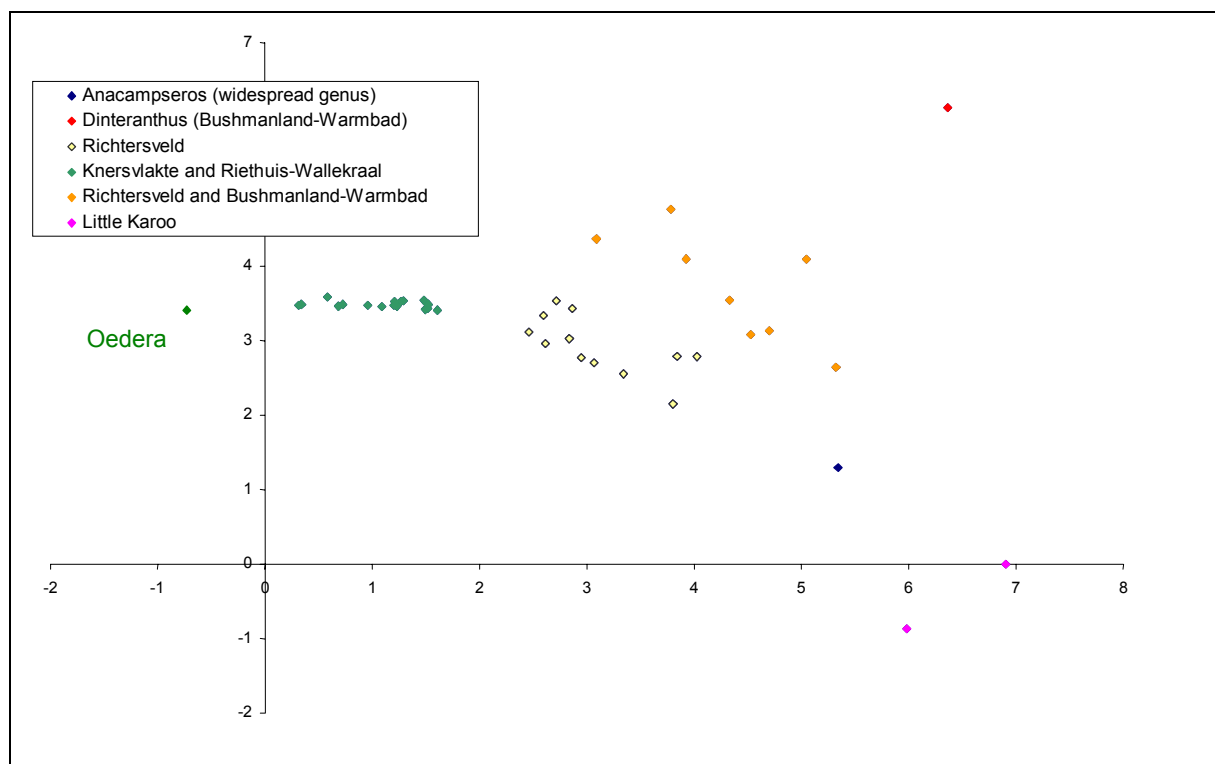


Figure 9. Phylogeographical subdivision of the obligate QFFs on genus level. Scatter diagram of the genera.

The genera that were plotted next to the QDS of the Knersvlakte formed a dense cluster which corresponded with the dense cluster of the QDSs (Figure 9). Only one genus (*Oedera*) was drawn aside. Apart from the dense cluster on the left hand side there were two groups of genera which were plotted in two loose clouds. In the left lower corner the genera of the Little Karoo were plotted separately from the rest. In the upper right corner *Dinteranthus* was plotted far off the other genera.

The genera of the Knersvlakte and the Riethuis-Wallekraal Phytochorion showed the densest cluster. This can be attributed to the high number of genera whose quartz-field species are restricted to both the Knersvlakte Phytochorion and the Riethuis-Wallekraal Phytochorion. The sparse cloud in the centre of the diagram corresponded well with the distribution of the QDSs of the Southern and Northern Richtersveld Phytochorion as well as the Bushmanland-Warmbad Phytochorion. The lower-left section of the cloud comprised these four genera (*Mitrophyllum*, *Nelia*, *Odontophorus*, *Polymita*, and *Schlechteranthus*) whose quartz-field taxa are restricted to the Richtersveld s.l. or which spread further to the south (into Riethuis-Wallekraal and Knersvlakte Phytochoria) These genera that occur in the Northern Richtersveld Phytochorion and in the Bushmanland-Warmbad Phytochorion were plotted in the upper-right section of the cloud.

Consequently, on genus level the two regional QFFs of the Richtersveld (Figure 9) were merely differentiated by four genera that are restricted to the Northern Richtersveld Phytochorion (*Adrocymbium*, *Cheiridopsis*, *Odontophorus*, and *Strumaria*), whereas the Southern Richtersveld does not house any endemic genus in the quartz-field flora. The Southern and Northern Richtersveld Phytochoria thus showed a relatively high correspondence on genus level. However, the genera of the obligate QFF of the Richtersveld s.l. were subdivided into two main groups. The left group showed main affinities to the southern obligate QFFs (Southern Richtersveld and Riethuis-

Wallekraal Phytochorion) the right group with the northern and eastern obligate QFFs (Northern Richtersveld Phytochorion and Bushmanland-Warmbad Phytochorion).

Dinteranthus, the only genus of the quartz-field flora that were entirely restricted to the Bushmanland-Warmbad Phytochorion was plotted in the upper right corner of the diagram.

Anacampseros, which occur in all phytochoria except in the Knersvlakte, was plotted in the gap between the genera of the Little Karoo Phytochorion and those of the Bushmanland-Warmbad Phytochorion and the Northern Richtersveld Phytochorion. It obviously causes the relative high correspondence between the Little Karoo, Bushmanland-Warmbad, and Northern Richtersveld Phytochoria.

Table 10. Genera of the obligate QFF sorted according to their occurrence (from right to left) in the scatter diagram of the genera (Figure 9). Genera that are largely or entirely restricted to quartz fields were underlined. Genera with a broad distribution within the obligate QFFs were written in *italics*.

Scores on Axis 1	Genus	Distribution of the quartz-field species within the genus
-0.7271	Oedera	Knersvlakte Phytochorion
0.3149	<u>Diplosoma</u>	Knersvlakte Phytochorion and outside the Knersvlakte in the south
0.3407	Babiana	Knersvlakte Phytochorion
0.5856	Lapeirousia	Knersvlakte Phytochorion
0.6857	<u>Dicrocaulon</u>	Knersvlakte Phytochorion and Riethuis-Wallekraal Phytochorion
0.7271	Pentzia	Knersvlakte Phytochorion
0.9554	Lasiopogon	Knersvlakte Phytochorion
1.0912	Pelargonium	Knersvlakte Phytochorion
1.2021	Eriospermum	Knersvlakte Phytochorion
1.2098	<u>Leucoptera</u>	Knersvlakte Phytochorion
1.2183	Othonna	Knersvlakte Phytochorion and Riethuis-Wallekraal Phytochorion
1.2348	<u>Oophytum</u>	Knersvlakte Phytochorion
1.2691	Zygophyllum	Knersvlakte Phytochorion
1.2895	<u>Argyroderma</u>	Knersvlakte Phytochorion
1.4840	<u>Jacobsenia</u>	Knersvlakte, Riethuis-Wallekraal and Southern Richtersveld
1.4908	<u>Monilaria</u>	Knersvlakte, Riethuis-Wallekraal and Southern Richtersveld
1.5196	<i>Senecio</i>	<i>Knersvlakte, Riethuis-Wallekraal and Southern and Northern Richtersveld Phytochorion</i>
1.5239	Lachenalia	Knersvlakte Phytochorion
1.6099	<i>Phyllobolus</i>	<i>Knersvlakte Phytochorion, Riethuis-Wallekraal Phytochorion, Southern and Northern Richtersveld Phytochorion</i>
2.4570	<u>Polymita</u>	Southern Richtersveld Phytochorion
2.5956	<u>Meyerophytum</u>	Riethuis-Wallekraal Phytochorion, Southern and Northern Richtersveld Phytochorion
2.6151	Cephalophyllum	Knersvlakte Phytochorion and Northern Richtersveld Phytochorion
2.7171	<i>Tylecodon</i>	<i>Knersvlakte Phytochorion, Northern Richtersveld Phytochorion and Bushmanland-Warmbad Phytochorion</i>
2.8369	Mitrophyllum	Southern and Northern Richtersveld Phytochorion
2.8665	<i>Bulbine</i>	<i>Knersvlakte, Southern and Northern Richtersveld Phytochorion</i>
2.9488	<u>Aspazoma</u>	Riethuis-Wallekraal, Southern and Northern Richtersveld Phytochorion
3.0671	Nelia	Southern and Northern Richtersveld Phytochorion
3.3396	Octopoma	Southern and Northern Richtersveld Phytochorion
3.8036	<u>Schlechteranthus</u>	Southern and Northern Richtersveld Phytochorion
3.8420	Strumaria	Northern Richtersveld Phytochorion
4.0255	Odontophorus	Northern Richtersveld Phytochorion
3.0911	Androcymbium	Northern Richtersveld Phytochorion
3.7808	Cheiridopsis	Northern Richtersveld Phytochorion
3.9252	<i>Conophytum</i>	<i>Knersvlakte Phytochorion, Riethuis-Wallekraal Phytochorion, Southern and Northern Richtersveld Phytochorion and Bushmanland-Warmbad Phytochorion</i>
4.3338	<i>Lithops</i>	<i>Knersvlakte Phytochorion, Southern and Northern Richtersveld Phytochorion, Bushmanland-Warmbad Phytochorion</i>
4.5302	Tridentea	Northern Richtersveld and Bushmanland-Warmbad Phytochorion
4.7021	Adromischus	Northern Richtersveld and Bushmanland-Warmbad Phytochorion
5.047	<u>Ihlenfeldtia</u>	Northern Richtersveld and Bushmanland-Warmbad Phytochorion
5.3233	Lapidaria	Bushmanland-Warmbad Phytochorion
6.3653	<u>Dinteranthus</u>	Bushmanland-Warmbad Phytochorion
5.3416	<i>Anacampseros</i>	<i>Little Karoo, Southern and Northern Richtersveld, Bushmanland-Warmbad Phytochorion</i>
5.9855	<u>Muiria</u>	Little Karoo Phytochorion
6.9058	Gibbaeum	Little Karoo Phytochorion and Swellendam area

Comparison of the structural and floral features of the phytocoria

III.1.4 Growth-form spectra

The entire obligate QFF

The obligate quartz-field flora (QFF) comprised a very narrow array of growth forms (Figure 10). In particular, dwarf shrubs which are smaller than 5 cm in height (nano-chamaephytes) were the most frequent growth forms. 58 % of the quartz field taxa belonged to this group of growth forms. All other growth-form groups were represented by a much lower percentage (a maximum of only 14 %).

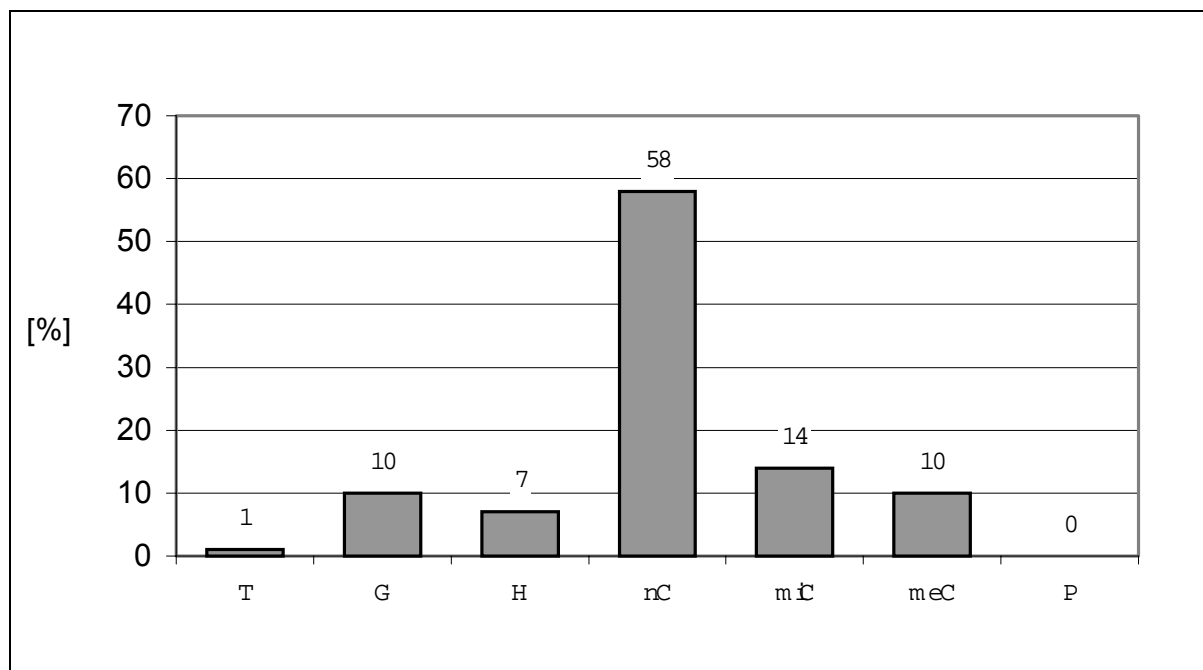


Figure 10. Growth-form spectrum of the QFF of Southern Africa (1)

Therophytes were represented by < 1 % (i.e., one species only) and phanerophytes, i.e., shrubs and trees taller than 50 cm in height, were entirely absent from the obligate QFF.

When the major group of nano-chamaephyteous growth forms were subdivided further into four subgroups, the following growth-form spectrum emerged (Figure 11).

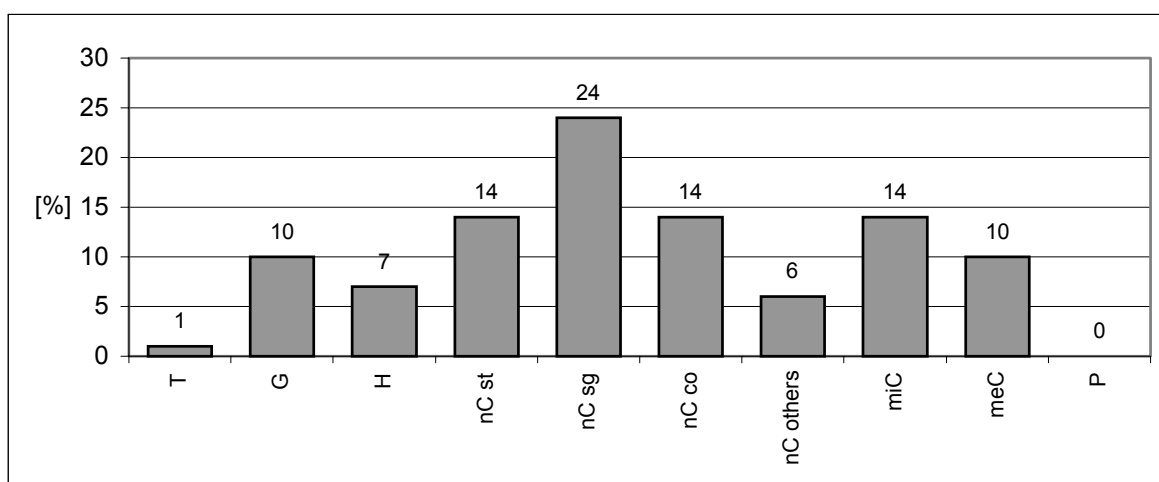


Figure 11. Growth-form spectrum of the southern African QFF (2) with special reference to the nano-chamaephyteous subgroups.

The most species-rich subgroup within the nano-chamaephytes were the subglobose nano-chamaephytes. This group also comprised the highest number of species and subspecies among all growth-form groups. Those nano-chamaephytes that did not fit in one of the three subgroups, the “other nano-chamaephytes”, represented a only small fraction of the nano-chamaephytes (6 % of the flora).

The regional QFFs

The phytogeographical analysis of the obligate QFF revealed six main phytochoria (see Chapter III.1.1). Each phytochorion was characterised by a number of endemic species or subspecies. Regarding the high percentage of regional endemic species the growth-form spectra of the regional quartz-floras was analysed to compare the regional particularities.

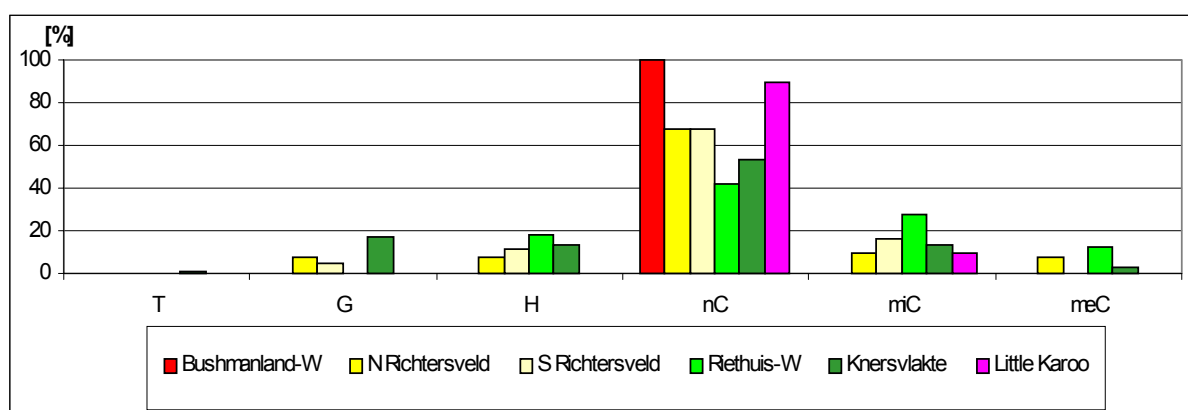


Figure 12. Growth-form spectra (percentage) of the six regional obligate QFFs. T = therophyte, G = geophytes, H = hemicryptophytes, nC = nano-chamaephytes (< 5 cm), miC = micro-chamaephytes (5-15 cm), meC = mega-chamaephytes.

Figure 12 shows the growth-form spectra of the regional obligate QFFs. They were arranged according to their geographical distribution, from north to south. The six floras showed strong correspondences: within all regional QFFs, the majority of the growth forms belonged to the group of nano-chamaephytes (i.e., shrubs < 5 cm in height). This growth group occurred in each of the floras. Also micro-chamaephytes were found in all floras except in the Bushmanland-Warmbad Phytochorion. They hence represented the second most frequent growth-form group within the floras. In contrast, geophytes, hemicryptophytes, and mega-chamaephytes (shrubs 15-50 cm in height) were absent in at least two of the regional floras. Therophytes were only found in the obligate QFF of the Knersvlakte Phytochorion.

Consequently, the regional obligate QFFs corresponded in being dominated by nano-chamaephyteous growth forms and by the fairly frequent occurrence of micro-chamaephytes and hemicryptophytes.

However, there were also clear differences between the regional floras. The most conspicuous divergence was found between the obligate QFFs of the Bushmanland-Warmbad Phytochorion as well as the Little Karoo Phytochorion on the one hand and the remaining obligate QFFs (of the Namaqualand *sensu lato*) on the other hand. The obligate QFFs of both the Little Karoo and the Bushmanland-Warmbad Phytochorion differed from those of the other phytochoria by an over-representation of nano-chamaephytes. In both phytochoria, the nano-chamaephytes contributed a very high percentage of the species and subspecies of the QFF (90 % in the Little Karoo Phytochorion and 100 % in the Bushmanland-Warmbad Phytochorion) whereas the percentages of nano-chamaephytes were considerably lower in the other four phytochoria (40-60 %). Other growth forms than nano-chamaephytes were rare (Little Karoo P.) or absent (Bushmanland-Warmbad P.).

The remaining four obligate QFF (Knersvlakte, the Riethuis-Wallekraal, the Southern and Northern Richtersveld Phytochorion) corresponded in having a similar percentage of hemicryptophytes, micro-chamaephytes, and mega-chamaephytes. All chamaephytes as well as hemicryptophytes were largely equally distributed within these floras. Only in the Southern Richtersveld Phytochorion mega-chamaephytes were absent. Geophytes and particularly therophytes, however, showed a slightly different distribution. The first were found in the Knersvlakte, the Southern and Northern Richtersveld Phytochorion but were absent in QFF of the Riethuis-Wallekraal Phytochorion. The therophytes, however, were only found in the obligate QFF of the Knersvlakte Phytochorion.

For a detailed comparison of the growth-form spectra of the regional obligate QFFs the most important group of the nano-chamaephytes were subdivided into the four subgroups (subterraneous, subglobose, compact nano-chamaephytes, and “others”; see Chapter II.2.1).

Again, particular similarity between Little Karoo and the Bushmanland-Warmbad Phytochorion could be detected (Figure 13). In both regional obligate QFFs the subglobose nano-chamaephytes formed the most important group. About half of the species / subspecies of these quartz floras belonged to this growth-form subgroup. The other nano-chamaephyteous subgroups were considerably less frequent in both floras. They comprised between 11 and 19 % of the nano-chamaephytes only.

In correspondence to the similarity regarding the main growth-form groups (Figure 12), again the obligate QFFs of the Namaqualand *sensu lato*, namely the Northern Richtersveld, Southern Richtersveld Phytochorion, Riethuis-Wallekraal Phytochorion, and the Knersvlakte Phytochorion showed distinct similarities. In the QFF of these phytochoria, the nano-chamaephyteous subgroups were more equally represented than in the Little Karoo and the Bushmanland-Warmbad Phytochoria. Moreover, the “other” nano-chamaephytes formed the most important

group of nano-chamaephyteous growth forms within all Phytochorion of the Namaqualand *sensu lato*, except in the Knersvlakte Phytochorion. The growth-form composition of the latter showed a generally balanced composition of the growth-form groups. None of the growth-form groups and subgroups represented more than 20 % of the species or subspecies.

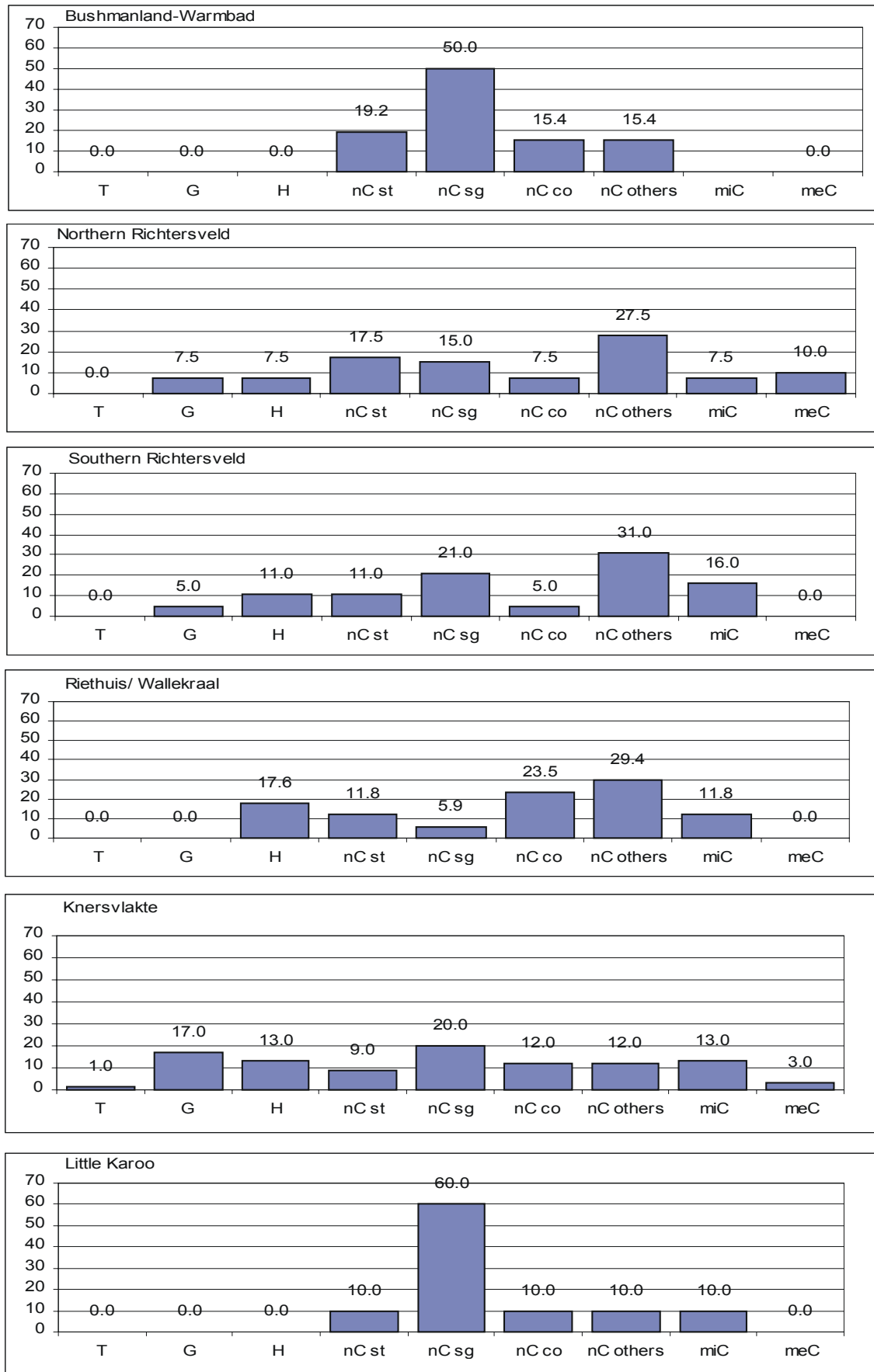


Figure 13. Growth-form spectra (percentage) of the six phytochoria of the obligate QFF. The nano-chamaephytes are subdivided into subgroups. The numbers give the percentage of the growth-form groups within the flora.

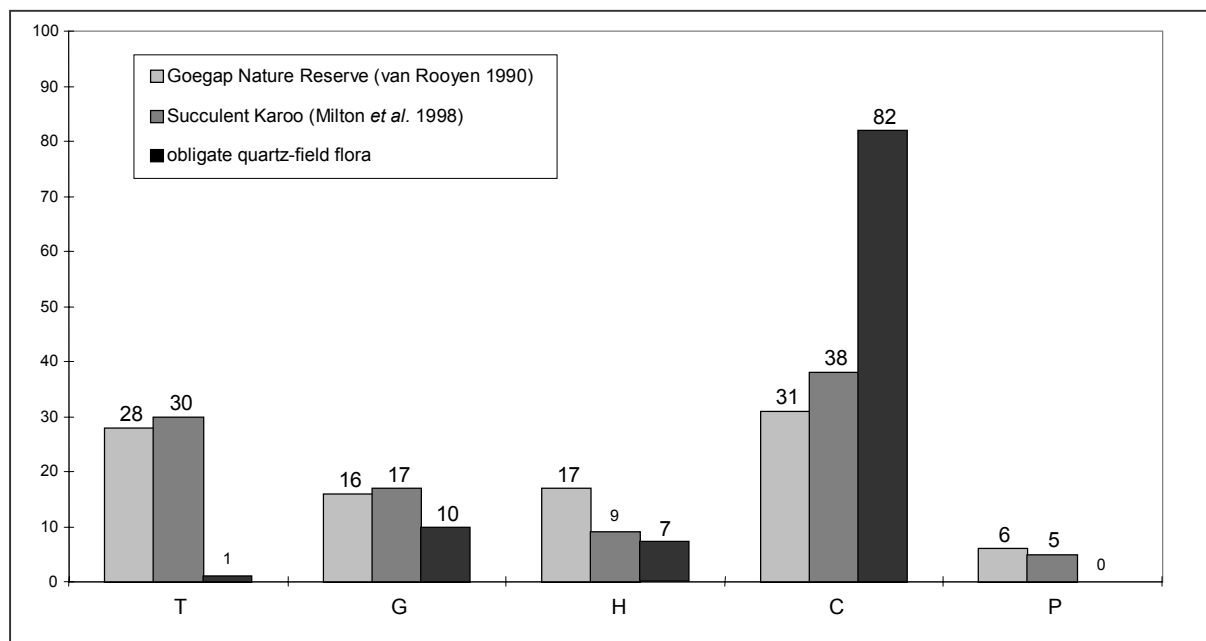


Figure 14. Comparison of the growth-form spectrum of the obligate quartz-field flora (QFF) and of the Succulent Karoo (data for the Succulent Karoo Flora taken from Milton *et al.* 1997 and van Rooyen *et al.* 1990). T = Therophytes, G = Geophytes, H = Hemicryptophytes, C = Chamaephytes, P = Phanerophytes.

For comparison purposes, growth-form spectra of the entire Succulent Karoo Flora (SKF, data from Milton *et al.* 1997) and of a small section of the Succulent Karoo (van Rooyen *et al.* 1990) was employed.

Figure 14 revealed the overwhelming dominance of chamaephytes in the obligate QFF. The percentage of chamaephytes in the obligate QFF is more than double as high as in the comparative floras of the Succulent Karoo. In contrast, phanerophytes, hemicryptophytes, geophytes and therophytes are considerably under-represented within the QFF.

Due to the lack of comparative data for the general SKF, the percentage of the other chamaephyteous groups, such as nano-, micro-, and mega-chamaephytes, as well as the percentage of the nano-chamaephyteous subgroups (compact, subglobose, subterraneous, others) cannot be considered here.

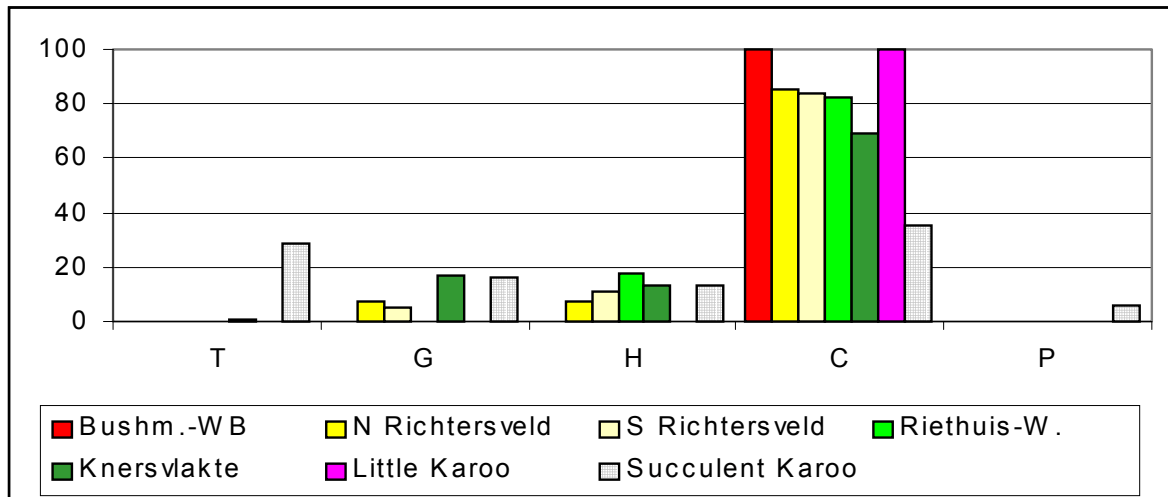


Figure 15. Comparison of the growth-form spectra (percentage of the species /subspecies) of the six regional QFFs and the general Succulent Karoo Flora (SKF). Figures refer to percentage of species and subspecies within the floras. Data for the Succulent Karoo are taken from Milton *et al.* 1997. T = Therophytes, G = Geophytes, H = Hemicryptophytes, C = Chamaephytes, P = Phanerophytes.

In Figure 15 the form spectrum of the general SKF was compared to that of the regional obligate QFFs. For the occurrence of the chamaephyteous growth form of different heights or even of the nano-chamaephyteous subgroups, no floral data for the entire SKF was available. In correspondence to the situation shown for the entire obligate QFF above, again the chamaephytes were strongly over-represented in all regional QFFs. In terms of percentage of hemicryptophytes and geophytes the QFFs of the Namaqualand *sensu lato*, i.e., Knersvlakte, Riethuis-Wallekraal, Southern and Northern Richtersveld, corresponded well with the entire SKF. In the obligate QFF of the Riethuis-Wallekraal Phytochorion, however, the geophytes were absent and therefore under-represented in comparison to the general SKF. Therophytes are highly under-represented in all regional QFFs, even in the Knersvlakte where they are represented by less than 1 % of the taxa.

III.1.5 Morphological and phenological features

The entire obligate QFF

The obligate QFF was clearly dominated by succulents (Table 11), only 2.6 % of the species and subspecies of the flora had no succulent organs at all. In addition to succulent leaves and stems, all organs that have particular tissues to store water, such as bulbs, roots, and tubers of geophytes, hemicryptophytes and other shrubs were interpreted as succulent organs. The majority of the succulent taxa within the QFF were leaf succulent (88 %). Only 4 % of the taxa were exclusively stem succulent (not having succulent leaves) whereas 7 % were both leaf and stem succulent. The percentage of species or subspecies with an assimilating succulent stem was comparatively low (2 %). In comparison to the low proportional representation of the stem succulents, taxa with a subterranean succulent axis (tubers) or succulent roots were relatively well represented within the QFF. 17 % of the quartz field taxa had tubers or succulent roots.

Table 11. Number of taxa and percentage of particular morphological and phenological features within the southern African obligate QFF. First figure = number of taxa (species and subspecies), second figure in brackets (percentage within the flora). Non-succulent = taxa without any succulent vegetative organs, leaf succ = leaf succulent taxa, stem succ TOTAL = total number and percentage of all stem succulent taxa (assimilating and non-assimilating, leaf succulent and non-leaf succulent); stem succ NOT leaf succ = stem succulent taxa without succulent leaves); stem succ and leaf succ = taxa that are stem AND leaf succulent; stem succulent (assim.) = taxa with succulent and assimilating stems; fleshy roots/ tubers = taxa with succulent roots or tubers;. Drought deciduous = drought-deciduous plants (excluding therophytes and geophytes)

Non-succulent	Leaf succulent	Stem succulent				Fleshy roots / tubers	Drought-deciduous
		Stem succ TOTAL	Stem succ NOT leaf succ	Stem succ AND leaf succ	Stem succulent (assim.)		
4 (2.6 %)	139 (87.7 %)	17 (9.7 %)	6 (3.9 %)	11 (7.1 %)	3 (1.9 %)	26 (16.8 %)	72 (46.5 %)

About half the taxa (46.5 %) had drought-deciduous leaves. This group included all taxa in which the leaves were either dropped during the dry period or where they remained on the plants as dry papery sheaths, often providing shelter and shade for the newly-formed leaves (e.g., Mitrophyllinae, Ihlenfeldt 1971b).

The regional QFFs

The six regional QFFs showed high correspondence with respect to frequency of succulence as well as phenological features. In all phytochoria the obligate QFFs comprised 80 to 100 % of **leaf-succulent** taxa whereas only 9 to 18 % of the taxa were stem succulent. However, taxa that were stem and leaf succulent were only found in the obligate QFFs of the Namaqualand *sensu lato*, they were absent in the Bushmanland-Warmbad Phytochorion and in the Little Karoo Phytochoria. Stem succulents with **assimilating** axis were either entirely absent (Knersvlakte and Little Karoo Phytochoria) or they were represented by a low percentage. The percentage of taxa with **subterranean succulent organs** like succulent roots and tubers was between 10 and 21 % in all regional floras except in the Riethuis-Wallekraal Phytochorion where this group comprised only 6 % of the obligate QFF. Also, the obligate QFF of the Knersvlakte housed the only taxa without any succulent organ. They comprised 6 % of that flora, though.

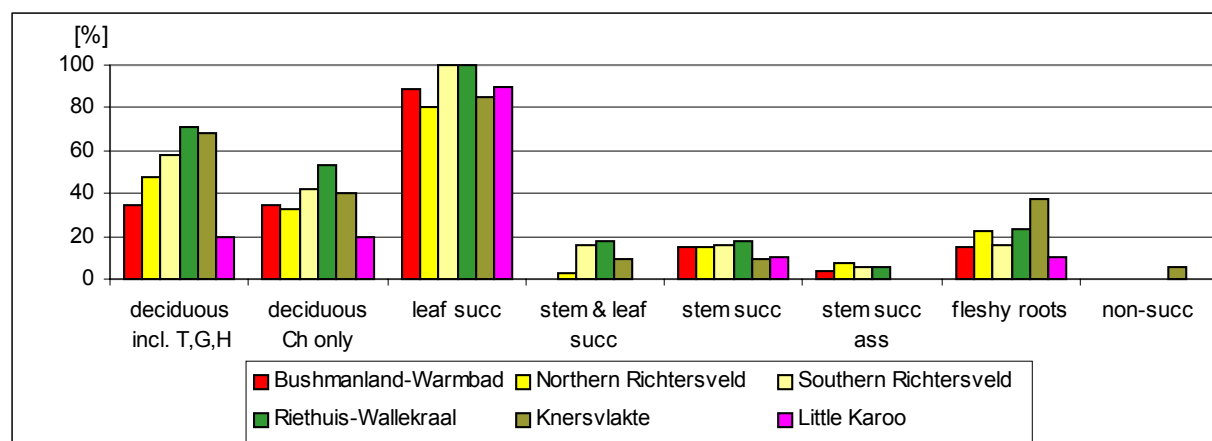


Figure 16. Percentage of taxa with particular morphological and phenological features within the regional obligate QFFs. deciduous = taxa with drought-deciduous leaves (incl. T, G, H = including

therophytes, geophytes, hemicryptophytes; Ch only = excluding therophytes, geophytes, hemicryptophytes); leaf succ = leaf-succulent taxa; stem & leaf succ = taxa with succulent leaves and stems; stem succ ass = taxa with succulent and assimilating axes; roots fleshy/ tubers = taxa with succulent / fleshy roots or tubers (includes geophytes), non-succ = taxa without any succulent organ.

Relatively low correspondence between the regional obligate QFFs was found regarding the **occurrence of drought-deciduous leaves**. This category was considered in two different versions: with and without having included therophytes and geophytes. Therophytes, hemicryptophytes, and geophytes are generally not acknowledged as drought-deciduous but in fact they are adapted to adverse or dry seasons by giving up the photosynthetic active organs (geophytes) or the entire plant (therophytes). Consequently, they were partly included into the group of drought-deciduous plants.

If the therophytes and geophytes were included, the highest percentages of drought-deciduous plants occurred in the Riethuis-Wallekraal Phytochorion and the Knersvlakte Phytochorion (Figure 16 and Table 12). Here about 70 % of the taxa shed their leaves at the beginning of the dry period. The Southern and the Northern Richtersveld Phytochorion still comprised roughly 50-60 % of drought-deciduous taxa. However, for the Bushmanland-Warmbad Phytochorion and particularly for the Little Karoo Phytochorion the percentage of drought-deciduous plants was considerably lower. If the therophytes and geophytes were excluded from this group, the percentage within the QFF of the Riethuis-Wallekraal Phytochorion remained the same but within the other QFFs of Namaqualand *sensu lato*, the percentages drop considerably.

Table 12. Morphological and phenological features of the species / subspecies of the regional obligate QFFs. First figure = number of species / subspecies; second figure in brackets = percentage within the regional obligate QFFs .

Phytochoria	Drought deciduous leaves		Leaf succulent	Stem succulent	Stem succulent (stems assimilating)	Stem and leaf succulent	Roots fleshy / tubers	Non-succulents
	incl. G & T	excl. G & T						
Bushmanland-Warmbad	9 (35%)	9 (35%)	23 (88 %)	4 (15 %)	1 (4 %)	0	4 (15 %)	0
Northern Richtersveld	19 (48%)	13 (33%)	23 (80 %)	6 (15 %)	3 (8 %)	1 (3 %)	6 (15 %)	0
Southern Richtersveld	11 (58%)	8 (42%)	19 (100 %)	3 (16 %)	1 (5 %)	3 (16 %)	3 (16 %)	0
Riethuis-Wallekraal	12 (71%)	9 (53%)	17 (100 %)	3 (18 %)	1 (6 %)	3 (18 %)	1 (6 %)	0
Knersvlakte	46 (69%)	27 (40%)	57 (85 %)	6 (9 %)	0	6 (9 %)	14 (21 %)	4 (6 %)
Little Karoo	2 (20%)	2 (20%)	9 (90 %)	1 (10 %)	0	0	1 (10 %)	0

In order to analyse the resemblance between the six phytochoria in terms of growth-form spectrum and occurrence of morphological and phenological features, a cluster analysis were conducted employing the percentage of nine growth-form groups, as well as eight morphological and phenological features as they are shown in Figure 13 and Figure 16. The resulting dendrogram (Figure 17) showed two main groups: the Bushmanland-Warmbad Phytochorion and the Little Karoo on the one hand and the Namaqualand *sensu lato* on the other hand. The

latter group again was subdivided into two pairs: Southern Richtersveld, Riethuis-Wallekraal Phytochorion and Northern Richtersveld, Knersvlakte.

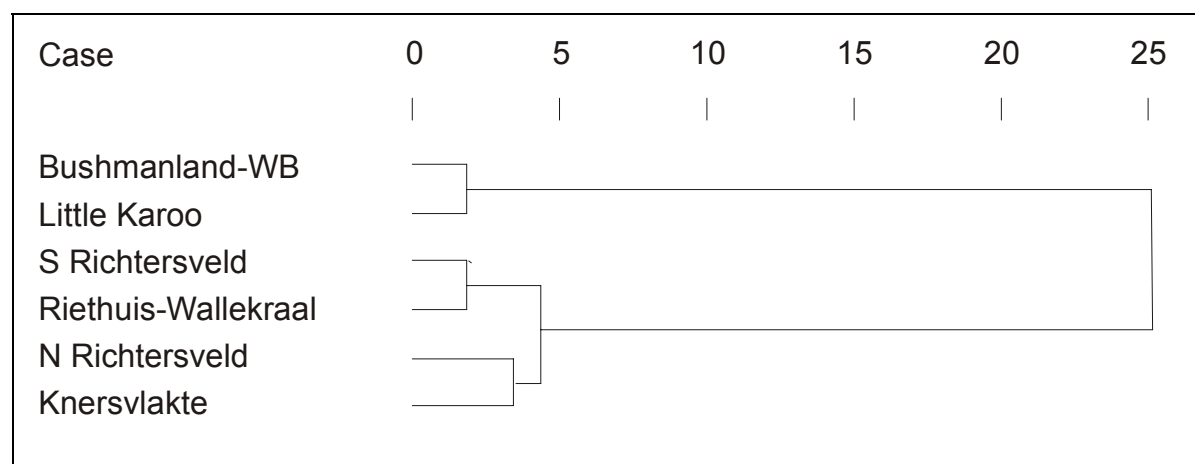


Figure 17. Dendrogram of a cluster analysis (using Ward Method) of the six regional obligate QFFs based the percentage of 17 structural features (9 growth-form groups, 8 morphological and phenological features).

III.2 Floral similarities between the phytochoria

In the following chapter the major taxonomic groups, the family spectra, the species to genera ratio, and finally the species inventories of the regional obligate QFFs will be analysed. The presentation of the floral spectra will be followed by a comparative analysis of the diversity of the regional floras with respect to various taxonomic levels. Finally, a synopsis of the floral interrelation of the floras will be given.

III.2.1 Major taxonomic groups

The obligate quartz-field flora in general

No pteridophytes were recorded to be an obligate quartz-field taxon.

Table 13 shows that the majority of the 155 obligate quartz-field taxa (species and subspecies) were dicotyledonae: 139 taxa (90 %) belonged to this group. In contrast, only 16 taxa (10 %) of were monocotyledonae.

The number of monocotyledonae genera (7 genera, 15 %) was similarly low compared to the number of the dicotyledonae genera (40 genera, 85 %). This relationship changed drastically when the number of families per major group was taken into account: there were 6 families of the monocotyledonae and only one more family (7 families) in the dicotyledonae group. Consequently, the number of species/subspecies per genus (compare species to genus ratios) was about the same in both major groups. However, there were about three times more species/subspecies per family in the dicotyledonae than in the monocotyledonae (compare the species to family ratio).

Table 13. The floral composition of the obligate QFF in terms of numbers of families, genera, taxa (species/subspecies) of the major taxonomic groups (Monocotyledonae, Dicotyledonae) and (*in brackets*) the percentage within the flora.

Major group	Species /subspecies	Genera	Families	Species to genus ratio	Species to family ratio
Pteridophyta	0	0	0	-	-
Monocotyledonae	16 (10.3 %)	7 (14.9 %)	6 (46.2 %)	2.4	2.8
Dicotyledonae	139 (89.7 %)	40 (85.1 %)	7 (53.8 %)	3.5	19.7
Total	155 (100 %)	47 (100 %)	13 (100 %)	3.3	11.9

The ratio of mono- and dicotyledonae, within the obligate QFF and the general Succulent Karoo flora (SKF)

Table 15 shows little difference on the lower taxonomic ranks, i.e., species and genera. In correspondence with the QFF, in the SKF the ratio of mono- to dicotyledonae on genus (1 : 2.7) and species / subspecies (1 : 3) level are similar. Also in the QFF the ratio on species/infraspecific taxa and genus level did not differ considerably (1 : 5.7 on genus level and 1 : 8.7 on species level). That is, in both floras the two major taxonomic groups are represented by about the same number of taxa on species and genus level. However, the floral composition of the obligate QFF in terms of major taxonomic groups diverges considerably from the SKF with respect of the ratio of mono- and dicotyledonae families.

Table 14. The percentage [%] of the major groups in terms of numbers of families, genera, and species/subspecies within the quartz field flora (QFF), in comparison with the Succulent Karoo flora (SKF). Data for the SKF from Hilton-Taylor 1996a.

Major group	Families (QFF)	Families (SKF)	Genera (QFF)	Genera (SKF)	Species / subspecies (QFF)	Species / subspecies / varieties (SKF)
Pteridophyta	0	5.9	0	1.4	0	0.5
Monocotyledonae	46.2	21.2	14.9	26.3	10.3	24.6
Dicotyledonae	53.8	72.9	85.1	72.3	89.7	74.9
Total	100	100	100	100	100	100

Table 15. Monocotyledonae / dicotyledonae ratio of the obligate quartz-field flora (QFF) and the Succulent Karoo flora (SKF) at different taxonomic ranks. Data for the SKF taken from Hilton-Taylor 1996a.

Flora	Family rank	Genus rank	Species / ssp. rank
QFF	1 : 1.2	1 : 5.7	1 : 8.6
SKF	1 : 3.4	1 : 2.7	1 : 3.0

In the SKF the percentage of mono- to dicotyledonae on family rank is about the same ratio as on genus and species rank. That is, in the monocotyledonae and the dicotyledonae of the SKF the relation between numbers of taxa is roughly the same at all taxonomic ranks. In the QFF, in contrast, the ratio on family rank differs considerably from those on the other taxonomic ranks: 1 : 1.16. Consequently, the relative low number of genera and species / subspecies per family of the monocotyledonae within the QFF is unusual and does not correspond at all with the situation in

the SKF. Consequently, on family level dicotyledonae are strongly under-represented within the QFF. Whereas, on genus and species level dicotyledonae are over-represented.

The regional obligate QFFs

Obviously, in all regional obligate QFFs the majority of the species and subspecies were dicotyledonae. In three of the regional obligate QFFs (Riethuis-Wallekraal, Bushmanland-Warmbad, Little Karoo), monocotyledonae were completely absent. In the other phytochoria the monocotyledonae comprised relatively few species or subspecies only. The highest proportion of monocotyledonae was found in the obligate QFF of the Knersvlakte. Here, they represented about 15 percent of the quartz-field species and subspecies. In the other two phytochoria where monocotyledonae belonged to the obligate QFF (Southern and Northern Richtersveld) they comprised less than 10 percent of the species and subspecies.

Table 16. Percentage of monocotyledonae and dicotyledonae taxa in the regional obligate QFFs of southern Africa

Phytochoria	Monocotyledonae [n]	Dicotyledonae [n]	Monocotyledonae [%]	Dicotyledonae [%]
Knersvlakte	10	57	14.92	85.07
Riethuis-Wallekraal	-	17	-	100.00
Southern Richtersveld	1	18	5.26	94.73
Northern Richtersveld	3	40	0.75	99.25
Bushmanland-Warmbad	-	26	-	100.00
Little Karoo	-	10	-	100.00

Monocotyledonae were best represented in the obligate QFF of the Knersvlakte which also comprised the highest number of quartz-field species in total. The second highest number and percentage of monocotyledonae were found in the obligate QFF of the Northern Richtersveld which had the second highest number of species and subspecies. But the percentage of monocotyledonae were not generally correlated with the species numbers of the obligate QFF: in the Bushmanland which was the third phytochorion with respect to richness in quartz-field species, no monocotyledonous species or subspecies occurred.

In Table 17 the percentage of monocotyledonous and dicotyledonous taxa within the regional obligate QFFs in comparison with their percentage within the entire flora of the areas covered by the phytochoria is shown. The lack of monocotyledonae in three of the regional obligate QFFs was not mirrored in the entire flora. In the flora of the Bushmanland-Warmbad Phytochorion as well as of the Little Karoo the monocotyledonae comprised about 20 % of the flora, where the percentage of monocotyledonae seems to be even higher than in the flora of the Namaqualand *sensu lato* (Desmet & Cowling 1999a).

Table 17. Comparison of the percentage of monocotyledonae and dicotyledonae within the obligate QFFs and general floras of the phytochoria.

Phytochoria	Regional obligate QFFs (see Table 16)		Entire floras of the areas covered by the phytochoria (data taken from literature)		References
	Monocotyledonae [%]	Dicotyledonae [%]	Monocotyledonae [%]	Dicotyledonae [%]	
Knervlakte	14.92	85.07	?	?	
Riethuis-Wallekraal	0	100.00	?	?	
Southern Richtersveld	5.26	94.73	12	88	Desmet & Cowling 1999a
Northern Richtersveld	0.75	99.25	12	88	Desmet & Cowling 1999a
Bushmanland-Warmbad	0	100.00	22	78	Werger 1986: Orange River Broken Veld
Little Karoo	0	100.00	18	82	Werger 1986: Succulent Karoo

III.2.2 Family spectra

The entire quartz-field flora

Table 18 shows the family spectrum of the southern African obligate QFF in terms of numbers of species or subspecies. By far the most important family of the obligate QFF are the Aizoaceae. 105 taxa (species and subspecies) – more than one third of the taxa – belonged to this group. All Aizoaceae taxa of the obligate QFF belonged to the Mesembryanthema, no taxa of the Aizoaceae s. str. were restricted to the quartz fields. The Crassulaceae, the second most highly represented family within the QFF, supplied only 17 taxa (10 %) to the flora. The Asteraceae and Asphodelaceae (Liliaceae s.l.) both contributed nine and seven taxa to the obligate QFF, respectively and form the third and fourth largest group. Each of the remaining families, several of them monocotyledons, contributed a few taxa only and form less than 2 % of the QFF.

Table 19 shows the family spectrum of the obligate QFF in terms of **numbers of genera and their percentage** within the obligate QFF. The Aizoaceae formed the most important group, it has the highest number of genera per family within the obligate QFF. With 28 genera and 61 % of the flora, the Aizoaceae ranked far above the Asteraceae (5 genera, 11 %), Crassulaceae (3 genera, 6 %), Iridaceae (2 genera, 4 %). The remaining families each contributed only one genus.

Table 18. Family spectrum of the flora of the southern African quartz fields (QFF). Percentages refer to importance of the families in terms of numbers of species and subspecies within the flora.

Family	Number of species / subspecies per family QFF	Percentage within the QFF
Aizoaceae	105	67 %
Crassulaceae	17	10 %
Asteraceae	9	5 %
Asphodelaceae	7	5 %
Portulacaceae	4	3 %
Iridaceae	3	2 %
Asclepiadaceae	2	1.5 %
Geraniaceae	2	1.5 %
Hyacinthaceae	1	1 %
Amaryllidaceae	1	1 %
Colchicaceae	1	1 %
Eriospermaceae	1	1 %
Zygophyllaceae	1	1 %
Total	155	100 %

Table 19. Numbers of genera per family represented in the flora of the southern African quartz fields (QFF) and their percentage in terms of numbers of genera.

Family	Numbers of genera per family within the QFF	Percentage within the QFF
Aizoaceae	28	61 %
Asteraceae	5	11 %
Crassulaceae	3	6 %
Iridaceae	2	4 %
Asphodelaceae	1	2 %
Asclepiadaceae	1	2 %
Hyacinthaceae	1	2 %
Geraniaceae	1	2 %
Amaryllidaceae	1	2 %
Portulacaceae	1	2 %
Colchicaceae	1	2 %
Eriospermaceae	1	2 %
Zygophyllaceae	1	2 %
Total	47	100 %

The family spectrum in terms of numbers of genera differs slightly from that in terms of numbers of species. The Asteraceae are more important than the Crassulaceae, the Iridaceae are more important than the Asphodelaceae and the Asclepiadaceae rank above the Portulacaceae when considering genera per family instead of species.

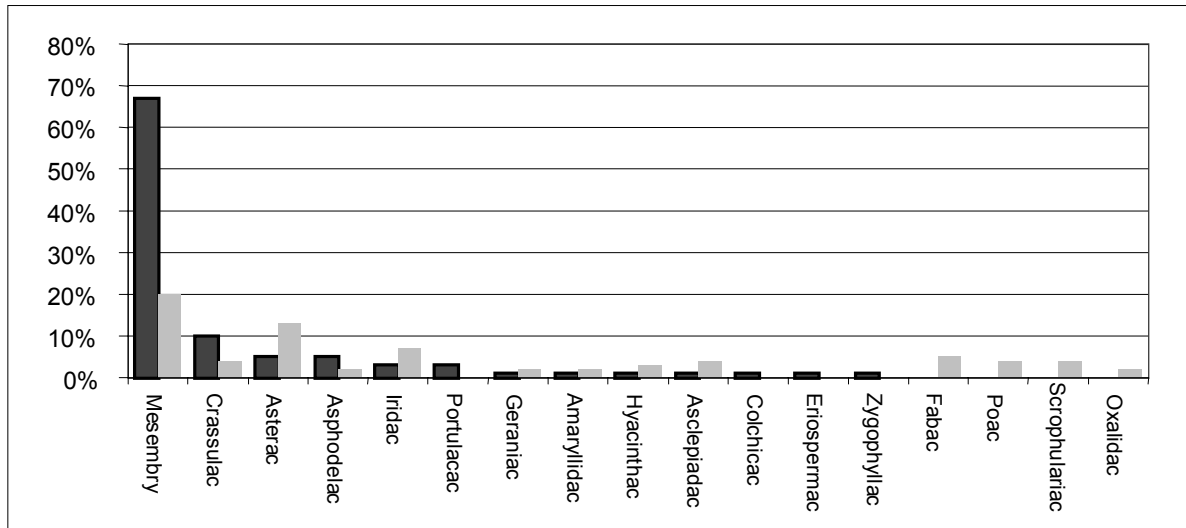


Figure 18. Percentage of families in terms of numbers of species / subspecies within the QFF (QFF) and the Succulent Karoo Flora (SKF). Black columns = obligate QFF, grey columns = SKF. Data for the SKF were taken from Hilton-Taylor (1996a).

The comparison with the family spectrum of the SKF give insight into the particularities of the composition of the obligate QFF (Figure 18). The comparative data for the SKF were taken from Hilton-Taylor (1996a). For his checklist, Hilton-Taylor (1996a) includes infraspecific taxa such as subspecies and varieties for most of the genera. Since subspecies rank was also included for the QFF, the data sets are largely comparable.

The family spectra of the two floras differed considerably on the species/subspecies level. Again in both floras the Aizoaceae represent the most important family, but the Aizoaceae are strongly over-represented within the QFF.

Also the Crassulaceae, the second group within the QFF in terms of species/subspecies are significantly over-represented within the obligate QFF (represented by 10 % of the species / subspecies in contrast to 4 % in the SKF). Consequently, the Aizoaceae and the Crassulaceae, the most species-rich families of the QFF were both represented by a 2.5 times higher percentage than in the SKF. Less significant but still obvious is the over-representation of the Asphodelaceae (5 % compared to 2 % in the SKF) and the Portulacaceae (2 % compared to < 1 % within the SKF). Colchicaceae, Eriospennaceae, Zygophyllaceae, four families that contributed 1 species (and about 1 % of the flora) to the QFF only, do not belong to the 20 most species-rich families of the SKF and are therefore not considered by Hilton-Taylor (1996a). On the other hand, a number of families are relatively under-represented within the QFF: Asteraceae and Iridaceae are the second or third most important families within the SKF (13 % and 7 % of the species), but in the QFF they contributed only 5 % and 2 % of the species / subspecies. Fabaceae s.l., Poaceae, and Scrophulariaceae which also belong to the ten most important families of the Succulent Karoo flora (representing 5 % or 4 % of the species/ infraspecific taxa) do not contribute any species to the flora of the quartz fields.

According to the comparison of the family spectra in terms of **numbers of genera** per family of the QFF and the SKF both floras correspond largely (Figure 19). The only difference is (i) the over-representation of the Aizoaceae and the Crassulaceae and (ii) the under-representation of the Poaceae, Fabaceae s.l. and the Scrophulariaceae within the QFF. The latter three families are ranked as the most important families within the SKF in terms of numbers of genera (contributing 8 %, 4 % and 3 %, respectively, to the genera of the SKF). They are entirely missing within the QFF. All other families of the QFF are fairly in line with the SKF.

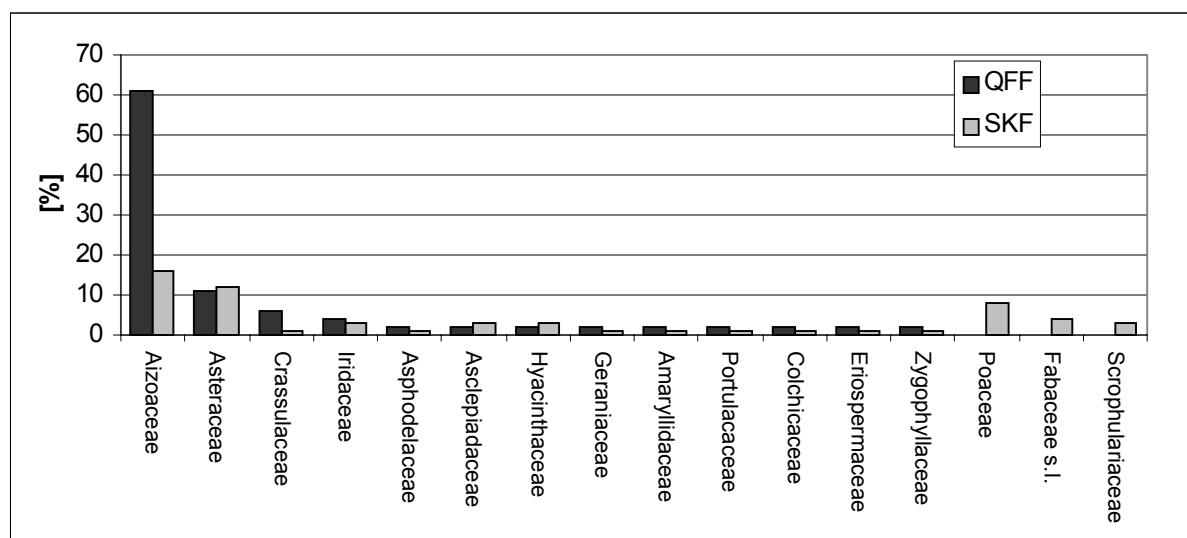


Figure 19. Percentage of families in terms of numbers of genera within the obligate quartz-field flora (QFF) and the Succulent Karoo Flora (SKF). Black columns = QFF, grey columns = SKF. Data for the SKF were taken from Hilton-Taylor (1996a).

Table 20. Families that are under- or over-represented in the obligate quartz fields flora (QFF) in terms of numbers of species/subspecies compared to the general Succulent Karoo flora (SKF). The families that are also under- or over-represented in terms of numbers of genera are given in bold letters.

Families that are under-represented	Families that are over-represented
Asclepiadaceae	Aizoaceae
Asteraceae	Asphodelaceae
Fabaceae	Crassulaceae
Hyacinthaceae	Portulacaceae
Iridaceae	
Oxalidaceae	
Poaceae	
Scrophulariaceae	

The **comparative ranking of the families in terms of numbers of genera** for the QFF and the SKF, shows a far higher conformity than the ranking in terms of numbers of species. Compared to the SKF only the Aizoaceae and the Crassulaceae and those families that are entirely absent from the QFF show considerable differences. Aizoaceae and Crassulaceae are clearly over-represented but in contrast to the family spectra in terms of numbers of species / subspecies, Asphodelaceae and Portulacaceae are not. They are represented roughly by the same percentage. Also, all the families that are listed in Table 20 as being under-represented in the QFF in terms of numbers of species / subspecies are represented to about the same percentage as in the SKF when the numbers of genera are taken into account.

The regional QFFs

In total 13 families were represented in the obligate QFF of southern Africa (Figure 20 and Figure 21). Only two families were found in all of the defined phytochoria, i.e., Crassulaceae and Aizoaceae (Mesembryanthema). The Asteraceae were the third group in terms of occurrence in the phytochoria. They were represented in the obligate QFFs of the Namaqualand *sensu lato* (Knersvlakte, Riethuis-Wallekraal, Southern and Northern Richtersveld) but were absent in the obligate QFFs of the Bushmanland-Warmbad Phytochorion and in the Little Karoo. The same applied for the Asphodelaceae which were also found only in the obligate QFFs of the Namaqualand *sensu lato*. However, they were absent in the Riethuis-Wallekraal Phytochorion. Geraniaceae were restricted to the obligate QFFs of the Knersvlakte and the Northern Richtersveld Phytochorion. Figure 20 and Figure 21 show the relative proportion of the plant families in the obligate QFF. By far the richest family in terms of species were the Mesembryanthema (Aizoaceae). In Bushmanland-Warmbad Phytochorion, the southern Richtersveld and the Little Karoo Mesembryanthema provide about three quarter of the quartz-field species and subspecies. In the other regional obligate QFFs, i.e., Northern Richtersveld, Riethuis-Wallekraal Phytochorion, and Knersvlakte, the Mesembryanthema comprised only up to two third of the species or subspecies respectively. The family spectrum of the obligate QFF of the Knersvlakte was particularly remarkable, because of the relatively small proportion of the two main groups of the southern African obligate QFF, i.e., Mesembryanthema and Crassulaceae. Here, the Mesembryanthema and the Crassulaceae contributed 56 % and 13 % of the regional quartz-field species only. In return, other families such as Asteraceae and Asphodelaceae were represented to a far higher proportion than in other regional obligate QFFs.

The highest **numbers of different plant families** in the regional obligate QFFs were found in the Knersvlakte and Northern Richtersveld Phytochorion. Nine families were encountered from these regional obligate QFFs. Besides an overlap of four plant families between the two regional QFFs, the family spectra of the obligate QFFs of the Knersvlakte comprised four families that were missing in the Northern Richtersveld (Eriospermaceae, Hyacinthaceae, Iridaceae, Zygophyllaceae) and in return, the obligate QFFs of the Northern Richtersveld Phytochorion comprised four families (Amaryllidaceae, Asclepiadaceae, Colchicaceae, Portulacaceae) that were missing in the obligate QFF of the Knersvlakte.

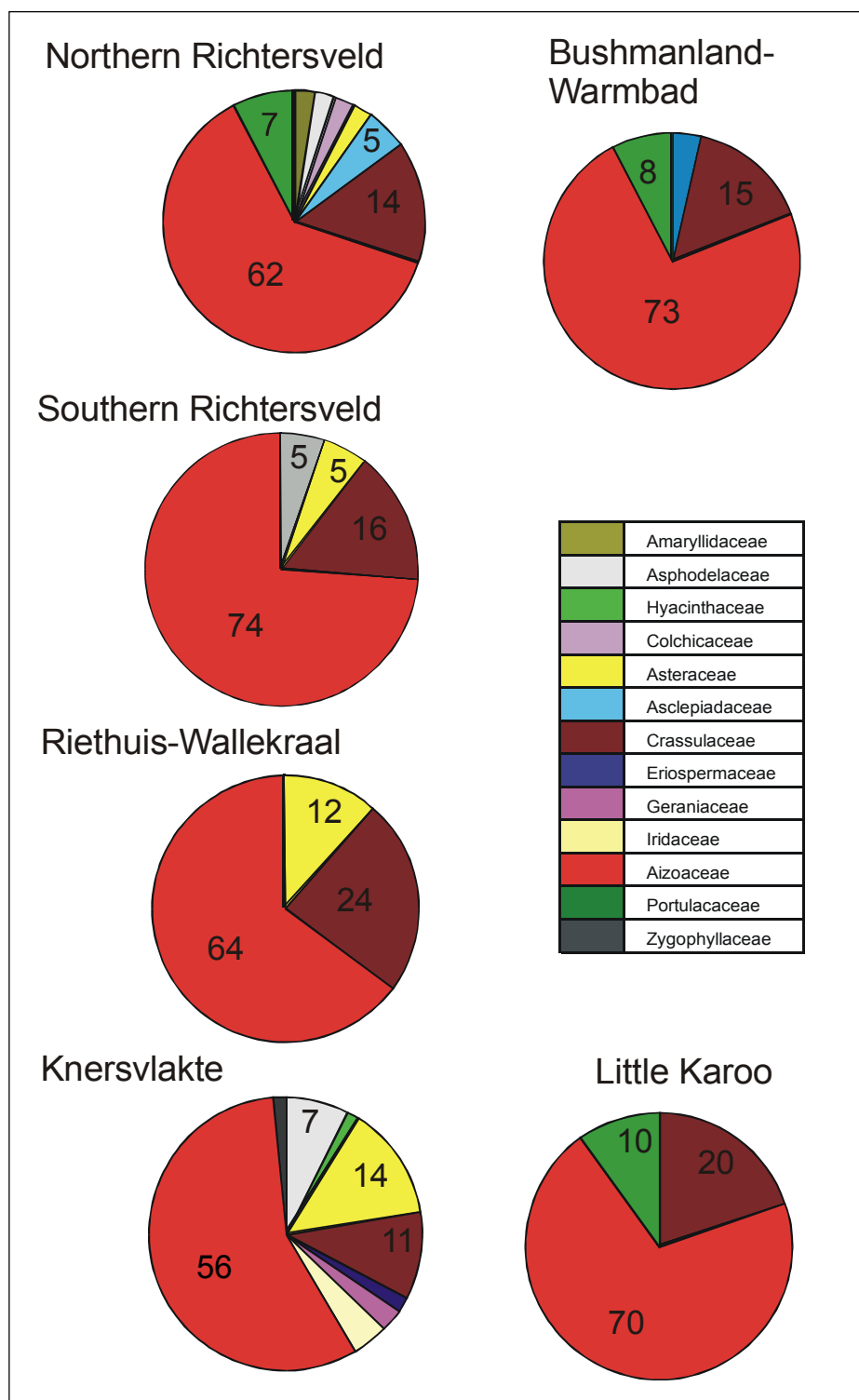


Figure 20. Family spectrum of the main regional obligate QFFs of southern Africa. The figures represent the numbers of species or subspecies per family in the obligate QFF of each area.

Table 21. Family spectra of the obligate QFF of the defined phytochoria

a) Numbers of species / subspecies per family.

Phytochoria	Mesembryanthema	Crassulaceae	Asteraceae	Asphodelaceae	Geraniaceae	Eriospermaceae	Hyacinthaceae	Zygophyllaceae	Iridaceae	Amaryllidaceae	Colchicaceae	Asclepiadaceae	Portulacaceae	Total (spp. /subsp.)
Knersvlakte	37	8	9	5	2	1	1	1	3					67
Riethuis-Wallekraal	11	4	2											17
Southern Richtersveld	14	3	1	1										19
Northern Richtersveld	25	6	1	1						1	1	2	3	40
Bushmanland-Warmbad	19	4										1	2	26
Little Karoo	7	2											1	10

b) Relative proportion [%] of the plant families in terms of numbers of species / subspecies.

Phytochoria	Mesembryanthem	Crassulaceae	Asteraceae	Asphodelaceae	Geraniaceae	Eriospermaceae	Hyacinthaceae	Zygophyllaceae	Iridaceae	Amaryllidaceae	Colchicaceae	Asclepiadaceae	Portulacaceae	Total
Knersvlakte	56	13	14	7	3	1	1	1	4					100
Riethuis-Wallekraal	64	24	12											100
Southern Richtersveld	74	16	5	5										100
Northern Richtersveld	62	15	2	2	2					2	2	5	8	100
Bushmanland-Warmbad	73	15										4	8	100
Little Karoo	70	20											10	100

There was a particular correspondence between the family spectrum of the obligate QFF of the **Northern Richtersveld and of the Bushmanland-Warmbad Phytochorion**: the two floras shared two of the four families (Asclepiadaceae, Portulacaceae) that were not found in the obligate QFFs elsewhere in the Namaqualand *sensu lato*. The overlap in the species inventories of the obligate QFFs of the Northern Richtersveld and the Bushmanland-Warmbad Phytochorion had been mentioned already when presenting the species inventories of the phytochoria (Chapter III.1.1).

Summarising, Mesembryanthema (Aizoaceae) and Crassulaceae were found in all regional obligate QFFs. Beyond this correspondence there were distinct differences between the regional obligate QFFs. Asteraceae and Asphodelaceae were restricted to (at least parts of) the obligate QFFs of the Namaqualand *sensu lato*. Five more families were only found in the obligate QFF of the Knersvlakte whereas four other families were found in the obligate QFF of the Northern Namaqualand only which shared two families with the obligate QFF of the Bushmanland-Warmbad Phytochorion and one with the Little Karoo.

The regional obligate QFFs differed considerably with respect of **numbers of plant families** (Table 22). Richest in species were the obligate QFFs of the Knersvlakte and the Northern Richtersveld Phytochorion. Both floras comprised 9 families. These two phytochoria also

comprised the highest numbers of species or subspecies within their obligate QFF (Knersvlakte 67 taxa and Northern Namaqualand 39 taxa). The obligate QFFs of the other phytochoria were considerably poorer with respect of plant families. They comprised 4 (Bushmanland-Warmbad and Southern Richtersveld) or three families (Riethuis-Wallekraal and Little Karoo) only. This largely corresponded with their lower numbers of quartz-field species.

Table 22 also shows the **Shannon-Wiener diversity index**. Besides the number of taxa (here families) this index also takes their abundance (here species per family) into account. The sequence of phytochoria in this table is sorted according to the Shannon-Wiener diversity index. The highest diversity index on family level was calculated for the Knersvlakte. The obligate QFF of the Northern Richtersveld Phytochorion had the second highest diversity index. Due to the more equal representation of the 3 families within the obligate QFF of the Riethuis-Wallekraal Phytochorion, the Shannon-Wiener diversity index was slightly higher than for the Southern Richtersveld Phytochorion where the obligate QFF comprised 4 families. The lowest diversity index was calculated for the obligate QFF of the Little Karoo. This regional obligate QFF comprised 3 families only of which one contributes 75 percent of the species.

Table 22. Number of families, diversity index and evenness on family level of the regional obligate QFFs.

Phytochoria	Number of families per phytochorion	Shannon-Wiener diversity index	Evenness
Knersvlakte	9	1.477	67.2
Northern Richtersveld	9	1.291	62.1
Riethuis-Wallekraal	3	0.873	79.5
Southern Richtersveld	4	0.826	59.6
Bushmanland-Warmbad	4	0.839	60.6
Little Karoo	3	0.802	72.9

The **evenness index** was calculated (column 4 in Table 22) to give insight into the equal or unequal composition of the family spectrum within the floras. The higher the evenness index the more equal the families were represented in the flora. The evenness indices did not correspond directly with the Shannon-Wiener index of diversity. By far the highest evenness indices were calculated for the obligate QFF of the Riethuis-Wallekraal Phytochorion and of the Little Karoo Phytochorion which both had an intermediate diversity index. This high evenness indices mirrored the relative equal representation of the families within the species spectra of the floras. In return, those floras that were most diverse on family level (Knersvlakte and Northern Richtersveld) had a rather intermediate evenness index. For the other regional obligate QFFs (Southern and Northern Richtersveld as well as Bushmanland-Warmbad Phytochorion) the evenness indices were equally low (about 60).

III.2.3 Spectrum of genera

The 155 species and subspecies of the obligate QFF formed part of 47 genera and 13 plant families. The number of species contributed to the obligate QFF was very heterogeneous among the genera 47 genera. As Table 23 shows 14 genera contributed three or more species or subspecies to the obligate QFF each whereas the remaining genera had one or two species only within the obligate QFF. The 14 most species rich genera within the obligate QFF contributed 105 species and subspecies, 67 % of the taxa.

Table 23. Fourteen most species-rich genera within the obligate quartz-field flora (QFF) and the total number of taxa (species and subspecies) per genus.

Genus	Family	Number of taxa within the QFF per genus	Total number of taxa per genus	Relative share of quartz field species within the genus	References
Conophytum	Mesembryanthema, Aizoaceae	21	120	18 %	S. A. Hammer, pers. comm.
Dicrocaulon	Mesembryanthema, Aizoaceae	12	12	100 %	H.-D. Ihlenfeldt, pers. comm.
Crassula	Crassulaceae	10 (9 species)	144 (exclusively species)	6 % (7 %)	Tölken 1977a
Argyroderma	Mesembryanthema, Aizoaceae	9	10	90 %	Hartmann 1977
Monilaria	Mesembryanthema, Aizoaceae	7	7	100 %	Ihlenfeldt & Jörgensen 1973
Gibbaeum	Mesembryanthema, Aizoaceae	7	15	47 %	J. Thiede, pers. comm.
Bulbine	Asphodelaceae	7	~ 50	14 %	Leistner 2000
Dinteranthus	Mesembryanthema, Aizoaceae	6	6	100 %	Sauer 1979, 1980
Tylecodon	Crassulaceae	5	27	18 %	Tölken 1985
Phyllobolus	Mesembryanthema, Aizoaceae	5	34	15 %	Gerbaulet 1997
Lithops	Mesembryanthema, Aizoaceae	5	51	8 %	Smith <i>et al.</i> 1998
Cephalophyllum	Mesembryanthema, Aizoaceae	4	30	13 %	Hartmann 1988
Anacampseros	Portulacaceae	4	29	12 %	Gerbaulet 1992a
Othonna	Asteraceae	3	96	3 %	Herman 1993
Total		105		67.7 %	

The most important genus in terms of numbers of species and subspecies was *Conophytum*. Twenty-one species and subspecies of *Conophytum* were recorded as quartz fields specialists. *Dicrocaulon* (Mesembryanthema), was the genus with the second-highest numbers of species within the obligate QFF. In addition to the Mesembryanthema, the Crassulaceae, Asphodelaceae (*Bulbine*), Portulacaceae (*Anacampseros*), and Asteraceae (*Othonna*) were also well represented amongst the most species-rich genera.

Table 24 shows the genera that were largely or completely restricted to quartz fields. Nine genera were completely restricted to quartz fields. Three of these contributed more than two species (*Dicrocaulon*, *Dinteranthus* and *Monilaria*) whereas the other six genera were monotypic (*Aspazoma*, *Muiria*) or nearly so (*Ihlenfeldtia*, *Meyerophytum*, *Oophytum*, *Schlechteranthus*). The genera that are largely or completely restricted to quartz fields belong, with only one exceptions (*Leucoptera*, Asteraceae), to the Mesembryanthema (Aizoaceae).

Table 24. Genera that were largely or completely restricted to the southern African quartz fields.

Genus	Number of species within the quartz flora	Total number of species	Percentage of quartz field species within the genus	References
Dicrocaulon	12	12	100	H.-D. Ihlenfeldt, pers. comm.
Argyroderma	9	10	90	Hartmann 1977
Gibbaeum	7	15	47	J. Thiede, pers. comm.
Monilaria	5	5	100	Ihlenfeldt 1973
Dinteranthus	4	4	100	Sauer 1979, 1980
Oophytum	2	2	100	Ihlenfeldt 1978
Jacobsenia	2	3	66	Ihlenfeldt 1997
Diplosoma	2	2	100	Ihlenfeldt 1988
Ihlenfeldtia	2	2	100	Hartmann 1992
Leucoptera	2	3	66	Nordenstam 1976
Meyerophytum	2	2	100	H.-D. Ihlenfeldt, pers. comm.
Schlechteranthus	2	2	100	Smith <i>et al.</i> 1998
Aspazoma	1	1	100	Smith <i>et al.</i> 1998
Muiria	1	1	100	Smith <i>et al.</i> 1998

In the following a short description of the most species-rich genera shall be given.

Conophytum N.E.Br., a genus that contribute the highest number of species and subspecies to the QFF (Schmiedel 2001a) comprises about 85 species and 35 subspecies (S. A. Hammer pers. comm.) and is therefore one of the most species-rich genera of the Mesembryanthema (Smith *et al.* 1998). With the only exception in *C. frutescens*, the *Conophytum* species are generally strongly reduced, cushion or cluster forming growth forms (Hammer 1993b). The leaves of the opposite leaf pairs are almost entirely united, forming distinct bodies (“Korpuskeln”). *Conophytum* is broadly restricted to the winter rainfall zone but also stretches into the arid parts of the summer rainfall zone in southern Namibia, north-western (Bushmanland) and in the transition zone in the south-eastern (Little Karoo) South Africa (Hammer 1993b, Hartmann 1991, Jürgens 1992). The quartz-field taxa within *Conophytum* are assorted to 10 of the 15 sections acknowledged by Hammer (1993b). Provided that these sections mirror the real infrageneric relationship of the genus, the quartz-field *Conophytum* taxa do not seem to be particularly closely related. Hence, the colonisation of the quartz fields by *Conophytum* taxa seems to have happened several times independently. This again may indicate that *Conophytum* taxa are generally pre-adapted to this kind of habitat.

Dicrocaulon N.E.Br. the next species-rich genus shows cushion-like to shrubby growth forms between 5 and 50 cm high (H.-D. Ihlenfeldt, pers. comm., Smith *et al.* 1998). *Dicrocaulon* belongs to the *Mitrophyllinae*, a subtribe which is characterised by succulent, semi-spheroid to oblong, mesomorphic, heterophyllous leaves (Ihlenfeldt 1971b). The genus comprises seven validly described species and at least five species that are undescribed still (H.-D. Ihlenfeldt, pers.

comm.). All *Dicrocaulon* taxa are restricted to quartz fields. The centre of diversity of the genus is the Knersvlakte but the two species are found in the Namaqualand region (Chapter III.1.1).

Crassula (Crassulaceae) is the third important group of the quartz field flora. Ten taxa (8 species and 2 subspecies) are restricted to the quartz fields. But with respect to the species-richness of the genus, *Crassula* comprises 144 species in total (Tölken 1977a), the percentage of species that are restricted to quartz fields is comparatively low (7 %). They can be either widespread (*C. columnaris*, *C. congesta* ssp. *laticephala*, *C. grisea*, *C. mesembryanthemopsis*) or have a rather restricted range-size (*C. susannae*, *C. obscurum* ssp. *violaciflorum* as well all *Tylecodon* and *Adromischus nanus* of the QFF).

Table 25. Quartz-field species/subspecies of *Crassula* their sections and distribution. Nomenclature follows Tölken (1977). All quartz-field species of the genus belong to the subgenus *Crassula*.

Species / subspecies	Section	Distribution
<i>C. congesta</i> ssp. <i>laticephala</i>	Columnares Haw. ex DC	Little Karoo
<i>C. columnaris</i> ssp. <i>columnaris</i>		Little Karoo and adjacent areas
<i>C. columnaris</i> ssp. <i>prolifera</i>		Namaqualand to Bushmanland-Warmbad Phytochorion
<i>C. multiceps</i>		Knersvlakte
<i>C. barklyi</i>		Knersvlakte to Riethuis-Wallekraal
<i>C. alstonii</i>	Argyrophylla (Schoenl.) Tölken	Southern and Northern Richtersveld Phytochorion
<i>C. susannae</i>		Riethuis-Wallekraal
<i>C. mesembryanthemopsis</i>		Warmbad area and southwestern Namibia
<i>C. grisea</i>	Arta (Schoenl.) Tölken	Riethuis-Wallekraal to Southern and Northern Richtersveld Phytochorion
<i>C. plegmatoides</i>		Northern Richtersveld Phytochorion

Argyroderma N.E.Br. (Mesembryanthema) is an endemic genus of the Knersvlakte. Nine of the 10 *Argyroderma* species (and 2 subspecies) are restricted to the quartz fields. Merely *A. fissum* (the only species of the subgenus *Roodia*) the putatively less derived species (Hartmann 1977) and the only species with oblong leaves, occurs also outside the quartz fields on loamy soils. The remaining species of the genus are characterised by hood-shaped or spheroid pairs of leaves and (in the putatively more derived taxa) little branching. Hartmann (1977) suggests that the colonisation took place at least three times independently. The putatively less derived, highly branched species (*A. framesii*, *A. subalbum*, *A. congregatum*) represent the intermediate links between ancestor *A. fissum* and the terminal species (*A. delaetii*, *A. patens*, *A. pearsonii*, *A. testiculare*). However, provided that the evolutionary trend as described by Hartmann (1977) proves right, the colonisation of the quartz-fields by *Argyroderma* might also have had taken place as a single event with subsequent adaptive radiation on the quartz fields. It is worth noticing that all ten *Argyroderma* species occur within a small area of about 100 by 60 km. Some of the species have broad distribution (*A. delaetii*, *A. fissum*) occur sympatrically with other species. But the locally restricted taxa show clear allopatric distributions. According to Hartmann (1977) they follow an ecological gradient parallel to the coast.

Gibbaeum (Haw.) N.E.Br. (Mesembryanthema) comprises 15 species (J. Thiede, pers. comm.) of which seven are restricted to quartz fields. According to recent findings, *G. pilosulum* and *G. cryptopodium* are the same taxon (J. Thiede, pers. comm.). Since *G. cryptopodium* (Kensit) Bolus is the older name *G. pilosulum* will be sunk. For the current studies, this still unpublished new combination has been acknowledged already and the formerly two species are named *G. cryptopodium*. *Gibbaeum* is largely restricted to the Little Karoo. Only one species, namely *G. gibbosum*, is also found north of the Swartberge in the southern Ceres Karoo. *G. gibbosum*, however, is not restricted to the quartz fields. Two other species (*G. haagei*, *G. esterhuyseniae*) occur beyond the southern border of the Little Karoo, south of the Langeberge. There, they inhabit the quartz fields of the Swellendam area. Within the range of the Little Karoo, *Gibbaeum* represents the most important group with respect to cover values of the vegetation and to species richness within the QFF. Those species that are not restricted to quartz fields are found on brown shale bands (*G. nebrownii*, *G. johnstonii*), sand stone gravel (*G. pachypodium*), light brown, soft shale (*G. velutinum*), or loamy soils (*G. angulipes*, *G. geminum*). The growth-form spectrum of *Gibbaeum* comprises a variety from frequently branched almost shrubby growth forms (*G. pachypodium*) to dwarf shrubs with oblong leaves to smaller growth forms with shorter, egg-shaped leaves. The revision of the *Gibbaeinae* by Glen (1974) hypothesises a phylogenetic trend from *G. pachypodium* as a basic taxon to increasing dwarfism and reduction of leaf-surface. However, there are indications for a polyphyletic status of the genus in its present delineation (J. Thiede, pers. comm.).

Bulbine Wolf (Asphodelaceae), a bulb with upright, oblong succulent leaves, is the most species-rich genus of the monocotyledonae in the QFF. The about 50 species of the genus are largely restricted to Southern Africa (Botswana, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe). Only five species are found in Australia. However, about three quarter of the species (approximately 37 of the about 50 species) are restricted to the winter rainfall zone of southern Africa. Seven species of the genus are restricted to quartz fields, all of them are very locally distributed, some of them are only known from their type locality (*B. wieseii*, *B. louwii*, *B. margaretha*). [Data on number of species and distribution of the presently unrevised genus were kindly supplied by D. Snijman, NBI Kirstenbosch.]

In correspondence with *Dicrocaulon*, all six taxa of **Monilaria** (Schwantes) Schwantes (5 species and 1 subspecies, Mesembryanthema) are restricted to quartz fields. But in contrast to *Dicrocaulon*, the genus *Monilaria* shows a broader distribution from the southern Knersvlakte to the Richtersveld. The three taxa that occur north of the Knersvlakte have a largely allopatric distribution. In the Knersvlakte, however, the distribution of the species overlap broadly, resulting in sympatric occurrence. Only the two species in terms of growth-form and leaf shape and size the species show very little variation. All taxa are dwarf shrubs with two different pairs of succulent leaves per axis (heterophylly) and succulent stems that are covered by persistent leaf bases (Ihlenfeldt & Jörgensen 1973).

Dinteranthus Schwantes (Mesembryanthema) comprises 4 species and 2 subspecies which are all restricted to quartz fields (Sauer 1979, 1980). The genus is endemic to the quartz fields of the Bushmanland and the Warmbad area where they occur largely allopatrically. *Dinteranthus* species are dwarf shrubs with reduced axis and highly succulent, egg-shaped, partly fused leaf pairs.

Tylecodon Tölken (Crassulaceae) comprises 28 species which are restricted to the western part southern Africa (Namibia and South Africa) (Leistner 2000). In correspondence to the genus *Crassula*, *Tylecodon* is fairly restricted to edaphically arid habitats. Again, only a relatively small percentage of the species, namely five species (18 %), are restricted to quartz fields. *Tylecodon* have tiny more or less succulent stems and deciduous, succulent leaves (Tölken 1985).

Four species and two subspecies of the QFF belong to *Phyllobolus* N.E.Br. (Mesembryanthema). *Phyllobolus* species are erect or creeping shrubs or dwarf shrubs or geophytes with deciduous succulent leaves. Although the genus is widespread in the western and central parts of South African and southern Namibia (Gerbaulet 1997), four of the five quartz-field species of the genus are restricted to the Knersvlakte Phytochorion. Only one species (*P. prasinus*) is found outside the Knersvlakte in the Riethuis-Wallekraal and the Southern Richtersveld Phytochorion.

The genus *Lithops* N.E.Br. (Mesembryanthema) comprises about 36 species and 15 subspecies (= 51 sp./ssp.). The distribution of the genus covers the central South African plateau and the western (arid) parts of Namibia (Cole 1988, Hartmann 1994). In general, *Lithops* mainly occurs on open, sloping sites or ridges with shallow, stony soils - with or without a surface layer of stones of different geological origin (Cole 1988). Considering the habitat ecology of the genus, the relative small share of the *Lithops* species within the QFF, i.e., six taxa only, is remarkable.

III.2.4 Species inventories of the phytochoria

The species inventories of the obligate QFFs will be presented according to their geographical distribution, from south (Little Karoo) to north (Bushmanland-Warmbad Phytochorion).

Little Karoo Phytochorion

The inventory of quartz-field species of the phytochorion of the Little Karoo (Table 26) was almost entirely restricted to *Gibbaeum* species. The only other taxa were *Crassula congesta* ssp. *laticephala*, *Crassula columnaris* ssp. *columnaris*, and *Muiria hortenseae* (Mesembryanthema).

Table 26. Quartz-field species that are endemic to the Little Karoo (* = endemic species)

<i>Crassula congesta</i> ssp. <i>laticephala</i> (Crassulaceae)*	<i>Muiria hortenseae</i> (Mesembryanthema)*
<i>Gibbaeum album</i> (Mesembryanthema)*	<i>Anacampseros papyracea</i> ssp. <i>papyracea</i> (Portulacaceae) Little Karoo, Great Karoo
<i>Gibbaeum cryptopodium</i> (Mesembryanthema)*	
<i>Gibbaeum dispar</i> (Mesembryanthema)*	
<i>Gibbaeum heathii</i> (Mesembryanthema)*	<i>Crassula columnaris</i> ssp. <i>columnaris</i> (Crassulaceae) SW Cape
<i>Gibbaeum petrense</i> (Mesembryanthema)*	
<i>Gibbaeum pubescens</i> (Mesembryanthema)*	

Only two taxa of the obligate QFF of the Little Karoo were not restricted to the area, both have a very broad distribution. They have to be considered as only moderately restricted to the quartz fields.

Knersvlakte Phytochorion

The obligate QFF of the Knersvlakte comprised 63 endemic species (Table 27) and thus houses the highest number of endemics of all regional QFFs. Several genera (mainly Mesembryanthema) provided numerous species to the obligate QFF (*Argyroderma*, *Bulbine*, *Dicrocaulon*, *Monilaria*, *Phyllobolus*, *Tylecodon*).

Table 27. Quartz-field species of the Knersvlakte (* = endemic species)

<i>Argyroderma congregatum</i> (Mesembryanthema)*	<i>Argyroderma crateriforme</i> (Mesembryanthema)*
------------------------------------------------------	-------------------------------------------------------

- Argyroderma delaetii* (Mesembryanthema)*
Argyroderma framesii ssp. *framesii*
(Mesembryanthema)*
Argyroderma framesii ssp. *hallii*
(Mesembryanthema)*
Argyroderma patens (Mesembryanthema)*
Argyroderma pearsonii (Mesembryanthema)*
Argyroderma ringens (Mesembryanthema)*
Argyroderma subalbum (Mesembryanthema)*
Argyroderma testiculare (Mesembryanthema)*
Babiana lewisiana (Iridaceae)*
Babiana pilosa (Iridaceae)*
Bulbine diphylla (Asphodelaceae)*
Bulbine haworthioides (Asphodelaceae)*
Bulbine louwii (Asphodelaceae)*
Bulbine margarethae (Asphodelaceae)*
Bulbine wiesei (Asphodelaceae)*
Cephalophyllum caespitosum
(Mesembryanthema)*
Cephalophyllum pulchellum
(Mesembryanthema)*
Cephalophyllum spissum
(Mesembryanthema)*
Conophytum calculus ssp. *calculus*
(Mesembryanthema)*
Conophytum subfenestratum
(Mesembryanthema)*
Richtersveld, Bushmanland-WB
Crassula multiceps (Crassulaceae)*
Dicrocaulon brevisfolium (Mesembryanthema)*
Dicrocaulon grandiflorum
(Mesembryanthema)*
Dicrocaulon humile (Mesembryanthema)*
Dicrocaulon longifolium (Mesembryanthema)*
Dicrocaulon microstigma (Mesembryanthema)*
Dicrocaulon nanum spec. nov.
(Mesembryanthema)*
Dicrocaulon neglectum spec. nov.
(Mesembryanthema)*
Dicrocaulon nodosum (Mesembryanthema)*
Dicrocaulon prostratum spec. nov.
(Mesembryanthema)*
Dicrocaulon pseudonodosum
(Mesembryanthema)*
Diplosoma luckhoffii (Mesembryanthema)*
Eriospermum titanopsoides (Eriospermaceae)*
Jacobsenia hallii (Mesembryanthema)*
Lachenalia patula (Hyacinthaceae)*
Lapeirousia lewisiana (Iridaceae)*
Lasiopogon minutus (Asteraceae)*
Leucoptera oppositifolia (Asteraceae)*
Leucoptera subcarnosa (Asteraceae)*
Lithops divergens var. *divergens*
(Mesembryanthema)*
Monilaria chrysoleuca (Mesembryanthema)*
Monilaria moniliformis (Mesembryanthema)*
Monilaria pisiformis (Mesembryanthema)*
Oophytum nanum (Mesembryanthema)*
Oophytum oviforme (Mesembryanthema)*
Othonna hallii (Asteraceae)*
Othonna intermedia (Asteraceae)*
Pelargonium caroli-henrici (Geraniaceae)*
Pelargonium quarciticola (Geraniaceae)*
Pentzia peduncularis (Asteraceae)*
Phyllobolus abbreviatus (Mesembryanthema)*
Phyllobolus digitatus ssp. *digitatus*
(Mesembryanthema)*
Phyllobolus digitatus ssp. *littlewoodii*
(Mesembryanthema)*
Phyllobolus herbertii (Mesembryanthema)*
Phyllobolus tenuiflorus (Mesembryanthema)*
Oedera silicola (Asteraceae)*
Tylecodon occultans (Crassulaceae)*
Tylecodon peculiaris (Crassulaceae)*
Tylecodon pygmaeus (Crassulaceae)*
Tylecodon tenuis (Crassulaceae)*
Zygophyllum teretifolium (Zygophyllaceae)*
Crassula barklyi (Crassulaceae) Knersvlakte,
Riethuis-W.
Crassula columnaris ssp. *prolifera*
(Crassulaceae), Knersvlakte, Riethuis-
W., S & N
Othonna lepidocaulis (Asteraceae)
Knersvlakte, Riethuis-W.
Senecio aloides (Asteraceae) Knersvlakte,
Riethuis-W., S & N Richtersveld, SW-
Namibia

Only four quartz-field taxa of the Knersvlakte were not endemic to the phytochorion. Two of them (*Crassula barklyi* and *Othonna lepidocaulis*) also occurred on the quartz fields of the Riethuis-Wallekraal Phytochorion. The other two species had a very broad distribution: *Crassula columnaris* ssp. *prolifera* covers all areas where quartz fields occur except the Little Karoo. *Senecio aloides* is only absent in the Bushmanland-Warmbad Phytochorion but reaches into the south-western part of Namibia (P.V. Bruyns, pers. comm.).

This high number of species and subspecies is mainly based a five of genera that contribute several species to the flora: *Argyroderma* (9 species and 2 subspecies), *Bulbine* (5 species), *Dicrocaulon* (10 species), *Phyllobolus* (4 species and 2 subspecies), and *Tylecodon* (4 species). The genus *Argyroderma* is of particular importance: Like *Gibbaeum* in the Little Karoo, the genus *Argyroderma* is endemic to the Knersvlakte experienced an adaptive radiation within the small area. Nine of 10 *Argyroderma* species are restricted to the quartz fields. *Bulbine* is a succulent geophyte which is

widespread in southern Africa and Australia. There are seven *Bulbine* species in the southern African QFF, of which 5 are restricted in the Knersvlakte. All of them show a very localised distribution. Some species are known from their type locality only (*B. louwii*, *B. wiesei*, *B. margarethae*). The genus *Dicrocaulon*, is not endemic to the Knersvlakte but its centre of diversity is located there. Only two of the twelve *Dicrocaulon* species (i.e., *D. spissum* and *D. ramulosum*) occur outside the Knersvlakte, on the quartz fields of the Riethuis-Wallekraal Phytochorion. Similar to *Argyroderma*, *Dicrocaulon* performed a radiation on the quartz fields of the Knersvlakte. *Phyllobolus*, a genus with 4 species and two subspecies in the QFF of the Knersvlakte, belongs to the specious genera of the Mesembryanthema, since Gerbault (1997) sunk the genera *Sphalmanthus* N.E.Br. and *Dactylopsis* N.E.Br. in *Phyllobolus*. The genus presently comprises 32 species and two subspecies. The genus is widespread in southern Namibia and in the western and central parts of South Africa but there is only one quartz-field species of *Phyllobolus* that occur outside the Knersvlakte: *Phyllobolus prasinus* inhabit the quartz fields of the Riethuis-Wallekraal Phytochorion and southern Richtersveld. Also *Tylecodon* is a species-rich (28 species, Le Roux & Boucher in prep.) and widespread genus of which only six species are restricted to the quartz fields. Four of the six quartz-field species of the genus are endemic to the Knersvlakte, the two others occur in the western part of the Bushmanland-Warmbad Phytochorion (*T. sulphureus*) or Northern Richtersveld Phytochorion (*T. pusillus*).

Oophytum (Mesembryanthema, Aizoaceae) is besides *Argyroderma* the only genus which is endemic to the Knersvlakte. The two *Oophytum* species, *O. nanum* and *O. oviforme*, are restricted to quartz fields. *O. nordenstamii* also occur on the quartz fields of the Knersvlakte. Since the taxonomic status of this taxon is ambiguous (Ihlenfeldt (1978) sunk it in *O. oviforme* whereas Smith *et al.* (1998) and S. A. Hammer (pers. comm.) acknowledge *O. nordenstamii* as a valid species this taxon was left out for the analysis.

Riethuis-Wallekraal Phytochorion

The obligate QFF of the Riethuis-Wallekraal Phytochorion comprised five species that were entirely restricted to the area (Table 28). Two species were represented by a subspecies only, *Monilaria scutata* ssp. *obovata* and *Conophytum obscurum* ssp. *vitreopapillum*. In *Monilaria scutata* the second subspecies, *M. s.* ssp. *scutata*, was also restricted to the quartz fields and occurred at the Riethuis-Wallekraal Phytochorion but has a broader distribution which stretches further to the north into the Southern Richtersveld Phytochorion. In *Conophytum obscurum* the subspecies *C. o.* ssp. *vitreopapillum* is the only taxon that is restricted to quartz fields (Hammer 1993b).

Most of the non-endemic taxa of the obligate QFF of the Riethuis-Wallekraal Phytochorion had a very broad distribution: *Crassula columnaris* ssp. *prolifera* and *Senecio aloides* covered almost the entire western part of the southern African quartz fields, whereas *Aspazoma amplexens*, *Crassula grisea*, *Meyerophytum meyeri*, and *Phyllobolus prasinus* occurred from the Riethuis-Wallekraal to the Northern Richtersveld Phytochorion. Four of the non-endemic taxa of the obligate QFF had a rather restricted distributions which stretched only into the adjacent phytochoria (Southern Richtersveld, Knersvlakte): *Crassula barkelyi*, *Jacobsenia vaginata*, *Monilaria scutata* ssp. *scutata*, and *Othonna lepidocaulis*.

Table 28. Quartz-field species of the Riethuis-Wallekraal Phytochorion (*= endemic species)

Conophytum concavum (Mesembryanthema)*	Meyerophytum globosum
Conophytum obscurum ssp. vitreopapillum	(Mesembryanthema)*
(Mesembryanthema)*	Monilaria scutata ssp. obovata
Crassula susannae (Crassulaceae)*	(Mesembryanthema)*
Dicrocaulon ramulosum (Mesembryanthema)*	
Dicrocaulon spissum (Mesembryanthema)*	

Aspazoma amplexans (Mesembryanthema) Riethuis-W., N & S Richtersveld	Meyerophytum meyeri (Mesembryanthema) Riethuis-W., N & S. Richtersveld
Crassula barklyi (Crassulaceae) Knersvlakte, Riethuis-W.	Monilaria scutata ssp. scutata (Mesembryanthema) Riethuis-W., Southern Richtersveld
Crassula columnaris ssp. prolifera (Crassulaceae) Knersvlakte, Riethuis- W., N & S Richtersveld, Bushmanland- WB	Othonna lepidocaulis (Asteraceae) Knersvlakte, Riethuis-W.
Crassula grisea (Crassulaceae) Riethuis-W., N & S Richtersveld	Phyllobolus prasinus (Mesembryanthema) Riethuis-W., N & S Richtersveld
Jacobsenia vaginata (Mesembryanthema) Riethuis-W., Southern Richtersveld	Senecio aloides (Asteraceae) Knersvlakte, Riethuis-W., N & S Richtersveld, Bushmanland-W

The widespread genus *Crassula* (Tölken 1977a) contributed four species to the QFF of the Riethuis-Wallekraal Phytochorion and thus represented the most species-rich genus of this regional QFF. The remaining genera contributed merely one or two (*Conophytum*, *Dicrocaulon*) species. None of the genera are endemic to the Riethuis-Wallekraal Phytochorion. But several of them are restricted to the surrounding: *Dicrocaulon* (12 species, H.-D. Ihlenfeldt, pers. comm.) and *Monilaria* (5 species, 2 subspecies, Ihlenfeldt & Jörgensen 1973) occur in the Knersvlakte and in the Riethuis-Wallekraal Phytochorion only. The distribution of *Jacobsenia* (Ihlenfeldt 1997) stretches from the north-western part of the Knersvlakte in the Southern Richtersveld Phytochorion. *Aspazoma* (one species, Smith *et al.* 1998) and *Meyerophytum* (two species, Smith *et al.* 1998, H.-D. Ihlenfeldt, pers. comm.) inhabit the quartz fields of the Riethuis-Wallekraal Phytochorion, to the Southern (*Jacobsenia*: three species) and Northern (*Aspazoma*, *Meyerophytum*) Richtersveld Phytochoria.

Southern Richtersveld Phytochorion

The obligate QFF of the Southern Richtersveld Phytochorion showed little particularity. The flora comprised merely seven endemic species and no endemic genera (Table 29). All endemic taxa had a very limited distribution, that is, they were known from one or two quarter-degree squares only.

The obligate QFF of the Southern Richtersveld was closely related to the adjacent phytochoria, the Riethuis-Wallekraal (Table 28) and the Northern Richtersveld Phytochorion (Table 30). Four taxa (*Conophytum maughanii* ssp. *armeniicum*, *Crassula alstonii*, *Nelia meyeri*, and *Schlechteranthus maximiliani*) were restricted to the Southern and Northern Richtersveld Phytochorion. Six out of twelve non-endemic species/subspecies of the obligate QFF of the Southern Richtersveld Phytochorion covered all three phytochoria, between the Riethuis-Wallekraal and the Northern Richtersveld Phytochoria. Among those, merely two taxa, i.e., *Crassula columnaris* ssp. *prolifera* and *Senecio aloides*, were widespread and were found beyond the borders of three phytochoria (see species inventory Knersvlakte Phytochorion, Riethuis-Wallekraal Phytochorion).

Table 29. Quartz-field species of the Southern Richtersveld Phytochorion (*= endemic species)

Bulbine truncata (Asphodelaceae)*	Polymita steenbockensis (Mesembryanthema)*
Conophytum hammeri (Mesembryanthema)*	
Conophytum violaciflorum (Mesembryanthema)*	Aspazoma amplexans (Mesembryanthema) Riethuis-W., S & N Richtersveld
Lithops helmutii (Mesembryanthema)*	Conophytum maughanii ssp. <i>armeniicum</i> (Mesembryanthema) S & N Richtersveld
Mitrophyllum mitratum (Mesembryanthema)*	
Monilaria obconica (Mesembryanthema)*	Crassula alstonii (Crassulaceae) S & N

Richtersveld
Crassula columnaris ssp. *prolifera*
 (Crassulaceae) Knersvlakte, Riethuis-
 W., S & N Richtersveld, Bushmanland-
 Warmbad
Crassula grisea (Crassulaceae) Riethuis-W., S
 & N Richtersveld
Meyerophytum meyeri (Mesembryanthema)
 Riethuis-W., S & N Richtersveld
Nelia meyeri (Mesembryanthema) S & N
 Richtersveld

Jacobsenia vaginata (Mesembryanthema)
 Riethuis-W., Southern Richtersveld
Monilaria scutata ssp. *obovata*
 (Mesembryanthema) Riethuis-W.,
 Southern Richtersveld
Phyllobolus prasinus (Mesembryanthema)
 Riethuis-W., S & N Richtersveld
Schlechteranthus hallii (Mesembryanthema) S
 & N Richtersveld
Senecio aloides (Asteraceae) Knersvlakte,
 Riethuis-W., S & N Richtersveld, S-
 Namibia

Northern Richtersveld Phytochorion

Forty quartz-field species/ subspecies occurred in the Northern Richtersveld Phytochorion (Table 30). The most species-rich group presented the *Conophytum* species (9 taxa). They provided both, endemic and non-endemic quartz-field taxa. Besides *Conophytum*, only *Anacampseros*, *Lithops*, and *Odontophorus* provided more than one species to the obligate QFF of the Phytochorion. Besides *Conophytum*, the genera *Crassula* and *Anacampseros* were the most specious taxonomic groups within the non-endemic QFF of the phytochorion.

Table 30. Quartz-field species of the Northern Richtersveld Phytochorion (*= endemic species)

<i>Anacampseros herreana</i> (Portulacaceae)*	<i>Aspazoma amplexans</i> (Mesembryanthema)
<i>Androcymbium cruciatum</i> (Colchicaceae)*	Riethuis-W., S & N Richtersveld
<i>Bulbine quartzicola</i> (Asphodelaceae)*	<i>Conophytum lithopsosides</i> ssp. <i>lithopsoides</i>
<i>Cephalophyllum regale</i> (Mesembryanthema)*	(Mesembryanthema) Northern
<i>Cheiridopsis velox</i> (Mesembryanthema)*	Richtersveld, Bushmanland-WB
<i>Conophytum armianum</i> (Mesembryanthema)*	<i>Conophytum maughanii</i> ssp. <i>armeniacum</i>
<i>Conophytum auriflorum</i> (Mesembryanthema)*	(Mesembryanthema) S & N
<i>Conophytum blandum</i> (Mesembryanthema)*	Richtersveld
<i>Conophytum irmae</i> (Mesembryanthema)*	<i>Conophytum maughanii</i> ssp. <i>maughanii</i>
<i>Conophytum maughanii</i> ssp. <i>latum</i>	(Mesembryanthema) Northern
(Mesembryanthema)*	Richtersveld, Bushmanland-WB
<i>Conophytum phoenicium</i>	<i>Crassula alstonii</i> (Crassulaceae) S & N
(Mesembryanthema)*	Richtersveld
<i>Crassula plegmatoides</i> (Mesembryanthema)*	<i>Crassula columnaris</i> ssp. <i>prolifera</i>
<i>Lithops herrei</i> (Mesembryanthema)*	(Crassulaceae) Knersvlakte, Riethuis-
<i>Lithops meyeri</i> (Mesembryanthema)*	W., S & N Richtersveld, Bushmanland-
<i>Mitrophyllum grande</i> (Mesembryanthema)*	WB
<i>Odontophorus angustifolius</i>	<i>Crassula grisea</i> (Crassulaceae) Riethuis-W., S
(Mesembryanthema)*	& N Richtersveld
<i>Odontophorus nanus</i> (Mesembryanthema)*	<i>Ihlenfeldtia excavata</i> (Mesembryanthema)
<i>Octopoma connatum</i> (Mesembryanthema)*	Northern Richtersveld, Bushmanland-
<i>Schlechteranthus maximilianii</i>	WB
(Mesembryanthema)*	<i>Meyerophytum meyeri</i> (Mesembryanthema)
<i>Strumaria villosa</i> (Amaryllidaceae)*	Riethuis-W., S & N Richtersveld
<i>Tridentea herrei</i> (Asclepiadaceae)*	<i>Nelia meyeri</i> (Mesembryanthema) S & N
<i>Tylecodon pusillus</i> (Crassulaceae)*	Richtersveld
<i>Adromischus nanus</i> (Crassulaceae) Northern	<i>Phyllobolus prasinus</i> (Mesembryanthema)
Richtersveld, Bushmanland-WB	Riethuis-W., S & N Richtersveld
<i>Anacampseros papyracea</i> ssp. <i>namaensis</i>	<i>Schlechteranthus hallii</i> (Mesembryanthema) S
(Portulacaceae) Northern Richtersveld,	& N Richtersveld
Bushmanland-WB	<i>Senecio aloides</i> (Asteraceae) Knersvlakte,
<i>Anacampseros recurvata</i> (Portulacaceae)	Riethuis-W., S & N Richtersveld, S-
Northern Richtersveld, Bushmanland-	Namibia
WB	

Tridentea umdausensis (Asclepiadaceae)
Northern Richtersveld, Bushmanland-

WB

Whereas *Conophytum* is a specious, widespread genus (Hammer 1993b, Smith *et al.* 1998) several others are endemic to the Southern and Northern Richtersveld Phytochorion (*Nelia*, *Odontophorus*, *Polymita*, *Schlechteranthus*) but comprise a few species only with. Only two of the genera are entirely restricted to quartz fields: *Schlechteranthus* (2 species, Smith *et al.* 1998) and *Nelia* (4 species, Smith *et al.* (1998); due to the lack of knowledge on the taxonomic status and distribution of the remaining species, only *N. meyeri* was acknowledged in this study). This is not the case for *Odontophorus* (5 species, Smith *et al.* 1998) and *Polymita* (2 species, Hartmann 1996, Smith *et al.* 1998).

Bushmanland-Warmbad Phytochorion

The obligate QFF of the Bushmanland-Warmbad Phytochorion comprised 17 regional endemic and 9 non-endemic species and subspecies (Table 31). The highest number of quartz-field species / subspecies were contributed by *Conophytum* (8 taxa). The second genus with respect to number of species / subspecies were *Dinteranthus* (6 taxa). This genus is entirely restricted to the quartz fields of the Phytochorion. Besides *Conophytum* and *Dinteranthus*, there were only two other genera that provided more than one species to the flora: *Crassula* and *Ihlenfeldtia*.

The non-endemic obligate QFF of the Bushmanland-Warmbad Phytochorion showed a strong affinity to the Northern Richtersveld Phytochorion. Seven out of 10 non-endemic quartz-field species occurred in the Bushmanland-Warmbad and Northern Richtersveld Phytochorion only. The other two taxa had a very broad distribution and covered almost the entire distribution of the southern African quartz fields (*Crassula columnaris* ssp. *prolifera*) or stretch from the Bushmanland-Warmbad Phytochorion far in the north to central Namibia (*Crassula mesembryanthemopsis*, Tölken 1977a).

The QFF of the Bushmanland-Warmbad Phytochorion was characterised by two genera that are endemic to the Phytochorion: *Dinteranthus* (4 species, 4 subspecies, Sauer 1980, Smith *et al.* 1998) and *Lapidaria* (1 species Smith *et al.* 1998). *Schwantesia* (8 species, Zimmermann 1996, Smith *et al.* 1998) and *Ihlenfeldtia* (2 species, Hartmann 1992), however, are centred in the Phytochorion but are not entirely restricted to it: Whereas *I. vanzylii* are found in the Bushmanland only, *I. excavata* also stretches in the Northern Richtersveld Phytochorion. Within the regional QFF three genera, i.e., *Dinteranthus*, *Lapidaria* and *Ihlenfeldtia* are entirely restricted to quartz fields.

Table 31. Quartz-field species of the Bushmanland-Warmbad Phytochorion (*= endemic species)

Conophytum burgeri (Mesembryanthema)*	(Mesembryanthema)*
Conophytum calculus ssp. vanzylii (Mesembryanthema)*	Dinteranthus pole-evansii (Mesembryanthema)*
Conophytum friedrichiae (Mesembryanthema)*	Dinteranthus vanzylii (L. Bolus) Schwantes
Conophytum lithopsoides ssp. koubergense (Mesembryanthema)*	(Mesembryanthema)*
Conophytum marginatum (Mesembryanthema)*	Dinteranthus wilmotianus ssp. impunctatus (Mesembryanthema)*
Conophytum smoreskaduense (Mesembryanthema)*	Dinteranthus wilmotianus ssp. wilmotianus (Mesembryanthema)*
Dinteranthus microspermus ssp. microspermus (Mesembryanthema)*	Ihlenfeldtia vanzylii (Mesembryanthema)*
Dinteranthus microspermus ssp. puberulus.	Lapidaria margaretae (Mesembryanthema)*
	Lithops olivacea (Mesembryanthema)*
	Schwantesia borchersdii (Mesembryanthema)*

Tylecodon sulphureus (Tölken) Tölken (Crassulaceae)*	Richtersveld, Bushmanland-WB
Adromischus nanus (Crassulaceae) Northern Richtersveld, Bushmanland-WB	Crassula columnaris ssp. prolifera (Crassulaceae) Knersvlakte, Riethuis- W., S & N Richtersveld, Bushmanland- WB
Anacampseros papyracea ssp. namaensis (Portulacaceae) Northern Richtersveld, Bushmanland-WB	Crassula mesembryanthemopsis (Crassulaceae) Bushmanland-WB, SW-Namibia
Anacampseros recurvata (Portulacaceae) Northern Richtersveld, Bushmanland- WB	Ihlenfeldtia excavata (Mesembryanthema) Northern Richtersveld, Bushmanland- WB
Conophytum lithopsoides ssp. lithopsoides (Mesembryanthema) Northern Richtersveld, Bushmanland-WB	Tridentea umdausensis (Asclepiadaceae) Northern Richtersveld, Bushmanland- WB
Conophytum maughanii ssp. maughanii (Mesembryanthema) Northern	

III.2.5 Species-to-genera ratio

The number of genera per phytochorion as well as the species-genera ratio of the different obligate QFFs varied considerably (Table 32). The highest ratio was found in the obligate QFF of the Knersvlakte which also was the most species-rich flora. The second highest species-to-genera ratio, however, was represented by the obligate QFF of the Little Karoo, which was characterised by the lowest number of species and subspecies. The Northern, Southern Richtersveld and the Riethuis-Wallekraal Phytochorion showed a species-to-genus ratio that was below the average (Figure 21). Consequently, there was only a very weak relationship between species number and species-to-genera ratio of the obligate QFFs.

Table 32. The species/ genera ratio of the regional obligate QFFs

Phytochorion	Species and subspecies	Genera	Species-to-genera ratio
Knersvlakte	67	25	2.68
Little Karoo	10	4	2.50
Bushmanland-Warmbad	26	11	2.36
Northern Richtersveld	40	23	1.74
Riethuis-Wallekraal	17	11	1.45
Southern Richtersveld	19	14	1.36

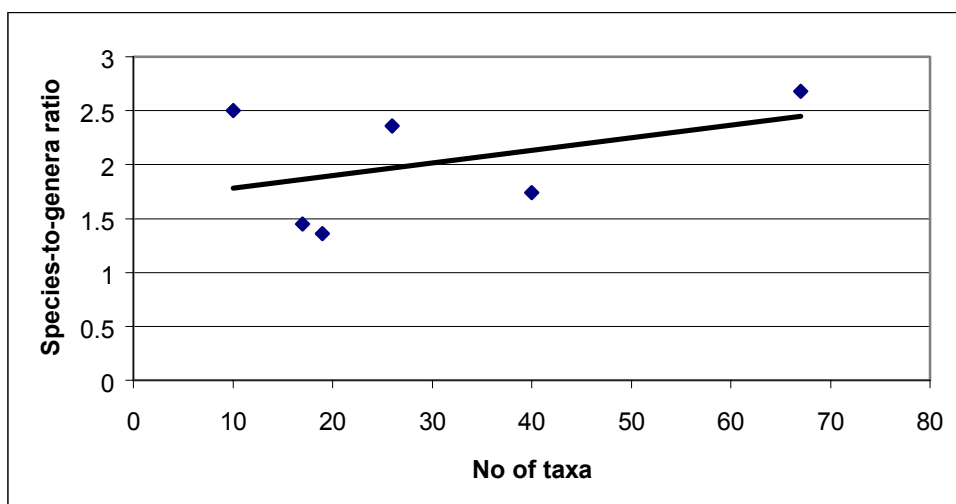


Figure 21. Relationship between number of quartz-field taxa (species and subspecies) and species-to-genera ratio of the regional obligate QFFs ($y = 0.012x + 1.66$, $r^2 = 0.18$).

III.3 Patterns of diversity within the phytochoria

III.3.1 Centres of diversity of the obligate QFF

The analysis of the regional obligate QFFs revealed that the six phytochoria differ significantly in terms of growth-form and species diversity. In order to get insight into the patterns of diversity and endemism, the taxonomic and growth-form data on QDS level were evaluated.

The highest numbers of quartz-field taxa (**species and subspecies**) per QDS (Figure 22) was found in the Knersvlakte Phytochorion (up to 40 taxa/ QDS, Table 33). Six of the QDS of the Knersvlakte housed more than 20 taxa each. Such a high density of quartz-field taxa per QDS is not found in any of the other phytochorion. The highest numbers of taxa per QDS that occurred outside the Knersvlakte were 13 in the Riethuis-Wallekraal Phytochorion and 12 in the Northern Richtersveld Phytochorion. The Bushmanland-Warmbad Phytochorion and the Southern Richtersveld housed 11 taxa per QDS as a maximum. Ten taxa per QDS was the highest number recorded for the obligate QFF of the Little Karoo.

The map also shows that the hot spots of quartz-field taxa were not scattered randomly but clustered to distinct areas of high occurrence of quartz-field taxa. The most obvious centre of high species richness (≥ 10 taxa / QDS, bold figures) lay in the Centre of the Knersvlakte. This area was also the largest in terms of numbers of QDS: nine adjacent QDS housed ≥ 10 taxa. Another important area of high occurrence of quartz-field taxa were found across the border between the Northern and the Southern Richtersveld Phytochorion and stretched to the western border of the Bushmanland-Warmbad Phytochorion (2817CC to 2917BB: west of Eksteenfontein to east of Steinkopf). Here five neighbouring QDS were inhabited by ≥ 10 quartz-field taxa. The other QDS' of ≥ 10 quartz-field taxa were less distinctly grouped or rather isolated: there were two QDS' in the Riethuis-Wallekraal Phytochorion, two unconnected QDS' in the western part of the Bushmanland-Warmbad Phytochorion (2918BB and 2919AB, vicinity of Pofadder) and one single QDS at the southern fringe of the Little Karoo (3321CC: Muiskraal and Springfontein area southwest of Vanwyksdorp).

A corresponding map (Figure 23) shows the numbers of **genera** of the obligate QFF per QDS. Again the same centres of diversity emerged as at species / subspecies level. They cover largely the same QDS'. Moreover, there are several QDS' that showed a high number of genera (≥ 5) but were not identical with the hot spots of species / subspecies diversity. This was the case in the Southern and Northern Richtersveld Phytochorion: in addition to the five QDS' with ≥ 10 species / subspecies, there were six more QDS' which housed ≥ 5 genera of the obligate QFF. Therefore, on genus level, the centre of diversity in the Southern and Northern Richtersveld Phytochorion stretched further to the west and northwest, covering large parts of the two phytochoria. The area of high genus richness in the vicinity of Pofadder was largely in line with the pattern on species / subspecies level.

In the Little Karoo Phytochorion none of the QDSs comprised ≥ 5 genera of the obligate QFF. The very species-rich QDS in the south of the Little Karoo (3321CC) housed the highest number of genera of the obligate QFF within the Little Karoo, though.

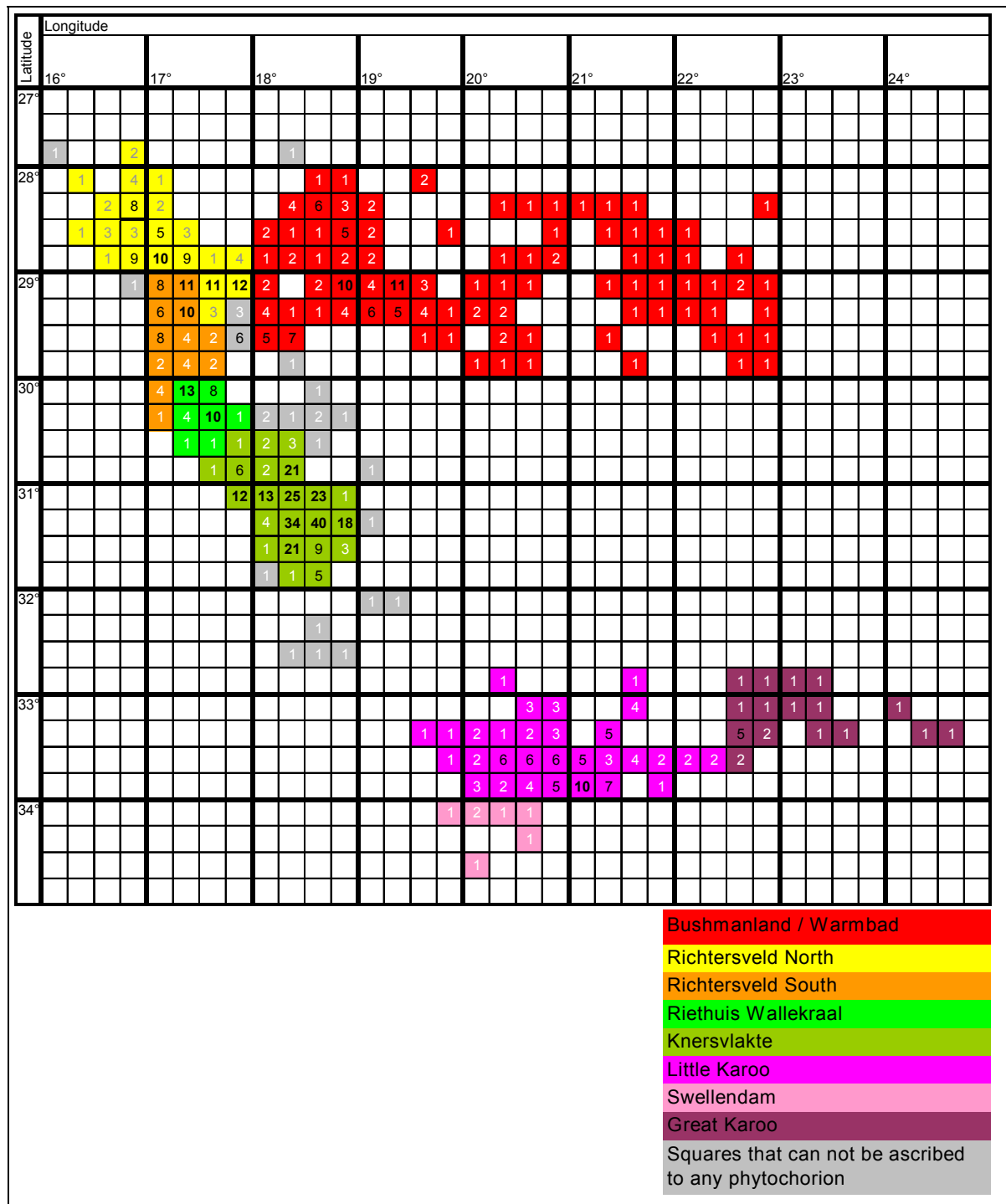


Figure 22. Obligate quartz-field species / subspecies per QDS within the main phytochoria.

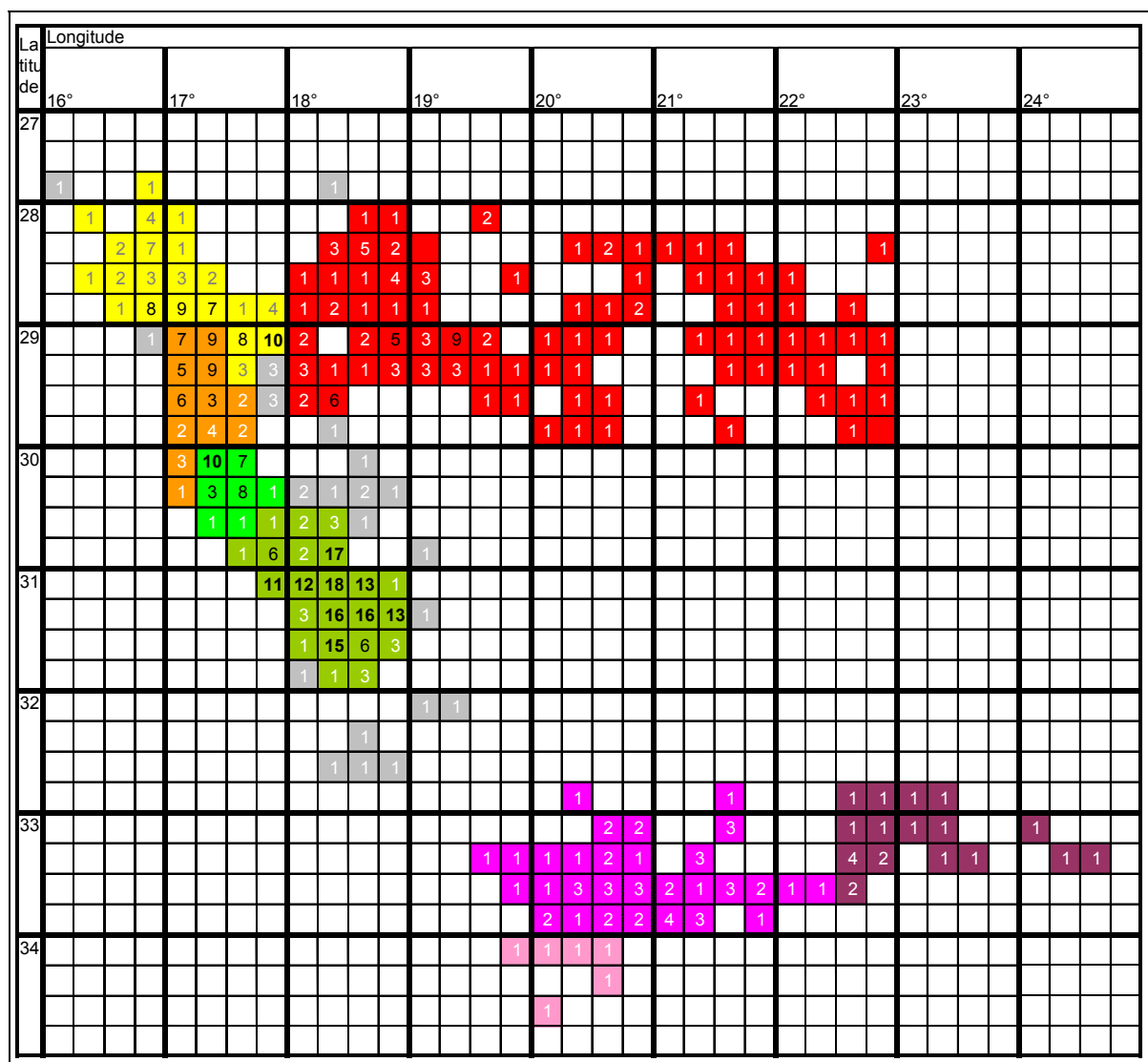


Figure 23. Numbers of genera of the obligate QFF per QDS within the main phytochoria.

On **family** level only two of the centres of species diversity were still detectable (Figure 24): two QDS in the Richtersveld and seven QDS in the Knersvlakte comprised ≥ 5 families of the obligate QFF. In contrast to the diversity on species / subspecies level, the centre of family diversity (2917BA, BB) of the Richtersveld was restricted to Northern Richtersveld Phytochorion only. The numbers of families per QDS in the other three centres of high species / subspecies richness were between one and three families per QDS only. Therefore, on family level they did not differ from the other QDS.

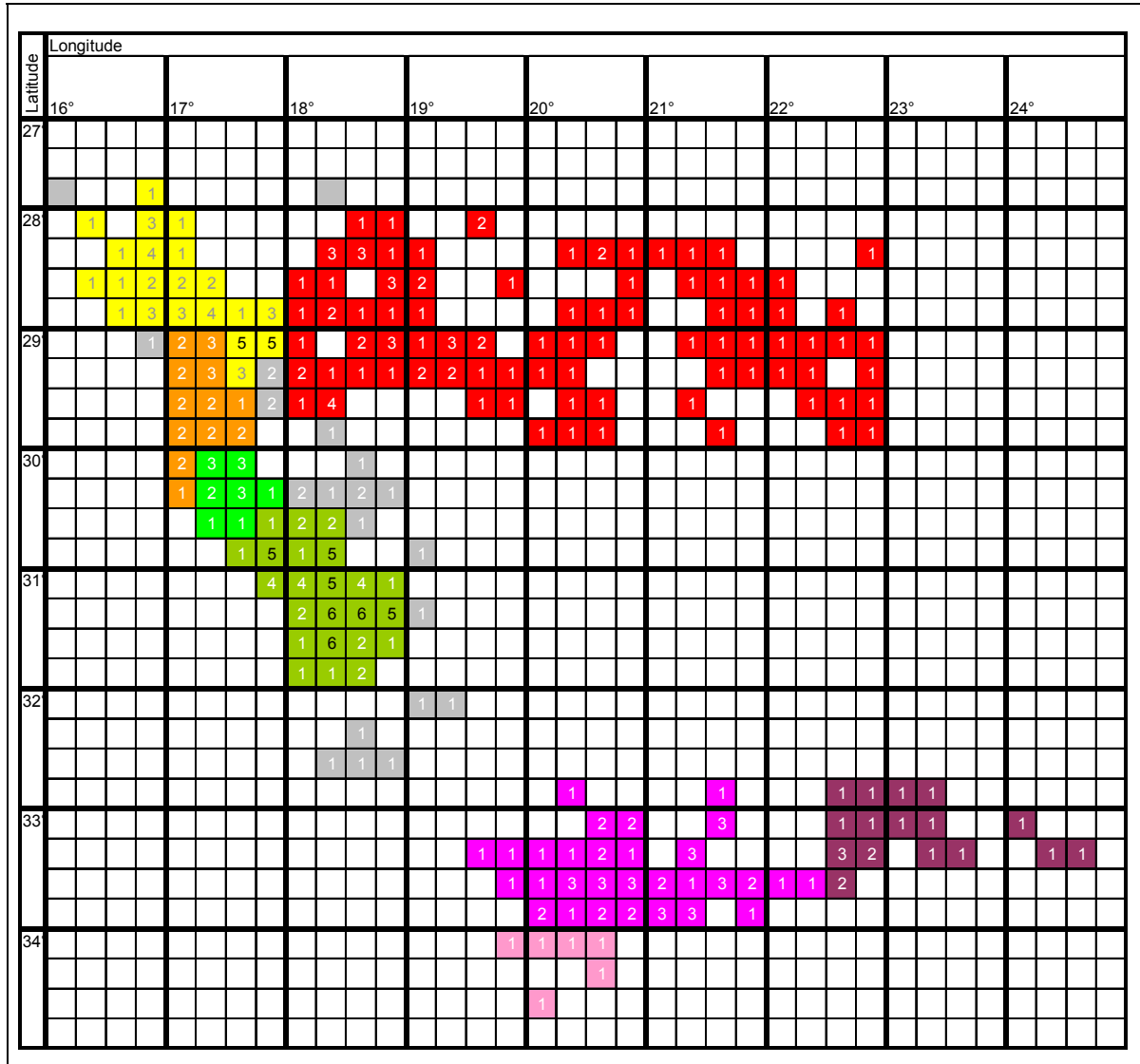


Figure 24. Numbers of families of the obligate QFF per QDS.

Nine different growth-form groups sensu Raunkiaer (1937), modified after Ellenberg & Müller-Dombois (1966), Jürgens (1986) and Schmiedel & Jürgens (1999) were defined for the obligate QFF (Chapter II.2.1). The number of **growth-form groups** per QDS was plotted according to their geographical distribution. The resulting map (Figure 25) revealed that the centres of highest growth-form richness (which housed ≥ 5 growth-form groups per QDS) corresponded largely with the centres of species / subspecies richness (Figure 22). In the Riethuis-Wallekraal Phytochorion, the Richtersveld Phytochoria, and in the Bushmanland-Warmbad Phytochorion the occurrence of QDS with ≥ 5 growth forms deviated from the QDS with ≥ 10 quartz-field species by only one single QDS each. These QDS however, still housed six (Bushmanland-Warmbad Phytochorion), eight (Riethuis-Wallekraal Phytochorion) or nine quartz-field species and subspecies (Northern Richtersveld Phytochorion), respectively. In addition there were three “satellites”, isolated QDS with ≥ 5 growth-form in the Northern Richtersveld Phytochorion (2816BD), in the western part of the Southern Richtersveld Phytochorion (2917DA) and at the southern fringe of Bushmanland-Warmbad Phytochorion (2918CB). All three isolated QDS with ≥ 5 growth forms comprised less than 10 species and subspecies but showed high numbers of genera (Figure 23) though.

There is a strong correspondence between species and growth from richness. But this relationship was not identical between the six phytochoria as it is shown in Figure 26. The highest coefficient for the relationship was found for the flora of the Northern Richtersveld Phytochorion ($y = 0.52x$) whereas the lowest coefficient was found for the Knersvlakte ($y = 0.24x$). The coefficients of the other floras lay in between.

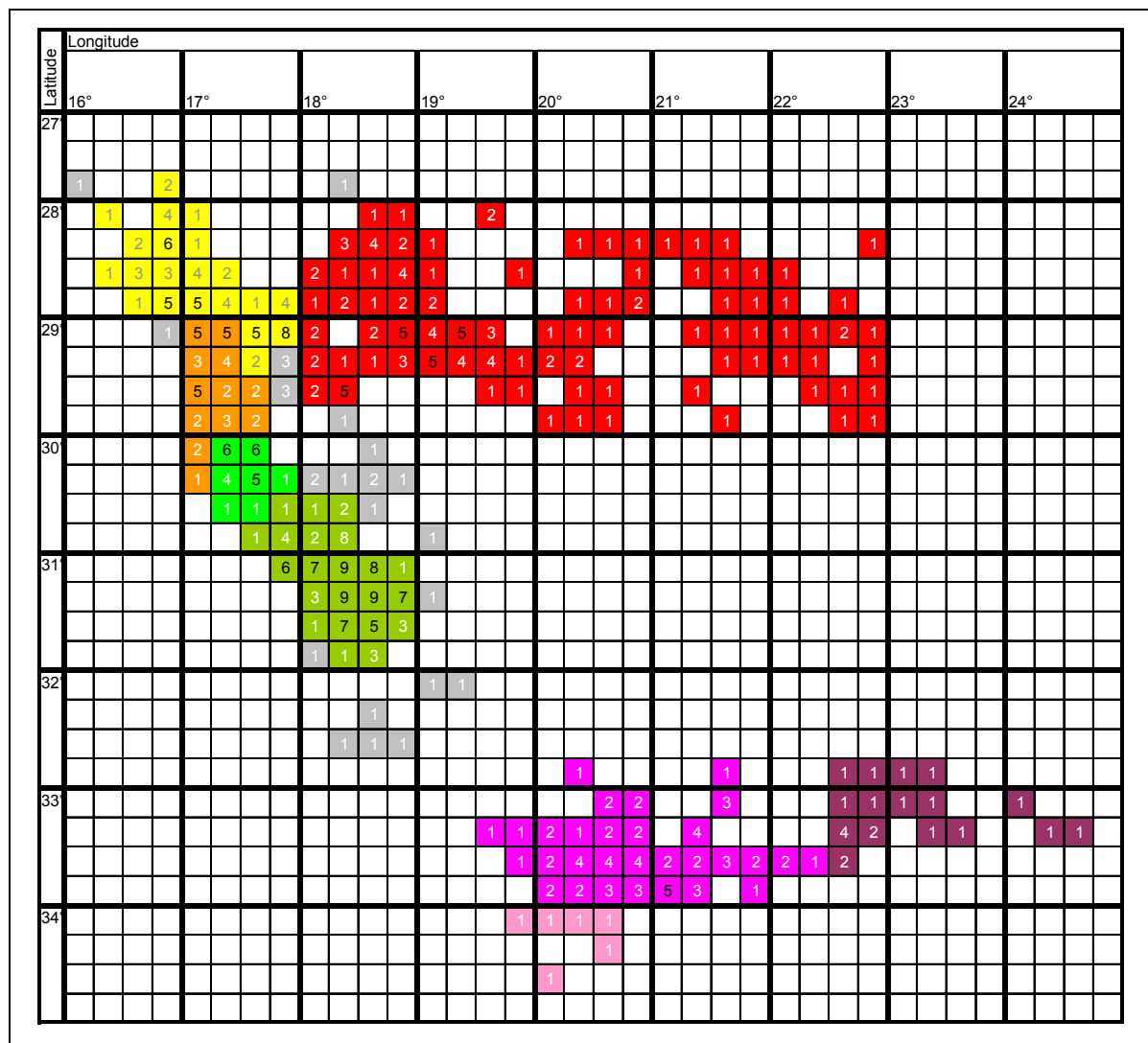


Figure 25. Number of growth-form groups within the obligate QFF per QDS.

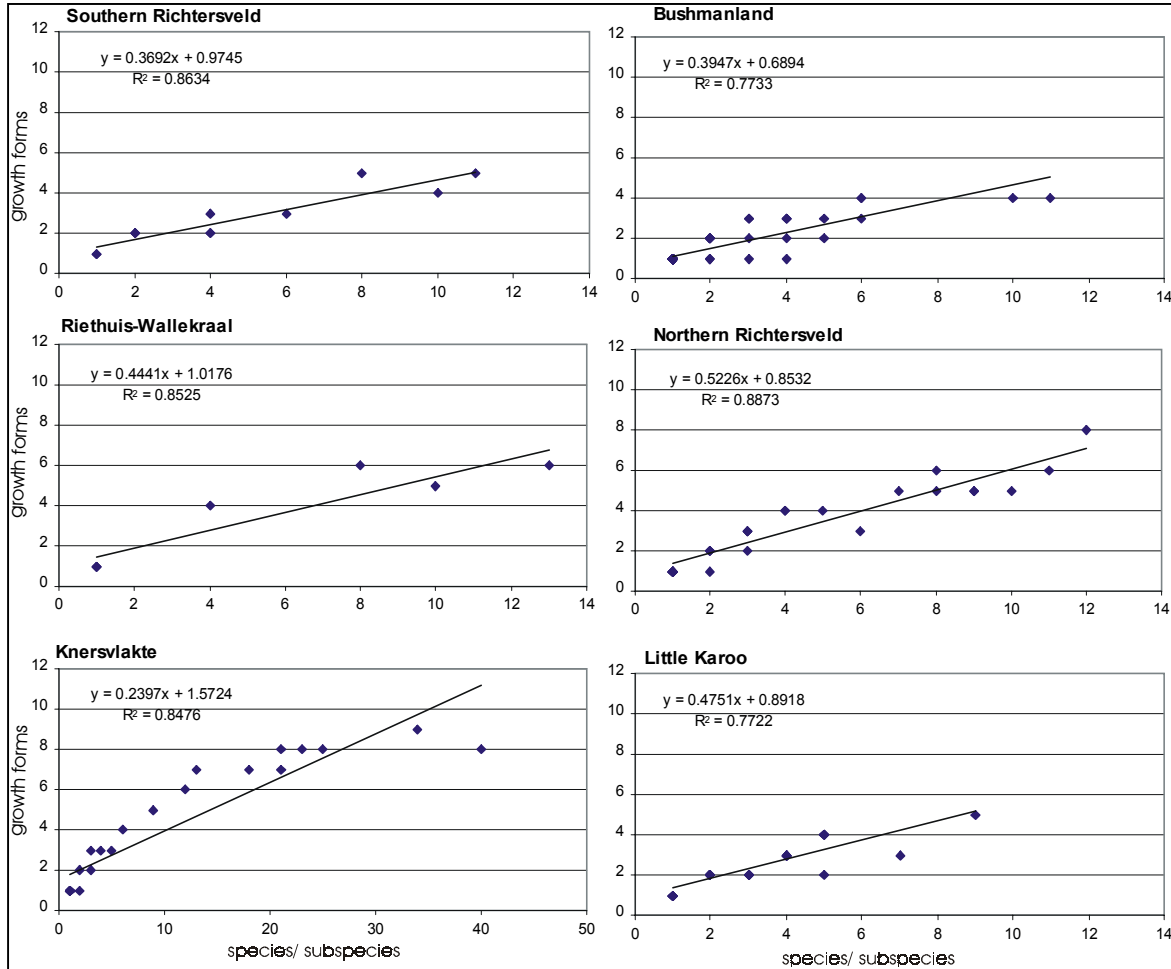


Figure 26. Relationship between richness of species / subspecies and growth forms per QDS in the six main phytochoria of the obligate QFF.

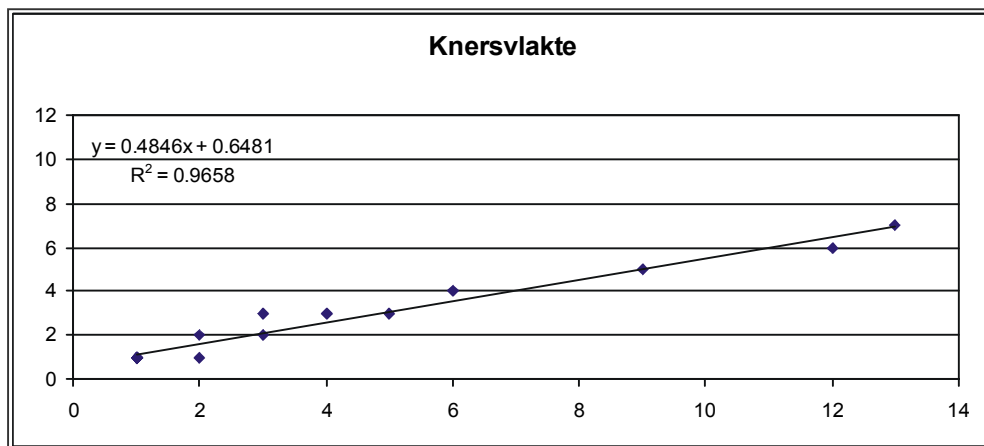


Figure 27. Relationship between richness of species / subspecies and growth forms in the Knersvlakte: QDS with low species richness only.

A separate analysis of the QDS that comprised less than 15 taxa (species/subspecies) per QDS (Figure 27) of the Knersvlakte Phytochorion showed a higher coefficient ($y = 0.48$ instead of $y = 0.24$ for the entire region).

Besides the Knersvlakte, the Southern Richtersveld ($y = 0.38$) and the Bushmanland-Warmbad Phytochorion ($y = 0.39$) had the lowest coefficients, indicating a comparably low relationship

between species numbers and growth-form numbers per QDS. The Riethuis-Wallekraal Phytochorion and the Little Karoo showed intermediate coefficients.

The measure of certainty (R^2) for the coefficient of the growth-form - species/subspecies relationship was relatively high for all regional obligate QFFs ($R^2 > 0.77$). Nevertheless, differences could be detected: the highest R^2 was found for the Northern Richtersveld ($R^2 = 0.88$) which also showed the highest coefficient (y). But for the Southern Richtersveld *Phytochorion*, the Riethuis-Wallekraal Phytochorion and the Knersvlakte the measure of certainty was similarly high ($R^2 > 0.84$). However, the Little Karoo and the Bushmanland-Warmbad Phytochorion showed the lowest measure of certainty ($R^2 = 0.77$). In the Bushmanland-Warmbad Phytochorion in particular, there were several QDSs of up to four species / subspecies per QDS that housed one growth form only. Such a low number of growth forms per species / subspecies was not found for any other phytochorion. Also, the richness of growth forms was relatively low in all QDS even if they comprised ten and more species / subspecies, hence the low coefficient.

III.3.2 Species richness and size of the phytochoria

To test whether the number of quartz-field taxa is controlled by the size of the phytochorion, the number of QDS that could clearly be ascribed to a particular phytochorion was determined (Figure 6). Table 33 shows the size of the defined phytochoria (expressed as number of QDS) as well as the density of quartz-field taxa and of endemic quartz-field taxa. By far the largest phytochorion is the Bushmanland-Warmbad Phytochorion in the northeast of the distribution of the quartz fields (see Figure 22). The second largest phytochoria is the Little Karoo, followed by the Northern Richtersveld and the Knersvlakte Phytochorion (both equally ranked), the Southern Richtersveld and the Riethuis-Wallekraal Phytochorion, which presents the smallest phytochorion. The largest phytochoria (Bushmanland-Warmbad and Little Karoo) showed the lowest density of both quartz-field species and regional endemics within the obligate QFF whereas the highest density of endemic and non-endemic species and subspecies of the obligate QFF was found in the Knersvlakte.

Table 33. Density of obligate quartz-field taxa within the defined phytochoria.

Phytochoria of the obligate QFF	Size of the phytochorion [QDS]	Density of obligate quartz-field taxa/QDS]	Density of endemic obligate quartz-field taxa [endemics/QDS]
Bushmanland-Warmbad	45	0.51	0.33
Little Karoo	30	0.36	0.30
Northern Richtersveld	22	1.77	1.00
Knersvlakte	22	3.03	2.86
Southern Richtersveld	11	1.54	0.55
Riethuis-Wallekraal	7	2.29	1.00

The relationship between the size of the phytochorion of the QFF and the number of corresponding taxa and endemics is shown in Figure 28. A high number of QDS per phytochorion was neither positively associated with a number of quartz-field species per *Phytochorion*, nor with the number of endemics within the regional QFF.

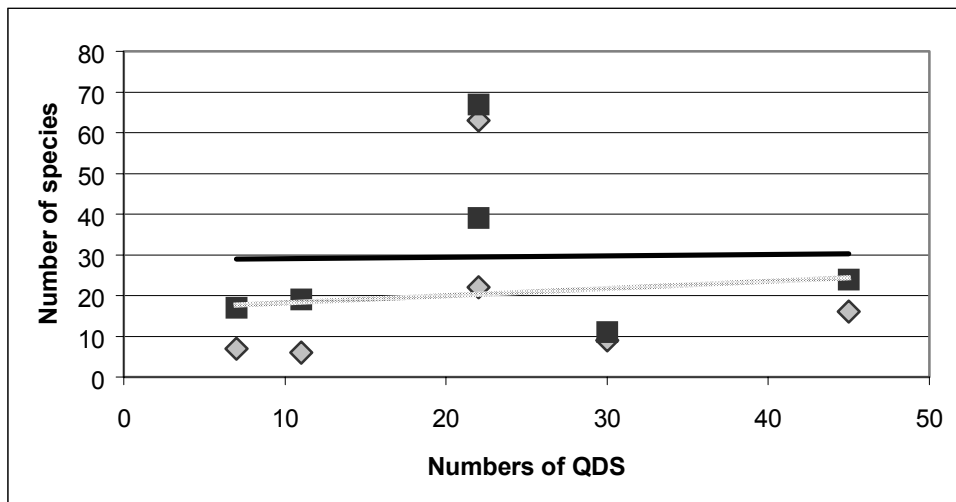


Figure 28. Relation between size of the quartz-field phytochoria and number of quartz-field taxa and regional endemics of the obligate QFF. Numbers of quartz-field taxa are shown by black squares ($y = 0.0305x + 28.804$, $r^2 = 0.0004$). Numbers of endemics within the regional QFFs are shown by grey squares ($y = 0.1781x + 16.433$, $r^2 = 0.0126$).

III.3.3 Relationship between growth-form diversity and species richness

The comparison of the growth-form spectra of the regional obligate QFFs (Figure 10 and Figure 11) revealed the differences between the regional floras also in terms of numbers of growth forms. Table 34 shows the number of growth-form groups, the Shannon-Wiener diversity index, and the evenness value on growth-form level of the obligate QFFs of the six phytochoria. The Knersvlakte Phytochorion showed the highest growth-form richness within the obligate QFF. It was the only obligate QFF that comprised nine different growth-form groups and subgroups. The Bushmanland-Warmbad Phytochorion in return, comprised the lowest number (four) of growth-form groups and subgroups. Here also the lowest diversity index was found. The diversity index of the obligate QFF of the Little Karoo hardly deviated from that of the former and comprised five growth-form groups only.

The Shannon-Wiener diversity index on growth form level of the regional obligate QFFs was directly related to the number of growth-form groups (i.e., growth-form richness) per regional obligate QFF. The evenness values, however, did not correspond strongly with the growth-form richness and the Shannon-Wiener diversity index. The highest evenness values ($E > 93$) were found for the Northern Richtersveld Phytochorion, the Riethuis-Wallekraal Phytochorion, and for the Knersvlakte Phytochorion. The lowest values were found for the Little Karoo Phytochorion ($E = 76.3$), the Southern Richtersveld Phytochorion ($E = 88.9$), and the Bushmanland-Warmbad Phytochorion ($E = 89.4$). That is, with respect to the evenness value, the obligate QFF of the Southern Richtersveld Phytochorion ranked below the Bushmanland-Warmbad Phytochorion which, however, was conspicuously poorer in growth-form diversity.

Table 34. Number of growth-form groups (including 4 nano-chamaephyteous subgroups), Shannon-Wiener diversity index, and evenness value on growth-form level of the regional QFFs (QFF).

Phytochorion	Number of growth forms within the regional QFF	Shannon-Wiener diversity index	Evenness
Knervlakte	9	2.045	93.12
Northern Richtersveld	8	1.952	93.87
Southern Richtersveld	7	1.731	88.95
Riethuis-Wallekraal	6	1.676	93.58
Little Karoo	5	1.294	76.27
Bushmanland-Warmbad	4	1.243	89.42

There was a trend for species-rich quartz-field phytochoria to have a high number of growth forms groups (Figure 29). However, the obligate QFF of the Bushmanland-Warmbad Phytochorion deviated conspicuously from those of all other phytochoria. Here, the relation between number of growth forms and number of species was considerably below the average. In contrast, in the Southern and the Northern Richtersveld Phytochorion the growth form to taxa relation was slightly above the average.

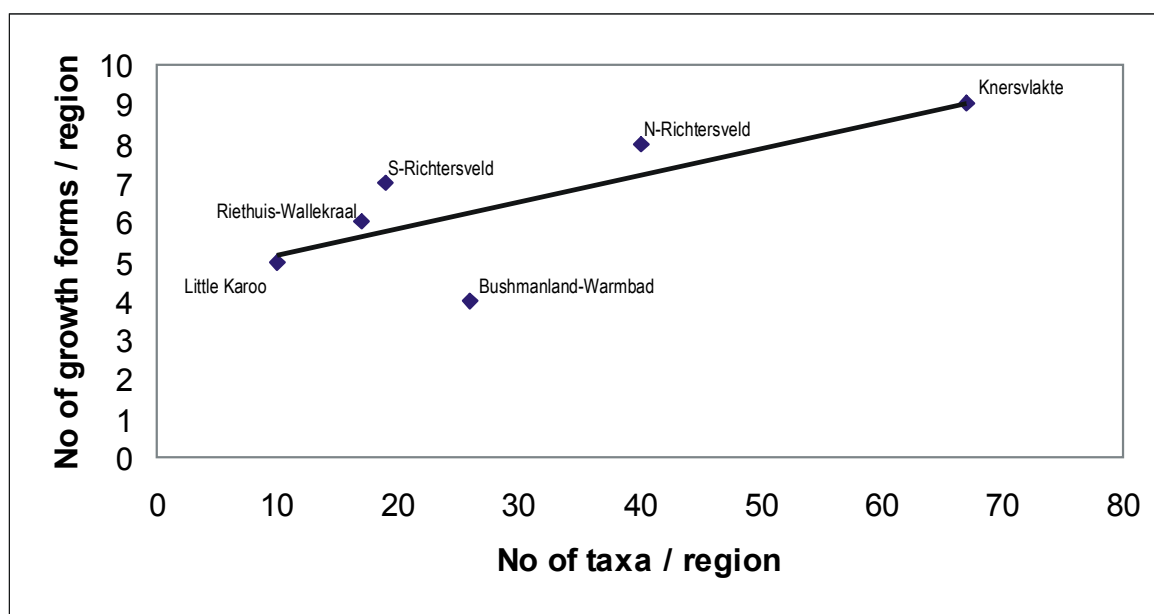


Figure 29. Relationship between number of quartz-field taxa and number of growth forms per phytochorion. Result of a linear regression: $y = 0.0683x + 4.4629$, $r^2 = 0.5794$.

III.4 Endemism in the obligate quartz-field flora

About 80 % of the quartz-field species and subspecies (124 taxa) were endemic to one of the six phytochoria of the obligate QFF (Chapter III.1.1). If the minor quartz-field regions, Swellendam region and Eastern Cape region (Chapter II.2.4), were also taken into account, the percentage of regional endemic species rose up to 84 %. Twenty-five species and subspecies or 16 % of the obligate QFF had a broad distribution which covered more than one phytochorion. In the following chapter, the endemic and non-endemic taxa will be compared. Which taxa were more widespread and which are locally restricted? Are there any structural or floral features that are more common in one of the groups?

For the following analysis of the endemic obligate QFF, all endemic quartz-field species were taken into account, that is, not only those that are endemic to the main phytochoria but also those that are endemic to the minor quartz-field regions in the Swellendam region (four species) and in the Eastern Cape (three species) (Chapter III.1.1).

III.4.1 Growth-form spectra

The spectrum of the endemic flora of the quartz fields was largely in line with that of the entire flora (Figure 30). The only difference was that the endemic flora comprised slightly more subglobose and compact nano-chamaephytes and less “other” nano-chamaephytes as well as micro-chamaephytes than the entire flora. In contrast, the growth-form spectrum of the non-endemic flora of the quartz fields differed considerably from the entire and the endemic obligate QFF. Therophytes and geophytes were completely absent from the non-endemic QFF. Distinctly lower percentages were found for the subglobose and (less distinct) for the subterranean nano-chamaephytes as well as mega-chamaephytes. The compact and other nano-chamaephytes as well as micro-chamaephytes were over-represented compared to the entire and the endemic obligate QFF. Generally, the growth-form groups within the non-endemic obligate QFF were more evenly apportioned than in the two other groups.

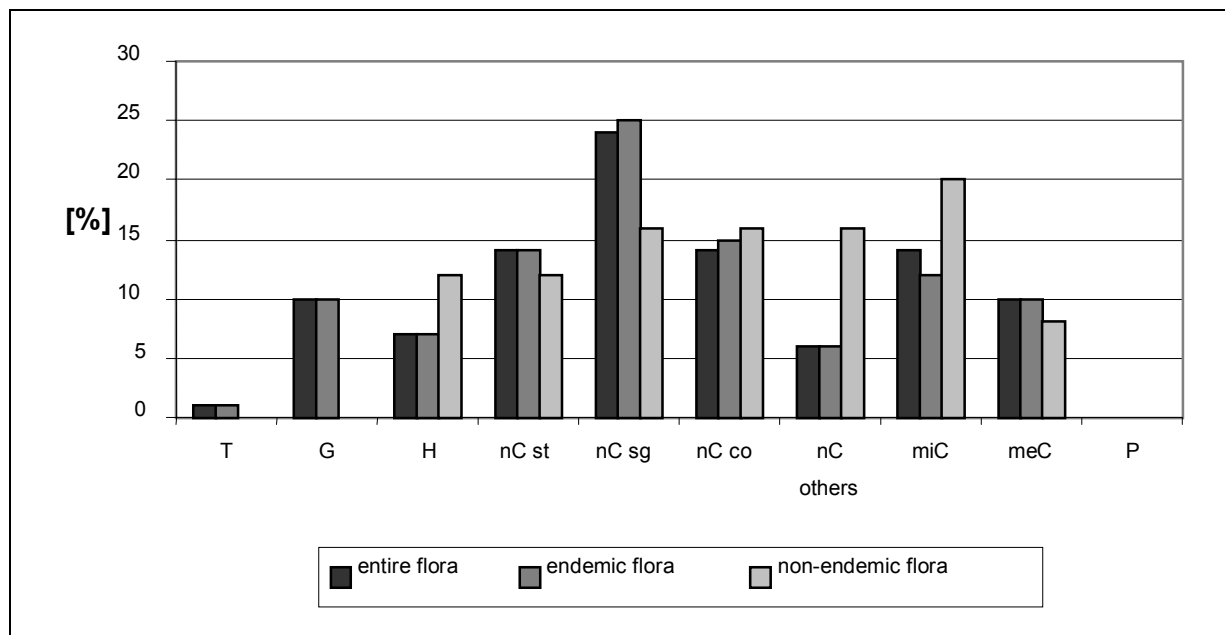


Figure 30. Percentage of different growth-form groups in terms of numbers of taxa (species and subspecies) of the entire flora, the endemic, and non-endemic species within the obligate QFF.

This was also confirmed by the very high evenness value ($E = 98.3$, Table 35) which is higher than the evenness values for the other two groups of the obligate QFF. In correspondence to the smaller number of growth-form groups the diversity index is lowest within the non-endemic obligate QFF. However, the differences among all three floral groups were rather small.

Summarising, the comparative analysis of the non-endemic, endemic and entire QFF emerged that the non-endemic QFF showed several differences to the endemic taxa within the QFF. They showed a narrower growth-form spectrum (no therophytes and geophytes belong in this group) and the growth forms were more evenly apportioned (each growth-form group was represented by 10 to 20 %), which was also mirrored by a very high evenness value. Most striking were their

very high percentage of “other” nano-chamaephytes which did not fit into the three common growth-form groups of the QFF (subterraneous, subglobose and compact nano-chamaephytes).

Table 35. Number of growth-form groups, Shannon-Wiener diversity index and evenness value on growth-form level of the entire obligate QFF, endemic and non-endemic quartz-field species.

Floral groups	Number of growth forms	Shannon-Wiener Diversity index	Evenness value
Entire obligate QFF	9	2.02	91.71
Endemic species	9	1.99	90.41
Non-endemic species	7	1.91	98.28

III.4.2 Morphological and phenological features

The spectrum of morphological and phenological features within the non-endemic species of the obligate QFF deviated considerably from the entire and endemic obligate QFF (Figure 31 and Table 36). Drought-deciduous taxa (with and without therophytes, geophytes, hemicryptophytes) were represented by a lower percentage in the non-endemic QFF. The percentage of stem succulents without succulent leaves and the stem succulents with assimilating axes was ten times higher than within the non-endemic quartz-field taxa than in the endemic flora. The percentage of taxa with succulent roots or tubers was only slightly higher among the non-endemic but when the geophytes were excluded, the percentage within the endemic QFF decreased, thus indicating a high over-representation of tubers and fleshy roots in this group. Regarding the percentage of leaf-succulent and stem *and* leaf succulent taxa the non-endemic quartz-field taxa did not vary conspicuously from that of the endemic flora. The endemic taxa within the obligate QFF showed generally high correspondence to the entire obligate QFF.

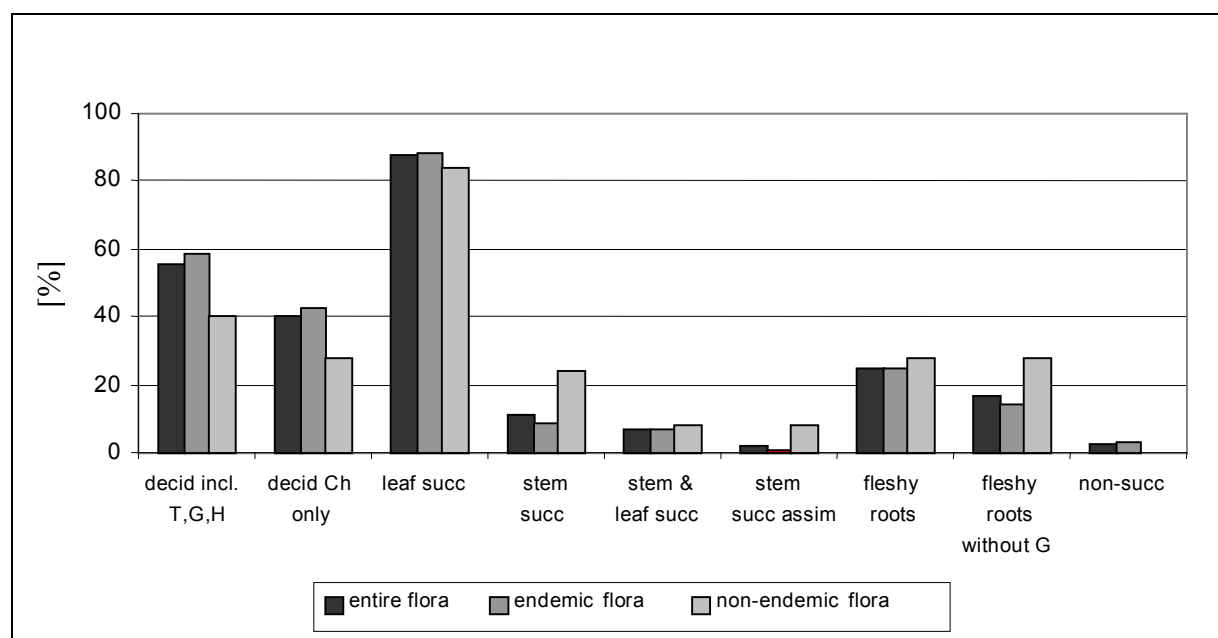


Figure 31. Percentage of morphological and phenological features of the entire obligate QFF as well as the endemic and non-endemic taxa.

Table 36. Number of species (above) and percentages (below) of particular morphological and phenological features of the regional endemic, non-endemic and entire flora of the quartz fields.

Group	No of species / subspecies	drought-deciduous	leaf succ	stem succ (without succ leaves)	stem & leaf succ	stem succ ass	roots fleshy/ tuber
Endemic taxa	131	77	116	2	9	1	32
Non-endemic taxa	25	10	21	4	2	2	7
Entire flora	156	87	137	6	11	3	39
	Percentage in terms of no of taxa	drought-deciduous	leaf succ	stem succ (without succ leaves)	stem & leaf succ	stem succ assim	roots fleshy/ tuber
Endemic taxa	83.9	58.8	88.5	1.5	6.9	0.8	24.6
Non-endemic taxa	16.1	40.0	84.0	16.0	8.0	8.0	28.0
Entire flora	100	55.8	87.8	3.8	7.1	1.9	25.0

III.4.3 Family spectra and major taxonomic groups

Table 39 and Figure 32 show the percentage of the families within the endemic and non-endemic taxa of the obligate QFF. The non-endemic taxa comprised 5 families only. In correspondence with the endemic obligate QFF, the Aizoaceae and the Crassulaceae represented the most important groups. The percentage of the Aizoaceae was considerably lower in the non-endemic than in the endemic obligate QFF, though. In return, the percentage of the four other families increased: in the non-endemic flora the Crassulaceae, Portulacaceae, Asteraceae, and Asclepiadaceae were over-represented compared to the endemic taxa of the QFF. Generally, there was a high similarity between the entire and the endemic obligate QFF whereas the non-endemic taxa of the QFF deviated considerably. No monocotyledonae belong to the group of non-endemic obligate QFF. All monocotyledonae within the obligate QFF had a fairly restricted distribution.

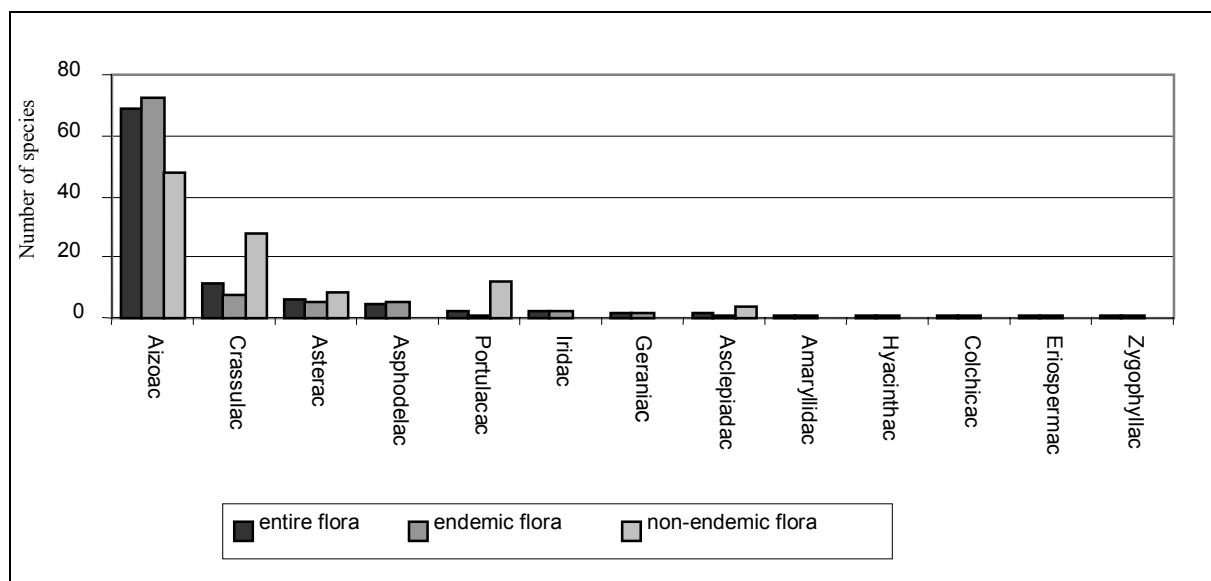


Figure 32. Family spectrum of the non-endemic compared to the entire and the endemic obligate QFF. Percentage of plant families in terms of numbers of species and subspecies.

Table 37. Comparison of the percentage of the families within the endemic and the non-endemic obligate QFF

Group	Mesembryanthema	Crassulaceae	Portulacaceae	Asteraceae	Asclepiadaceae	Asphodelaceae	Iridaceae	Geraniaceae	Hyacinthaceae	Zygophyllaceae	Eriospermaceae	Amaryllidaceae	Colchicaceae	Total
Entire obligate QFF [n = 156 sp. or ssp.]	67	10	3	5	1	5	3	1	1	1	1	1	1	100
Regional endemic spp. / subsp. of the obligate QFF (incl. Swellendam and Eastern Cape) [n =131 sp. or ssp.]	71	7	1	5	1	5	3	2	1	1	1	1	1	100
Non-endemic flora of the quartz fields [n = 25 sp. Or ssp.]	48	28	12	8	4									100

Although the Aizoaceae represented the biggest group within the non-endemic obligate QFF, only 11 % of the Aizoaceae within the entire QFF are non-endemic. In contrast, in the Portulacaceae, Asclepiadaceae and Crassulaceae the share of non-endemic quartz-field taxa within the obligate QFF was considerably higher.

Table 38. Percentage of non-endemic compared to their occurrence within the entire quartz field taxa of the plant families.

Family	Number of taxa within the entire flora	No of taxa within the non-endemic flora	Percentage of non-endemic taxa within the entire obligate QFF
Portulacaceae	4	3	75.00
Asclepiadaceae	2	1	50.00
Crassulaceae	17	7	41.18
Asteraceae	9	2	22.22
Aizoaceae	107	12	11.21

Due to the relatively lower percentage of the Aizoaceae, the family spectrum of the non-endemic flora was more evenly apportioned. Consequently, the non-endemic obligate QFF had a much higher **evenness value** ($E = 93.3$) than the endemic ($E = 46.7$) and entire ($E = 49.0$) obligate QFF (Table 39). However, the **Shannon-Wiener diversity indices** of the three groups differed only insignificantly (Table 39).

Table 39. Shannon-Wiener diversity index and evenness value for the family spectra of the entire, endemic and non-endemic QFF.

Group	No of families	Diversity index (on family level)	Evenness value (on family level)
Entire obligate QFF	13	1.71	48.71
Endemic obligate QFF	13	2.01	46.71
Non endemic obligate QFF	5	1.293	93.34

III.4.4 Spectra of widespread genera and species

In Table 41 the taxa (species and subspecies) of the obligate QFF that occurred in more than one phytochorion are listed according to their distribution. The synopsis makes emerge that the non-endemic obligate QFF not only comprised a very narrow array of families but also was largely restricted to a few genera only. Most of the species belonged to *Crassula*, *Anacampseros*, or *Conophytum* which were also the only genera that contributed more than one taxon to the non-endemic obligate QFF. The percentage of non-endemic to total quartz-field taxa within the genera differed considerably (Table 40). Whereas in *Crassula* and *Anacampseros* the majority of the quartz-field species occurred in more than one phytochorion, in *Conophytum* the majority of the taxa were local endemic to one phytochorion. *Conophytum* contributed the highest number of taxa to the obligate QFF (Chapter III.2.3) but only 14.3 % of these taxa had a broad distribution.

Table 40. Genera that contribute more than one species / subspecies to the non-endemic obligate QFF. Number of taxa within the non-endemic and the entire obligate QFF and the percentage of non-endemic taxa within the entire obligate QFF.

Genus	Number of taxa within the non-endemic obligate QFF	Number of taxa within the entire obligate QFF	Percentage [non-endemic / entire obligate QFF]
Crassula (Crassulaceae)	6	10	60.0 %
Anacampseros (Portulacaceae)	3	4	75.0 %
Conophytum (Mesembryanthema)	3	21	14.3 %

The names and distribution of taxa that occur in more than one phytochorion are listed in Table 41a-f. Among those taxa that had a particularly broad distribution in terms of numbers of phytochoria covered by their distribution (Table 41f), no Mesembryanthema were listed. This group only comprised Crassulaceae, Portulacaceae, and Asteraceae.

Table 41. Quartz-field species that occur in more than one phytochorion.

a) Species that occur in the Knersvlakte and the Riethuis-Wallekraal Phytochorion only	
Crassula barklyi	Crassulaceae
Othonna lepidocaulis	Asteraceae

b) Species that only in the Riethuis-Wallekraal and Southern Richtersveld Phytochorion	
Jacobsenia vaginata	Mesembryanthema (Aizoaceae)
Monilaria scutata ssp. obovata	Mesembryanthema (Aizoaceae)

c) Species that only in the Riethuis-Wallekraal, Southern and Northern Richtersveld Phytochorion	
Aspazoma amplexans	Mesembryanthema (Aizoaceae)
Crassula grisea	Crassulaceae
Meyerophytum meyeri	Mesembryanthema (Aizoaceae)
Phyllobolus prasinus	Mesembryanthema (Aizoaceae)

d) Species that only in the Southern and Northern Richtersveld Phytochorion	
Conophytum maughanii ssp. armeniacum	Mesembryanthema (Aizoaceae)
Crassula alstonii	Crassulaceae
Nelia meyeri	Mesembryanthema (Aizoaceae)
Schlechteranthus maximilianii	Mesembryanthema (Aizoaceae)

e) Species that only occur in the Northern Namaqualand and Bushmanland-Warmbad Phytochorion	
Adromischus nanus	Crassulaceae
Anacampseros papyracea ssp. namaensis	Portulacaceae
Conophytum lithopsoides ssp. lithopsoides	Mesembryanthema (Aizoaceae)
Conophytum maughanii ssp. maughanii	Mesembryanthema (Aizoaceae)
Ihlenfeldtia excavata	Mesembryanthema (Aizoaceae)
Tridentea umdausensis	Asclepiadaceae

f) Taxa with a broad distribution		
<i>Crassula mesembryanthemopsis</i>	Crassulaceae	Bushmanland-Warmbad to central Namibia
<i>Senecio aloides</i>	Asteraceae	Knersvlakte to southwest Namibia
<i>Crassula columnaris</i> ssp. <i>prolifera</i>	Crassulaceae	Knersvlakte to Northern Richtersveld and Bushmanland-Warmbad
<i>Crassula columnaris</i> ssp. <i>columnaris</i>	Crassulaceae	Southwestern Cape
<i>Anacampseros papyracea</i> ssp. <i>papyracea</i>	Portulacaceae	Little Karoo, Great Karoo
<i>Anacampseros recurvata</i>	Portulacaceae	Southern to Northern Richtersveld and Bushmanland-Warmbad Phytocorion

III.5 Vegetation classification

III.5.1 Main groups within the vegetation

The phytogeographical analysis of the obligate QFF revealed six main phytocoria which differed considerably with respect to species inventories (Chapter III.1.1). The vegetation of the quartz fields, however, did not only comprise obligate quartz-field taxa but also eurytopic species. Therefore, the broad subunits of the vegetation did not necessarily mirror the phytogeographical subdivision of the obligate QFF.

The analysis of the entire data set of the vegetation of the quartz fields showed two main groups (Figure 33): a broad represent the relevés from the Little Karoo. The broad cloud along Axis 1 represented the relevés of the quartz fields of the Little Karoo Phytocorion the and Swellendam area. The dense cloud on the left hand side represented the relevés of the Namaqualand *sensu lato* and the Bushmanland-Warmbad Phytocorion. The Knersvlakte relevés were plotted furthest to the right, thus indicating highest affinity to the relevés of the Little Karoo.

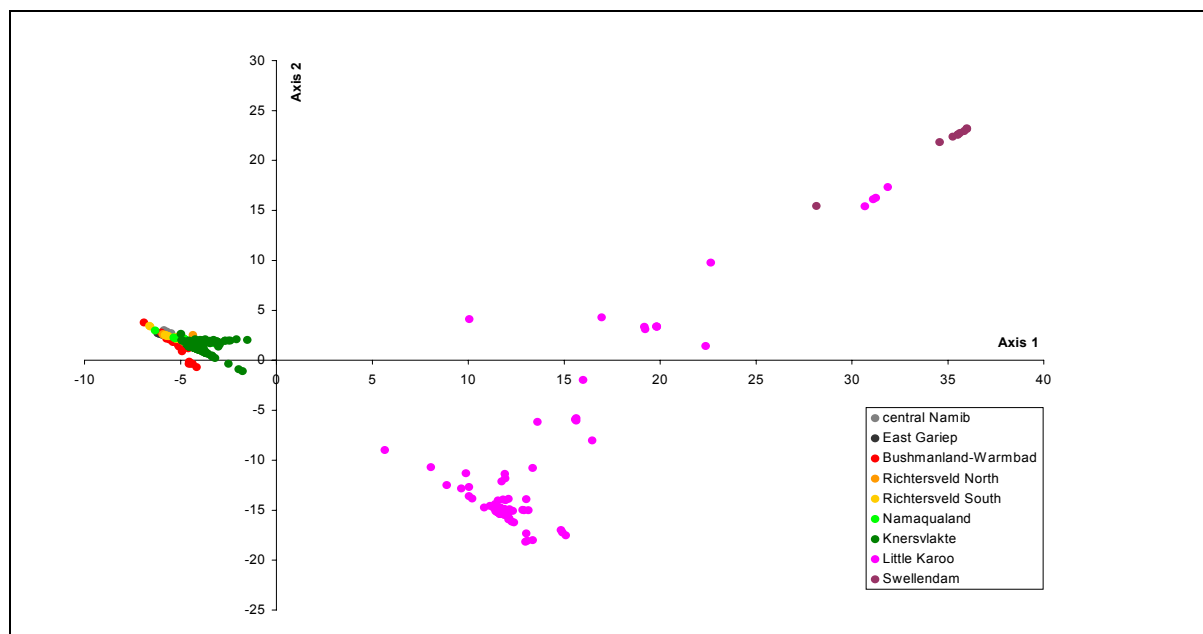


Figure 33. CA ordination of all quartz-field relevés of the study area. Scatter diagram of relevés.

Figure 33 showed three main groups: species occurring in the Namaqualand *sensu lato* as well as the Warmbad-Bushmanland on the left side, the species largely restricted to relevés of the Little Karoo Phytochorion in the centre and those from the Swellendam area in the upper right corner.

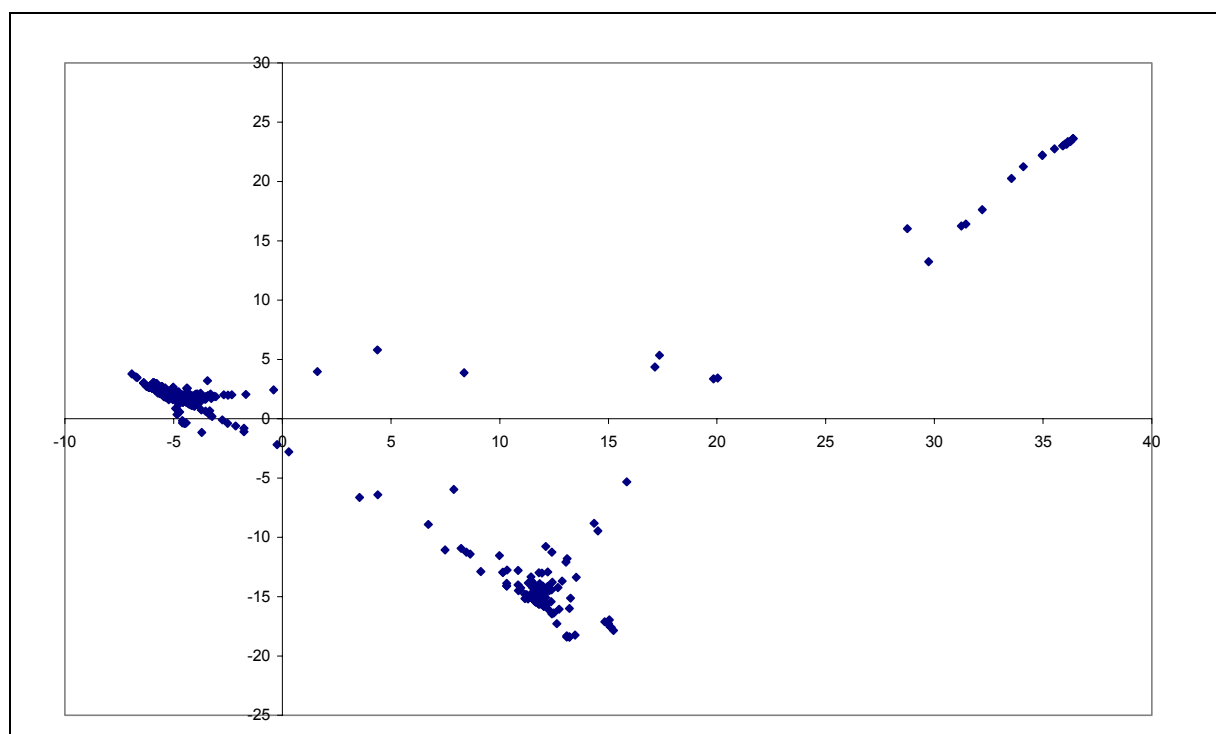


Figure 34. CA ordination of species of quartz-field relevés of all phytochoria

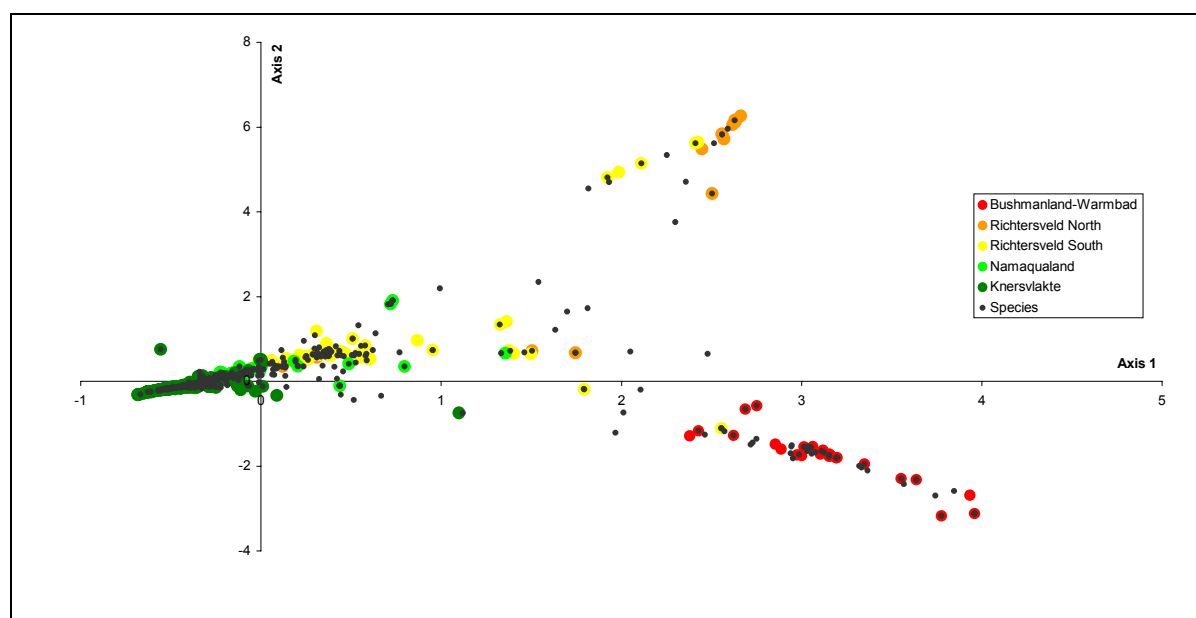


Figure 35. CA ordination of quartz-field relevés of the Namaqualand and Bushmanland-Warmbad Phytochorion. Joint plot of relevés and species.

The intrinsic relationship within the quartz-field relevés of the Namaqualand *sensu lato* and of the Bushmanland-Warmbad Phytochorion has been analysed by a separate CA. The scatter diagram of the relevés (Figure 35) revealed a clear geographical gradient from south (left) to north (right) along Axis 1. The relevés of the Knersvlakte were plotted in the highest density. From south to

north the distribution of relevés within the ordination became more broadly scattered. The northern phytocoria (Bushmanland-Warmbad and Richtersveld s.l.) were separated into the western (Richtersveld s.l., above Axis 1) and the eastern section (Bushmanland-Warmbad Phytocorion, below Axis 2). The relevés of the Richtersveld s.l. were split into two distinct groups each comprising both, relevés of the southern and northern Richtersveld. The lower group showed close relationship to the relevés of the central Namaqualand (Riethuis-Wallekraal area) on the one hand and of the Bushmanland-Warmbad area on the other hand. The upper group of Richtersveld relevés were strongly separated from all other relevés. The most important species that were associated with the second group were *Drosanthemum inornatum*, *Brownanthus pubescens*, *Ruschia inconspicua* (Mesembryanthema, Aizoaceae), and *Portulacaria pygmaea* (Portulacaceae), i.e., the Community # 51 (Chapter IX.1.5).

Based on the results of the CA ordination of all quartz-field relevés (Figure 33 and Figure 35), the classification of the vegetation the data set was subdivided into three parts, resulting in three phytosociological tables: the Little Karoo and adjacent areas (Appendix 12), the Namaqualand *sensu lato* (Appendix 10), and the Bushmanland-Warmbad area (Appendix XX).

The description of the communities comprises the diagnostic species (character and differential taxa), additional data on the vegetation community: vegetation cover, species richness (species numbers per relevé) as well as growth-form composition. For each community a habitat description is given comprising the distribution area, the topography, inclination, exposition, physical soil properties (soil depth, stone content, soil texture, geology) and chemical soil properties (electrical conductivity, soil acidity, carbonate content and composition of the water soluble ions).

III.5.2 Little Karoo and adjacent areas

All references to species groups (SG) and numbers of communities refer to the phytosociological table I of the Little Karoo (Appendix 11).

Hierarchical classification

The phytosociological table of the Little Karoo and adjacent areas comprises 200 relevés which form part of 16 communities (# 1-16) and two sub-communities of quartz fields and related habitats. The CA of the data matrix of the synoptic table (Figure 36) revealed a clear subdivision along Axis 1 into two Major Communities, Community # 1 on the one hand and # 2-16 on the other hand. The second Major Community (comprising Community # 2-16) comprises four subgroups of lower hierarchy: Communities # 2-4 as well as Community # 16 were plotted apart from the rest (i.e., Communities # 5-15) along Axis 2, thus revealing a sub-division of the Major Community into Community Group B, C & D, and E (left). Community Groups C and D showed the highest similarities and were only separated in the CA after having omitted Communities # 1-4 from the analysis (Figure 41, right). In the classification they were merely separated by the occurrence of the differential species in SG F and J, respectively.

The communities were all characterised by a low number of diagnostic species. Also, very few species revealed to be appropriate to separate community groups of higher hierarchical level. The only species groups were SG F, combining Communities # 5-7, as well as species group SG J, combining Communities # 8-15. Numerous species are common for the majority of the communities (SG E, T and U). Among those *Hereroa tenuifolia* (SG E), *Pteronia pallens*, *Malephora lutea*, *Tetragonia robusta* (both SG T), and *Psilocaulon articulatum* (SG U) occurred with high constancy in the majority of the communities.

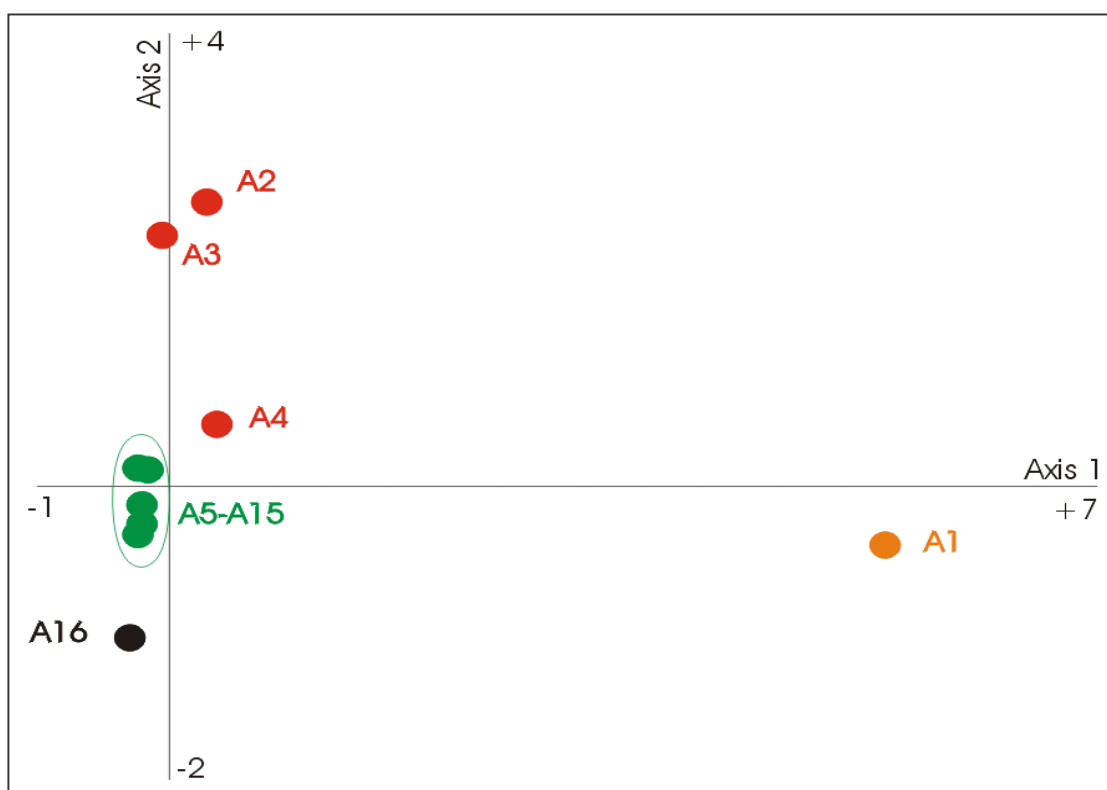


Figure 36. CA ordination of the data matrix of the synoptic table.

The resulting community groups (A-E) based on the hierarchical classification (Figure 37) mirror largely the geographical distribution of the communities:

A) Major Association: Swellendam area, south of the Langeberge
 1 *Gibbaeum haagei*-*Delosperma asperulum* Community

B-D Major Association: Little Karoo and adjacent areas to the north

B) Association Group: Barrydale-Vanwyksdorp area, southern fringe of the Little Karoo

2 *Gibbaeum velutinum* Community

3 *Gibbaeum angulipes* Community

4 *Gibbaeum album* Community

Association Group: Barrydale-Vanwyksdorp area, southern fringe of the Little Karoo

5 *Gibbaeum dispar* Community

6 *Zeuktophyllum suppositum* Community

7 *Gibbaeum petrense* Community

Association Group: Central and northern part of the Little Karoo between Kruisrivier in the east and Calitzdorp in the west as well as southern fringe of the Ceres Karoo, north of the Swartberge.

- 8 *Gibbaeum cryptopodium* Community
- 9 *Gibbaeum pubescens* Community
- 10 *Pteronia pallens*-*Aridaria noctiflora* ssp. *defoliata* Community
- 11 *Gibbaeum gibbosum* Community
- 12 *Gibbaeum geminum* Community
- 13 *Gibbaeum shandii* Community
- 14 *Gibbaeum heathii* Community
- 15 *Gibbaeum pachypodium* Community

Association: Widespread in the Little Karoo

- 16 *Psilocaulon junceum* Community

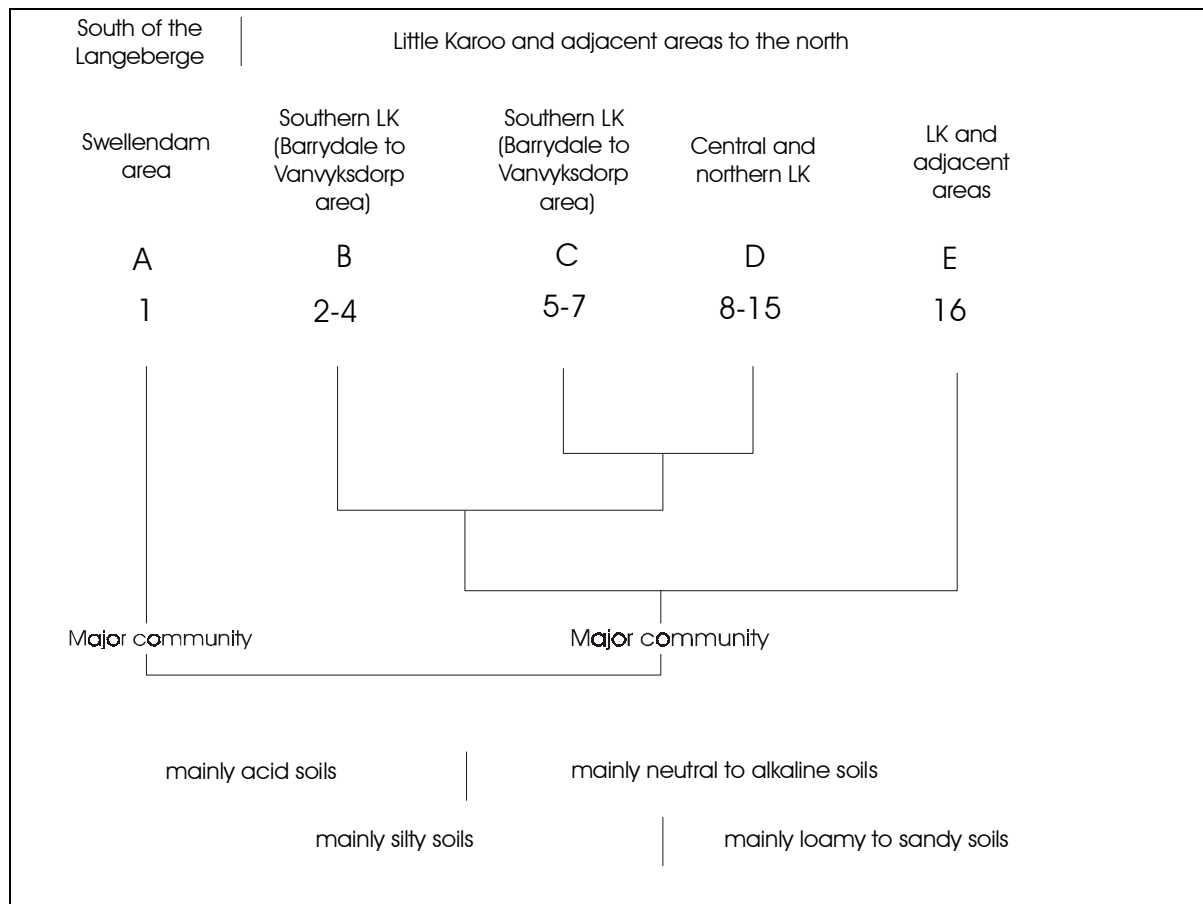


Figure 37. Hierarchical cladogram of the plant communities, Little Karoo.

Total cover values and species richness

The mean total cover values were low for most of the communities (4.4-10.8 %). Only the *Gibbaeum haagei*-*Delosperma asperulum* Community (# 1) and the *Psilocaulon junceum* Community (# 16) had considerably higher mean cover values (17 and 59 %, respectively).

For the majority of the communities the mean species numbers per relevé (25 m²) were below 10 spp. per relevé. Considerably higher value (17 spp/ relevé) was only found for the *Zeuktophyllum suppositum* Community (# 6) (Figure 38 and Table 42).

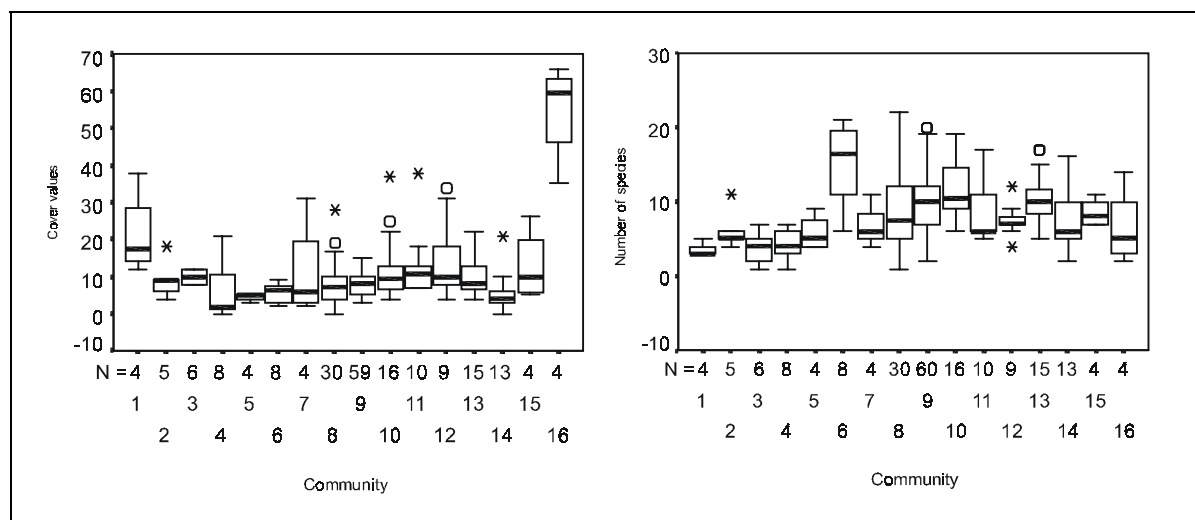


Figure 38. Box-Whisker plots of total cover values and species numbers of communities # 1-16 of the Little Karoo and adjacent areas.

Table 42. Plant cover and number of species for the communities # 1-16 of the Little Karoo and adjacent areas (mean, minimum, maximum).

Community		1	2	3	4	5	6	7	8	9.1	9.2	10	11	12	13	14	15	16
Plant cover values	Mean	17.5	8.7	10.1	2.1	5.2	6.5	6.3	6.7	7.7	7.6	9.6	10.8	10.4	8.4	4.4	9.8	59.1
	Min	12.0	4.2	8.0	0.1	3.1	1.7	2.1	0.1	3.1	2.6	4.4	6.6	4.1	3.6	0.2	4.7	35.1
	Max	38.1	18.3	12.2	21.2	5.5	8.8	30.5	27.6	14.7	14.1	37.0	37.7	33.6	22.0	21.4	26.2	66.1
Number of species	Mean	3	5	4	4	5	17	6	8	8	10	11	6	7	10	6	8	5
	Min	3	4	1	1	4	6	4	1	4	2	6	5	4	5	2	7	2
	Max	5	11	7	7	9	21	11	22	18	20	19	17	12	17	16	11	14

The vegetation of the Namaqualand *sensu lato*

All references to species groups (SG) and numbers of communities refer to the Synoptic Table II and Phytosociological Table II (Appendix 9 and Appendix 10).

III.5.3 Knersvlakte

Major habitat units of the Knersvlakte

The Knersvlakte is the most southern section of the Namaqualand (Cowling *et al.* 1999b) and forms part of the Lowland Succulent Karoo (Hoffman 1996a) of the Succulent Karoo Biome (Cowling *et al.* 1986, Rutherford & Westfall 1986). The area is situated between 30° 15' and 31° 45'S where the escarpment draws back towards east and opens up a broad and gently undulated lowland plain of roughly 10 000 km² in size between the west coast and the escarpment. The average annual rainfall ranges between 100-120 in the southeast, 120-140 mm in the northeast and 140-160 mm/a in the southwest (Figure 39) and occurs mainly during winter months

(June/July, Figure 2). The variance of rainfall is higher in the west than in the east but generally low between 20 and 30 mm (Max - Min) of the long-term average. Rainfall is thus low but very predictable.

Based on the land and soil types by Ellis (1988) the Knersvlakte can be subdivided into five major habitat units (MHU): sandy soils, moderately deep loamy soils, quartz fields, shale bands, and dolomite outcrops. Three of them comprise geographically and geomorphologically defined sub-sections as listed in Table 43 (compare also Figure 40):

Table 43. Major habitat unites of the Knersvlakte and their geographical subsections.

1	Sandy soils
1.1	Coastal Sandveld
1.2	The inland stretching sand strip north of Vanrhynsdorp
1.3	The alluvial fans in the northern Knersvlakte
1.4	Sandy plains along the Sout Rivier and Groot-Graafwater Rivier in the central Knersvlakte
2	Moderately deep loamy soils: sandy loam plains with heuweltjies in the central and northern Knersvlakte
2.1	Heuweltjie veld in the north-eastern Knersvlakte
2.1.1	Southern section of the heuweltjie veld: homogeneous, little structured into heuweltjies and the interspace.
2.1.2	Northern section of the heuweltjie veld: strongly structured into heuweltjies and the interspace, which is characterised by shallow, impoverished soils and vegetation communities of its own
2.2	Sandy loam plains south of the sand strip in the southern Knersvlakte and between the shale bands in the east
3	Quartz fields, small scale mosaics of quartz covered desert pavements, loamy soils without cover of quartz gravel, and heuweltjies
3.1	along the upper Geelbek Rivier (= northern quartz fields)
3.2	along the lower Geelbek Rivier (= central quartz fields, Arizona area)
3.3	along the lower Sout and Varsch Rivier north of the sand strip (central quartz fields, Quaggas Kop area)
3.4	in the Rooiberg-Moedverloren area in the western Knersvlakte (central quartz fields).
4	Shale bands in the eastern Knersvlakte parallel to the Bokkelveldberge (escarpment)
5	Limestone outcrops with shallow soils

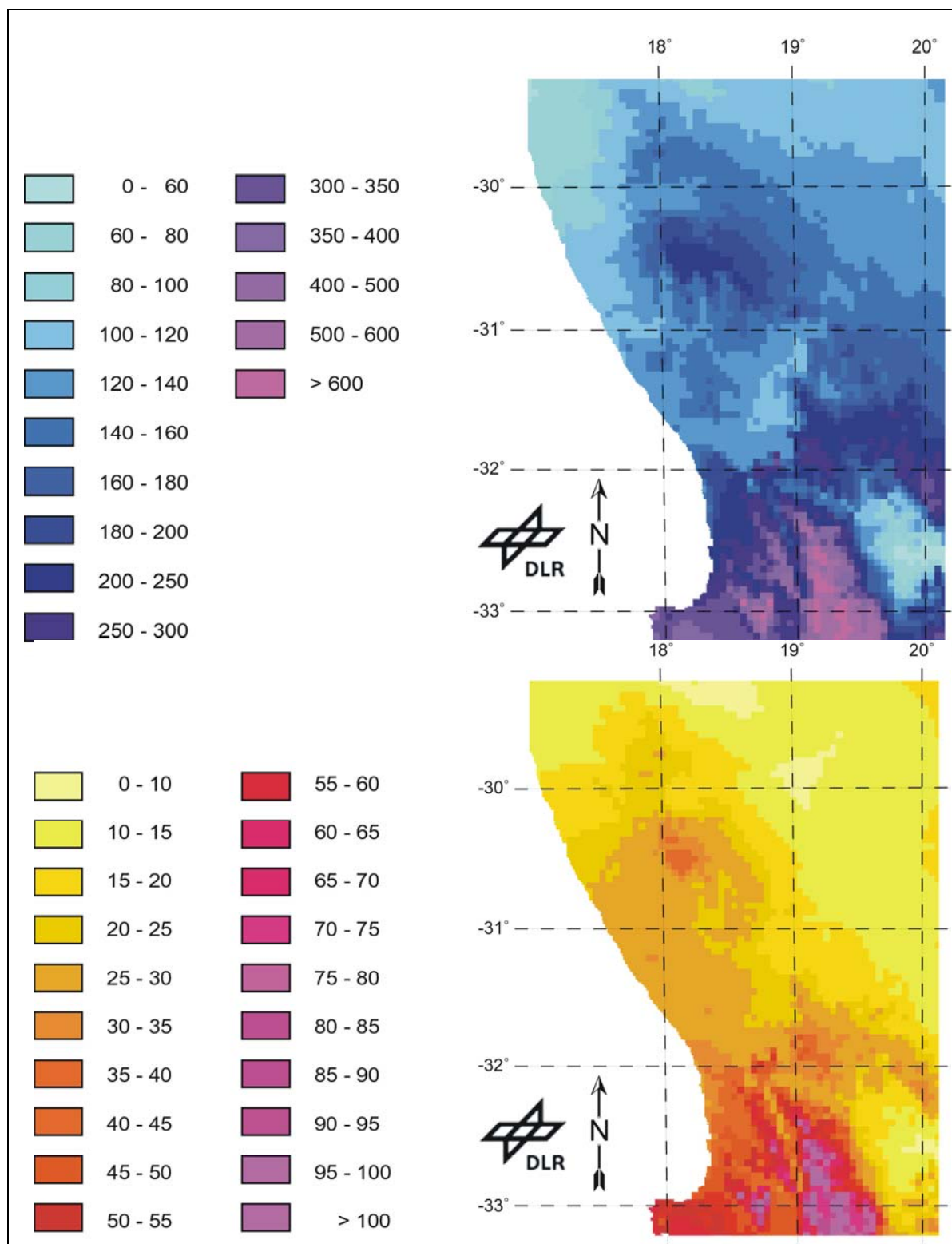


Figure 39. Spatial distribution precipitation in the Knersvlakte and surroundings on a resolution of 5 x 5 km. Above: Long-term average of total annual precipitation. Below: Variance (Max - Min) of the long-term average of total annual precipitation. Maps kindly supplied by the German Aerospace Centre, DLR.

The Knersvlakte comprises four different areas with **sandy soils** of different origin. The white coastal sand (MHU 1.1) and the inland stretching red sand strip (MHU 1.2) seems to originate from the coast, whereas the sand in the northeastern Knersvlakte presents an extensive alluvial fan which extends down from the escarpment between Loerriesfontein, Kliprand and

Kamieskroon (De Beer *et al.* in press). Of alluvial and aeolian origin is the sand along the Sout River and the Groot-Graafwater-River in the Central Knersvlakte (Gresse 1992). Due to the distance to the coast, the sandy habitats at the coast and those further inland differ considerably regarding climatic conditions, i.e., temperature regime and precipitation in particular. But also regarding the soil conditions the four sandy habitat types can be distinguished. The coastal sand is generally very deep (> 100-150 cm) and poorly structured. The red sand strip (MHU 1.2) differs with shallow (< 50 cm) to very deep (>> 150 cm) soils with low dunes even. The alluvial sands in the central and northern Knersvlakte, in return, is typically more shallow and hardly reach depths of > 100 cm.

Moderately deep, **loamy sandy soils** cover broad plains in the northeastern, eastern and the southern Knersvlakte. In the northeast (MHU 2.1), they reach largest extension and form a hardly undulated plain which borders to the alluvial plains in the north (MHU 1.3), to the escarpment and the shale bands (4) in the north and to the quartz fields in the southwest (MHU 3). The whole plain is characterised by the frequently and regularly occurrence of mainly deserted heuweltjies. Particularly in the northern section (MHU 2.1.1) this plain is strongly structured into heuweltjies and the interspace with shallow, impoverished sandy soils, whereas this pattern is less strongly developed in the southern section (MHU 2.1.2). Here, the vegetation which is associated with the heuweltjies typically extend into a broad circle around the heuweltjies often cover a broad area without leaving any gaps with non-heuweltjie vegetation. The other type of loamy soils either occur as two disjunct islands within the shale bands or cover the entire southern Knersvlakte, south of the red sand strip. In contrast to the sandy loamy plain in the northeast, the southern and eastern loamy soils largely lack of heuweltjies. The eastern and the southern subsection of the loamy correspond largely regarding the vegetation which is characterised by disturbance and overgrazing (Steinschen *et al.* 1996).

Quartz fields (MHU 3) represent an unusual habitat type which is widespread in the semiarid parts of the winter rainfall area of Southern Africa. But in the Knersvlakte, quartz fields reach their broadest extension and highest habitat diversity. Quartz fields are edaphically induced special habitats with shallow soils and which are either extremely saline or they are rich in stone content and have a very low soil pH. The quartz derives from weathering quartz veins. In the Knersvlakte they are found in the central part, along and west of the N7 as well as along the northwestern border of the Knersvlakte, west of the loamy plains (MHU 2.1). The quartz fields of the central Knersvlakte, again comprise three zones which are geographically fairly distinct and also differ regarding climatic conditions (more influence of fog in the west) and vegetation composition. Quartz fields typically form a small scale mosaic comprising quartz fields of different habitat types, closely mingled with loamy soils without quartz cover as well as heuweltjies with an island-like occurrence. These soils without quartz cover within the quartz-field mosaics largely house vegetation units of its own (Community # 10-13) but also shares communities of the loamy sandy plains (MHU 2).

In the western Knersvlakte, largely parallel to the escarpment, dominate the poorly weathered **shale bands** of the Besonderheid Formation (Gresse 1992). The topography is gently undulated comprising ridges or plateaux of shale and shallow valley bottoms which are partly covered by alluvial deposits of the Kleinfontein and Vars Rivier. The soils at the slopes and plateaux are typically shallow and skeletal whereas in the valleys they are rich in loamy sand.

West of Vanrhynsdorp, along the Widouw and the Troe-Troe Rivier **limestone** of the Widouw Formation (Gresse 1992) occurs and present a small but distinct Major Habitat Unit (5). Carbonate which is elsewhere in the Knersvlakte largely restricted to heuweltjies and their surrounding (only in the Varsche Rivier Extension, south of the Sout Rivier, limestone outcrops are found along the River), presents a very important feature here. Particularly on plateaux and

outcrops where the limestone is exposed, communities occur which are absent elsewhere in the Knersvlakte. However, spiny species clearly dominate and beyond that the slopes and valleys are largely covered by the Australian invader *Atriplex lindleyi* ssp. *inflata*. This an severe soil erosion indicate strong overgrazing and disturbance in this area.

The major habitat units again consist of geographical sub-sections and comprises a certain array of different small scale habitats, controlled by changes in soil conditions, geology or topography (e.g., soil depth, salinity, run-off and run-on areas, heuweltjies, micro dunes, angle of slope). The number of habitats within a land type depends on the soil and geo-diversity and therefore differs between the major habitat units.

The vegetation of the Knersvlakte outside the quartz fields

Most of the communities and even the alliances can be clearly associated with particular habitat units. In the formal description of the communities (Chapter III.5.3, Appendix) and in Table 44 their association to particular major habitat units is given.

Table 44. Vegetation communities and sub-communities of the Knersvlakte (without quartz-field vegetation) and their association with Major Habitat Units.

Major habitat unit (MHU)		(Deep) sandy soils				Loamy soils			Quartz-field mosaics				Shale	Dolomite
Com.	Sub-com.	1.1	1.2	1.3	1.4	2.1.1	2.1.2	2.2	3.1	3.2	3.3	3.4	4	5
1		x												
2	1		x	x	x									
	2	x	x											
3		x												
4				x	x									
5				x										
6				x	x									
7	1						x							
	2		x	x			x							
	3			x										
8			(x)			x								
9	1-4			(x)									x	
10										x	x	x		
11					x					x	x			x
12				x						x	x	x		
13												x		
14								x						
15								x						
16	1							x						x
	2												x	
	3			x		x								
17					x		x							
18														x
19	1-3					x			x	x	x	x		
20	1									x	x	x	x	
	2									x	x	x		

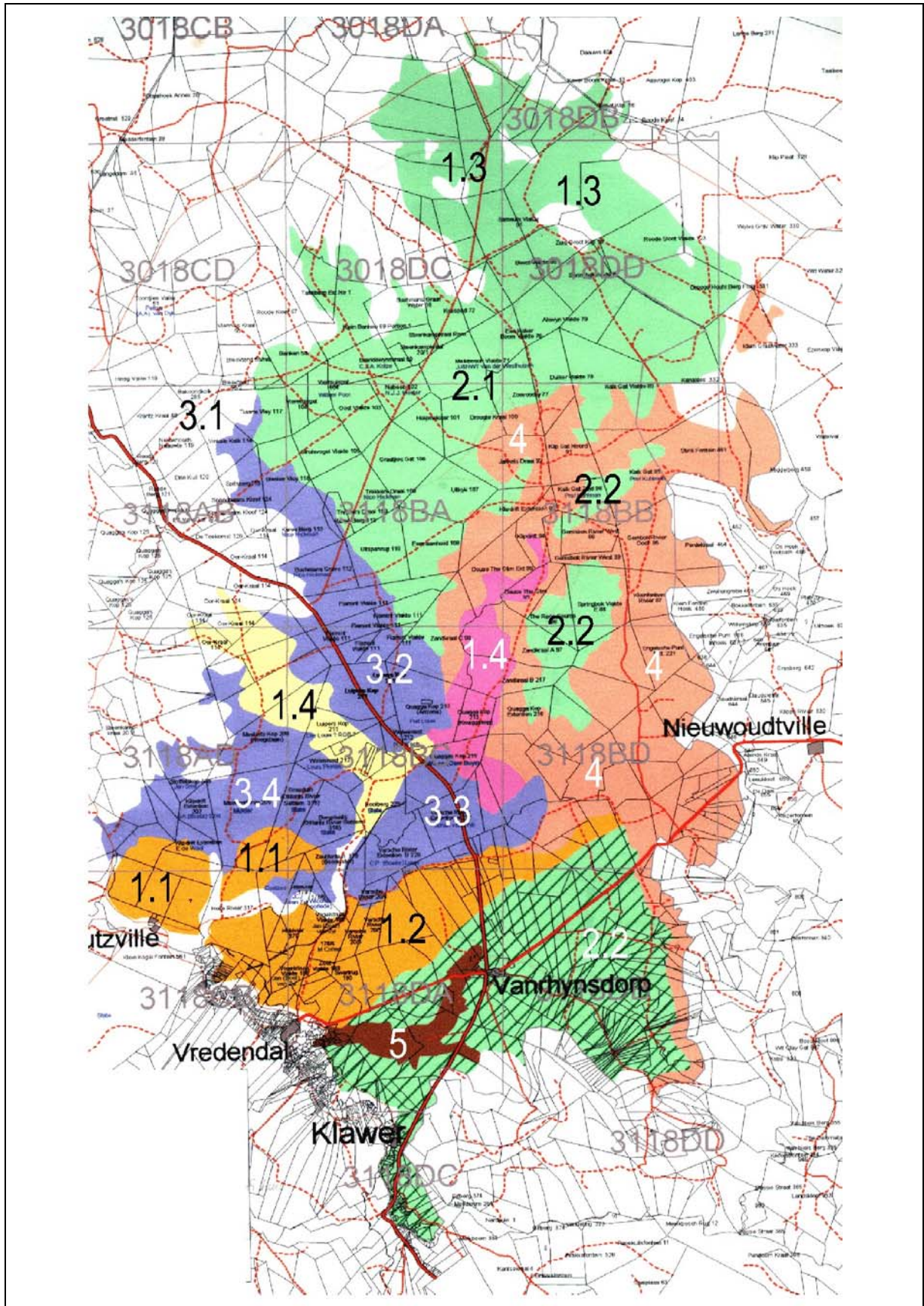


Figure 40. Distribution and delimitation of the Major Habitat Units of the Knersvlakte. GIS map by Annelise Le Roux, Western Cape Nature Conservation Board, based on data of Ute Schmedel and Freddy Ellis.

The vegetation of the very deep, sandy soils: *Zygophyllum morgsana-Othonna cylindrica* Alliance

- 1 *Eriocephalus racemosus-Lebeckia multiflora* Strandveld Community
- 2 *Cladoraphis spinosa* Spiny Grass Community
 - 2.1 *Cladoraphis spinosa* dominated Sub-Community
 - 2.2 *Cladoraphis spinosa-Euphorbia burmannii* Sub-Community
- 3 *Ruschia ruschiana* aff. (Schmiedel 93302 HBG)-*Antimima excedens* Succulent Shrub Community

Deep to moderately shallow, sandy soils of the central and northern Knersvlakte: *Ruschia* sp. (Schmiedel 104621 HBG)-*Drosanthemum curtophyllum* Alliance

- 4 *Stipagrostis namaquensis* Grass Veld Community
- 5 *Ruschia robusta* Succulent Shrub Community
- 6 *Ruschia versicolor* Succulent Shrub Community
- 7 *Leipoldtia calandra-Ruschia lisabeliae* Succulent Shrub Community
 - 7.1 *Leipoldtia calandra*-dominated Succulent Dwarf Shrub Sub-Community
 - 7.2 *Drosanthemum curtophyllum* Succulent Dwarf Shrub Sub-Community
 - 7.3 *Ruschia* sp. (Schmiedel 104621 HBG) Succulent Shrub Sub-Community
- 8 *Cephalophyllum parvibracteatum* Dwarf Shrub Community

Vegetation of the shale bands: *Brownanthus ciliatus-Ruschia spinosa* Dwarf Shrub Community

- 9 *Brownanthus ciliatus-Ruschia spinosa* Dwarf Shrub Community
 - 9.1 *Brownanthus ciliatus*-dominated Dwarf Shrub Sub-Community
 - 9.2 *Ruschia spinosa*-dominated Dwarf Shrub Sub-Community
 - 9.3 *Rhinephyllum macradenium* Dwarf Shrub Sub-Community
 - 9.4 *Arenifera stylosa* Dwarf Shrub Sub-Community

Vegetation of loamy-sandy soils of the Knersvlakte: *Psilocaulon leptarthron-Euphorbia muricata* Alliance

- 10 *Ruschia patulifolia* Succulent Shrub Community
- 11 *Drosanthemum roseatum* Succulent Shrub Community
- 12 *Cephalophyllum framesii* Succulent Dwarf Shrub Community
- 13 *Ruschia stricta* var. *turgida* Succulent Shrub Community
- 14 *Drosanthemum deciduum* Succulent Shrub Community
- 15 *Drosanthemum hispidum* Succulent Shrub Community
- 16 *Atriplex lindleyi* ssp. *inflata* Annual Weed Community
 - 16.1 *Atriplex lindleyi* ssp. *inflata-Stipa capensis* Sub-Community
 - 16.2 *Atriplex lindleyi* ssp. *inflata-Malephora purpureo-croccea* Sub-Community
 - 16.3 *Atriplex lindleyi* ssp. *inflata-Augea capensis* Sub-Community
- 17 *Salsola zeyheri* Semi-Succulent Shrub Community

18 *Melolobium candicans*-*Hermannia cuneifolia* Thorny Shrub Community19 *Ruschia subsphaerica* Succulent Shrub Community19.1 *Ruschia subsphaerica* dominated sub-community19.2 *Ruschia subsphaerica* - *Ruschia patulifolia* sub-community19.3 *Ruschia subsphaerica*-*Drosanthemum roseatum* sub-community20 *Aridaria serotina*-*Ruschia* sp. (Bartels 93268 HBG) Succulent Shrub Community20.1 *Aridaria serotina*-dominated Sub-Community20.2 *Aridaria serotina*-*Ruschia* sp. (Bartels 93268 HBG) Sub-Community

Communities of the quartz-field vegetation of the Knersvlakte

The quartz-field vegetation of the Namaqualand *sensu lato*, including the Knersvlakte, central Namaqualand and the Richtersveld, was characterised by species group (SG) W, which comprises *Crassula columnaris* ssp. *prolifera*, *C. deceptor* and *Senecio aloides* as the most constant species. The vegetation of the quartz fields of the Knersvlakte was subdivided into two main groups (alliances) which covered all but two intermediate communities. Despite the differences in species composition, all quartz-field communities of the Knersvlakte were characterised by common species which were grouped in SG X (*Drosanthemum diversifolium*, *Argyroderma fissum*, *Phyllobolus spinuliferus*) and Y (*Argyroderma delaetii*, *Cephalophyllum spissum*, *Othonna intermedia*, *Zygophyllum teretifolium*, and others). SG X had a broader distribution, though. It was also recorded for the relevés outside the quartz fields in the Knersvlakte and for communities that were also recorded for the central Namaqualand (Riethuis-Wallekraal area).

The *Salsola* sp. (Schmiedel 93110 HBG)-*Argyroderma pearsonii* Alliance was defined by SG Z (*Argyroderma pearsonii*, *Mesembryanthemum fastigiatum*, *M. stenandrum*, *Salsola* sp. Schmiedel 93110 HBG, and *Tylecodon pygmaeus*). The communities of this alliance occurred on saline quartz fields of the Knersvlakte. The majority of the communities were poorly defined by diagnostic species. However, each community typically was by one single species which often also occurred on other communities but with very low cover values only. Therefore, several communities were defined the dominating species and not by a diagnostic species.

The *Conophytum calculus* ssp. *calculus* Alliance is restricted to acid, moderately to non-saline quartz fields of the Knersvlakte. It was defined by the occurrence of *C. calculus* ssp. *calculus* only. Also species Group AH (*Antimima dualis*, *Phyllobolus tenuiflorus*, *Anacampseros retusa*, *Lachenalia patula*, *Ruschia vanbeerdei*, *Mesembryanthema longistylum*, *Trachyandra tortilis*, *Pentzia peduncularis*, *Dicrocaulon humile*) covered large parts of the Alliance but with low constancy values only. The SG was absent from the quartz-field communities of the northern Knersvlakte (# 38 *Dicrocaulon longifolium* and # 39 *D. nodosum* Community). Due to the SG AG (*Spergularia media*, *Conophytum minutum* v. *pearsonii*, *Cephalophyllum pulchrum*, *Aspalathus* sp. (Schmiedel 110253 HBG), *Crassula capitella* ssp. *thyrsiflora*, *Ficinia lateralis*, *Euphorbia hamata*, *Hirpicium alienatum*, *Salsola* sp. Schmiedel 102410 HBG) the Alliance was related to the communities of the Riethuis-Wallekraal area. Species Group AF (*Pteronia ciliata*, *Gazania krebsiana*, *Pelargonium crithmifolium*, *Phyllobolus deciduus*) were characteristic species of the non-saline quartz fields of the Namaqualand *sensu lato*. In contrast to the communities of the saline quartz-field of the Knersvlakte, the communities of this alliance were all defined by diagnostic species, However, the number of diagnostic species per community were low for the majority of the communities.

***Salsola* sp. (Schmiedel 93110 HBG)-*Argyroderma pearsonii* Alliance (# 21-30)**

- 21 *Drosanthemum diversifolium*-dominated Community
- 22 *Argyroderma fissum*-dominated Community
- 23 *Argyroderma delaetii*-dominated Community
- 24 *Cephalophyllum spissum*-dominated Community
- 25 *Argyroderma pearsonii*-dominated Community
- 26 *Mesembryanthemum fastigiatum*-dominated Community
- 27 *Oophytum nanum* Community
- 28 *Phyllobolus digitatus* ssp. *digitatus* Community
- 29 *Oophytum oviforme* Community
- 30 *Monilaria pisiformis* Community
- 31 *Conophytum minutum* var. *minutum* Community
- 32 *Brownanthus corallinus* Community

The *Conophytum calculus* ssp. *calculus* Alliance (Community # 33 - 39)

- 33 *Ruschia burtoniae* Community
- 34 *Monilaria chrysoleuca* var. *chrysoleuca* Community
- 35 *Monilaria moniliformis* Community
- 36 *Dicrocaulon brevifolium* Community
- 37 *Dicrocaulon pseudonodosum* Community
- 38 *Dicrocaulon longifolium* Community
- 39 *Dicrocaulon nodosum* Community

III.5.4 Riethuis-Wallekraal area

The communities that were largely restricted to the quartz-field habitats of the Riethuis-Wallekraal Phytochorion showed a low internal subdivision. The regional communities were combined by the SG AR (*Othobna incisa*, *Phyllobolus prasinus*, *Othobna rechingeri*, *Meyerophytum meyeri*, *Senecio sulcicalyx*, *Meyerophytum globosum*, *Cephalophyllum inaequale*) but also shared SG AG with the acid non-saline quartz fields of the Knersvlakte and SG AF with the acid quartz fields of the Knersvlakte and the Richtersveld. In correspondence with the communities of the non-saline, acid quartz fields of the Knersvlakte, the communities were clearly defined by diagnostic species and not only by dominating species.

- 40 *Monilaria scutata* var. *obovata* Community
- 41 *Jacobsenia vaginata* Community
 - 41.1 *Jacobsenia vaginata*-*Meyerophytum globosum* Sub-Community

41.2 *Jacobsenia vaginata*-dominated Sub-Community

- 42 *Dicrocaulon spissum* Community
- 43 *Dicrocaulon ramulosum* Community
- 44 *Ruschia viridifolia* Community
- 45 *Monilaria scutata* var. *scutata* Community

III.5.5 Richtersveld

The vegetation of the Richtersveld was separated from the vegetation of the Riethuis-Wallekraal area by the occurrence of *Cheiridopsis robusta* and *Euphorbia ephedroides* (SG BG). Only the *Aspazoma amplexans* Community (# 46) which was grouped together with the plant communities of the Richtersveld was also found in Riethuis-Wallekraal area. The communities which occur exclusively (# 46-48, # 50-51) or facultatively (# 49) on quartz fields were defined by species group BH (*Sarcocaulon crassicaule*, *Crassula grisea*, *Euphorbia decussata*, *Trachyandra muricata*, *Othonna obtusiloba*, *Cephalophyllum numeesense*, *Anacampseros papyracea* ssp. *namaesis*, *Crassula expansa* ssp. *expansa*, *Tetragonia reduplicata*, *Zygophyllum prismatocarpum*). The quartz-field communities of the Richtersveld were again subdivided into two groups. One group was defined by the occurrence of SG AY (*Antimima* sp. Schmiedel 104874 HBG, *Suaeda* sp. Schmiedel 102015 HBG, *Adenoglossa decurrens*, *Lithops meyeri*, *Octopoma connatum* etc.) and comprised Communities # 46-48 which were hardly defined by diagnostic species but by the dominance of particular species. The second group (Communities # 49-51) was not defined by joint species and its communities were defined by several diagnostic species each.

- 46 *Ruschia leucosperma* Community
- 47 *Cephalophyllum regale*-dominated Community
- 48 *Aspazoma amplexans* Community
- 49 *Eberlanzia cyathiformis* Community
- 50 *Schlechteranthus hallii* Community
- 51 *Brownanthus pubescens* Community
 - 51.1 *B. pubescens*-dominated Community
 - 51.2 *B. pubescens*-*Ruschia inconspicua* Community

The zonal lowland vegetation of the Richtersveld were represented by the *Brownanthus pseudoschlichtianus* Community (# 51) that strongly dominates the loamy-sandy soils of the lowland plains of the Richtersveld. The community is very poor in species and hardly share species with any of the other major groups, except *Cheiridopsis robusta* and *Euphorbia ephedroides* (SG BG).

- 52 *Brownanthus pseudoschlichtianus* Community

III.5.6 Bushmanland-Warmbad area

All references to species groups (SG) and numbers of communities refer to the Phytosociological Table III. Detailed description of the communities are given in Chapter IX.1.6.

The Bushmanland-Warmbad area only comprised a low number of quartz-field communities of which only the *Lithops julii* Community is entirely restricted to quartz fields.

- 1 *Zygophyllum decumbens* Community
- 2 *Lithops julii* Community

3 *Oropetium capense* Community

- 3.1 *Oropetium capense*-*Ruschia odontocalyx* Sub-Community
- 3.2 *Oropetium capense*-*Lithops julii* Sub-Community
- 3.3 *Oropetium capense*-*Galenia fruticosa* Sub-Community
- 3.4 *Oropetium capense* species-poor Sub-Community

4 *Drosanthemum* sp. (Schmiedel 102344 HBG) Community

III.6 Environmental variables controlling the species composition

Quartz fields represent special habitats which are defined by properties of the soil surface (Chapter I.4). The vegetation classification (Chapter III.5) revealed the occurrence of distinct Community groups within the vegetation which, in return were associated with certain habitat conditions. In order to make the main gradients within the vegetation emerge, correspondence analyses (CA of the computer programme CANOCO) were applied. The main gradients were interpreted by employing the direct gradient analyses, based on canonical correspondence analysis (CCA, of the same computer programme). The unconstrained relevé scores were used to investigate the relationship between the communities and the environment whereas the constrained relevé scores revealed the (linear) relationships between the relevés and the environmental variables. To exclude the overruling influence of geographical particularities, based on the high degree of endemism, the regional data sets were always analysed separately.

The following environmental variables were used: inclination of slope, quartz cover on soil surface, stone cover on soil surface of other lithology as quartz, soil depth, stone content in soil, electrical conductivity, soil pH (H^+ concentration was employed here in order to obtain a linear relation), and carbonate. Due to the fact that the quartz fields mainly occur in plains or on very moderate hills exposition plays a minor role for the vegetation.

III.6.1 Little Karoo

Indirect gradient analyses

The CA ordination of the communities # 1-16 (Figure 41, left) of the Little Karoo and adjacent areas mirrored the hierarchical classification of the vegetation as described above (Figure 37). Communities # 1-4 were clearly separated from the remaining communities: *Gibbaeum haagei* Community (# 1), *G. velutinum* Community (# 2), and the *G. album* Community (# 4) were plotted from left to right along Axis 1 of the scatter diagram, whereas the *G. angulipes* Community (# 3) was plotted at the distal end of Axis 2. The remaining communities (Community # 5-16) were plotted in a dense cloud in the left lower corner of the scatter diagram.

The summary statistics of the correspondence analysis (Table 45) had high eigenvalues (> 0.9). The species-environment correlation was considerably low (< 0.5) though. Eleven percent of the variance of the species data and 22 % of the species-environment relationship was explained by the ordination. The environmental variable H^+ concentration had the strongest positive correlation with the first two axes. Although the correlation was slightly higher with Axis 2 than Axis 1. Quartz cover (< 6 cm in diameter) was positively correlated with Axis 1 and the variable coarse quartz cover (> 6 cm in diameter) was positively associated with Axis 4. The other

environmental variables showed very poor correlation with any of the axes. Thus, the clear separation of the data set along Axis 1 and 2 was not entirely explained by the employed environmental variables which were mainly based on environmental properties.

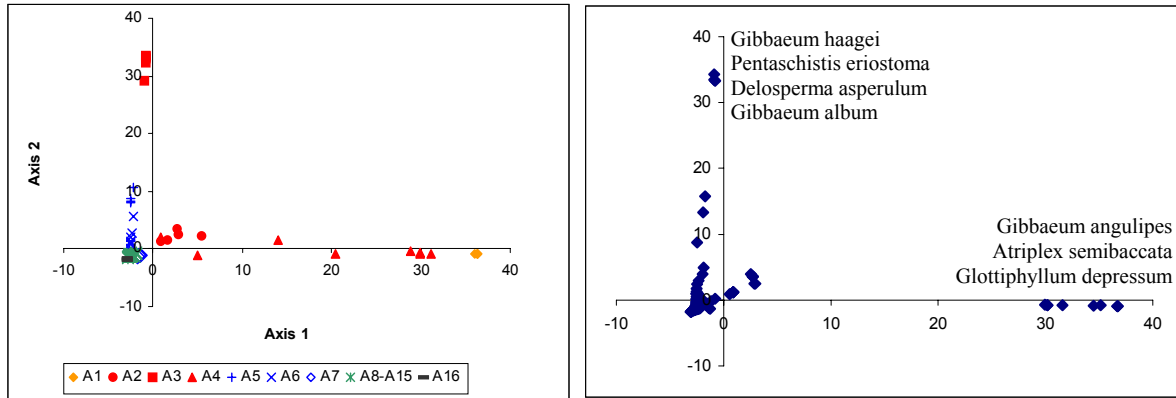


Figure 41. CA ordination of species data of quartz fields and related habitats of the Little Karoo and adjacent areas. Communities # 1-16. Left: Scatter plot of relevés. Right: Scatter plot of species.

Table 45. Summary statistics of the CA of species data of the quartz-field and related habitats of the Little Karoo and adjacent areas.

Axes	1	2	3	4
Eigenvalues:	.993	.973	.881	.828
Species-environment correlations:	.464	.482	.206	.503
Cumulative % of variance				
of species data:	5.6	11.0	15.9	20.6
of species-environment relation:	10.7	22.0	23.9	34.3
Sum of all unconstrained eigenvalues:				17.868
Sum of all canonical eigenvalues:				1.999

Table 46. Correlation matrix of the supplementary environmental variables and CA axes of species data of the Little Karoo and adjacent areas.

Axis	1	2	3	4
incl	.1163	.1476	-.0232	.0234
soildpth	-.0614	-.1253	-.1053	-.0260
coarseq	-.0311	.0982	.0733	.4710
quartz	.2559	.1091	-.0199	-.0183
stonecov	-.1932	-.0869	.0983	.0142
stonecon	-.1452	-.0650	.0278	-.0688
elconduc	.0383	-.0172	-.0639	-.0538
carbonat	-.0869	-.0650	-.0198	-.0051
H ⁺ conc	.3588	.4656	-.0538	-.0230

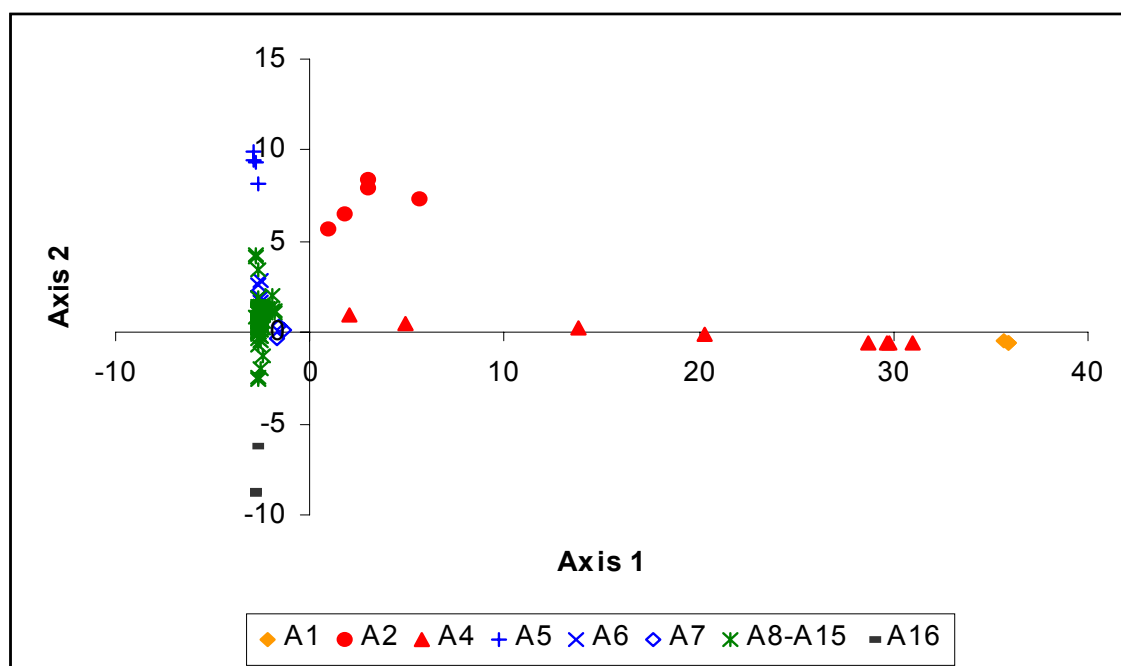


Figure 42. CA ordination of species data of quartz fields and related habitats of the Little Karoo and adjacent areas. Without the *G. angulipes* Community (# 3). Scatter plot of relevés.

A subsequent correspondence analysis of the same data set but without the *G. angulipes* Community (# 3) (Figure 42, right) revealed the same pattern as before but allowed the *G. velutinum* Community (# 2) and the *G. dispar* Community (# 5) to move up along Axis 2.

Table 47. Summary statistics of the CA ordination of species and environmental variable data of quartz fields and related habitats of the Little Karoo and adjacent areas.

Axes	1	2	3	4
Eigenvalues:	.992	.888	.829	.786
Species-environment correlations:	.467	.203	.506	.612
Cumulative % of variance of species data:	5.9	11.1	16.0	20.7
of species-environment relation:	11.7	13.7	25.2	41.1
Sum of all unconstrained eigenvalues:				16.916
Sum of all canonical eigenvalues:				1.845

Table 48. Correlation matrix of the supplementary environmental variables and CA axes of species data of the Little Karoo and adjacent areas.

Axes	1	2	3	4
incl	.0549	.0088	.0252	-.1395
soildpth	-.0483	-.1206	-.0270	.0226
coarseq	-.0533	.0843	.4784	-.1035
quartz	.2379	-.0077	-.0167	-.5194
stonecov	-.1784	.0885	.0132	.2701
stonecon	-.1512	.0263	-.0692	-.3337
elconduc	.0622	-.0715	-.0531	-.2924
carbonat	-.0782	-.0282	-.0060	.1781
H ⁺ conc	.3504	-.0147	-.0350	-.2674

The ordination had high eigenvalues (< 0.8 for the first three axes). but the species environment correlation for the first two axes was comparably low (< 0.5). Particularly Axis 2 was very poorly

explained by any of the variables. Nevertheless, coarse quartz cover (> 60 mm diameter) was strongly associated with Axis 3 (0.47) and several environmental variables (i.e., quartz cover, stone cover, stone content, electrical conductivity) showed significantly strong associations with Axis 4. The high correlation of environmental variables with Axes 3 and 4 revealed that the environmental variables explained certain aspects of the variance in species data but were not relevant for the strongest separation of the species data along Axis 1 and 2.

Direct gradient analyses

The scatter diagram of the unconstrained relevé scores of the Canonical Correspondence Analysis of the species data of the Little Karoo and adjacent areas (Figure 43) revealed the habitat preferences of the communities classified above.

Axis 1 represented a gradient of increasing quartz cover on soil surface which revealed to be the most important gradient (longest arrow) and - with lower importance - of electrical conductivity. Soil depth was negatively associated with quartz cover on soil surface. H⁺ concentration was positively associated with both, Axis 1 and Axis 2. Stone cover of other lithology than quartz stones and carbonate were negatively associated with Axis 2 and negatively associated with H⁺ concentration. Consequently, quartz cover on soil surface was positively associated with electrical conductivity, stone content in soil, and less strongly associated with low soil pH (high H⁺ concentration) and inclination of slope. They were negatively associated with soil depth and, with lower importance, carbonate content in soil and stone cover of other lithology than quartz.

Table 49. Summary statistics of the CCA ordination of species and environmental variable data of quartz fields and related habitats of the Little Karoo and adjacent areas.

Axes	1	2	3	4	
Eigenvalues:	.610	.473	.340	.312	
Species-environment correlations:	.855	.757	.721	.691	
Cumulative % of variance					
of species data:	2.2	4.0	5.2	6.4	
of species-environment relation:	23.7	42.1	55.4	67.5	
Sum of all unconstrained eigenvalues:					27.2466
Sum of all canonical eigenvalues:					2.56

The CCA ordination (Table 49) had high eigenvalues and very high species environmental correlations (>0.75) for the first two axes. the cumulative percentage of variance of species data was relatively low (4 %) but more than 40 % of the variance of species-environment relation was explained was explained by the ordination.

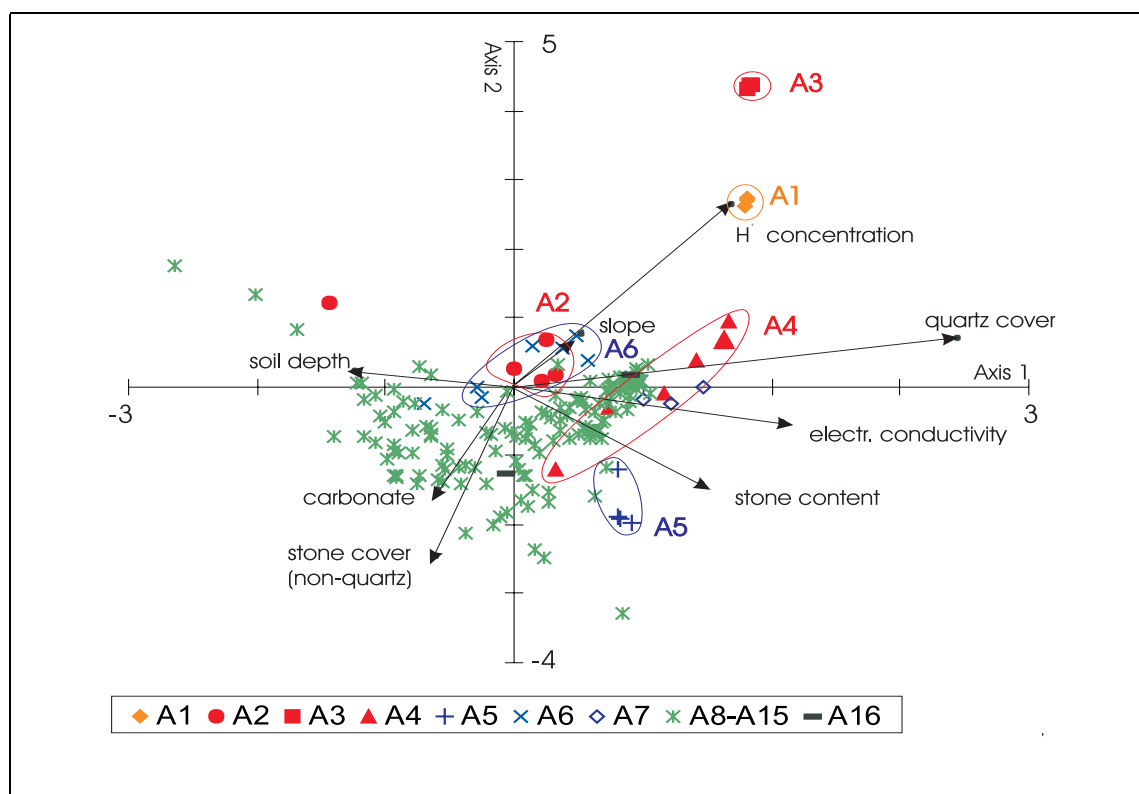


Figure 43. Joint plot of the unconstrained relevé scores of the CCA ordination of the Communities # 1-16 and eight edaphic variables (H^+ concentration, inclination of slope, quartz cover on soil surface, electrical conductivity, stone content in soil, stone cover of other lithology than quartz, carbonate content in soil, and soil depth) of the Little Karoo and adjacent areas.

The scatter plot of the **unconstrained relevé scores** showed a high correspondence between communities and particular environmental variables. The majority of the relevés of the community groups A, B, C and E (Communities # 1-7 and # 16), were plotted in the right sector of the scatter diagram whereas the relevés of community group D (Communities # 8-15) represented the dense cloud below Axis 1 at both sides of Axis 2 (see details in Figure 44). The majority of the relevés of the southernmost communities (# 1-4) were positively associated with quartz cover, electrical conductivity, and with stone content in soil. The *Gibbaeum angulipes* Community (# 3) and the *Gibbaeum haagei-Delosperma asperulum* Community (# 1) showed the strongest association with H^+ concentration. The majority of the relevés of the *Gibbaeum velutinum* Community (# 2) and the *Zeuktophyllum suppositum* Community (# 6) were plotted near the centre of the diagram without an association with any of the environmental variables except H^+ concentration and inclination of slope. The typical habitat of the two communities are characterised by a desert pavement of both quartz stones and stones of other lithology as quartz. The *Gibbaeum album* Community (# 4) and the *Gibbaeum petrense* Community (# 7) were plotted next to each other. They were positively associated with quartz cover, stone content in soil, electrical conductivity and negatively associated with soil depth. The *Gibbaeum dispar* Community (# 5) was positively associated with stone content in soil and stone cover of other lithology than quartz. It was negatively associated with soil depth.

The majority of the community group C (Communities # 8-15) as well as the *Psilocaulon junceum* Community (# 16) were plotted in a cloud below Axis 1 near the centre of the diagram. The details of the central part of the ordination diagram are shown in Figure 44. The figure showed a clear sequence of the communities # 8-15 along the main gradients that were represented by Axis 1 (i.e., high soil depth to quartz cover and high electrical conductivity). The *G. cryptopodium* Community (# 8) was the only community that was broadly scattered along Axis 1, covering a

broad range of environmental gradients. The strongest positive association with quartz cover was revealed for the *Gibbaeum pubescens* Community (# 9). However, the two sub-communities (# 9.1 and # 9.2) showed different habitat preferences: the *Gibbaeum pubescens*-*Berkheya cuneata* Sub-Community (# 9.2) was more positively associated with H^+ concentration than the *G. pubescens*-*G. cryptopodium* Sub-Community (# 9.1). The latter revealed to be more positive associated with electrical conductivity and a closer relationship with the *G. cryptopodium* Community (# 8) than the first (Sub-Community # 9.1). The relevés of *G. heathii* Community (# 14) were positively associated with stone content in soil and with stone cover of other lithology than quartz. They showed little association with quartz cover on soil surface. The relevés of the *G. gibbosum* Community (# 11) were plotted near the centre of the scatter diagram showing no clear association with any of the environmental variables. The *G. shandii* Community (# 13) was positively associated with carbonate content and stone cover of other lithology than quartz and was negatively associated with inclination of slope, H^+ concentration, as well as quartz cover. The relevés of the *Pteronia pallens*-*Aridaria noctifloru* ssp. *defoliata* Community (# 10), a common lowland community outside quartz fields in the Little Karoo, were plotted between the *G. geminum* Community (# 12) and the *G. shandii* Community (# 13) revealing a positive association with soil depth and carbonate content in soil. The *G. geminum* Community (# 12) showed the strongest positive association with soil depth.

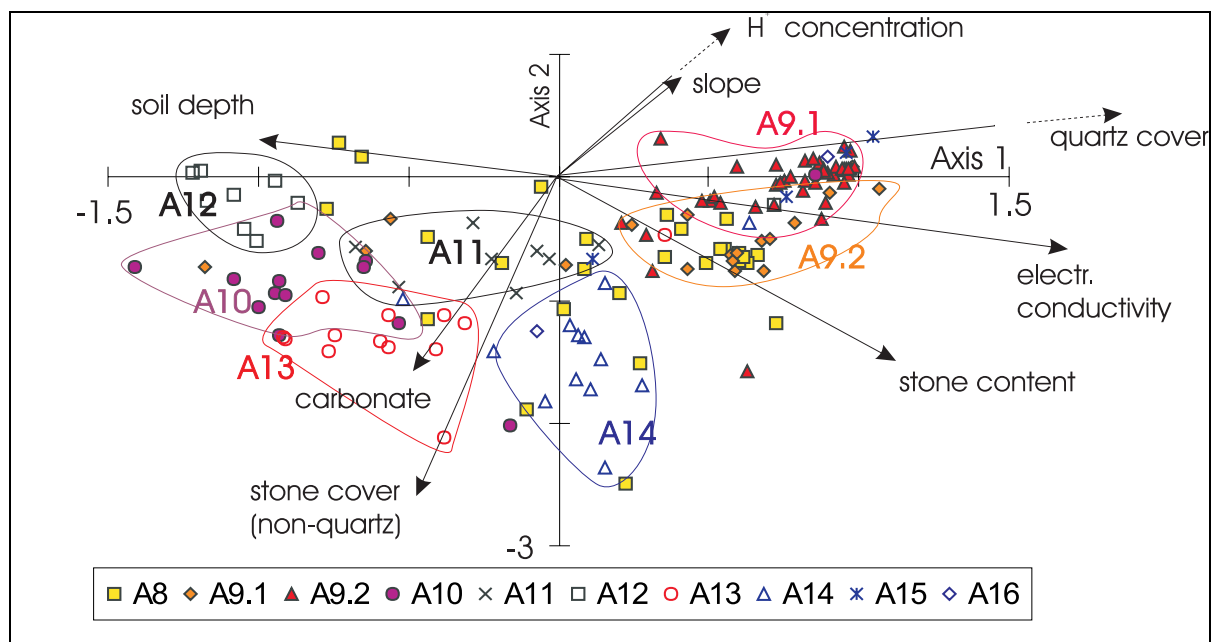


Figure 44. Details of the central part (extract) of Figure 43. Joint plot unconstrained relevé scores of the CCA ordination of species and edaphic variable data of communities # 1-16 from the Little Karoo and adjacent areas.

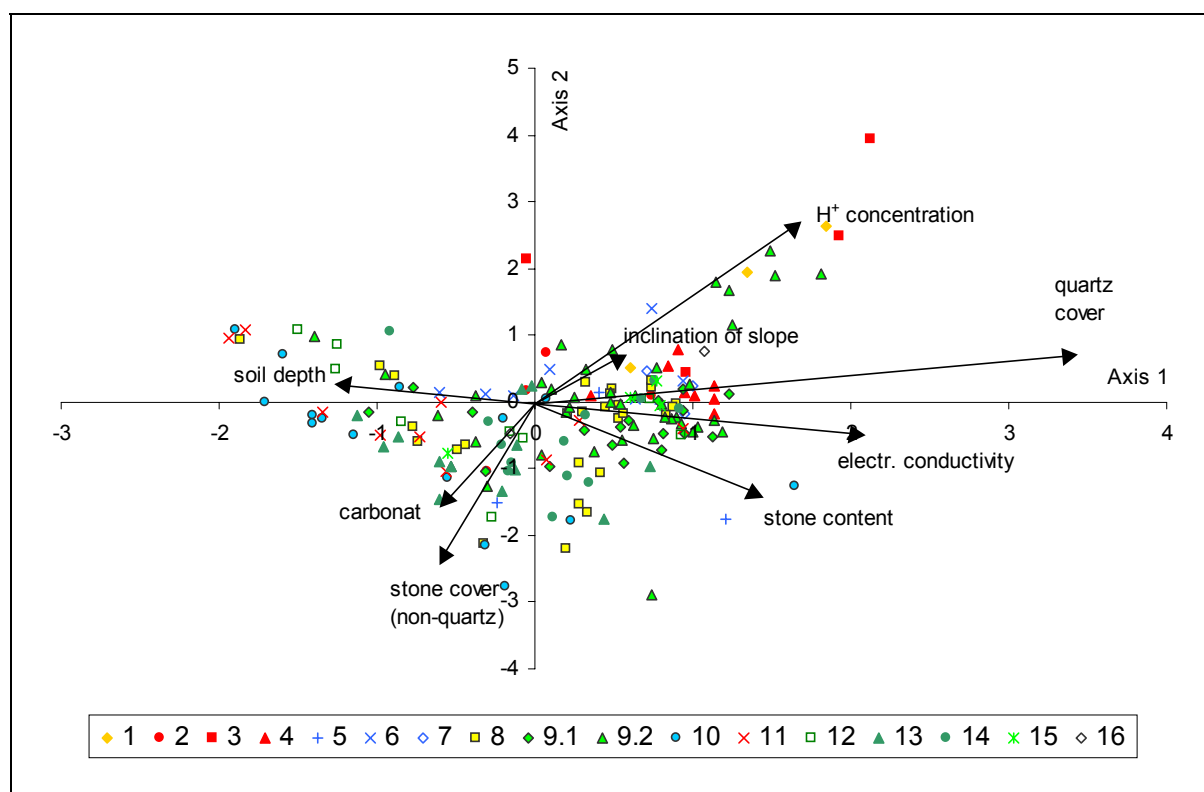


Figure 45. Joint plot of the constrained relevé scores of the CCA ordination of the communities # 1-16 and eight edaphic variables (H^+ concentration, inclination of slope, quartz cover on soil surface, electrical conductivity, stone content in soil, stone cover of other lithology than quartz, carbonate content in soil, and soil depth) of the Little Karoo and adjacent areas.

The joint plot of **constrained relevé scores and environmental variables** of the 16 communities of the Little Karoo and adjacent areas was largely in line with that of the unconstrained relevé scores. The majority of the relevés of communities # 1-7 were scattered on the right hand side of the ordination diagram. They were mainly positively associated with the environmental variables quartz cover on soil surface, electrical conductivity and H^+ concentration which were plotted parallel to Axis 1. For some communities particular habitat preferences emerged: the *G. haagei* Community (# 1) and the *Gibbaeum angulipes* Community (# 3) were significantly positively associated with H^+ concentration. The *Gibbaeum album* Community (# 4) and with lower significance, the *Gibbaeum petrense* (# 7) as well as the *Gibbaeum pachypodium* Community (# 15) showed a positive association with quartz cover on soil surface and electrical conductivity. The relevés of the *Pteronia pallens*-*Aridaria noctiflora* ssp. *defoliata* Community (# 10), the *Gibbaeum gibbosum* Community (# 11), the *Gibbaeum geminum* Community (# 12) and the *Gibbaeum shandii* Community (# 13) were generally positively associated with soil depth, carbonate in soil, and stone cover of other lithology than quartz. They were negatively associated with quartz cover, electrical conductivity and H^+ concentration. The relevés of the remaining communities (# 2, 5, 8, 9, 14, and 16) were scattered more broadly in the ordination diagram, thus covering a broad gradient of environmental variables.

The **Box-Whisker plots of the environmental variables** determined for the relevés of the 16 communities (Figure 46) showed strongest inter-community differences for the variables quartz cover on soil surface, stone cover of other lithology, electrical conductivity, soil pH, and carbonate content.

In contrast to all other communities the mean quartz cover on soil surface for the communities 10 to 14 and 16 were very low (1-36 %). The lowest values were determined for the *Pteronia*

pallens-Aridaria noctiflora ssp. *defoliata* Community (# 10) as well as the *Psilocaulon junceum* Community (# 16) which both represent widespread communities of the surroundings of quartz fields in the study area. Those communities that showed low mean values for quartz cover, typically showed high mean values for stone cover of other lithology (> 33 %) except the *P. junceum* Community (# 16) which typically occurs on soils without any stone cover. Only the *G. dispar* Community (# 5) showed a similarly high mean value for both, quartz cover (75 %) and stone cover of other lithology (52 %). The electrical conductivity was high for all quartz-field and related habitats (>> 0.5 mS/cm) compared to the communities # 10 and # 16 (mean electrical conductivity << 0.5). For community # 4 and # 7, the mean values for electrical conductivity were extremely high (>> 3 mS/cm). The mean values for soil pH for the majority of the communities lay > 6 pH, whereas community # 1-3 generally occurred on acid soils (mean values between pH 4.1 and 5). High mean values for carbonate content in soil was only shown for the *Pteronia pallens-Aridaria noctiflora* ssp. *defoliata* Community (# 10) and the *P. junceum* Community (# 16).

Other variables showed lower variation. The mean inclination of slope was low for most of the habitats (<< 10 %). Only the *Zeuktophyllum suppositum* Community (# 6) was associated with steeper slopes (11-25 %) whereas the other communities were typically found on moderate slopes or level sites. Soils of quartz fields are typically shallow. The mean soil depth for all communities of quartz fields and related habitats were low (< 20 cm). Only the *Psilocaulon junceum* Community (# 16) showed a mean value of 38 cm. The stone content in soils of quartz fields and related habitats was generally high (> 20 % weight). Even the values for the zonal *Pteronia pallens-Aridaria noctiflora* ssp. *defoliata* Community (# 10) and of the *Psilocaulon junceum* Community (# 16) lay within the range. Mean values for carbonate were low for most of the communities. Only the soils of the surroundings of quartz fields and related habitats (Communities # 10 and # 16) showed mean values above 0 (Class 1.5 - 4.1).

The **composition of ions** of the soils of different communities of the Little Karoo and adjacent areas showed a strong variance within the data set. The total amount of ions of some samples exceeded other by more than 100 times. Such strong differences were even found between relevés of the same community (i.e., in Communities # 2, 3, 12, and 13). The variance between the communities did not exceed the variance within the community. The strong variance between the samples of the same community revealed hardly any particular preferences of the communities regarding the ion composition in soil. Only the *Gibbaeum velutinum* Community (# 2) had low content of sodium in all three samples whereas the magnesium content increased relatively. Also, a general trend was that for the relevés of the community groups A (Community # 1), B (Community # 2-4), and C (Communities # 5-7) the absolute carbonate content tended to be lower than for the community groups D (Communities # 8-15).

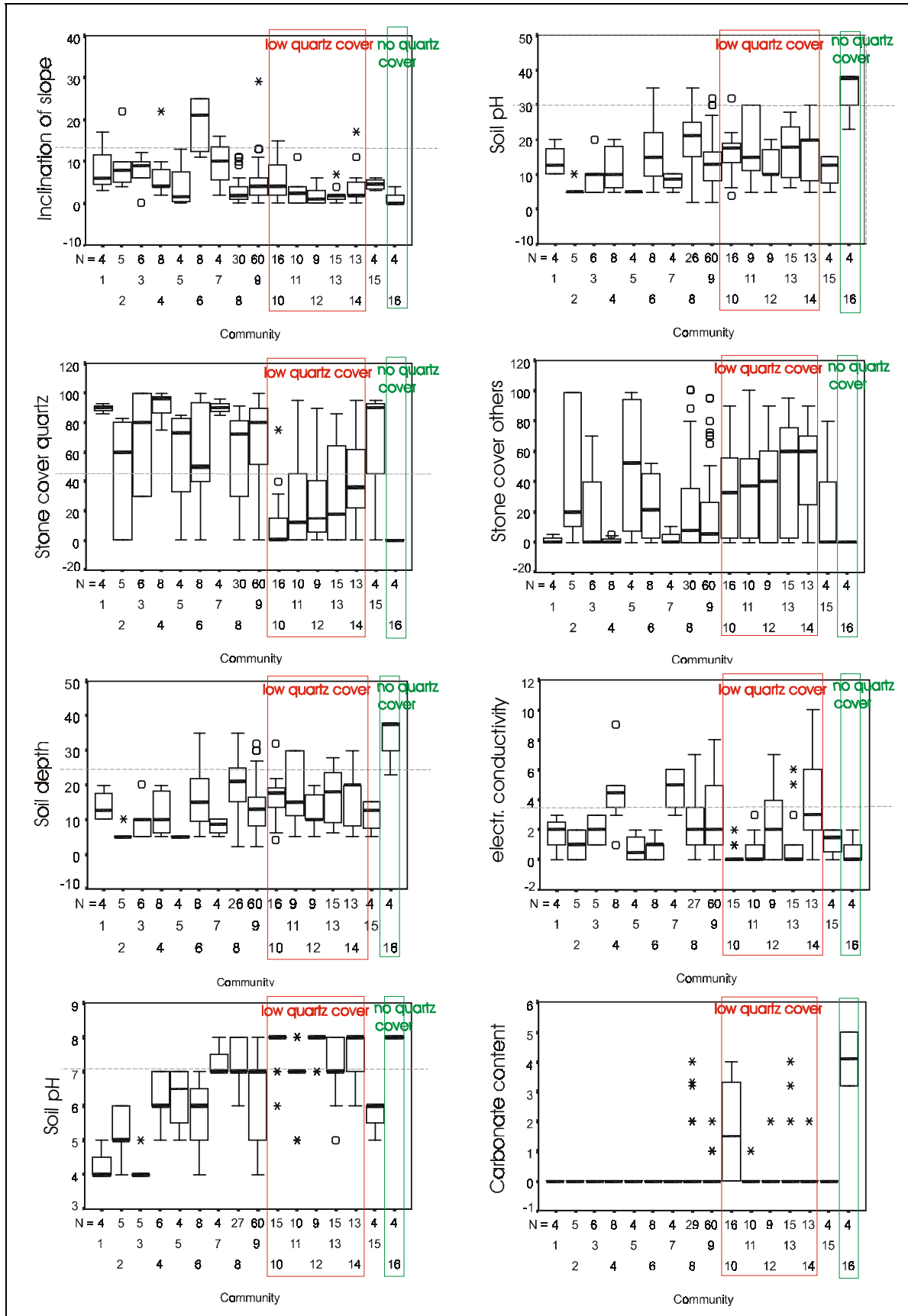


Figure 46. Box-Whisker-plots showing the range of the environmental variables within community # 1-16 of the Little Karoo and adjacent areas.

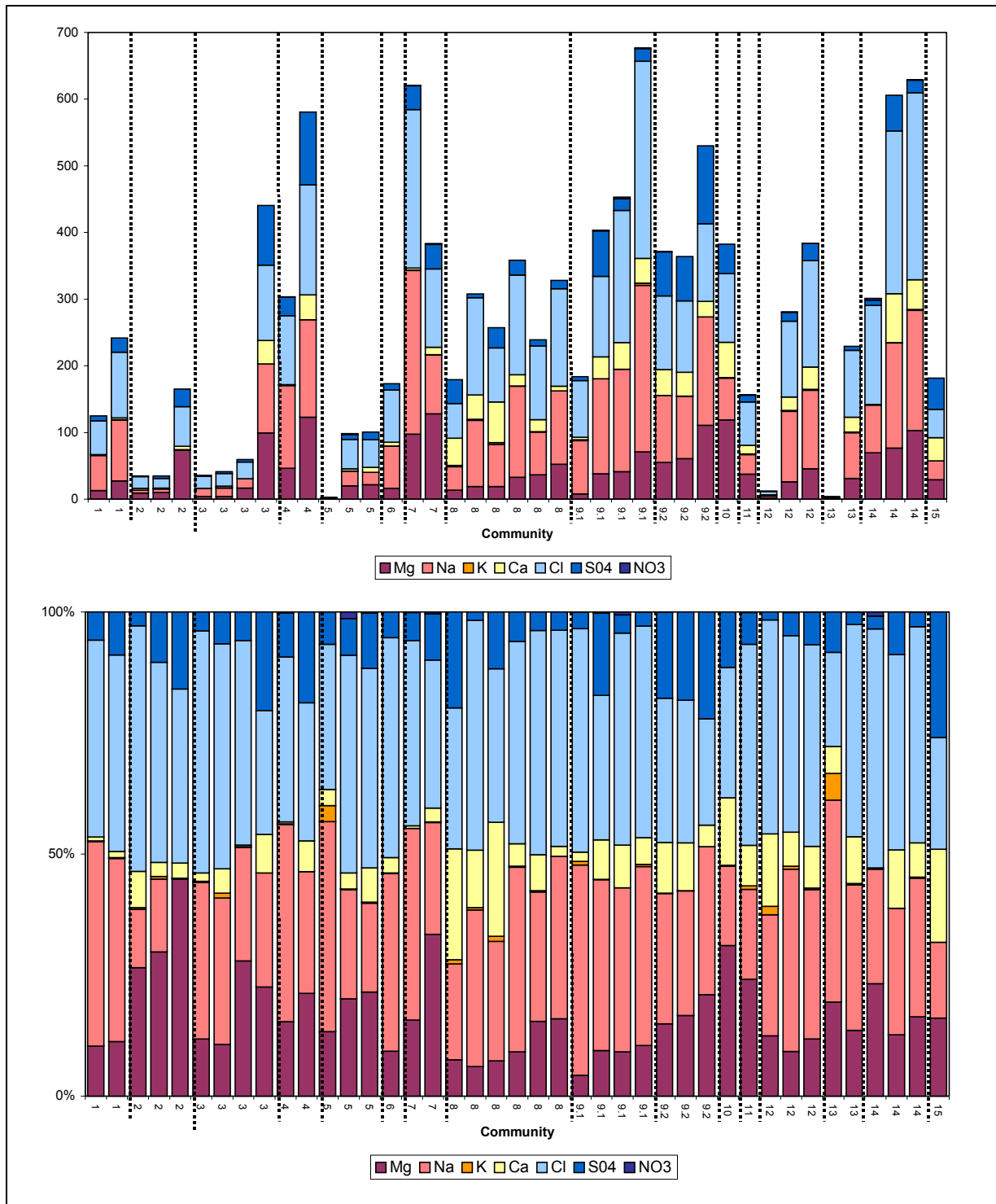


Figure 47. Absolute (above, in meq/kg) and relative (below) composition of cations and anions of selected relevés of the communities (# 1-15) in the Little Karoo and adjacent areas.

Namaqualand *sensu lato*: Knersvlakte, Riethuis-Wallekraal, Richtersveld

In the following, the species group (SG) and numbers of communities refer to Phytosociological Table II (Appendix 10) and Synoptic Table II (Appendix 9).

III.6.2 Knersvlakte

The scatter diagram of the relevés based on a CA ordination clearly showed a division of the data set into two main parts plotted on both sides of the Axis 2 (Figure 48). On the left hand side of the diagram, the relevés of the saline quartz fields (shown in red) were plotted. The majority of the relevés were clustered densely close to Axis 1. Merely the relevés of the *Oophytum oviforme* Community (# 29) were split off and drawn in the upper left quarter of the diagram. On the right hand side of the diagram, the communities that are mainly restricted to non-saline, acid quartz fields were plotted (shown in blue). They were broadly scattered along Axis 2 whereas the communities formed distinct clusters which were clearly separated from each other.

The *Monilaria pisiformis* Community (# 30) was plotted in the middle (along Axis 2) thus revealing an intermediate position between the two main groups. In contrast, among the saline relevés of the quartz fields, only the *Oophytum oviforme* Community (# 31) was clearly separated as such, whereas the other were plotted in a dense sequence: the *Mesembryanthemum fastigiatum* Community (# 26) was plotted furthest to the left, directly bordering to a dense cluster representing the *Argyroderma pearsonii* Community (# 25) and, further to the right, the *Phyllobolus digitatus* ssp. *digitatus* Community (# 28). The *Cephalophyllum spissum* (# 24), *Argyroderma fissum* (# 22), *A. delaetii* (# 23), *Oophytum nanum* (# 27) and *Drosanthemum diversifolium* Community (# 21), in return, were plotted very closely together without showing any resolution on community level. The communities of the non-saline, acid quartz fields on the right hand side of the diagram were clearly separated from each other. The clusters representing communities were scattered parallel to Axis 2.

In order to explain some aspects of the variance within the species data, environmental variables were subsequently included into the analysis. The direction of strongest variation within the data set were presented by arrows. Axis 1 which presented the axis of strongest variance of species data was best explained by the environmental variables stone content, H⁺ concentration, and electrical conductivity. Whereas the latter was negatively associated with Axis 1. Coarse quartz cover on the one hand and stone cover of other lithology than quartz on the other hand largely explained the divergent distribution of the communities of the non-saline quartz fields along Axis 2. But the remaining variables were of lower importance for the variance of species data. The low importance of quartz cover was due to the low variance of quartz cover within the data set which comprised quartz-field relevés only. However, the quartz cover which was restricted to fine to medium sized quartz gravel (< 60 mm in diameter) decreased with increasing percentage of coarse quartz gravel (> 60 mm in diameter) which was characteristic for the *Browmanthus corallinus* Community (# 32), the *Monilaria chrysoleuca* Community, the *Dicrocaulon longifolium* (# 38) as well as the *D. nodosum* Community (# 39). The *Ruschia burtoniae* (# 33) and the *Conophytum minutum* var. *minutum* Community (# 31), in return, was plotted in the lower right section of the ordination which was positively associated with stone cover of other lithology than quartz. The separation of the *Oophytum oviforme* Community (# 29) from the other saline quartz fields was interpreted by a more positive association with inclination of slope, soil depth and coarse quartz cover.

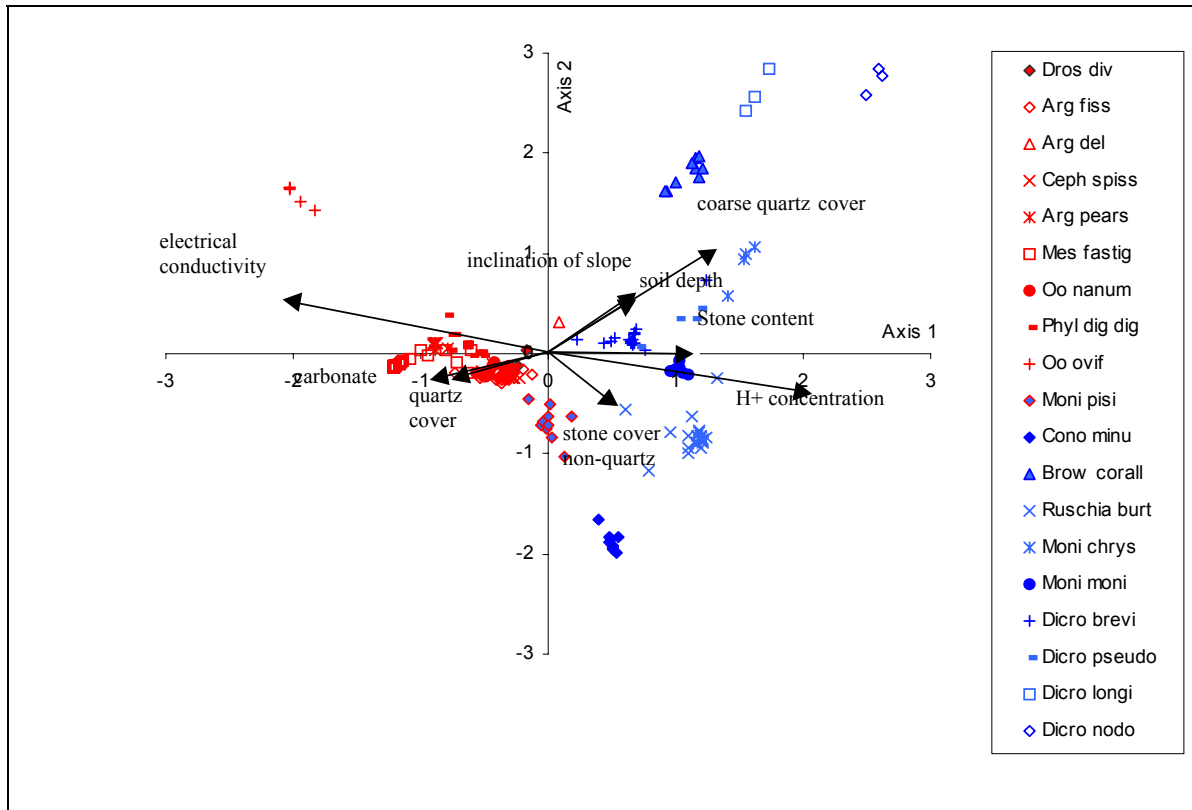


Figure 48. CA ordination of species data of all quartz-field relevés of the Knersvlakte.

The ordination without the outlying *Oophytum oviforme* Community (Figure 49) was largely in line with the previous. The dense cluster of the relevés of the saline quartz fields remained. However, in contrast to the previous ordination they were arranged in a row largely parallel to Axis 1. In the row furthest to the left and slightly separated from the rest, the *Mesembryanthemum fastigiatum* Community (# 24) was plotted. This community was recorded for the most extremely saline quartz fields in the Knersvlakte. It was followed by the other relevés which were less distinctly arranged according to the communities.

But the communities of the acid quartz fields were spread even broader thus revealing a strong positive association between the *Brownanthus corallinus* Community (# 32) and the *Dicrocaulon longifolium* Community (# 38) and soil depth whereas the *Dicrocaulon nodosum* Community (# 39) was more strongly associated with coarse quartz cover.

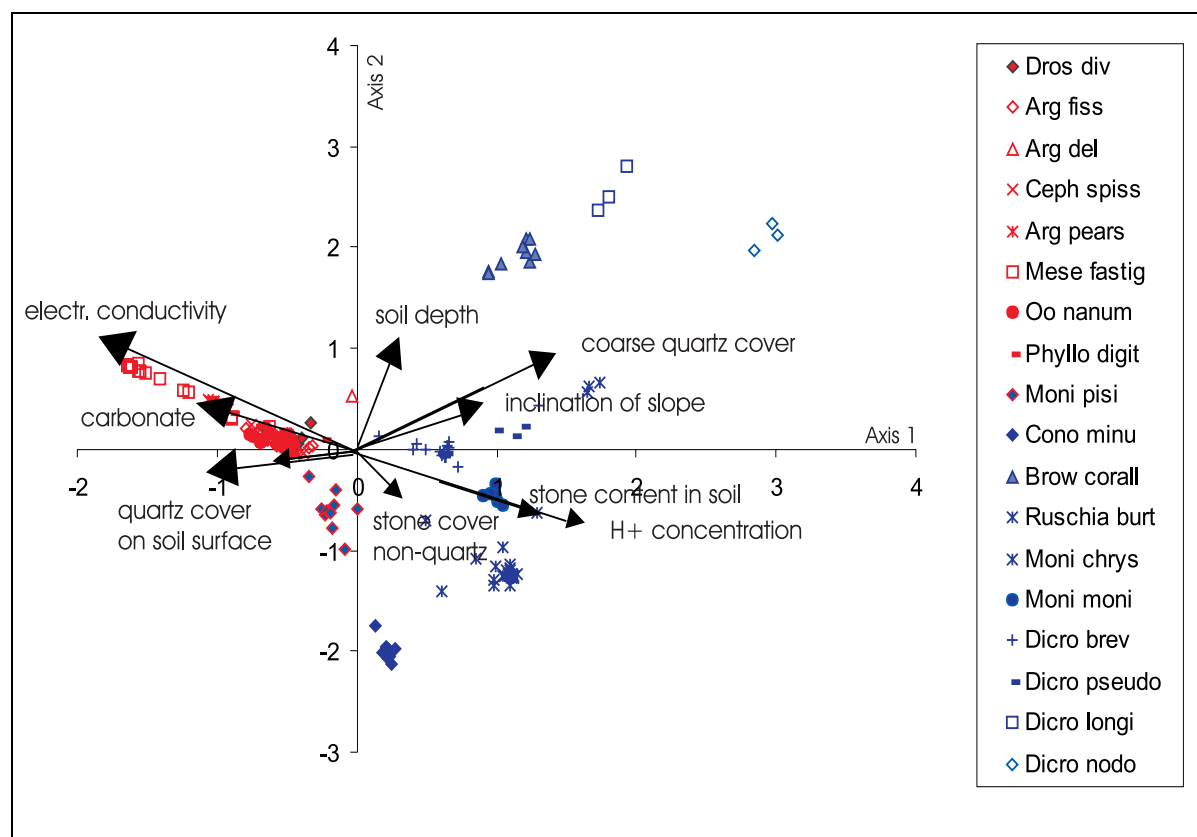


Figure 49. CA ordination of species data of the quartz fields of the Knersvlakte calculated without *Oophytum oviforme* Community (# 29).

Table 50. Summary statistics for the CA of species data of the quartz-field relevés from the Knersvlakte.

Axes	1	2	3	4
Eigenvalues:	.944	.923	.916	.900
Cumulative % of variance of species data:	4.3	8.5	12.7	16
of species-environment relation:	19.1	27.5	37.3	40.5
Species-environment correlations:	.680	.460	.493	.287
Cumulative % of variance				
Sum of all unconstrained eigenvalues:				21.840
Sum of all canonical eigenvalues:				2.314

Table 51. Summary statistics for the CA of species data of the quartz-field relevés from the Knersvlakte without *Oophytum oviforme* Community (# 29).

Axes	1	2	3	4
Eigenvalues :	.939	.921	.901	.894
Cumulative % of variance of species data :	4.4	8.8	13.1	17.3
of species-environment relation:	21.0	34.2	37.2	40.9
Species-environment correlations :	.709	.569	.275	.303
Sum of all unconstrained eigenvalues				21.099
Sum of all canonical eigenvalues				2.280

The eigenvalues and the species environment correlations for both CA ordinations were very high. The correspondence analysis without the outlying *Oophytum oviforme* Community (# 39) even revealed higher species-environment correlations for the first two axes. However, the cumulative percentage of variance of species data explained by the ordinations was comparatively low (< 10

% for the first two axes) (Table 50 & Table 51). In both analyses about one third of the variance of species-environment relation was explained by the ordinations. However, despite the increase of statistical values for the CA, the changes in the data set did not result into a better resolution of the communities of the saline quartz fields. Subsequent analyses were therefore conducted with the complete data set.

In order to dissolve the cluster of relevés of the **saline quartz fields**, a separate CA analysis of the corresponding data was conducted (Figure 50). For this analysis, however, the outlying *Oophytum oviforme* community (# 29) was omitted. The correspondence analysis had high eigenvalues, high species-environment correlation and explained about 20 % of the variance of species data and 35 % of the variance of the species-environment relation (Table 52).

The resulting ordination revealed a clear separation of the *Oophytum nanum* Community (# 27) from the rest. It showed strongest positive association with H⁺ concentration and, less significantly, with stone content in soil. The *Mesembryanthemum fastigiatum* Community (# 26), the *Argyroderma pearsonii* Community (# 25) and the *Cephalophyllum spissum* Community (# 23) were plotted on the right hand side of the diagram along Axis 1. They were associated with highest values of electrical conductivity. In return, the *Argyroderma fissum* C., the *A. delaetii* Community (# 23), the *Phyllobolus digitatus* ssp. *digitatus* Community (# 28) as well as the *Drosanthemum diversifolium* Community (# 21), were plotted next to each other at the lower left corner of the diagram. The *D. diversifolium* and *Argyroderma fissum* Community (# 22) showed the strongest overlap with each other whereas *Argyroderma delaetii* and the *Phyllobolus digitatus* ssp. *digitatus* Community were plotted in distinct clusters each.

Table 52. Summary statistics for the CA analysis (Figure 50) of the species data of saline quartz fields of the Knersvlakte with subsequently included environmental variables.

Axes	1	2	3	4	
Eigenvalues:	.893	.849	.763	.732	
Species-environment correlations:	.519	.540	.390	.430	
Cumulative % of variance					
of species data:	10.3	20.1	28.9	37.4	
of species-environment relation:	17.0	34.5	42.7	52.2	
Sum of all unconstrained eigenvalues:					8.654
Sum of all canonical eigenvalues:					1.414

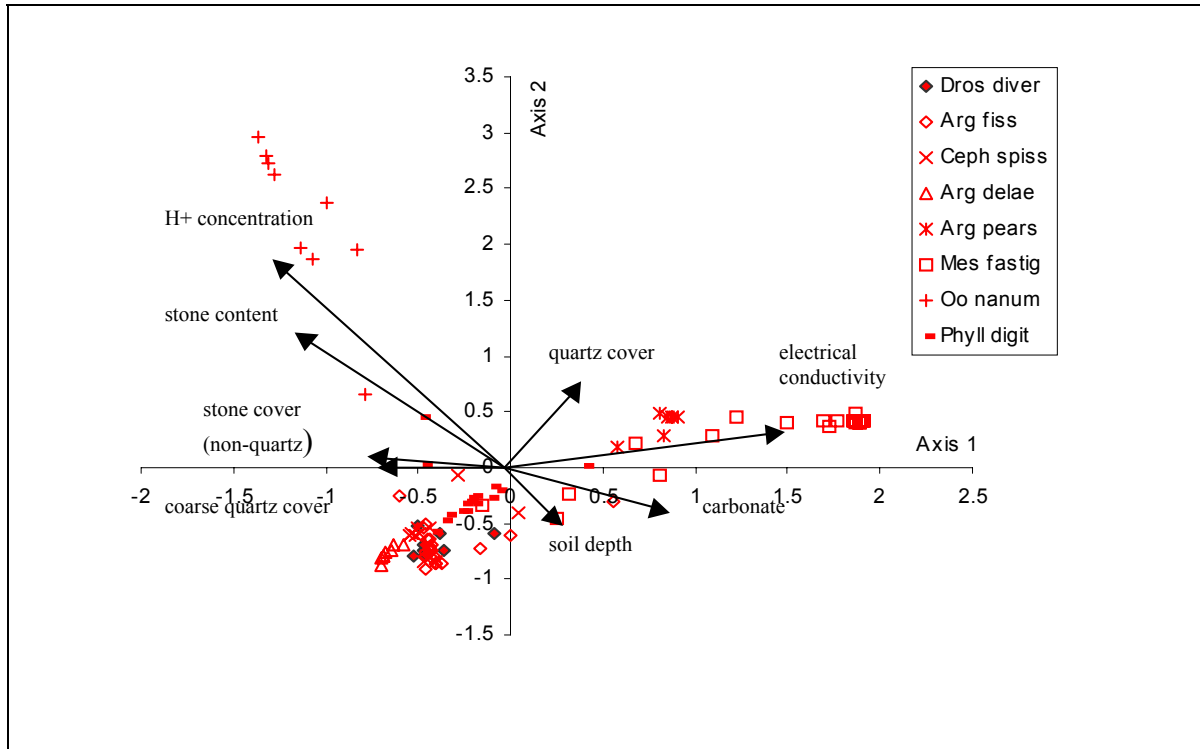


Figure 50. CA ordination of species data of saline quartz fields of the Knersvlakte. Arrows indicate the direction of strongest variance of the environmental variables.

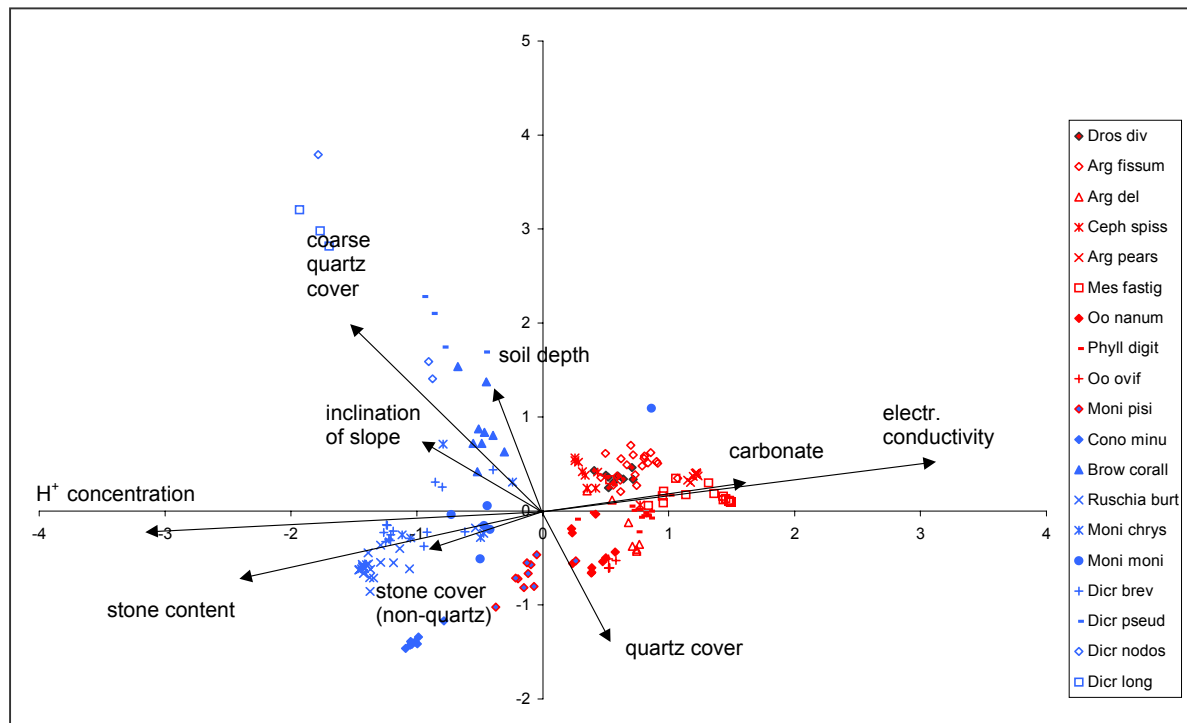


Figure 51. Joint plot of the unconstrained relevé scores of the CCA ordination with species data and environmental variables of the saline quartz fields of the Knersvlakte (without *Oophytum oviforme* Community # 29).

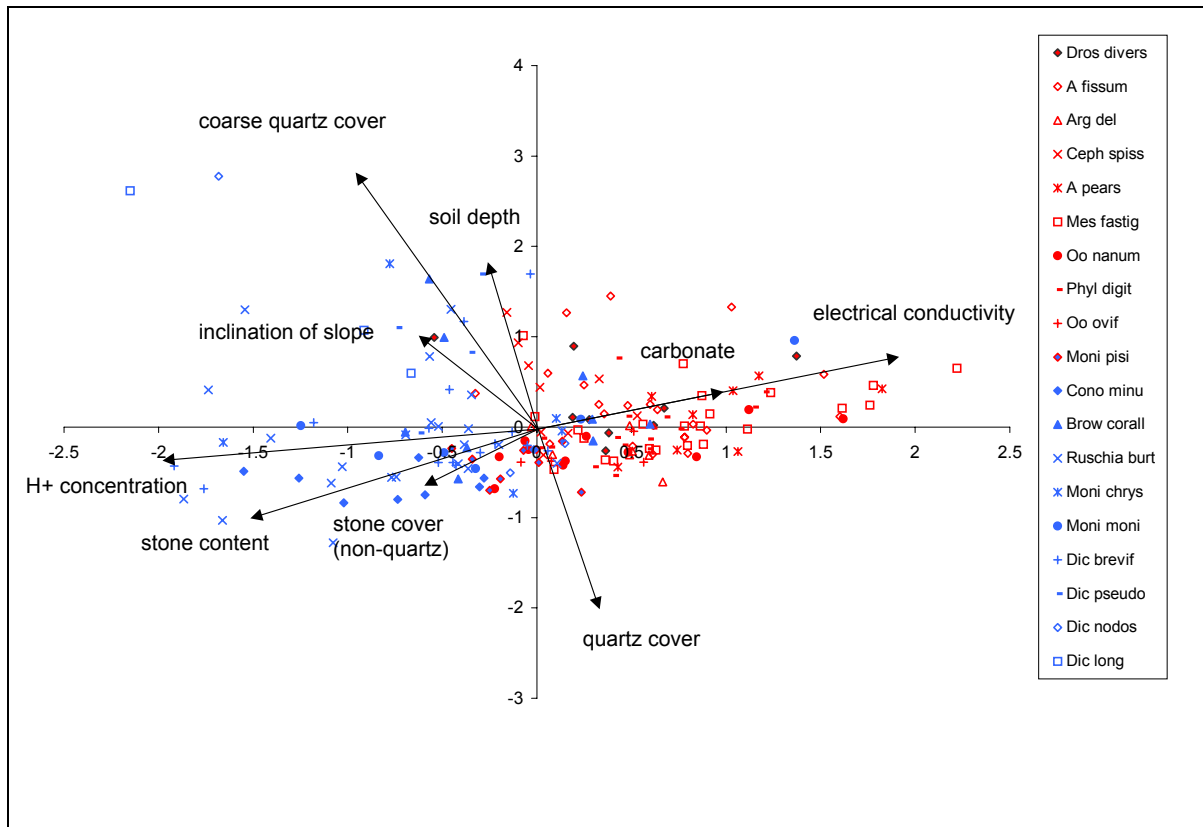


Figure 52. Joint plot of the constrained relevé scores of the CCA ordination of the species and environmental variable data from all quartz-field relevés of the Knersvlakte.

The eigenvalues and the species-environment correlations were high, indicating a robust ordination. Almost half of the cumulative percentage of variance of species-environmental relation was explained by the ordination (Table 53).

Table 53. Summary statistics of the CCA ordination of the species and environmental variable data from quartz fields of the Knersvlakte.

Axes	1	2	3	4
Eigenvalues:	.618	.417	.281	.244
Species-environment correlations:	.830	.736	.644	.570
Cumulative percentage variance of species data:	2.9	4.9	6.2	7.4
of species-environment relation:	27.1	45.4	57.7	68.4
Sum of all unconstrained eigenvalues:				21.099
Sum of all canonical eigenvalues:				2.280

In correspondence with the CA ordination, the joint plot of **unconstrained** relevé scores of the CCA ordination (Figure 51) separated the relevés into two main groups: those on saline quartz fields and those non-saline, acid quartz fields. The arrow that presents salinity (high electrical conductivity) directed to the right thus indicating a positive association with Axis 1. The arrow presenting H^+ concentration (inversion of soil pH) were plotted at the left hand side of the diagram and was negatively associated with Axis 1. Both environmental variables were represented by the longest arrows and therefore revealed to be of highest importance for the variance in species data. Carbonate was positively associated with electrical conductivity whereas stone content in soil as well as stone cover of other lithology than quartz were negatively

associated with electrical conductivity and positively associated with low soil pH (H^+ concentration). Quartz cover of coarse fractions (> 60 mm diameter), soil depth and inclination of slopes had positive associations with Axis 2 whereas quartz cover of small fractions (< 60 mm) was negatively associated with Axis 2.

In correspondence with the CA ordination, the relevés of the non-saline, acid quartz fields (*Conophytum minutum* var. *minutum* Community # 31 to *Dicrocaulon nodosum* Community # 39) were scattered broadly along both, Axis 1 and 2. The communities of the saline quartz fields (*Drosanthemum diversifolium* Community # 21 to *Oophytum oviforme* Community # 29), in contrast, were densely plotted along Axis 1 which were positively associated with electrical conductivity and negatively associated with H^+ concentration. The sequence of communities along Axis 1 mirrored the habitat preferences of the community. The *Mesembryanthemum fastigiatum* Community (# 26), the *Argyroderma pearsonii* Community (# 25) and the *Phyllobolus digitatus* ssp. *digitatus* C. (# 28) showed the strongest association with salinity. The other communities were less strongly correlated with salinity but also associated with the other environmental variables, such as soil depth (*Drosanthemum diversifolium* C. # 21, *Argyroderma fissum* C. # 22, and *Cephalophyllum spissum* C. # 24) or quartz cover on soil surface (*Argyroderma delaetii* C. # 23, *Oophytum nanum* C. # 27, *Oophytum oviforme* C. # 29), respectively. The *Oophytum oviforme* Community (# 29) which was an outlier in the CA ordination did not reveal any particularities regarding its association with any of the variables taken into account here.

The communities of the non-saline, acid quartz fields (shown in blue) were roughly split into two parts. One group was positively associated with Axis 2 and thus positively associated with coarse lithology. This group comprised the *Dicrocaulon nodosum* C. (# 39), the *D. longifolium* C. (# 38), the *D. pseudonodosum* C. (# 37) and the *Brownanthus corallinus* Community (# 32). Another group was plotted in negative association with Axis 2 and Axis 1 thus revealing a strong positive association with H^+ concentration and stone content in soil (*Ruschia burtoniae* C. # 33), the *Conophytum minutum* var. *minutum* C. # 31, and *Dicrocaulon brevifolium* Community # 36). The *Monilaria moniliformis* C. (# 35) and the *Monilaria chrysoleuca* C. (# 34) were plotted at the proximal end of the of the gradients H^+ concentration and stone content, thus indicating a less strong affinity to any of the variables that were included into the analysis. In correspondence with the CA ordination, the *Monilaria pisiformis* C. (# 30) was plotted in the centre of the ordination, in an intermediate position between the saline and non-saline quartz fields.

The joint plot of the **constrained relevé scores** and the environmental variables of the same CCA ordination (Figure 52) presented the linear combinations of relevés and environmental variables. In correspondence with the CA ordination and the joint plot of the unconstrained relevé scores of the CCA ordination, the relevés of the saline (shown in red) and non-saline, acid quartz fields (shown in blue) were clearly separated from each other. The saline quartz fields were merely associated with three out of eight environmental variables, i.e., electrical conductivity, carbonate content and quartz cover on soil surface, among which electrical conductivity and carbonate direct into the identical direction. The non-saline, acid quartz fields were associated with five divergent environmental variables and were thus dispersed more broadly than those the relevés of the saline quartz fields. Due to the linear combination of the relevés and the environmental variables of the constrained relevé scores, the communities were more broadly scattered than in the unconstrained relevé scores of the same CCA ordination.

However, several communities showed a distinct association with particular environmental variables. The *Argyroderma fissum* C. and *Cephalophyllum spissum* C. were both positively associated with coarse quartz cover, soil depth, and inclination of slope and negatively associated with small to medium sized quartz cover on soil surface. The *Argyroderma pearsonii* C., *Mesembryanthemum fastigiatum* C. and the *Phyllobolus digitatus* ssp. *digitatus* C. The *Argyroderma delaetii* C., in return was

plotted along the proximal end of the arrow presenting electrical conductivity and with positive association with quartz cover on soil surface, thus indicating its preference of less saline quartz-field habitats. The *Oophytum nanum* C. and the *Oophytum oviforme* C. were plotted in the centre of the diagram. They did not show any alliance with the environmental variables employed.

Among the communities of the non-saline, acid quartz fields the *Monilaria moniliformis* C. (# 35), *Monilaria chrysoleuca* C. (34), the *Monilaria pisiformis* C. (# 30), and the *Brownanthus corallinus* Community (# 32) were plotted in the centre of the diagram. That is, some relevés area positive associated with electrical conductivity. They thus did not show any particular association with the environmental variables employed. The *Dicrocaulon brevifolium* C. (# 36), and the *Ruschia burtoniae* C. (# 33) were broadly scattered on the right hand side of the diagram, revealing a generally positive association with coarse quartz cover, H⁺ concentration, and stone content in soil. The *Conophytum minutum* var. *minutum* C. (# 31), in contrast, was restricted to the lower left section of the ordination, thus revealing a positive association with H⁺ concentration and stone content in soil. The *Dicrocaulon longifolium* C. (# 38), the *D. nodosum* C. (# 39), and the *D. pseudonodosum* C. (# 39) were largely restricted to the upper left section of the ordination which make emerge their strong association with soils with coarse quartz cover on soil surface, relatively high soil depth, and relatively high inclination of slope.

A separate CCA ordination was calculated with a data set which was restricted to the saline quartz fields from the Knersvlakte (after having omitted the *Oophytum oviforme* Community # 29). The ordination did not have very high eigenvalues for the axes and the cumulative percentages of variance of species data explained by the ordination were comparatively low (Table 54). However, nearly 50 % of the cumulative percentage of variance of species-environment relation were explained by the ordination.

Table 54. Summary statistics of the CCA ordination of species and environmental variable data from the saline quartz fields of the Knersvlakte (without *Oophytum oviforme* Community # 29).

Axes	1	2	3	4	
Eigenvalues :	.394	.301	.240	.169	
Species-environment correlations:	.704	.643	.644	.535	
Cumulative % of variance					
of species data:	4.2	7.5	10.1	11.9	
of species-environment relation:	26.2	46.2	62.1	73.4	
Sum of all unconstrained eigenvalues:					9.298
Sum of all canonical eigenvalues:					1.505

The joint plot of the **unconstrained** relevé scores and environmental variables of the vegetation data from the saline quartz fields in the Knersvlakte (Figure 54) revealed a clear separation of the vegetation communities from each other. Each community showed a clear graphical relationship with any of the environmental variables employed. The *Mesembryanthemum fastigiatum* C. (# 26) was plotted in strong positive association with electrical conductivity whereas the *Argyroderma pearsonii* C. (# 25) showed a stronger correlation with quartz cover on soil surface. The *Phyllobolus digitatus* ssp. *digitatus* C. (# 28), in contrast, showed a less pronounced affinity to electrical conductivity. The *Argyroderma fissum* C. (# 22) and the *Drosanthemum diversifolium* C. (# 21) were both positive associated with carbonate in soil and soil depth, whereas the *Cephalophyllum spissum* C. (# 24), which is closely related to the *A. fissum* C., showed a higher affinity to inclination of slope and coarse quartz cover. The *Oophytum nanum* C. (# 27) and, less pronounced though, the *Argyroderma delaetii* C. (# 23) were positively associated with H⁺ concentration and stone content in soil.

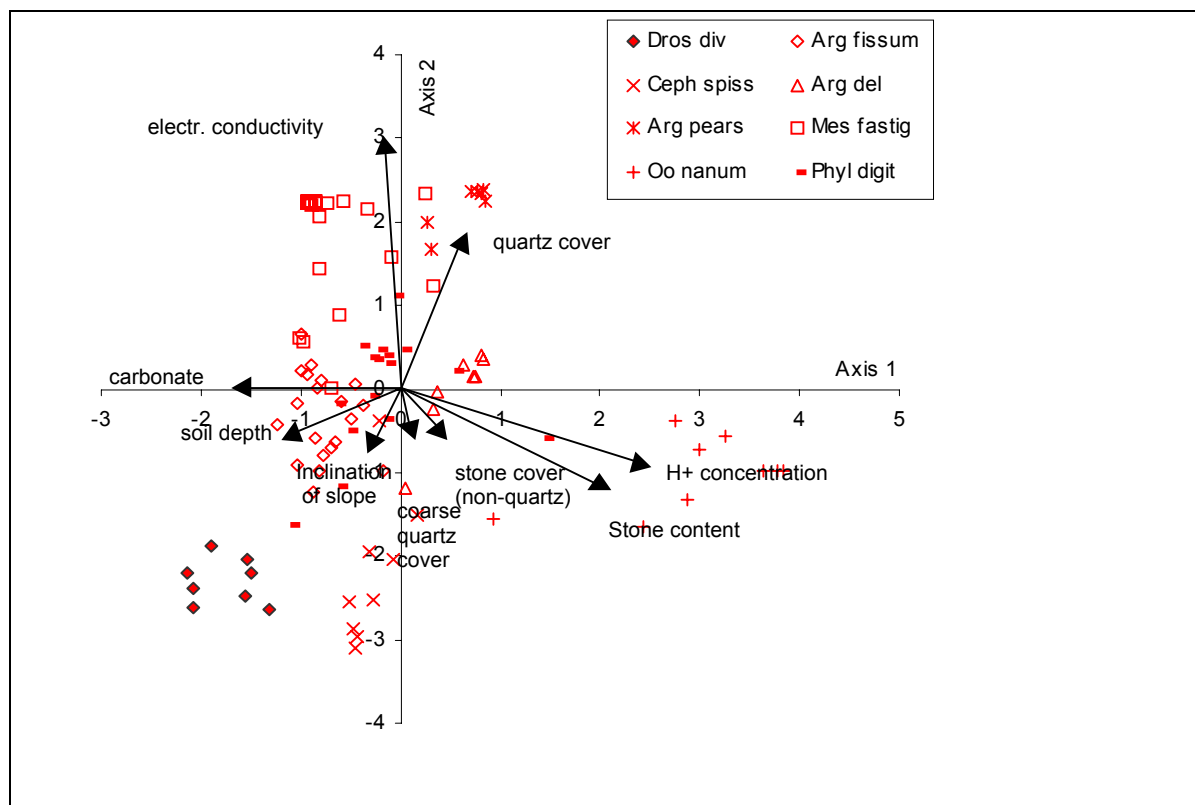


Figure 53. Joint plot of the unconstrained relevé scores of the CCA ordination of the species and environmental variable data from the saline quartz fields of the Knersvlakte (without *Oophytum oviforme* Community # 29).

The joint plot of **constrained** relevé scores and environmental variables of the canonical correspondence analysis of data from the saline quartz fields of the Knersvlakte (Figure 53) again revealed the H^+ concentration and electrical conductivity as the environmental variables which are most relevant for the variance in species data. The *Argyroderma fissum* C. (# 22) and the *Phyllobolus digitatus* ssp. *digitatus* C. (# 28) were broadly scattered and showed weak correlation with any of the environmental variables. The *Argyroderma pearsonii* Community (# 25) and the *Mesembryanthemum fastigiatum* Community (# 26), in contrast, were positively associated with electrical conductivity and quartz cover on soil surface, whereas *A. delaetii* Community (# 23) had a stronger correlation with low soil pH, presented by H^+ concentration as well as with stone content in soil. *Cephalophyllum spissum* Community (# 24) and *Drosanthemum diversifolium* Community (# 21) were both positively associated with inclination of slope, carbonate and soil depth.

The spectrum of the absolute ion content in the soil samples of quartz-field communities of the Knersvlakte (Communities # 21-39) (Figure 55) revealed a high variance regarding the total values with most of the communities. This variance did not differ from the variance between the communities. Merely the *Monilaria pisiformis* C. (# 30), the *Conophytum minutum* C. (# 31), the *Dicrocaulon pseudonodosum* Community (# 37), and the *Dicrocaulon longifolium* Community (# 38) showed a strong similarity among the relevés of the same communities. With respect to the relative composition of the ions (Figure 56) the same variance within and among the quartz-field communities emerged. However, three communities seemed to be generally associated with soils with a low percentage of magnesium in the ion spectrum, i.e., the *Drosanthemum diversifolium* dominated C. (# 21), the *Brownanthus corallinus* C. (# 32), and the *Dicrocaulon longifolium* C. (# 38).

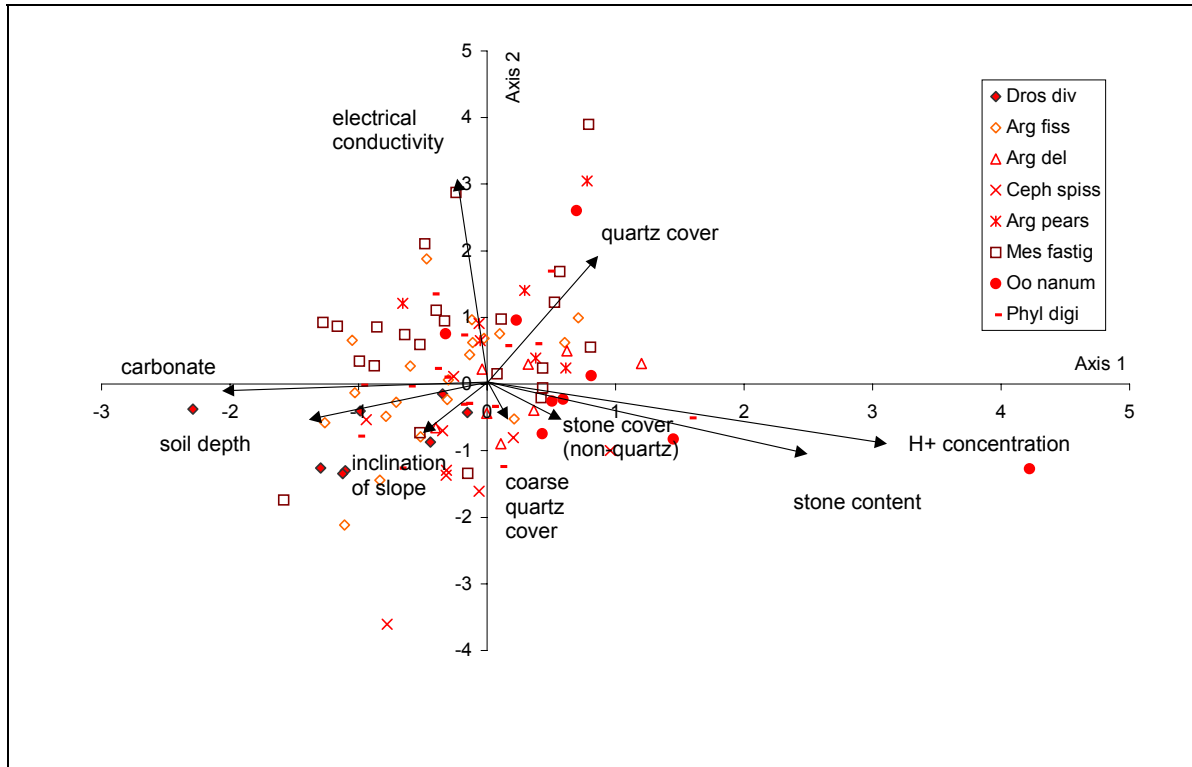


Figure 54. Joint plot of the constrained relevé scores of the CCA ordination of the species and environmental variable data from the saline quartz fields of the Knersvlakte (without the *Oophytum oviforme* Community # 29).

Beyond the particularities of singular communities there was a general difference between the ion composition of soils of the saline quartz fields (Communities # 21-30) and that of non-saline, acid quartz fields (Communities # 31-39). Acid quartz fields tended to have a relatively higher percentage of magnesium, calcium, and sulphate than the saline quartz fields. Among the saline quartz fields, sodium and chloride were presented with higher percentages.

The ion composition of both groups of quartz-field habitats differed considerably from the soils outside quartz fields (Communities # 1-20) which largely had lower total values of ion content for most of the samples. Only the samples from the *Salsola zeyheri* Community (# 17), the *Ruschia subsphaerica* C. (# 19) and the *Aridaria serotina-Ruschia* sp. (Bartels 93268 HBG) Community (# 20) had similarly high total content of ions than the quartz-field communities. For these samples where the ion content was generally low (Community # 1-14) the ion spectrum was composed more equally: the relative share of sodium and chloride was smaller whereas that of the other ions increased. Potassium and nitrate, in particular, were presented with a far higher percentage than in the samples with high total content of ions. The high content of ions in the samples of communities # 17, # 19, and # 20 were closely related to the high electrical conductivity which is typical for these communities.

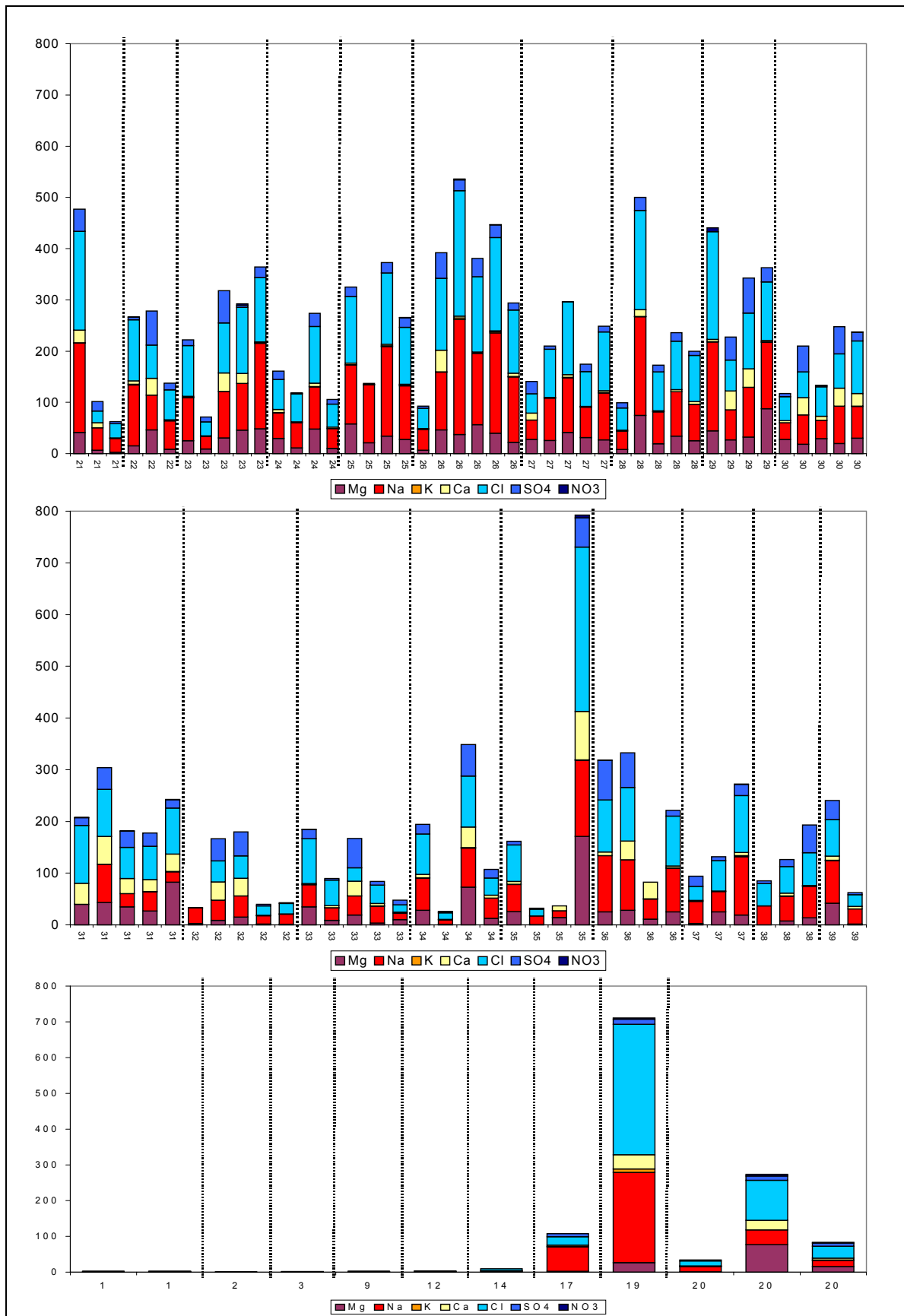


Figure 55. Absolute content of ions (given in meq/kg) of selected relevés of the communities of saline quartz fields (Communities # 21-30, top), non-saline acid quartz fields (Communities # 31-49, middle), and outside the quartz fields (Communities # 1-20, bottom) of the Knersvlakte.

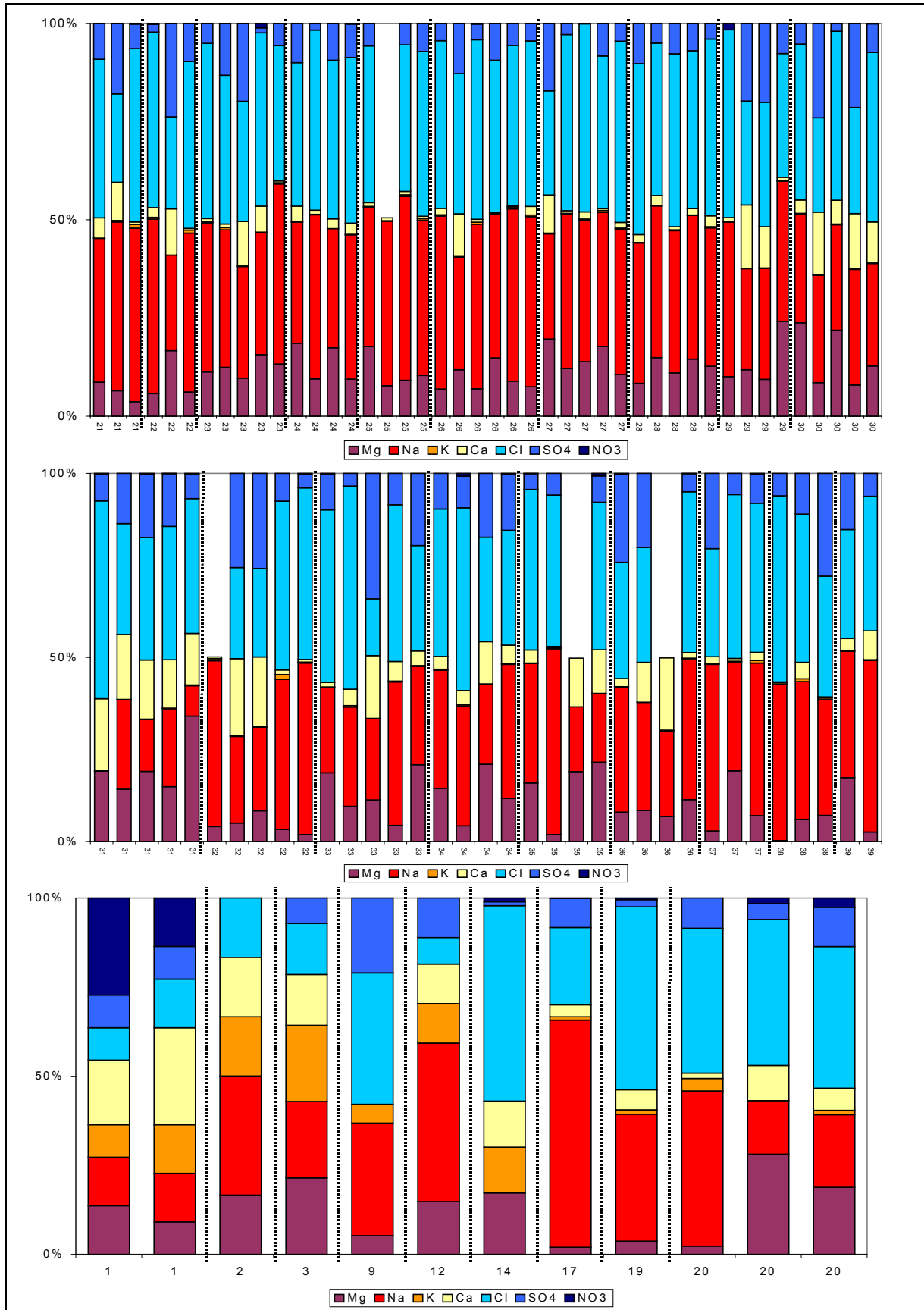


Figure 56. Relative composition of ions of selected relevés of the communities of saline quartz fields (Communities # 21-30, top), non-saline acid quartz fields (Communities # 31-49, middle), and outside the quartz fields (Communities # 1-20, bottom) of the Knersvlakte.

III.6.3 Riethuis-Wallekraal area

The CA ordination of the species data of the Riethuis-Wallekraal area (Figure 57) revealed a trichotomy of the quartz-field vegetation: one group comprised non-saline, acid quartz fields and two other groups comprised saline quartz fields. Communities that mainly occur outside the quartz fields (i.e., *Drosanthemum roseatum* C. # 11 and *Ruschia leucosperma* Community # 46) were again plotted in a fourth group, in negative association with quartz cover on soil surface.

The summary statistics Table 55 indicated a robust ordination: the eigenvalues (> 0.9 for the first three axes) and the species-environment correlations (0.79) were extremely high and up to 20 % of the variance of species data and about one third of the species-environment relation were explained by the ordination.

Table 55. Summary statistics of the CA ordination of species data and subsequently added environmental variables of quartz-field and adjacent relevés of the Riethuis-Wallekraal area.

Axes	1	2	3	4
Eigenvalues:	.948	.935	.908	.888
Species-environment correlations :	.662	.797	.858	.458
Cumulative % of variance				
of species data:	10.2	20.2	30.0	39.5
of species-environment relation:	12.3	29.8	49.5	55.0
Sum of all unconstrained eigenvalues:				9.310
Sum of all canonical eigenvalues:				3.392

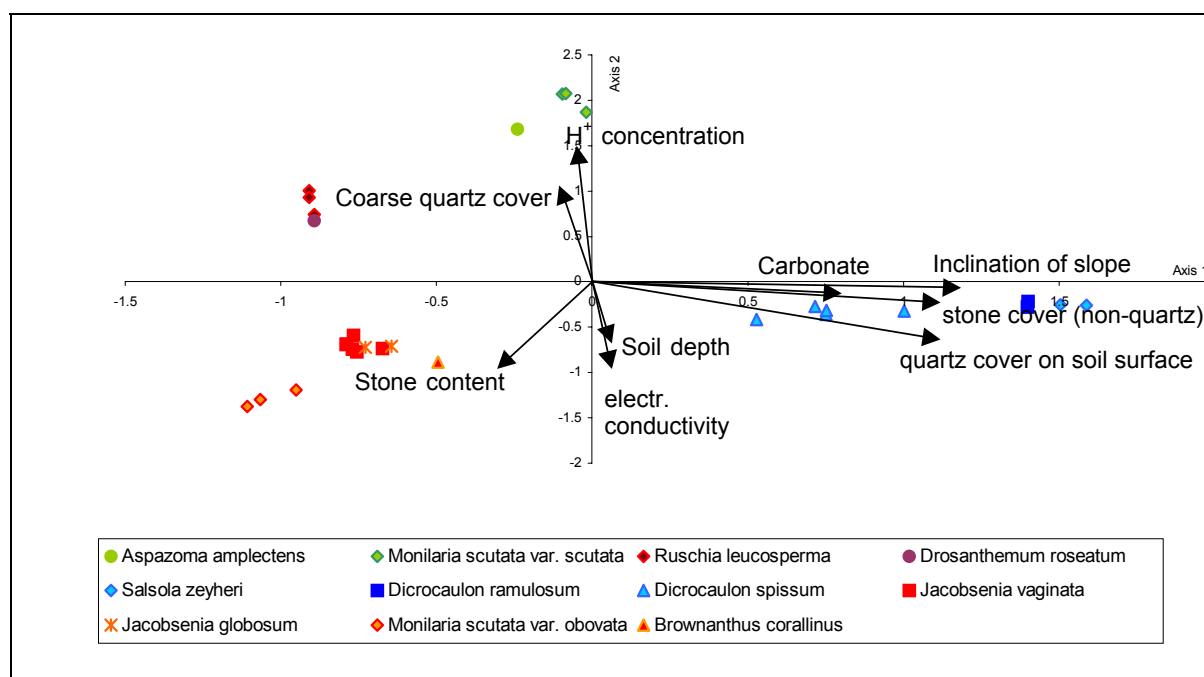


Figure 57. CA ordination of species and subsequently added environmental variable data of the quartz fields and adjacent relevés of the Riethuis-Wallekraal area.

Each community (as defined in Chapter IX.1.4) was associated to one of these groups and thus with particular environmental variables. The *Monilaria scutata* var. *scutata* Community (# 45) as well as the *Aspazoma amplexens* Community (# 48), shown in green in Figure 57, showed a strong positive association with low soil pH (H^+ concentration) and coarse quartz cover on soil surface. They were the only communities that were negatively associated with salinity. Salinity, however, was of secondary importance for the variance in species data (presented by a short arrow). Salinity was generally positively correlated with soil depth.

The saline quartz fields comprised communities that were positively associated with inclination, quartz cover as well as stone cover of other lithology than quartz, and carbonate content in soil. The latter environmental variable had lower importance for the variance in species data. The separation of the *Salsola zeyheri*-*Galenia fruticosa* Community (# 17), the *Dicrocaulon ramulosum* Community (# 43) and less strongly the *Dicrocaulon spissum* Community (# 42) were mainly explained by the variance of these environmental variables. The *Monilaria scutata* var. *obovata* C. (# 40), the *Jacobsenia vaginata* Community (with the *J. globosum*-*M. globosum* Sub-C. # 41.1 and the *J. vaginata*-dominated Sub-C. # 41.2) as well as the *Brownanthus corallinus* Community (# 32) were grouped next to each other. They were negatively associated with inclination of slope, quartz cover on soil surface, stone cover of other lithology than quartz on soil surface. But they were positively associated with stone content in soil and had a more positive association with soil depth and electrical conductivity.

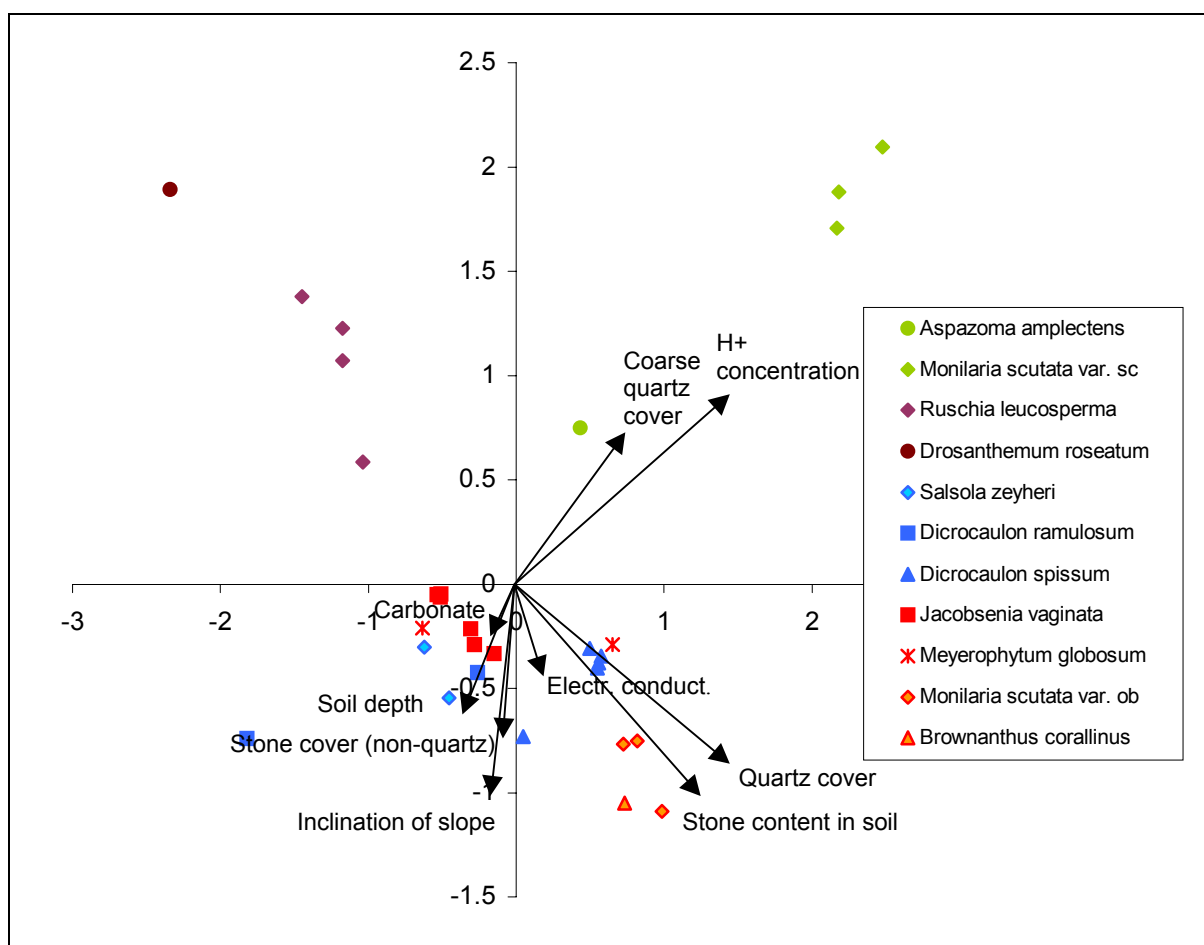


Figure 58. Joint plot of the unconstrained relevé scores and environmental variables of the CCA ordination of the quartz-field and adjacent relevés of the quartz fields in the Riethuis-Wallekraal area.

The *Ruschia leucosperma* Community (# 46) as well as the *Drosanthemum roseatum* Community (# 11) formed a fourth group which was not associated with quartz cover at all. The *Ruschia leucosperma* Community (# 46) has been recorded for quartz fields in the Richtersveld. The *Drosanthemum roseatum* Community (# 11), however, typically inhabit heuweltjies or their surrounding in the Knersvlakte and were never recorded for the quartz fields. For the Riethuis-Wallekraal area they were negatively associated with quartz cover and stone cover of other lithology on soil surface, inclination of slope, and carbonate content in soil. However, their separation from the remaining relevés were not explained by the positive by any of the environmental variable.

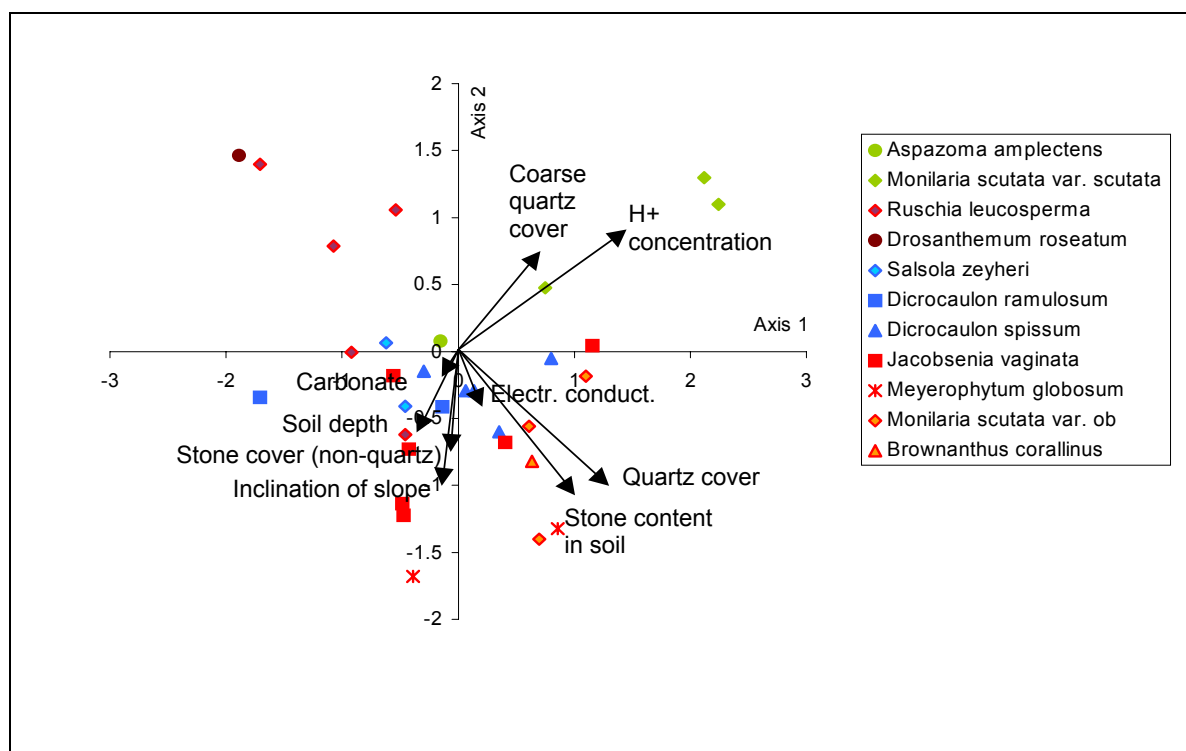


Figure 59. Joint plot of the constrained relevé scores and environmental variables of the CCA ordination of the quartz-field and adjacent relevés of the quartz fields in the Riethuis-Wallekraal area.

The CCA ordination of species and environmental variables of the relevés of quartz fields and adjacent habitats (Figure 58 and Figure 59) strongly supported the results of the CA ordination. The ordination was based on high eigenvalues (> 0.7), extremely high species-environment correlations (> 0.9) (Table 56). More than 15 % of the cumulative percentage of variance of species data and 44 % of the species-environment relation were explained by the ordination.

Table 56. Summary statistics of the CCA ordination of species and environmental variable data of quartz-field and adjacent relevés of the Riethuis-Wallekraal area.

Axes	1	2	3	4
Eigenvalues:	.760	.725	.623	.555
Species-environment correlations:	.927	.914	.899	.833
Cumulative % of variance				
of species data:	8.0	15.7	22.3	28.2
of species-environment relation:	22.6	44.1	62.6	79.1
Sum of all unconstrained eigenvalues:				9.455
Sum of all canonical eigenvalues:				3.367

Both joint plots, those of the unconstrained and of the constrained relevé scores, revealed the separation of the quartz fields into saline and acid quartz fields. The latter were characterised by relatively high cover values of coarse quartz debris whereas the latter were strongly positively associated with cover of medium sized (< 60 mm) quartz debris (quartz cover). The environmental variable electrical conductivity was presented by a very short arrow, thus indicating the poor importance of this variable for the variance in species data within the ordination. This separation of the species data of the saline quartz fields into the two groups which emerged from the CA ordination (Figure 57) was not mirrored in either of the joint plots

of the CCA ordination. Again, the *Ruschia leucosperma* Community (# 46) and the *Drosanthemum roseatum* Community (# 11) were clearly separated from other communities. Their negative association with quartz cover, stone content in soil and inclination of slope which was indicated by the CA ordination was strongly supported by the unconstrained and constrained relevé scores of the CCA ordination. The two communities did not show any positive association with any of the environmental variables employed.

The two joint plots of the CCA ordination, based on unconstrained and constrained relevé scores were largely in line. They both revealed a strong correlation between the communities and particular environmental variables, thus indicating strong habitat preferences of the communities.

III.6.4 Richtersveld

The CA ordination of quartz-field and adjacent habitats of the Richtersveld (Figure 60) revealed a clear separation between the quartz-field relevés (shown in blue and green) and those of the *Brownanthus pseudoschlichtianus* Community (# 52). The quartz fields again were divided into two subgroups: The *Brownanthus pubescens* Community (# 51, which comprises two sub-communities, shown in blue) was separated from the *Aspazoma amplexans* C. (# 48), the *Cephalophyllum regale* C. (# 47), and the *Schlechteranthus hallii* Community (# 50). Some of the relevés of the *Cephalophyllum regale* Community, however, were scattered quite broadly along Axis 1. The *Ruschia leucosperma* Community (# 46) was plotted close to the latter group of quartz-field communities and the *Eberlanzia cyathiformis* Community (# 46) had a intermediate position between the latter and the *Brownanthus pseudoschlichtianus* Community (# 52).

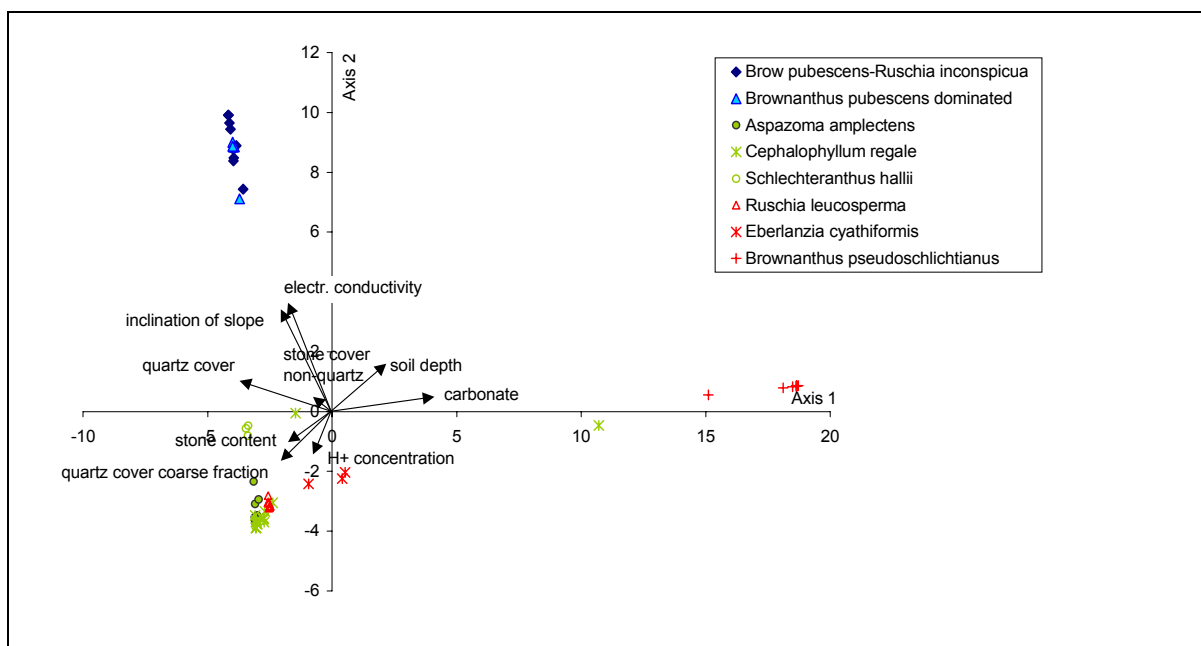


Figure 60. CA ordination of species and subsequently added environmental variable data of quartz-field and adjacent habitats of the Richtersveld. Seven communities and two sub-communities were distinguished.

The correlation with the subsequently added environmental variables revealed that the two main groups of quartz-field habitats were associated with contrasting environmental variables each. The *Brownanthus pubescens* Community (# 51) was positively associated with electrical conductivity, inclination of slope and - less strongly - cover of small to medium sized quartz debris (quartz cover). The remaining quartz-field communities were positively associated with the

environmental variables H^+ concentration, stone content in soil, and stone cover of coarse fraction (> 60 mm) of quartz debris. The *Schlechteranthus hallii* Community (# 50) in particular was plotted in a very close association with the environmental variable stone content in soil. The *Brownanthus pseudoschlichtianus* Community (# 52) showed a positive association with carbonate content in soil and - less strongly - with soil depth. Soil depth was generally negatively associated or independent with both quartz-field habitats. However, it had a less negative association with the saline quartz fields than with the non-saline, acid quartz-field relevés.

Table 57. Summary statistics for the CA of species data from quartz fields and surroundings in the Richtersveld

Axes	1	2	3	4	
Eigenvalues:	.982	.958	.908	.857	
Species-environment correlations:	.749	.559	.604	.651	
Cumulative % of variance					
of species data:	7.1	14.1	20.7	27.0	
of species-environment relation:	18.7	28.9	40.1	52.5	
Sum of all unconstrained eigenvalues:					13.731
Sum of all canonical eigenvalues:					2.941

The ordination was supported by high eigenvalues and high species-environmental correlations (Table 57). About one third of the variance of species-environment relation but only 14 % of the variance species data was explained by the ordination.

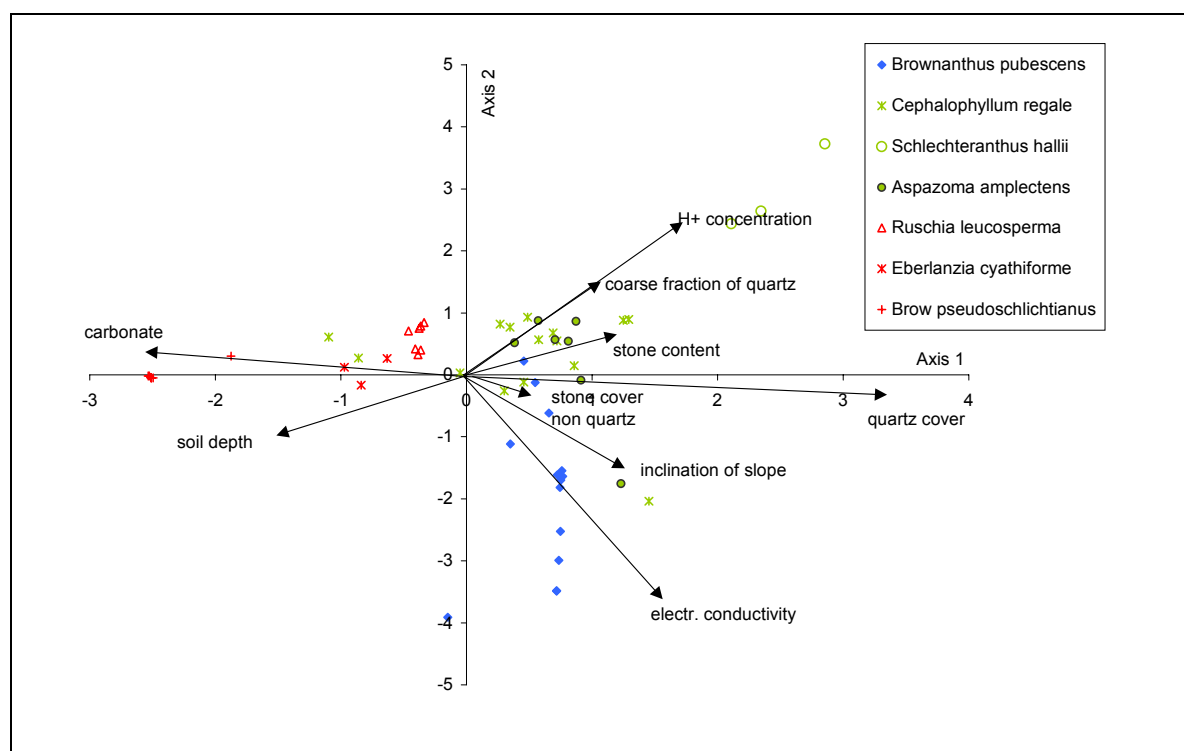


Figure 61. Joint plot of unconstrained relevé scores of the species and environmental variable data from the quartz-field and adjacent habitats of the Richtersveld.

In the joint plot of the relevé scores of the species and environmental variable data of quartz-field and related habitats of the Richtersveld (Figure 61), the separation of the habitats inside and outside the quartz became even more obvious. The communities that were largely or completely restricted to habitats outside quartz fields (shown in red) showed a strong positive association

with carbonate in soil and with soil depth, they were negatively associated with quartz cover on soil surface. The two main habitat types of the quartz fields which emerged in the CA ordination already, were clearly separated by the unconstrained relevé scores of the CCA ordination. The environmental variables H^+ concentration on the one hand and electrical conductivity on the other hand explained the majority of the variance in species data within the quartz-field habitats.

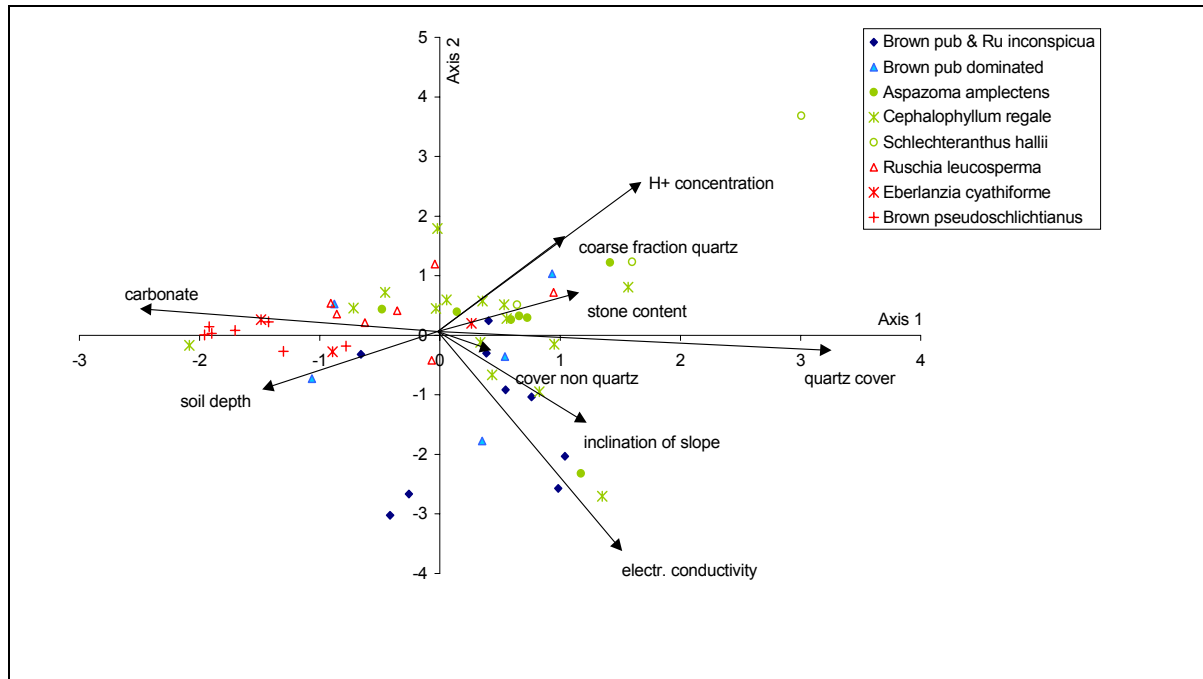


Figure 62. Joint plot of constrained relevé scores of the CCA ordination of quartz-field and adjacent habitats of the Richtersveld.

The joint plot of the constrained relevé scores of the CCA ordination (Figure 62) which are the linear combination of environmental variables strongly supported the separation of saline and non-saline, acid quartz fields. The communities of the habitats outside quartz fields, i.e., the *Brownanthus pseudoschlichtianus* Community (# 52), the *Eberlanzia cyathiforme* Community (# 49), and to a smaller extend the *Ruschia leucosperma* Community (# 46) were positively correlated with carbonate content in soil and soil depth. The latter community, however, was found on both, inside and outside quartz fields. Its ecological position was mirrored by its pattern of scatter within the ordination where it was plotted around its centre. The *Cephalophyllum regale* Community (# 47) which was mainly associated with non-saline, acid quartz fields in the CA ordination and the unconstrained relevé scores of the CCA ordination showed a comparatively broad ecological amplitude along the gradients. The same was true for the *Brownanthus pubescens*-dominated Sub-Community (*Brownanthus pubescens* Community # 51).

The CCA ordination was robust (Table 58): the eigenvalues and the species-environment correlations were high. Forty percent of the variance of the species-environment relation was explained by the ordination. However, the cumulative percentage of variance of species data explained by the ordination was rather low (8.8 %).

Table 58. Summary statistics for the CCA of species and environmental data from quartz fields and surrounding habitats in the Richtersveld.

Axes	1	2	3	4	
Eigenvalues:	.651	.551	.464	.385	
Species-environment correlations:	.846	.860	.767	.725	
Cumulative % of variance					
of species data:	4.7	8.8	12.1	14.9	
of species-environment relation:	22.1	40.9	56.7	69.8	
Sum of all unconstrained eigenvalues:					13.731
Sum of all canonical eigenvalues:					2.941

The ion spectrum and composition of the quartz fields of the Riethuis-Wallekraal area (Communities # 40-45) and the Richtersveld (Communities # 48-51) (Figure 63) revealed a generally higher content of ions for the samples from the Riethuis-Wallekraal area (# 40-45) which was mainly due to an increase of sodium and chloride. The samples from the Riethuis-Wallekraal area showed very low variance within and among the communities. Most of the samples from quartz fields of the Richtersveld had lower total values of ion content and a more equal distribution among them. With respect to the relative composition of ions (Figure 63, below) the samples of the *Aspazoma amplexans* Community (# 48) and the *Schlechteranthus ballii* Community (# 50) had a very high percentage of sulphate, and - less significantly - calcium. Both communities were also associated with relatively low values of electrical conductivity (< 1 mS/cm) and moderately acid soil pH. The samples of the *Brownanthus pubescens* Community (# 51), in return, had high very low values of magnesium with respect to both, relative share and absolute values.

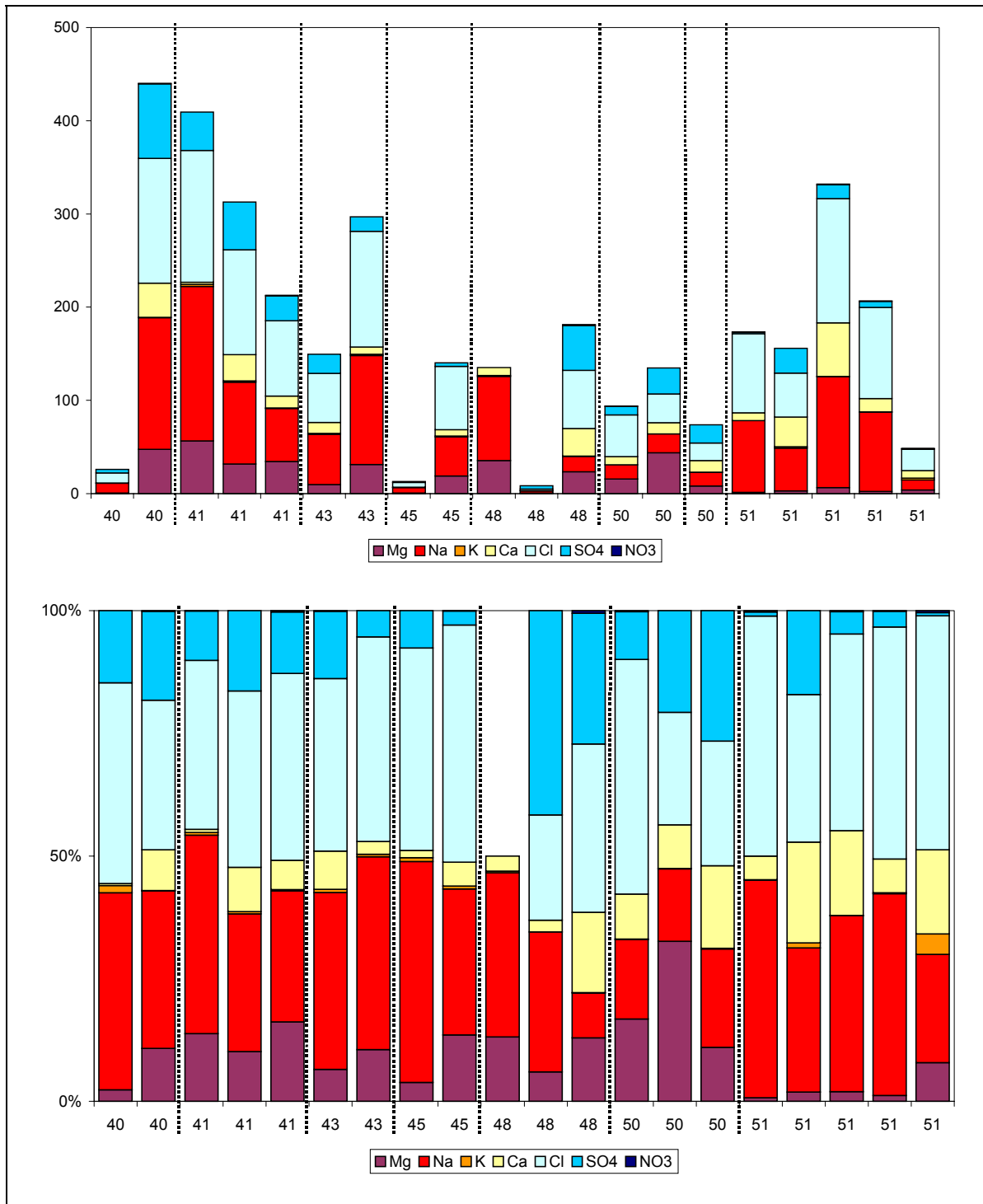


Figure 63. Absolute (above, values given in meq/kg) and relative (below) composition of cations and anions of selected relevés of the communities in the Riethuis-Wallekraal area (# 40-45) and the Richtersveld (# 48-51).

III.6.5 Bushmanland-Warmbad area

In the CA ordination of the species data of quartz-field habitats of the Bushmanland-Warmbad area (Figure 64) the *Zygophyllum decumbens* C. (# 1 B-W) and the *Oropetium capense*-*Ruschia odontocalyx* Sub-Community (# 3.1 B-W) were separated from the rest. The relevés of the other sub-communities of the *Oropetium capensis* Community were plotted next to each other, whereas those of the *Lithops julii* Community (# 2 B-W) were scattered broadly. The strongest variance in species data along Axis 1 was positively associated with the variance of the environmental variables quartz cover on soil surface, inclination of slope, and stone content in soil. The *Oropetium capensis*-*Ruschia odontocalyx* Sub-Community (# 3.1 B-W) which was plotted along Axis 2 was positively associated with soil depth and negatively associated with electrical conductivity. The ordination had very high eigenvalues and high species-environment correlations (Table 59).

Table 59. Summary statistics for the CA ordination of species data and subsequently added environmental variables from quartz-field habitats in the Bushmanland-Warmbad area.

Axes	1	2	3	4
Eigenvalues:	.964	.831	.803	.713
Species-environment correlations:	.412	.451	.397	.511
Cumulative % of variance				
of species data:	13.1	24.5	35.4	45.1
of species-environment relation:	9.4	19.1	26.4	37.1
Sum of all unconstrained eigenvalues:				7.338
Sum of all canonical eigenvalues:				1.739

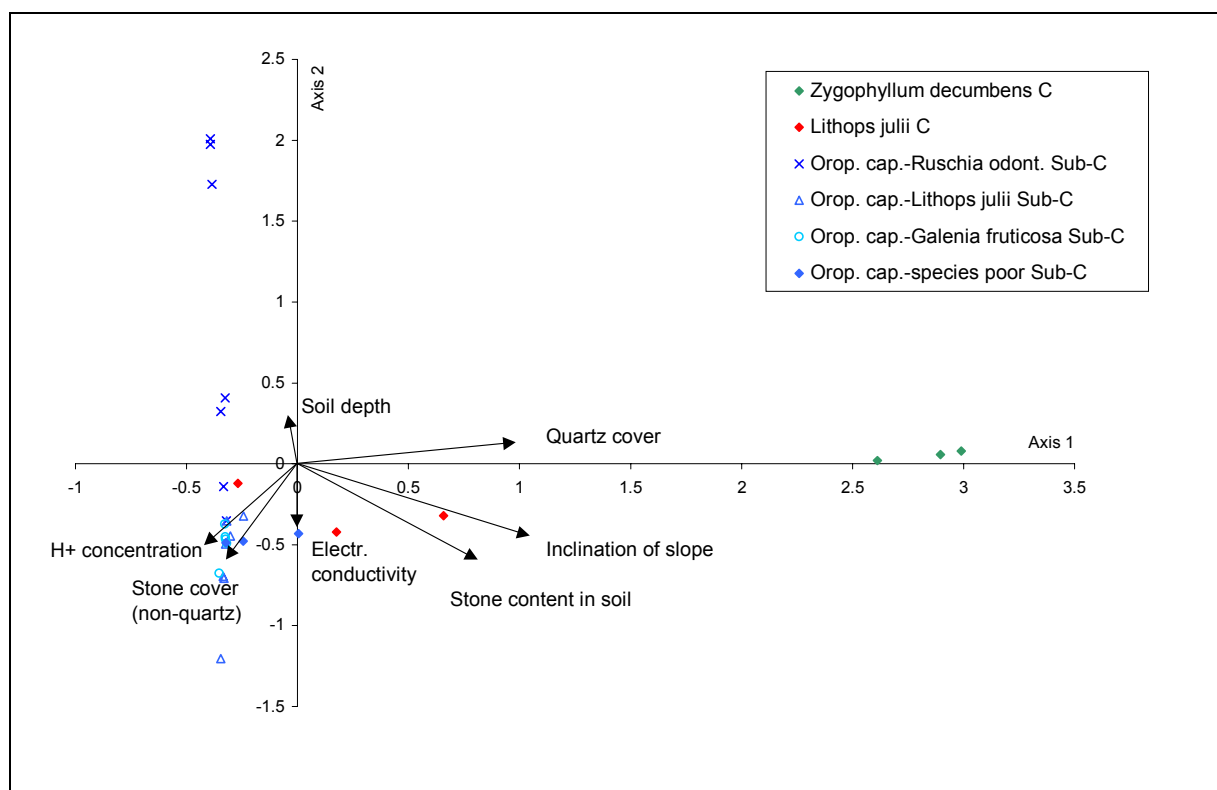


Figure 64. CA ordination of species data and subsequently added environmental variables of quartz-field habitats in the Bushmanland-Warmbad area.

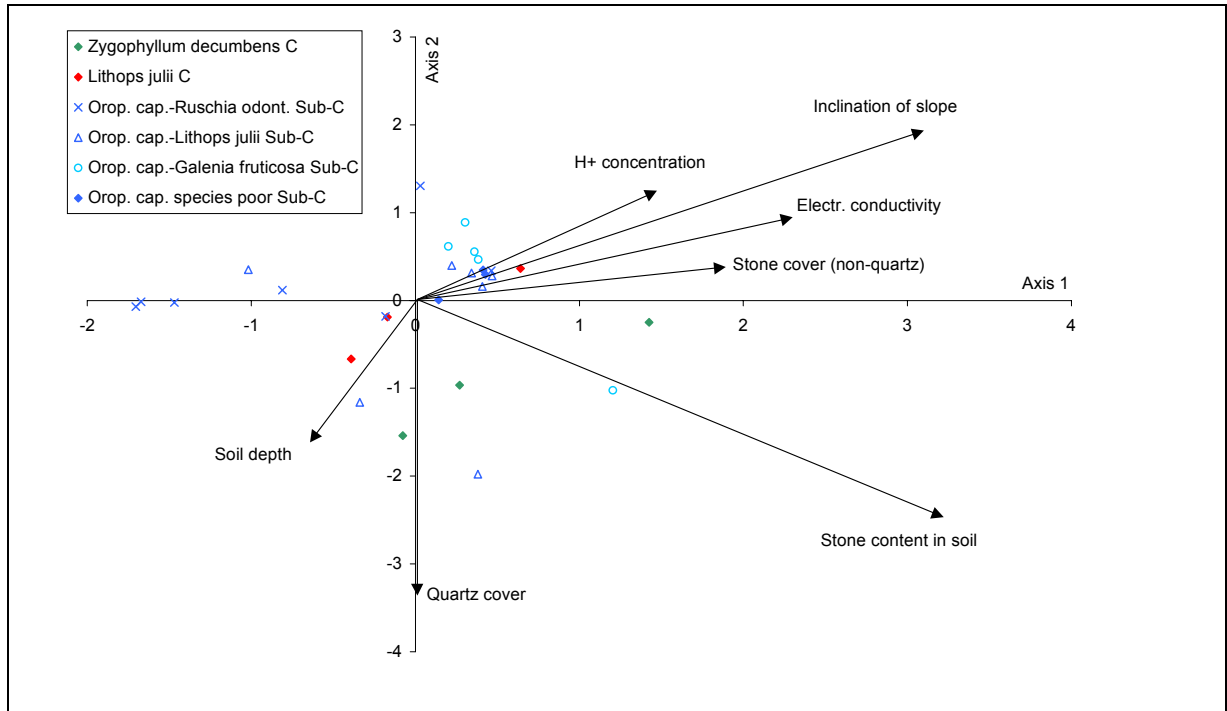


Figure 65. Joint plot of unconstrained relevé scores of quartz-field habitats of the Bushmanland-Warmbad area.

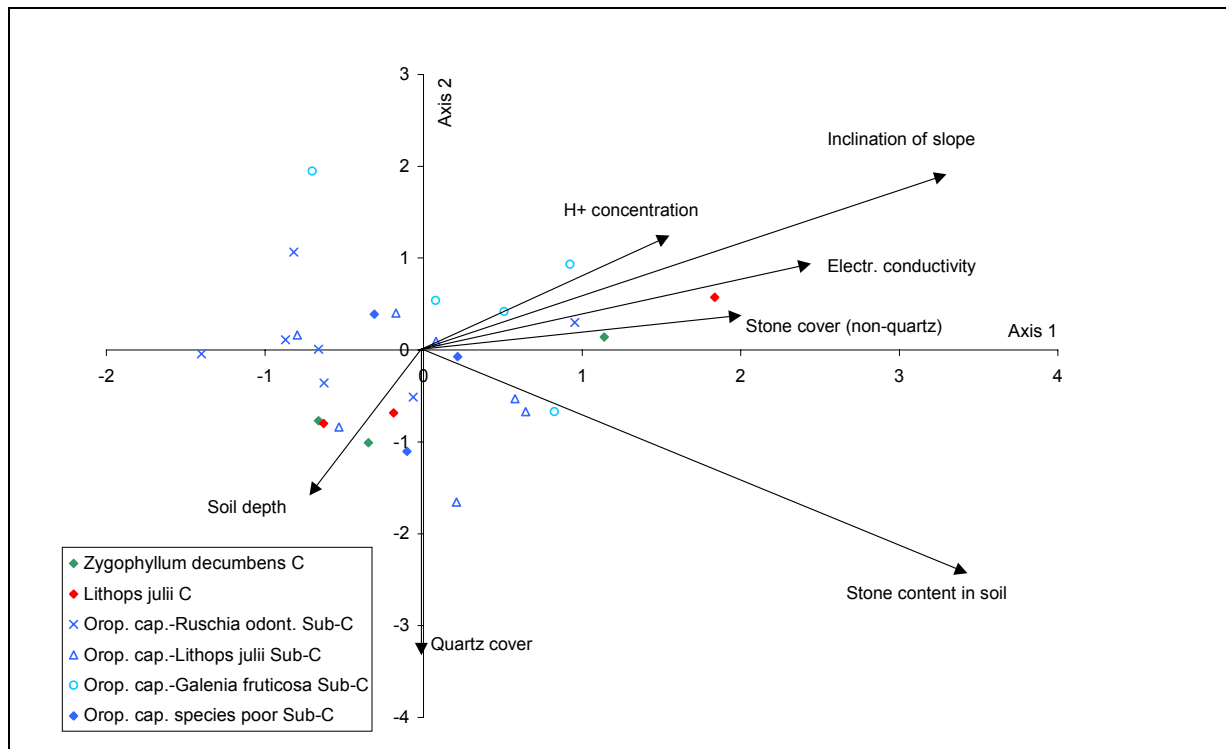


Figure 66. Joint plot of constrained relevé scores of quartz-field habitats of the Bushmanland-Warmbad area (Community 1-4 B-W)

Among the environmental variables that were employed for the CCA ordination (Figure 65 and Figure 66), inclination of slope and stone content in soil was of highest importance for the variance in species data. The arrows representing quartz cover, stone cover of other lithology as quartz, H^+ concentration, electrical conductivity, and soil depth were of comparatively low

importance. Axis 1 represented a gradient of increasing inclination, increasing stone content and decreasing soil depth. Axis 2 represented a gradient of decreasing quartz cover on soil surface.

In general, the communities showed a low affinity to any of the environmental variables employed, not even for the unconstrained relevé scores (Figure 65). Only the *Oropetium capensis-Galenia fruticosa* Sub-Community (# 3.3 W-B) showed a positive association with H⁺ concentration in soil. The strong separation of the *Zygophyllum decumbens* Community (# 1 B-W) from the rest which emerged from the CA ordination was not explained by environmental variables in the CCA ordination. Its positive association with quartz cover and inclination of slope (in CA) was also not supported by the constrained relevé scores of the CCA ordination.

The CCA of the species and environmental variable data of the quartz-field habitats of the Bushmanland-Warmbad area had high eigenvalues for the first two axes and very strong species-environment correlations (Table 60). About 50 % of the variance of species species-environment relation was explained by the ordination.

Table 60. Summary statistics for the CCA ordination of species and environmental variable data from quartz-field and surrounding habitats in the Bushmanland-Warmbad area.

Axes	1	2	3	4	
Eigenvalues:	.517	.449	.293	.238	
Species-environment correlations:	.836	.899	.689	.732	
Cumulative & of variance					
of species data:	7.6	14.2	18.6	22.1	
of species-environment relation:	28.2	52.7	68.7	81.7	
Sum of all unconstrained eigenvalues:					6.785
Sum of all canonical eigenvalues:					1.833

Table 61. Weighted means (above) and weighted standard deviation (below, in brackets) of environmental variable data employed for ordinations for the different areas.

Area	Inclination of slope [°]	Soil depth [cm]	Quartz cover coarse gravel [%]	Quartz cover [%]	Stone cover non-quartz [%]	Stone content in soil [% weight]	Electr. conductivity [mS/cm]	Carbo-nate content in soil [Class 1-5]	H ⁺ concentration (*100 000)
Little Karoo	4.2126 (4.9157)	15.4447 (7.8363)	-	50.1866 (38.125)	26.841 (34.825)	40.296 (22.871)	2.0225 (2.0524)	0.3489 (0.9778)	0.4712 (1.4794)
Kners-vlakte	7.1924 (6.6778)	17.351 (7.525)	3.4152 (7.152)	88.808 (18.077)	1.599 (4.217)	46.286 (20.499)	3.019 (2.567)	0.2067 (0.550)	1.9616 (3.3374)
Riethuis-Walle-kraal	8.5099 (7.2843)	14.180 (6.898)	0.8073 (4.544)	68.165 (31.381)	7.6339 (16.595)	31.399 (15.819)	2.1667 (1.802)	0.0950 (0.5517)	1.2770 (2.8208)
Richters-veld	8.603 (1.317)	19.574 (10.031)	1.673 (2.485)	54.858 (42.219)	3.6948 (14.519)	39.2714 (17.699)	0.9503 (1.4807)	0.2462 (0.606)	0.9516 (3.380)
Bushman land-WB	3.3221 (2.584)	14.119 (7.357)	-	77.276 (18.366)	0.7941 (2.4892)	47.752 (19.319)	0.0754 (0.0671)	-	0.0933 (0.1806)

III.7 Growth-form composition of the vegetation

III.7.1 Growth-form composition inside and outside the quartz fields of different phytochoria

The comparison of the growth-form composition of the vegetation of the quartz fields and the surrounding zonal habitats in five different phytochoria with frequent occurrence of quartz fields revealed a high correspondence within both the quartz fields and the surrounding zonal habitats of the Succulent Karoo (Figure 67). In these phytochoria, the average canopy cover (Table 62) on the quartz fields was app. 8-10 % and more than half of this comprised nano- and micro-chamaephytes (NaCh, MiCh). The average cover of zonal vegetation was higher than of the quartz-field relevés. Highest average cover for zonal vegetation was recorded for the Knersvlakte (22 %) whereas it was considerably lower for the other phytochoria (between 5 and 12.3 %). Mega-chamaephytes (meCh) comprised about 70-80 % of this cover, whereas on the quartz fields mega-chamaephytes were poorly represented (average canopy cover < 3.5 %). Other growth forms, i.e., phanerophytes, hemicryptophytes, and geophytes had very low cover values on both habitat types. In contrast to the other regions, the Knersvlakte had a relatively high average canopy cover of therophytes in both zonal habitats (3.4 %) and quartz fields (0.6 %). On quartz fields, these therophytes were mainly succulent (e.g., *Mesembryanthemum fastigiatum* Thunberg [syn. *Opophytum aquosum* (L. Bolus) N. E. Brown] and *Mesembryanthemum stenandrum* (L. Bolus) L. Bolus.) both Mesembryanthemaceae, whereas on zonal habitats they were non-succulent (mainly Asteraceae species). The growth-form composition of the vegetation inside and outside the quartz fields in the Bushmanland differed considerably from the other regions. In contrast to the Succulent Karoo vegetation, mega-chamaephytes reached higher cover values (average = 3.3 %) inside than outside quartz fields. Hemicryptophytes, which generally occurred with low cover values on the relevés of the Succulent Karoo, reached high values in (average = 3.9 %) on the quartz fields of the Bushmanland-Warmbad area.

Table 62. Average canopy cover (mean values) of quartz-field and zonal vegetation in five different areas with frequent occurrence with quartz fields.

	Buschmanland-Warmbad		Richtersveld		central Namaqualand		Knersvlakte		Little Karoo	
	outside	inside	outside	inside	outside	inside	outside	inside	outside	inside
%	5.06	9.74	9.53	7.53	11.3	8.5	22.09	9.43	12.3	7.9
n	9	37	30	66	13	46	329	364	66	121

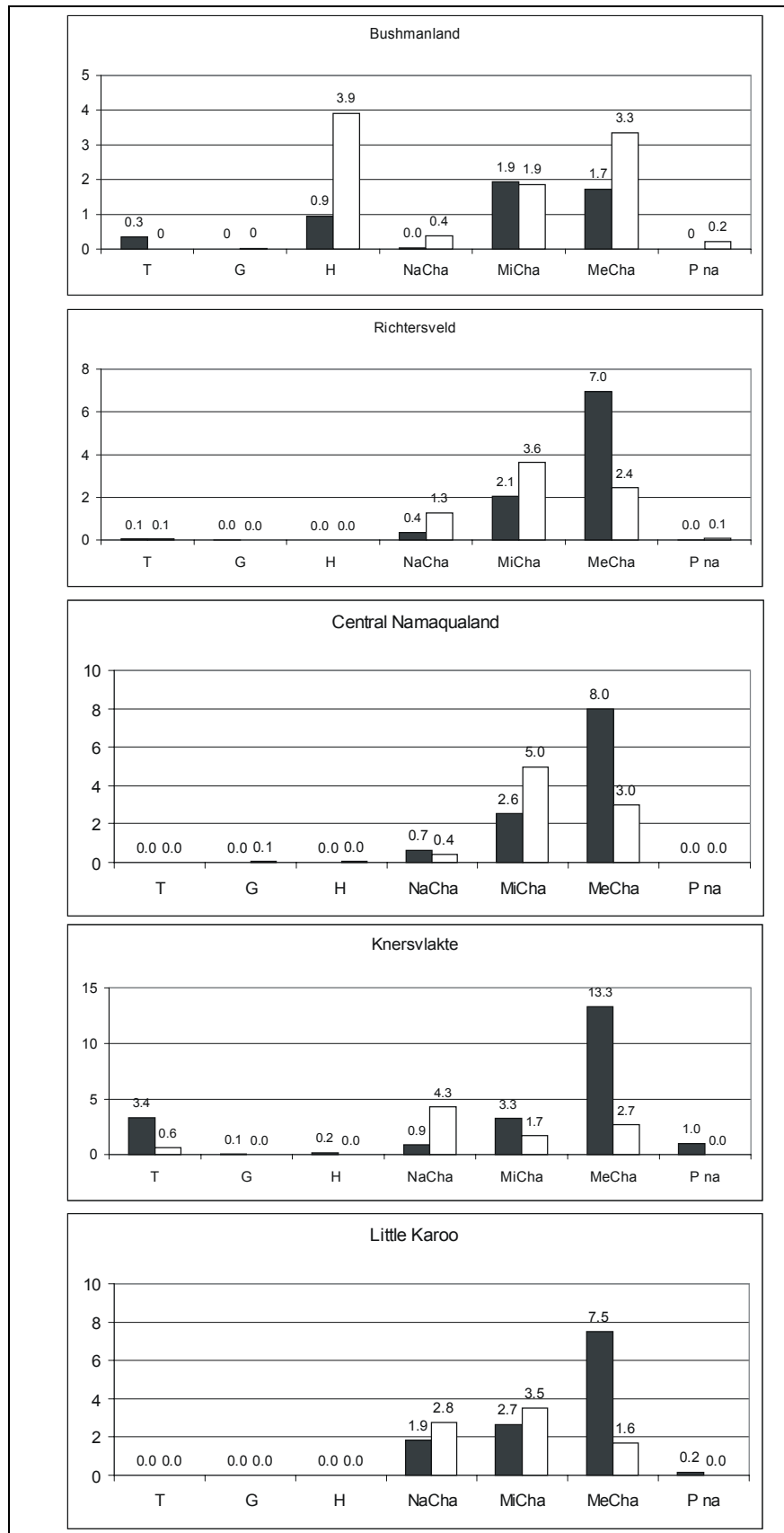


Figure 67. Mean canopy cover [%] of the growth forms on relevés with quartz cover (white columns) and without quartz cover (black columns) of five geographical regions. T= therophytes, G = geophytes, H = hemicryptophytes, NaCha = nano-chamaephytes (0-5 cm), MiCha = micro-chamaephytes (5-15 cm), MeCha = mega-chamaephytes (15-50 cm), Pna = Nano-phanerophytes).

III.7.2 Environmental variables controlling the growth-form composition of the vegetation

The analyses of distribution of growth forms within the regional sets of growth-form data were carried out by employing the correspondence analysis, using the programme CANOCO 4.0 (ter Braak & Smilauer 1998). For the CCA direct gradient analyses the species names were replaced by the species' growth-form type. For all regional data sets the same array of environmental variables and the same growth-form groups were employed.

Little Karoo

The constrained ordination of the CCA analysis of growth-form and environmental variable data from quartz fields and adjacent habitats of the Little Karoo is shown in Figure 68. The arrows presenting the environmental variables quartz cover and electrical conductivity were plotted next to each other, directing into the opposite direction of carbonate content, soil depth, and stone cover of other lithology than quartz. H^+ concentration, inclination of slope, and cover of coarse fragments of quartz were plotted in a rectangle to the other variables but opposite to soil depth.

Table 63. Summary statistics for the CCA analysis of growth-form and environmental variable data from quartz fields in the Little Karoo and adjacent regions.

Axes	1	2	3	4
Eigenvalues:	.319	.124	.064	.056
Growth form-environment correlations:	.775	.428	.330	.307
Cumulative % of variance				
of growth-form data:	8.9	12.4	14.2	15.7
of growth form-environment relation:	55.0	76.5	87.5	97.2
Sum of all unconstrained eigenvalues:				3.575
Sum of all canonical eigenvalues:				0.579

The constrained eigenvalues for the ordination were moderate, however, more than 75 % of the cumulative variance of the fitted growth-form data were explained by the CCA (Table 63).

The joint plot of growth forms and environmental variables show the correspondence between the distribution of growth forms and environmental gradients (Figure 68) thus indicating the habitat preferences of the different chamaephyteous growth forms. High cover values of mega-chamaephytes were negatively associated with the environmental variables quartz cover, electrical conductivity, inclination of slope, and coarse quartz cover. It was positively associated with soil depth, carbonate content, and (with low importance) stone cover of other lithology. High cover values of micro-chamaephytes also had a broad distribution. Highest values of micro-chamaephytes were recorded for quartz fields with high electrical conductivity. The relevés with the highest cover values for compact nano-chamaephytes were plotted in the centre of the ordination diagram with no obvious association with any of the environmental variables, but a negative association with soil depth.

Each particular subtype of the nano-chamaephyteous growth forms revealed strong preferences regarding habitat conditions (Figure 68). Compact and reptant nano-chamaephytes reached highest cover values on relevés with high H^+ concentration (low soil pH), high inclination and coarse cover of quartz. They were largely absent from relevés with deep soils and high carbonate content. Subglobose nano-chamaephytes were mainly restricted to quartz fields which either have acid soil pH (high H^+ concentration) or high electrical conductivity. High cover values of subterranean nano-chamaephytes, in contrast, were plotted at the lower right fringe of the ordination diagram, thus indicating a positive association with high quartz cover and high electrical conductivity.

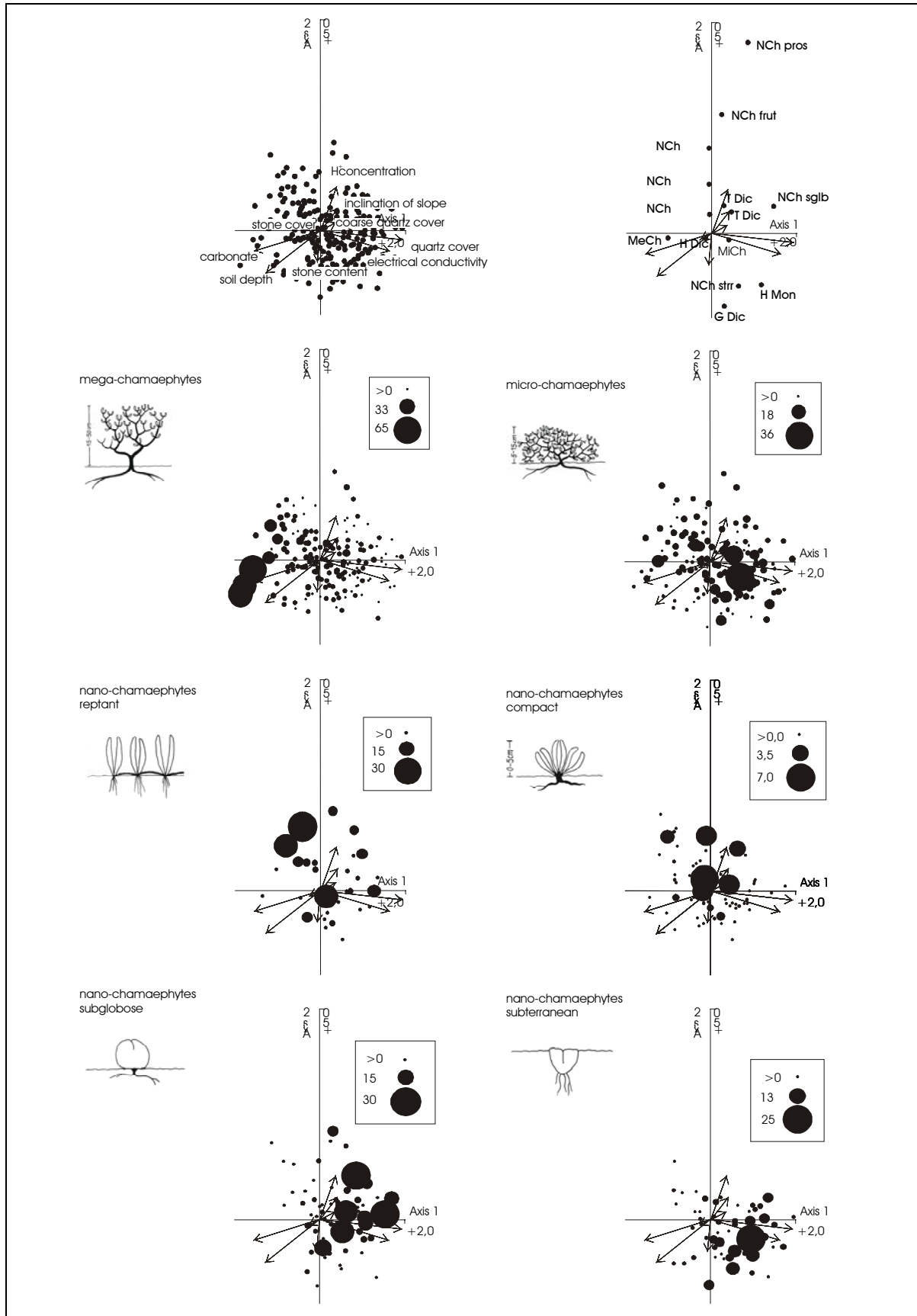


Figure 68. CCA ordination of growth-form and environmental variable data of quartz-field and related habitats in the Little Karoo and adjacent areas. For the analysis species names were replaced by the species' growth form.

Namaqualand *sensu lato*: Knersvlakte, Central Namaqualand, Richtersveld

Knersvlakte

The ordination diagram of the CCA (Figure 69) which was based on the growth-form composition of the vegetation and its association with environmental variables showed an identical pattern of environmental variables as was shown for the vegetation composition on species level (see Chapter III.6.2). The arrow representing the environmental variable electrical conductivity was plotted parallel to Axis 1. It had the longest extension, thus indicating a high explanatory value for the distribution of growth forms within the data set. H^+ concentration was negatively associated with electrical conductivity and positively associated with stone content in soil, thus emerging the two main groups of the quartz-field habitats as has been shown above (Chapter: III.6.2). Also in correspondence with the CCA ordination on species level (Figure 51), Axis 2 was mainly explained by the environmental variables soil depth and, with a negative association, quartz cover on soil surface. The majority of the environmental variables employed were shown by particularly long arrows except the variables inclination of slope and stone cover of other lithology than quartz which were of lower importance for the growth-form composition of the vegetation.

The ordination was relatively robust: the first two axes had relatively high eigenvalues, strong growth form-environmental correlation and explained more than 80 % of the variance in the growth form-environment relationship (Table 64).

Table 64. Summary statistics for the CCA of growth-form and environmental variable data from quartz fields and surrounding sites in the Knersvlakte.

Axes	1	2	3	4	
Eigenvalues:	.346	.229	.066	.025	
Species-environment correlations:	.668	.558	.332	.223	
Cumulative % of variance					
of species data:	8.9	14.8	16.5	17.2	
of species-environment relation:	50.7	84.3	94.0	97.7	
Sum of all unconstrained eigenvalues:					3.874
Sum of all canonical eigenvalues:					.682

The CCA joint plot of environmental variables and species as well as the plots of growth-form abundance per relevé revealed that the growth-form types differentiated within the studies differed regarding their habitat preferences. The cover values (relative percentage at each relevé) of the mega-chamaephytes showed positive association with the environmental variables soil depth, quartz cover of coarse fragments, and inclination of slopes. They were positively associated with stone content in soil, although less conspicuous. They were negatively associated with electrical conductivity and quartz cover.

Micro-chamaephytes were positively associated with H^+ concentration and stone content in soil. They occurred with low cover values only on quartz relevés with high soil depth and were largely absent from quartz-field relevés with high electrical conductivity. The nano-chamaephytes in general (combining all nano-chamaephyteous subtypes) showed a broad distribution but occurred with significantly lower cover values on relevés with high soil depth and coarse quartz cover.

The cover values of the three main subtypes of nano-chamaephyteous growth forms, i.e., compact, subglobose, and subterranean nano-chamaephytes) differed significantly from each other regarding their habitat preferences.

The cover values of compact nano-chamaephytes showed a nearly opposite pattern to those of the micro-chamaephytes. High cover values of compact nano-chamaephytes were negatively associated with stone content but positively associated with electrical conductivity and, less prominently though, with soil depth. They were negatively associated with stone content and H^+ concentration. They showed no strong association with quartz cover but were plotted also in negative association with quartz cover. Subglobose nano-chamaephytes were strongly positively associated with stone content in soil and quartz cover on soil surface. They were scattered on the lower left margin of the joint plot diagram, thus indicating a strong association with highest values of stone content and quartz cover. High cover values of subterranean nano-chamaephytes were restricted to soils with quartz cover and electrical conductivity but largely absent from soils with high stone content.

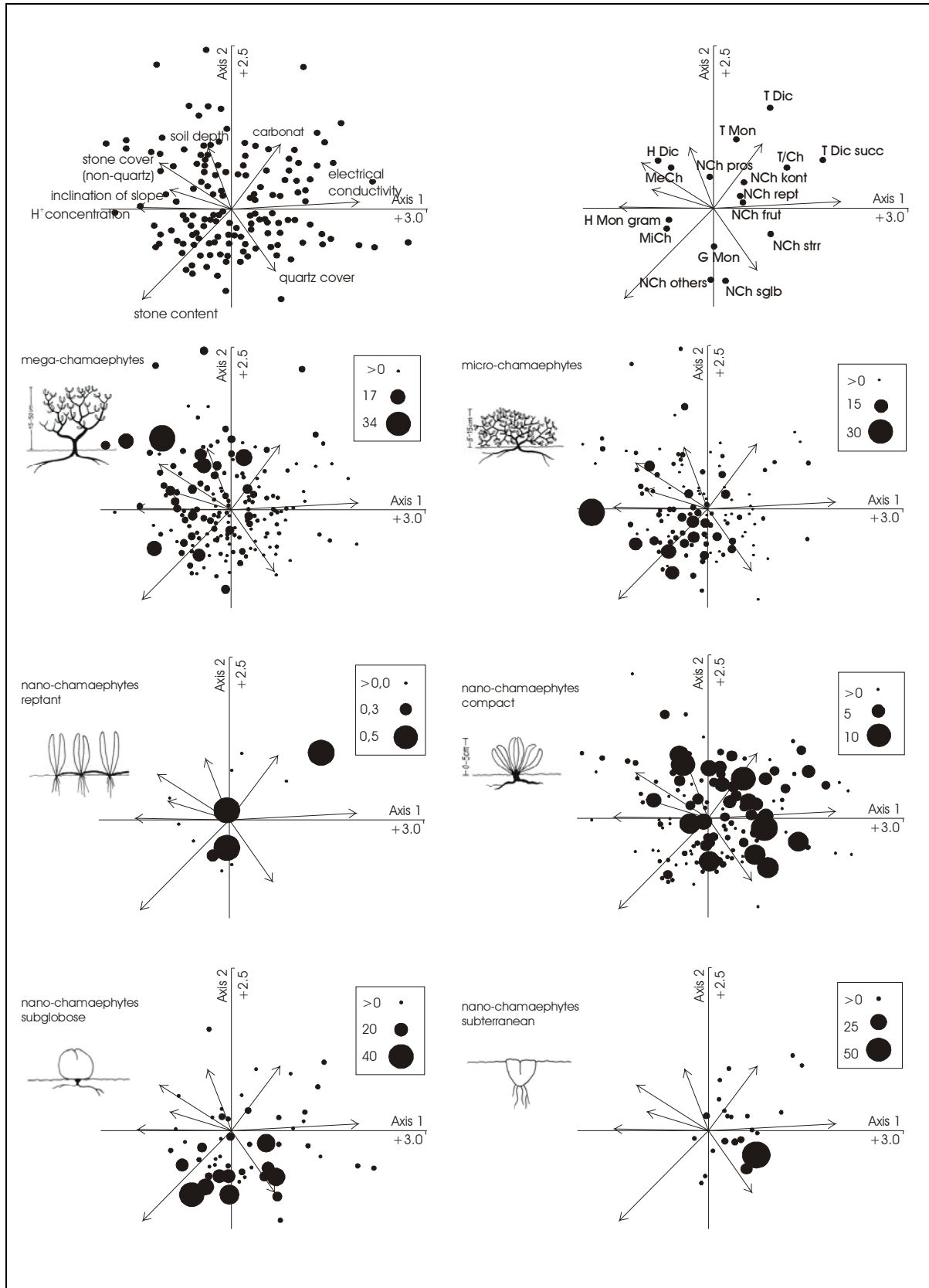


Figure 69: CCA ordination of data from the Knersvlakte. For the analysis species names were replaced by the species' growth form.

Riethuis-Wallekraal area

The CCA ordination (Figure 70) of growth-form data correlated with environmental variables of quartz fields and adjacent habitats in the central Namaqualand (Riethuis-Wallekraal area) separated the mega-chamaephytes and the reptant nano-chamaephytes from the remaining chamaephyteous growth forms along Axis 1. This separation is mainly explained by the environmental variables quartz cover on soil surface, stone content in soil, and H^+ concentration. In contrast to other data sets of quartz-field relevés, electrical conductivity is of subordinate importance for the variance in species data.

The values in the summary statistics of the CCA ordination (Table 65) show relatively high eigenvalue for the first axis and low eigenvalues for the following axes. The cumulative percentages of variance of growth-form as well as growth form-environment data explained by the ordination were very high.

Table 65. Summary statistics of CCA analysis of growth-form and environmental variables of quartz-field and adjacent relevés in the Riethuis-Wallekraal area

Axes	1	2	3	4
Eigenvalues:	.249	.050	.033	.019
Growth form-environment correlations:	.727	.676	.513	.406
Cumulative % of variance				
of growth-form data:	27.4	32.9	36.6	38.7
of growth form-environment relation:	68.7	82.4	91.5	96.8
Sum of all unconstrained eigenvalues:				.907
Sum of all canonical eigenvalues:				.362

Micro- and mega-chamaephytes showed contrasting patterns regarding their distribution and abundance. High cover values of mega-chamaephytes were positively associated with high carbonate and inclination of slope, and electrical conductivity. They were negatively associated with quartz cover on soil surface, H^+ concentration, and stone content in soil. Micro-chamaephytes occurred with highest values on relevés which were positively associated with quartz cover on soil surface and had lowest cover values on saline soils without quartz cover but were otherwise broadly scattered.

Repent nano-chamaephytes were restricted to relevés without quartz cover, high soil depth, and high electrical conductivity. Compact nano-chamaephytes, which occur with low cover values on all relevés (< 3 %) showed largely the same distribution than micro-chamaephytes. Subglobose nano-chamaephytes also had a broad distribution. It only occurred with cover values > 1 % on relevés that were positively associated with quartz cover on soil surface and inclination of slope. Subterranean nano-chamaephytes, in contrast, were only recorded for relevés with high quartz cover, high stone content, H^+ concentration, and high electrical conductivity. “Other” chamaephyteous groups which did not correspond with any of the three main subtypes of nano-chamaephytes (i.e., compact, subglobose and subterranean) were had too low frequency and cover values on the relevés employed to be plotted.

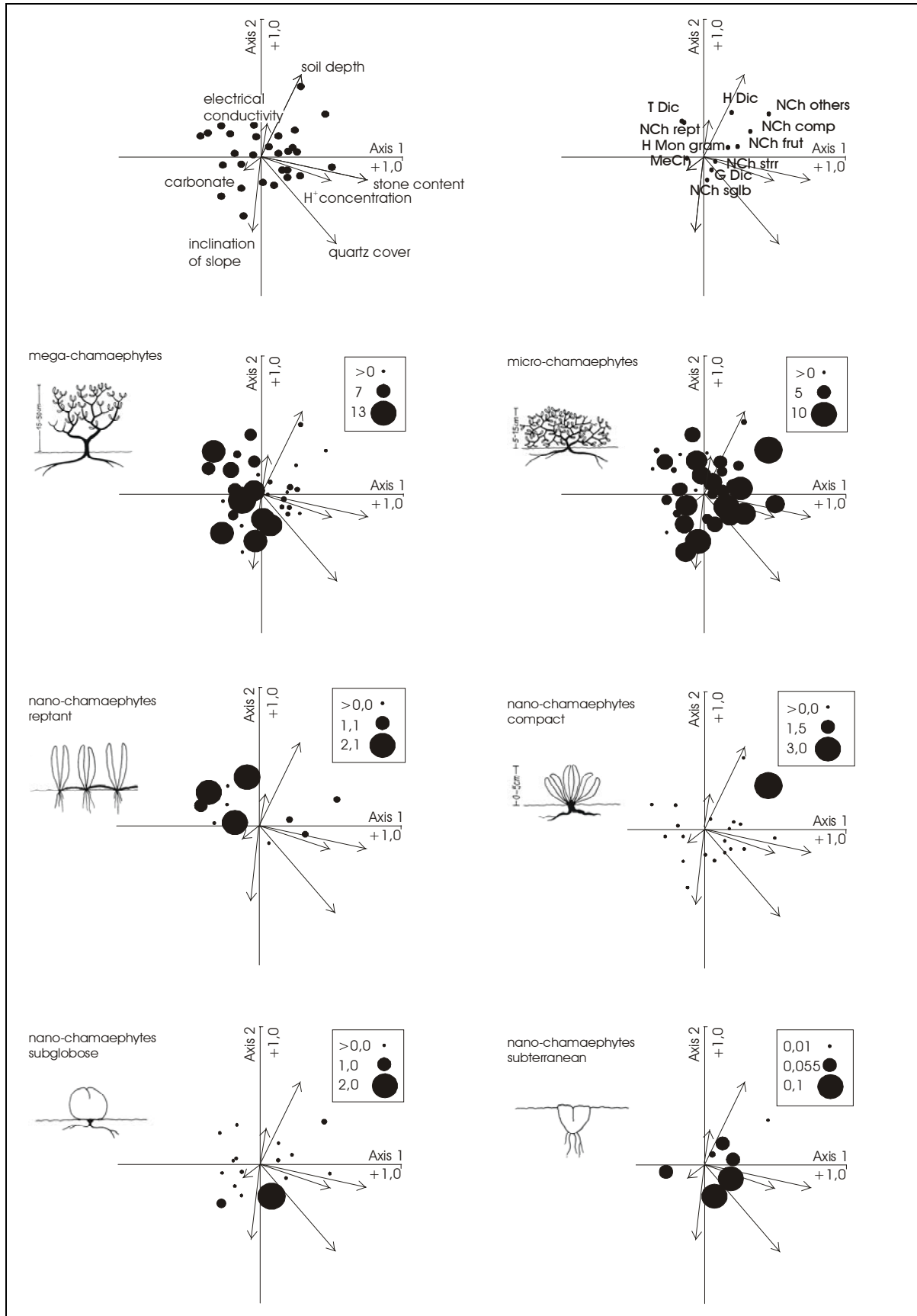


Figure 70. CCA ordination of growth-form and environmental variables of quartz-field and adjacent relevés from the Riethuis-Wallekraal area. For the analysis species names were replaced by the species' growth form.

Richtersveld

The CCA ordination of growth-form data correlated with environmental variables of quartz fields and adjacent habitats in the Richtersveld (Figure 71) revealed that the variable quartz cover on soil surface explained most of the variance within the growth-form data. It was presented by the longest arrow which was plotted parallel to Axis 1. Another strong variable was “soil depth” which was negatively associated Axis 2. Numerous relevés were plotted along Axis 2, indicating a negative association with soil depth and electrical conductivity but did not show a positive association with any environmental variable. Consequently, the eigenvalues for Axis 2, 3 and 4 were very low but the growth form-environment correlation and the cumulative percentage of variance of growth-form and of growth form-environment relation were high (Table 66).

Table 66. Summary statistics of CCA analysis of growth-form and environmental variable data of quartz fields and adjacent habitats of the Richtersveld.

Axes	1	2	3	4	
Eigenvalues:	.302	.072	.037	.017	
Growth form-environment correlations:	.684	.405	.421	.281	
Cumulative % of variance					
of growth-form data:	13.9	17.2	18.9	19.7	
of growth form-environment relation:	67.3	83.3	91.5	95.4	
Sum of all unconstrained eigenvalues:					2.168
Sum of all canonical eigenvalues:					.448

In the data set from the Richtersveld, mega- and micro-chamaephytes showed contrasting patterns regarding distribution of high cover values. The first group was positively associated with carbonate in soil and soil depth and negatively associated with quartz cover. Micro-chamaephytes, in contrast, occurred with high cover values on relevés with high quartz cover, high stone content and high electrical conductivity. Nano-chamaephytes, in return, were largely restricted to the quartz fields which were negatively associated with soil depth: compact nano-chamaephytes were broadly scattered in positive association with quartz cover and electrical conductivity and in negative association with carbonate. Subglobose nano-chamaephytes occurred on quartz-field relevés which were positively associated with stone content and inclination. They were negatively associated with soil depth. Subterranean nano-chamaephytes, were restricted to quartz fields with high electrical conductivity and high electrical conductivity. Other chamaephyteous groups which did not correspond with any of the three main subtypes of nano-chamaephytes (i.e., compact, subglobose and subterranean) were had too low frequency and cover values on the relevés employed to be plotted.

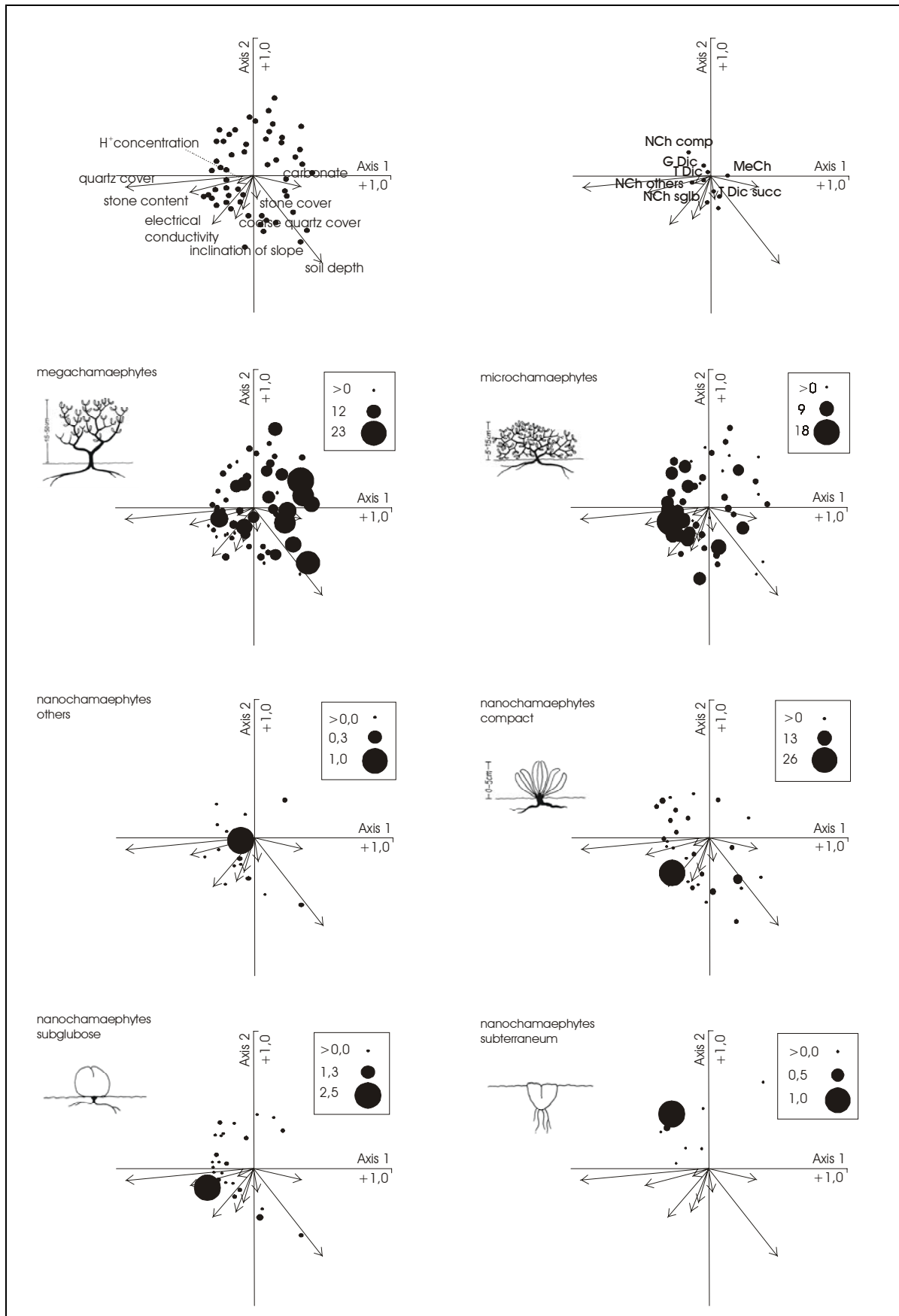


Figure 71. CCA ordination of growth-form and environmental variable data of quartz-field and adjacent relevés from the Richtersveld. For the analysis, species names were replaced by the species' growth form type.

Bushmanland-Warmbad area

The CCA ordinations of the growth-form and environmental variable data from the Bushmanland-Warmbad area (Figure 72) showed high correspondence regarding distribution of environmental variables and growth forms. The growth-form variance along Axis 1 was explained by the environmental variables stone and carbonate content in soil, whereas the variance along Axis 2 was explained by inclination and electrical conductivity. Quartz cover on soil surface was of low importance and was negatively associated with soil depth and H⁺ concentration.

Table 67. Summary statistics of the CCA analyses of the growth-form and environmental variable data of relevés from the Bushmanland-Warmbad area

Axes	1	2	3	4	
Eigenvalues:	.401	.320	.099	.066	
Growth form-environment correlations:	.756	.716	.388	.309	
Cumulative % of variance of growth-form data :	11.0	19.8	22.5	24.3	
of growth form-environment relation:	42.1	75.7	86.1	93.0	
Sum of all unconstrained eigenvalues:					3.646
Sum of all canonical eigenvalues:					.952

The summary statistics of the analysis was robust (Table 67). It had high eigenvalues for the first two axes and explained high cumulative percentages of variance of growth forms and growth form-environment relation.

Mega-chamaephytes and micro-chamaephytes showed contrasting patterns of distribution regarding high cover values in both analyses. High cover values of mega-chamaephytes were positively associated with soil depth and electrical conductivity. Micro-chamaephytes occurred with highest cover values on relevés which were positively associated with carbonate and stone content. Nano-chamaephytes generally occurred with low cover values only. Compact, subterranean, and “other” nano-chamaephytes were plotted in the centre of the ordination without particular association with any of the environmental variable in the direct gradient analysis. Only the subglobose nano-chamaephytes which also reached the highest cover values among the nano-chamaephyteous growth forms, showed a positive association with inclination of slope and stone content. They were negatively associated with soil depth.

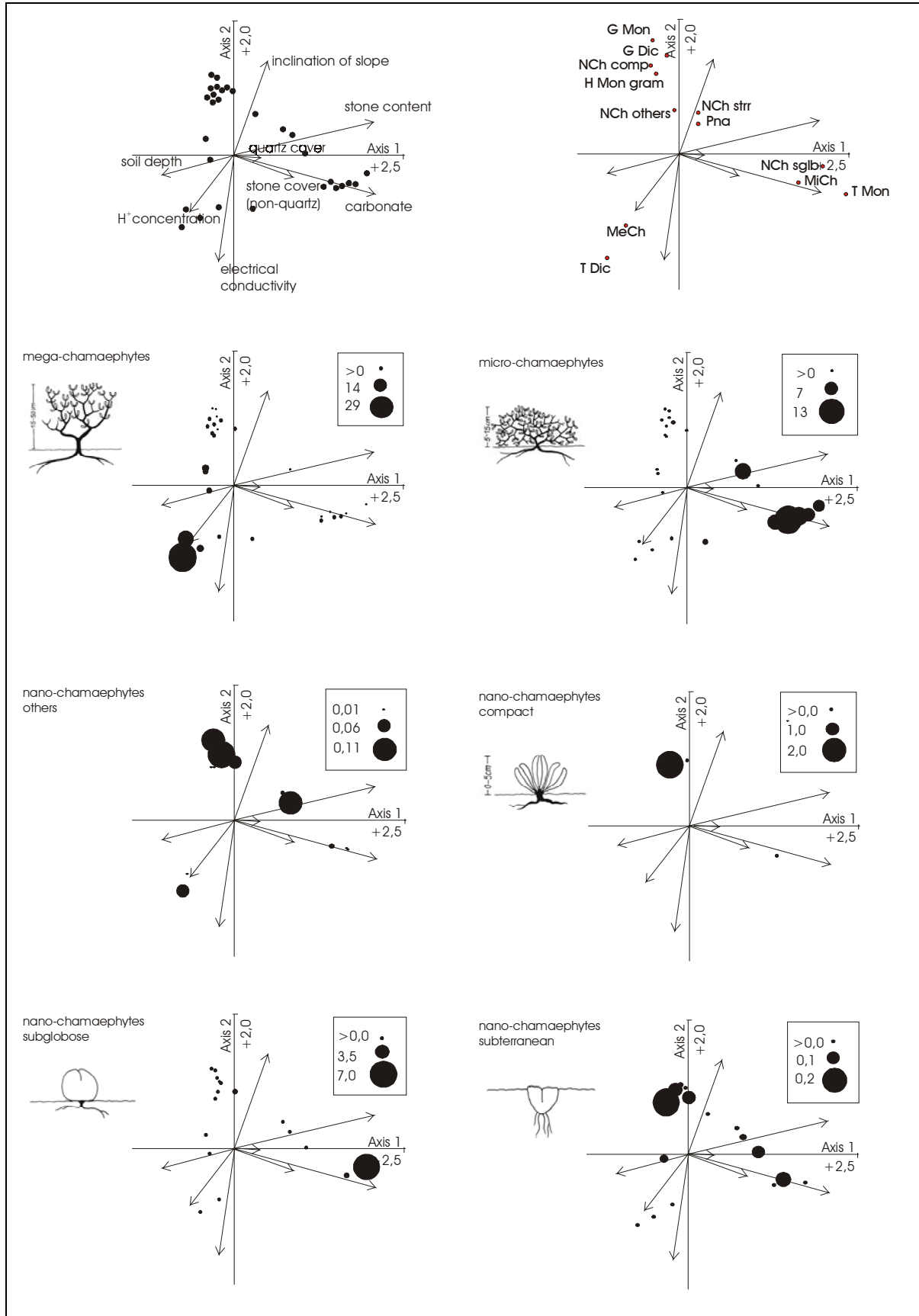


Figure 72. CCA analysis of growth-form and environmental variable data of quartz fields and adjacent relevés of the Bushmanland-Warmbad area.

III.7.3 Distribution of growth forms along gradients of increasing quartz cover and salinity

The distribution of growth forms (shown in average cover values) along gradients of increasing density of quartz cover and electrical conductivity increasing quartz cover (Figure 73) showed a high correspondence between the four regions of the Succulent Karoo but a divergent pattern for the Nama Karoo (Bushmanland-Warmbad area). In the Succulent Karoo the cover values of mega-chamaephytes decreased with increasing quartz cover. Micro- and nano-chamaephytes responded indifferent. The relative dominance of nano- and/or micro-chamaephytes on quartz-field relevés is therefore due to the significant decrease of cover values of mega-chamaephytes and nano-phanerophytes but not to the absolute increase of dwarf growth forms. This is also in line with the average cover values of growth forms inside and outside the quartz fields (Figure 67). Nano-phanerophytes only reached high cover values on relevés without quartz cover. Their cover values increased considerably when the density of quartz cover increased.

In the Bushmanland-Warmbad area cover values of mega- and micro-chamaephytes were largely indifferent to the increase of quartz cover. Whereas nano-phanerophytes only occurred on relevés with > 60 % quartz cover.

The response of therophytes, geophytes and hemicryptophytes to the increase of quartz cover was largely indifferent in all regions. Therophytes were only recorded for the Knersvlakte with considerable cover values. Their cover values decreased only slightly with increased quartz cover. Geophytes generally occurred with very low average cover values (< 1 %) but were sporadically recorded for the entire range of quartz cover. Hemicryptophytes covered the entire range of quartz cover but had very low average cover values in the Succulent Karoo. In the Bushmanland-Warmbad area they reached average cover between 3.5 and > 8 %.

The growth-form distribution along a gradient of increased salinity in soil (Figure 74) revealed a low correspondence between average cover values per growth-form environmental variable. Only the data set from the Knersvlakte mega-chamaephytes clearly decreased with increasing salinity whereas nano-chamaephytes increased. Micro-chamaephytes had highest cover values on relevés with intermediate salinity (1-3 mS/cm).

In the Little Karoo, mega-chamaephytes were only represented with high cover values (> 5 mS/cm) on relevés with low salinity (< 1 mS/cm). Micro- and nano-chamaephytes were quite evenly distributed along the gradient. In the Richtersveld and in the central Namaqualand (Riethuis-Wallekraal area), the distribution of all growth-form types seemed to be indifferent from the edaphic salinity. In the Bushmanland-Warmbad area, maximum values of electrical conductivity which have been recorded were < 1.5 mS/cm.

Consequently, the dominance of dwarf growth forms on quartz fields is not exclusively controlled by electrical conductivity. In contrast, only in the Little Karoo and the Knersvlakte, this correspondence have been detected. It can therefore be concluded that the dominance of dwarf growth forms on the quartz fields is also influenced by other factors which are often associated with quartz fields, such as relatively low soil depth and high H⁺ concentration.

However, the low correspondence between growth forms and conductivity in the Central Namaqualand and Richtersveld can partly be attributed to the low number of relevés taken into account (46 and 82 relevés, respectively) compared to the number of relevés from the Knersvlakte and Little Karoo (> 200 relevés on quartz fields and related habitats). Therefore, the distribution might be biased by a low number of relevés with very high salinity values (> 10

mS/cm; 5 and 7 relevés in the Richtersveld and Riethuis-Wallekraal area versus 28 and 56 relevés in the Little Karoo and Knersvlakte, respectively).

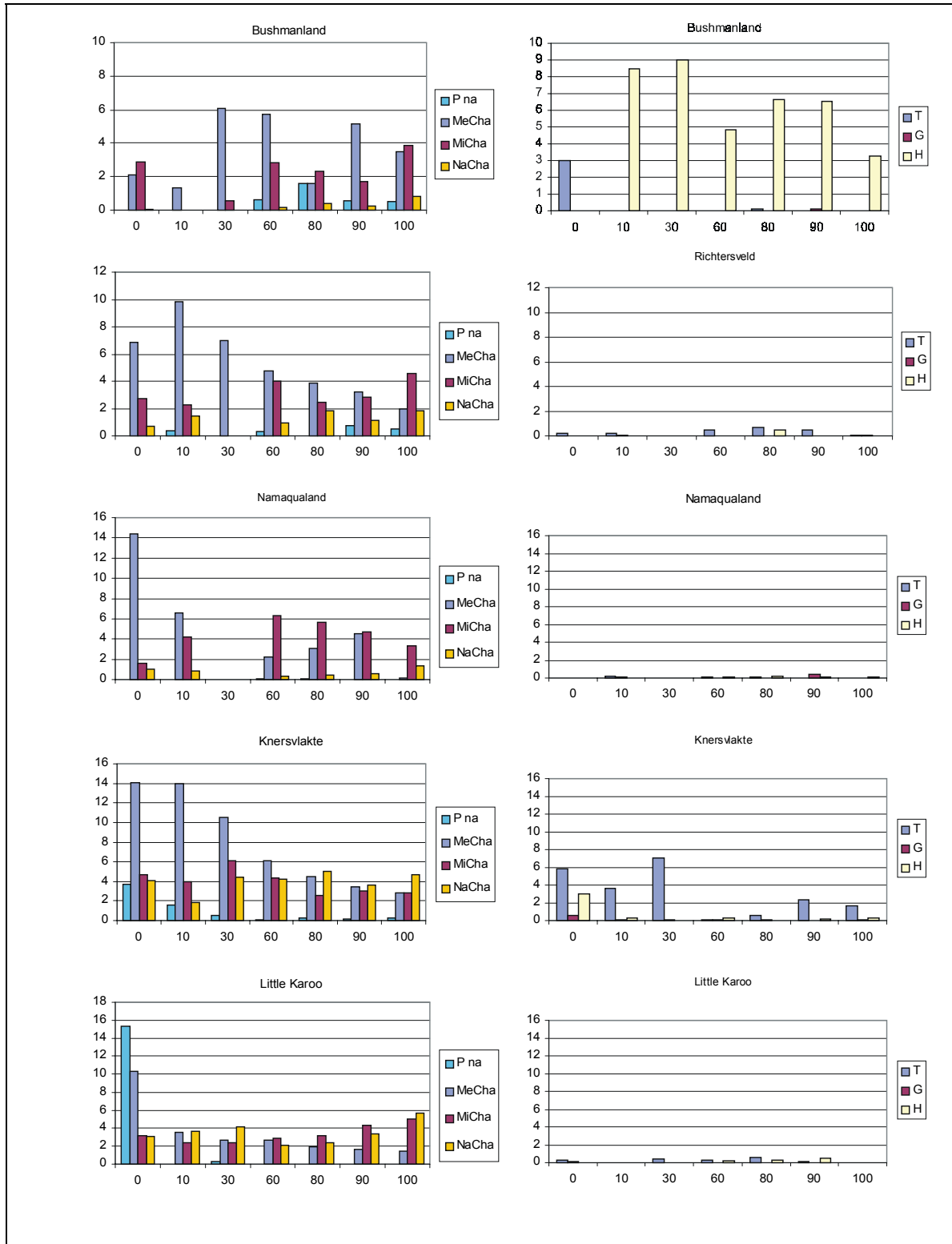


Figure 73. Distribution of growth forms (average cover values per growth form) along a gradient of increasing density (0-100 %) of quartz cover in different regions.

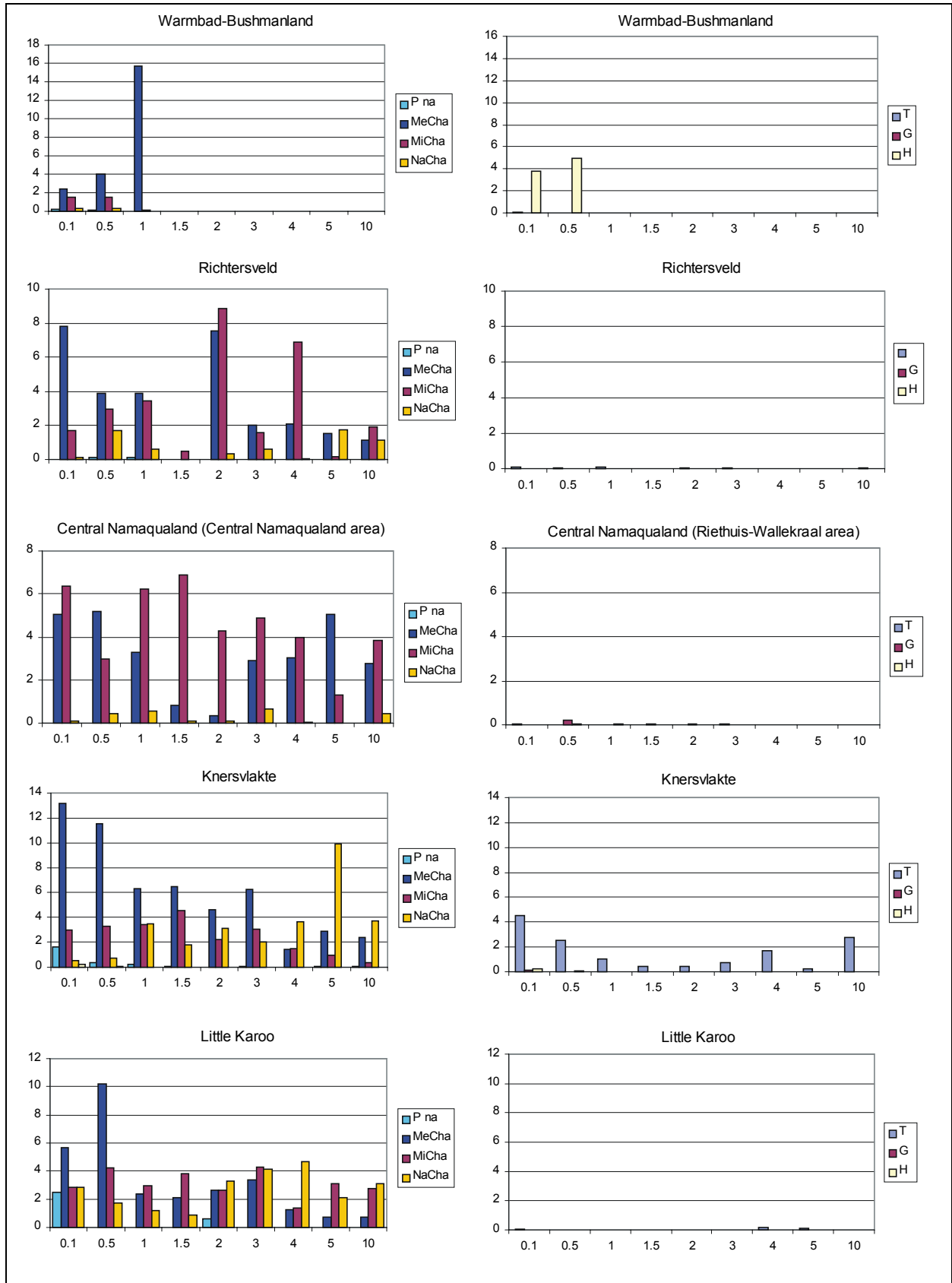


Figure 74. Distribution of growth forms (average cover values per growth form) along a gradient of increasing salinity in soil (> 0.0 -> 10 mS/cm) for the vegetation of different regions.

III.8 Microclimatic conditions

III.8.1 Radiation

In spring 1996, the incoming global solar radiation in the Knersvlakte was about 900 W/m^2 (Figure 75 above). At some exceptional days the global solar radiation went up to 1100 W/m^2 . Quartz fields and soils without quartz cover reflected about 300 W/m^2 or 30 to 40 % of the incoming global solar radiation. The net radiation on soils with and without quartz cover was between 600 and 800 W/m^2 .

Quartz fields reflected slightly more radiation than soils without quartz (Figure 75 below). The daily maximum difference between net radiation inside and outside the quartz fields was between 10 and 15 W/m^2 , i.e., 1.5 % of the global solar radiation. Quartz fields reflected about 15 % more global solar radiation than neighbouring soils without quartz cover.

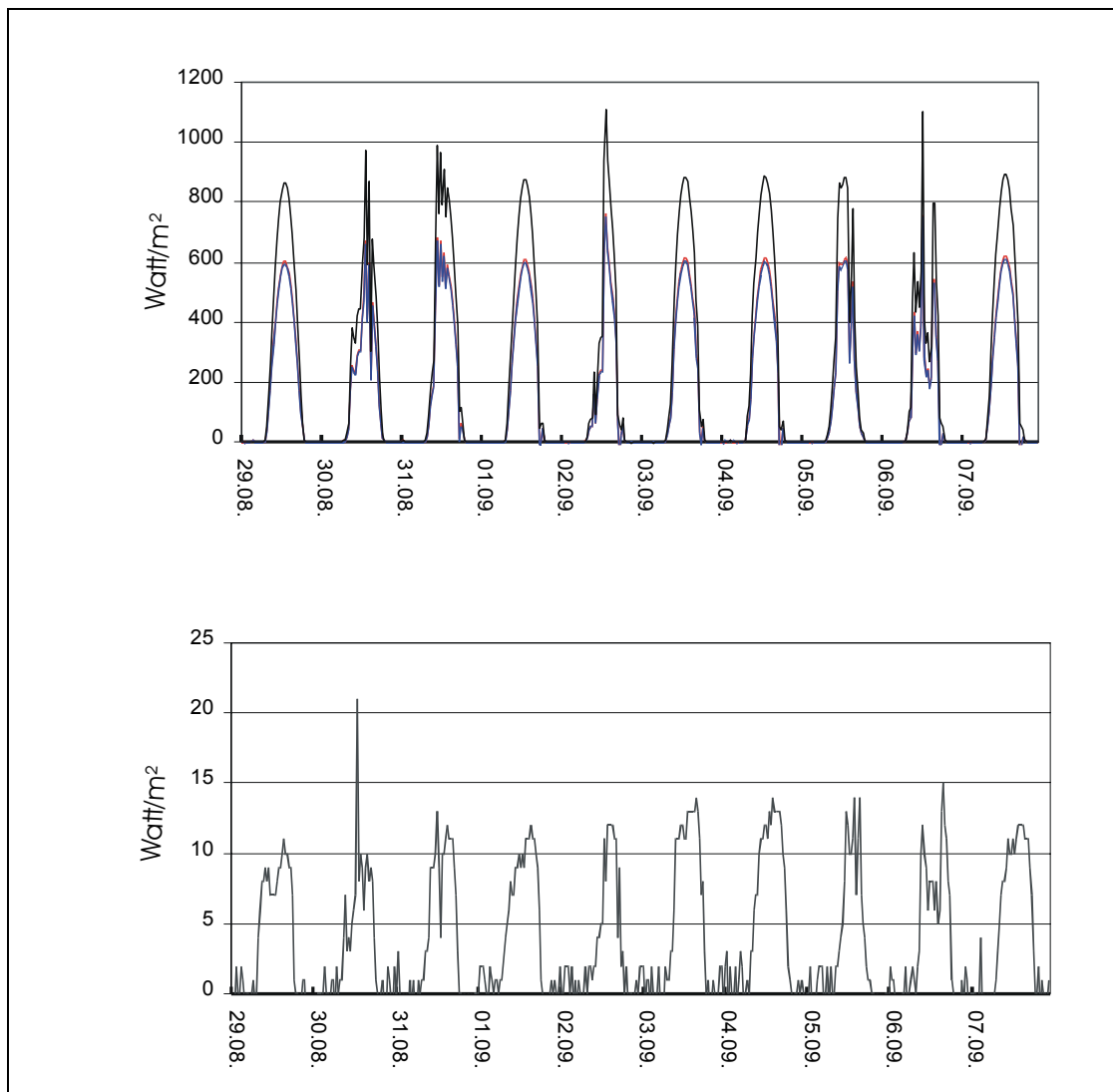


Figure 75. Above: incoming global solar radiation (300-3000 nm) (black line), net radiation on soils with (blue line) and without (red line) quartz cover. Below: difference between reflected solar radiation (300-3000 nm) by quartz fields and soils without quartz cover (quartz fields — soils without quartz cover). Knersvlakte, September to October 1996.

III.8.2 Air temperature near the ground

Figure 76 (left column) shows the air temperature at 10 mm above soil surface measured in the Knersvlakte on quartz fields and on neighbouring soils without quartz cover compared to air temperatures at 2 m height in winter and summer. The daily maximum temperatures in the course of one year (XI 1997-X 1998) are given in Figure 77.

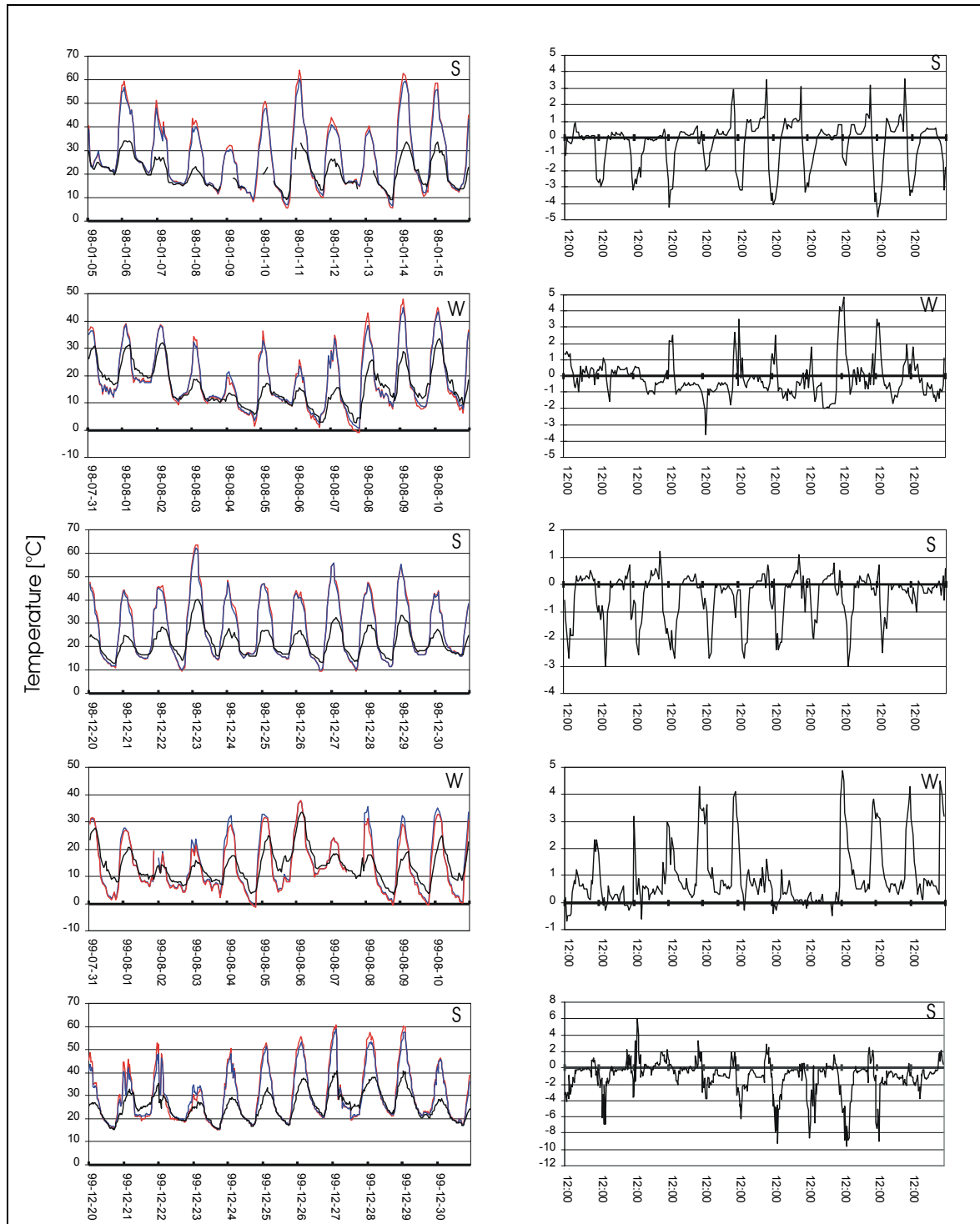


Figure 76. Air temperature 10 mm above soil surface on soils with (blue line) and without quartz cover (red line) compared to air temperature in 2 m height (black line) under winter (W) and summer (S) conditions in the Knersvlakte. Left: Course of temperatures. Right: Net differences of temperature (quartz fields — soils without quartz cover).

During winter the daily maximum temperatures of the air near the ground on both soil types stayed below 40°C for most of the days. During the coolest days, the temperatures did not exceed 25 to 30°C. In summer, the daily maximum temperatures were considerably higher (i.e., above 40°C for most of the days). During the hottest summer days, the air temperatures near the ground of both soil types reached more than 60°C and surpassed those of the air in 2 m height by > 20°C (e.g., summer 1998). The nocturnal minimum air temperature near the ground ranged between 0 and 10°C in winter, whereas it seldom went below 10°C in summer.

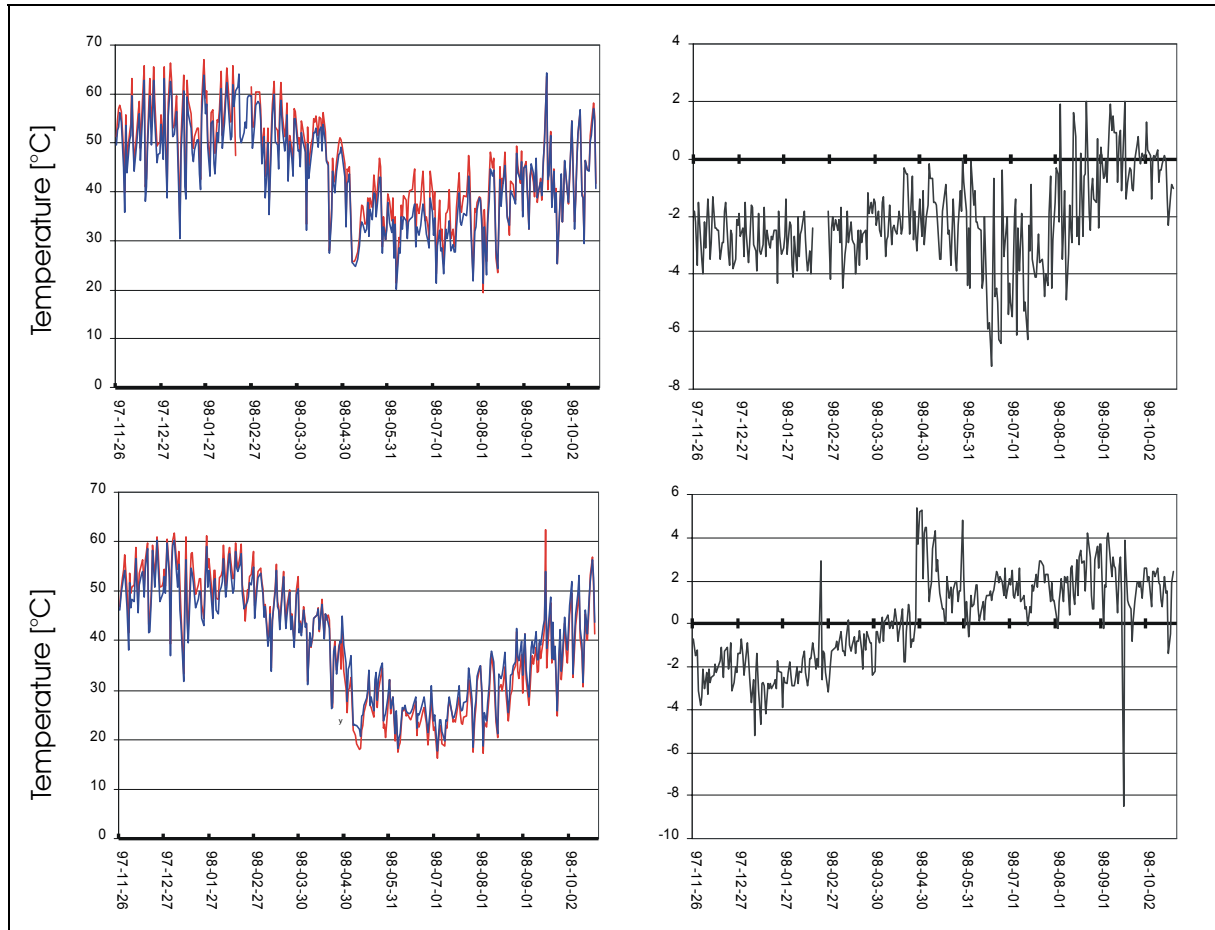


Figure 77. Right column: Daily maximum temperatures on soils with (blue line) and without (red line) quartz cover. Left column: Net differences of temperatures (with quartz — without quartz). Above: Air temperature 1 mm above the ground. Below: Soil surface temperature. Knersvlakte XI 1997- X 1998.

In summer and in winter, the daily maximum air temperatures near the ground were lower on soils with quartz cover than on soils without quartz cover for most days of the year (4–8°C, Figure 78 and Figure 79 right columns). The differences in temperatures varied extremely. In December 1999 (summer) the maximum air temperature near the ground of quartz fields was > 9°C below that of soils without quartz cover whereas the differences were merely < 3°C in December 1998. In August 1999 (winter) the air temperatures on the quartz field revealed to be even warmer (up to 5°C) than of the surrounding soil. The maximum differences were determined for the hottest time of the day between noon and 2h p.m.

III.8.3 Soil-surface temperature

The daily maximum temperatures on top (Figure 78) as well as 3 mm underneath the soil surface (Figure 79) varied between 25–40°C in winter and 40–60°C in summer. Only in December 1998,

the daily maximum temperatures were below 30°C for most of the days. The nocturnal minimum temperatures were between 0 and 10°C in winter and between 10 and 20°C in summer and ranged close to or below the air temperature in 2 m height.

In winter, soil surfaces with quartz cover had higher daily maximum temperatures than those without quartz cover. The daily maximum differences were up to 4°C. In summer the relationship was typically inverse: the daily maximum temperature on soil surface of quartz fields were up to 5°C lower than those of soils without quartz cover. In December 1998, however, very low maximum temperatures in 2 m height (< 30°C for most of the days) were determined. At that time also the daily maximum temperatures near the ground were low (> 50°C for most of the days) and the maximum temperatures of the quartz fields exceeded those of the soils without quartz fields by a few degrees.

In summer and winter, the maximum differences occurred during the hottest time of the day, between noon and 2h p.m.

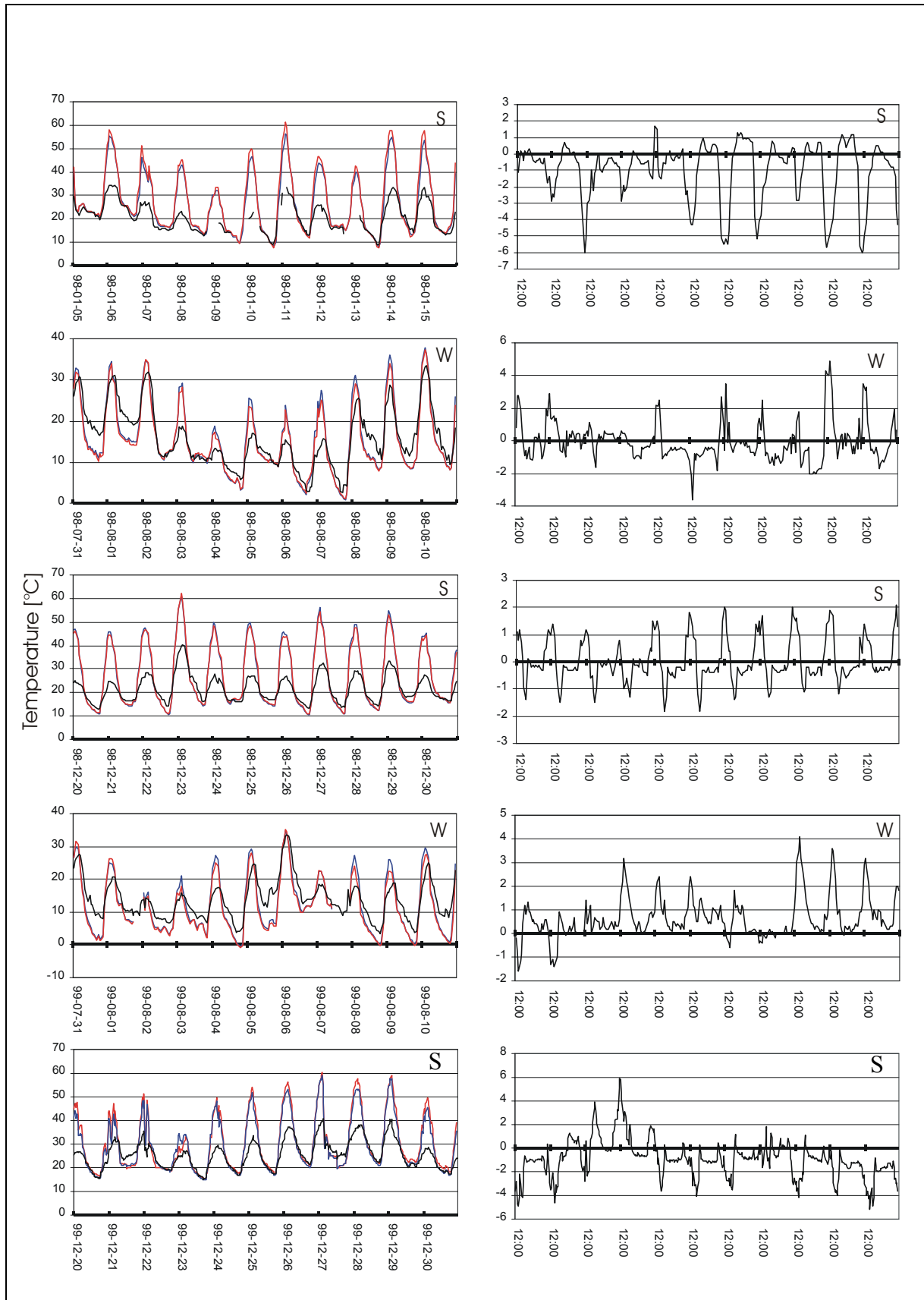


Figure 78. Surface temperature of soils with (blue line) and without (red line) quartz cover compared to air temperature in 2 m height (black line) under winter (W) and summer (S) conditions in the Knersvlakte. Left: Course of temperatures. Right: Net differences of temperatures (quartz fields — soils without quartz cover).

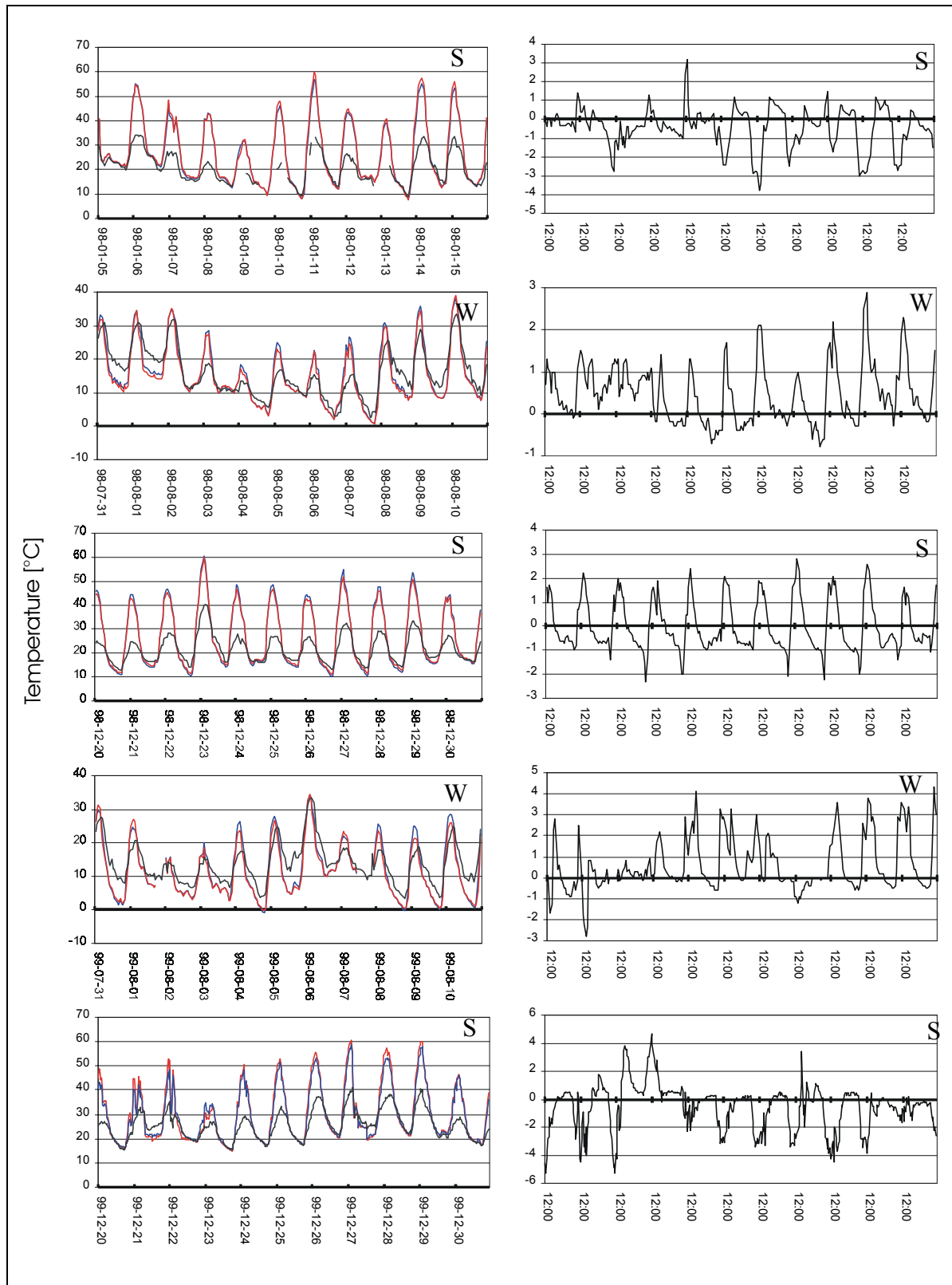


Figure 79. Surface temperature 3 mm underneath the soil surface of soils with (blue line) and without quartz cover (red line) compared to air temperature in 2 m height (black line) under winter (W) and summer (S) conditions in the Knersvlakte. Left: Course of the temperatures. Right: Net differences of temperatures (quartz fields — soils without quartz cover). Knersvlakte, December 1999.

III.8.4 Leaf-surface temperature

Measurements of leaf-surface temperature of *Argyroderma pearsonii* and *Argyroderma delaetii* (Knersvlakte) growing inside and outside of quartz fields (Figure 80) showed maximum temperatures of nearly 60°C during the summer months. The daily maximum temperatures during winter were considerably lower and seldom exceeded 35°C. The nocturnal minimum temperatures were < 5°C in winter and spring (October 1998) and > 15°C in summer (1999/2000).

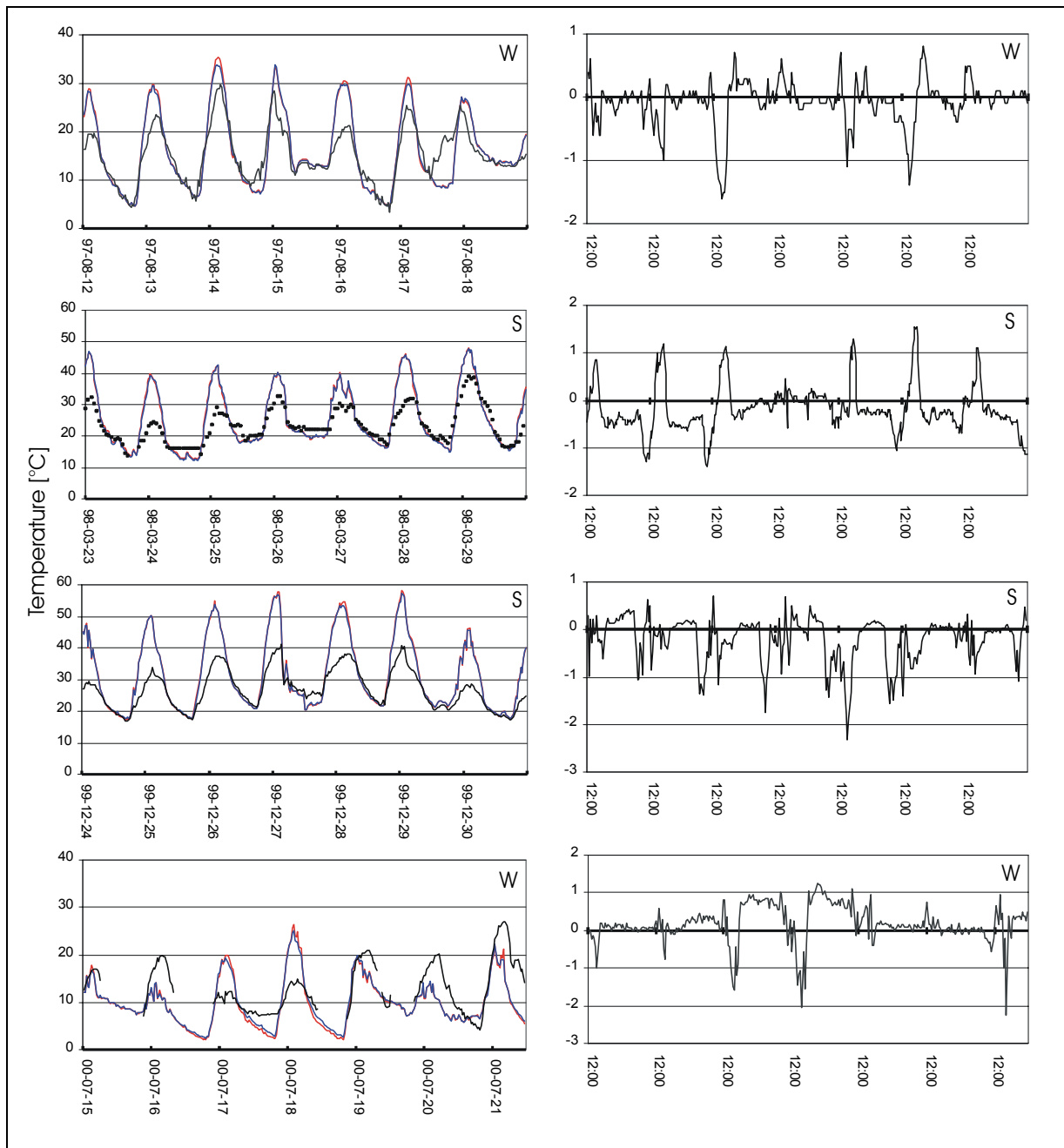


Figure 80. Leaf surface temperatures (median) of four *Argyroderma* spp. plants growing inside (blue line) and outside (red line) quartz fields compared to air temperature in 2 m height (black line) under winter (W) and summer (S) conditions in the Knersvlakte. Left: Course of temperatures. Right: Net differences of temperatures (surface temperatures of plants inside quartz fields — surface temperatures of plants outside quartz fields). Knersvlakte.

The *Argyroderma* plants growing on quartz fields showed lower maximum surface temperatures of leaves than plants growing outside quartz fields. Highest differences of 3-5°C were determined for warm winter- and spring-days. The measurements carried out in mid- and late summer showed minor differences only (on most days < 1°C).

In agreement with the studies in the Knersvlakte, measurements on *Gibbaeum cryptopodium* growing inside and outside the quartz fields of the Little Karoo (Figure 81) showed similar results: during late summer (March 1998), the *G. cryptopodium* plants on quartz fields had lower daily maximum temperatures than the specimens on the neighbouring soils without quartz cover.

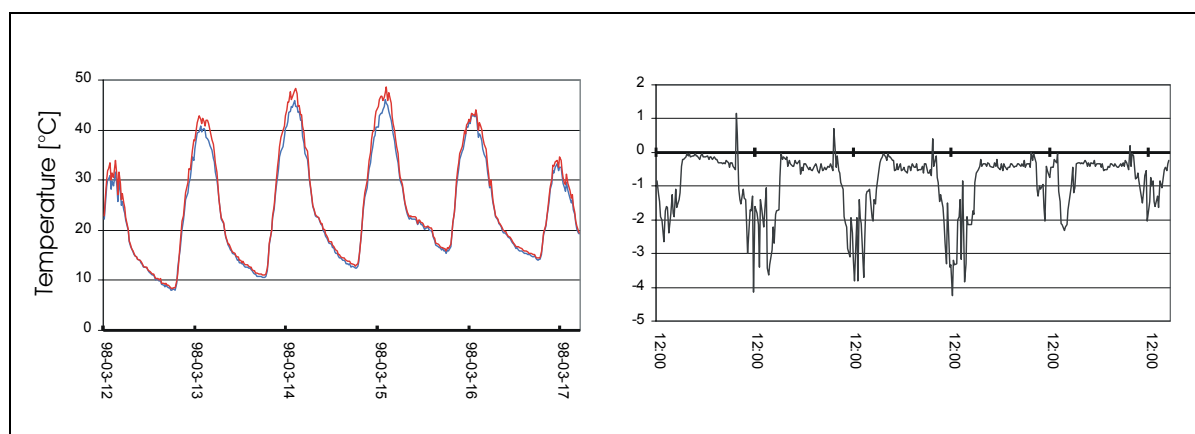


Figure 81. Left: Leaf surface temperatures (median) of four *Gibbaeum cryptopodium* plants growing inside (blue line) and outside (red line) quartz fields. Right: Differences (surface temperatures of plants growing inside quartz fields — surface temperatures of plants growing outside quartz fields). Little Karoo, March 1998.

III.8.5 Surface temperatures of a quartz stone

The daily maximum temperatures of the upper surface of quartz stones in the Knersvlakte (August 1997) ranged between 25°C and 35°C and were up to 15°C below that of the ambient air (Figure 82). During night the minimum surface temperature of the quartz stone differed considerably from that of the ambient air. It was either several degrees above or below that of the ambient air. The dew-point temperature of the ambient air during the day time was very low (10-20°C, except on the August 18, 1995). The nocturnal dew-point temperature varied strongly from night to night between several degrees above and below the temperature of the ambient air and the quartz stone.

During night the minimum surface temperature of the quartz stone differed considerably from that of the ambient air. It was either several degrees above or below that of the ambient air. The dew-point temperature of the ambient air during the day time was very low (10-20°C, except on the August 18, 1995). The nocturnal dew-point temperature varied strongly from night to night between several degrees above and below the temperature of the ambient air and the quartz stone.

Similar measurements of the surface temperatures of a quartz stone in comparison with a shale stone in the Little Karoo in September 1995 showed almost identical temperatures for both stones during night but lower maximum temperatures of the quartz stone during daytime (Figure 83). The strongest differences of up to 4°C were determined when both stones reached high maximum temperatures (September 18 and 19). In correspondence to the measurements in the Knersvlakte, the dew-point temperature varied strongly and was either above or below the temperature of the ambient air. However, it stayed below the temperature of the stones' surfaces.

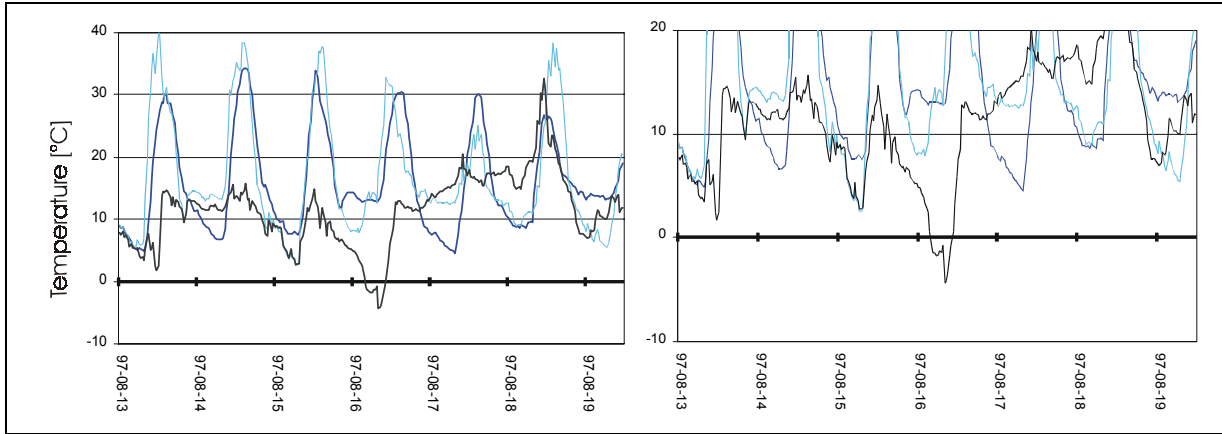


Figure 82. In situ surface temperatures of a quartz stone (dark blue line), temperatures (light blue line) and dew-point temperature (black line) of the ambient air. Above: diurnal course of temperatures. Below: Detail, showing the nocturnal minimum temperatures. Knersvlakte, August 1997.

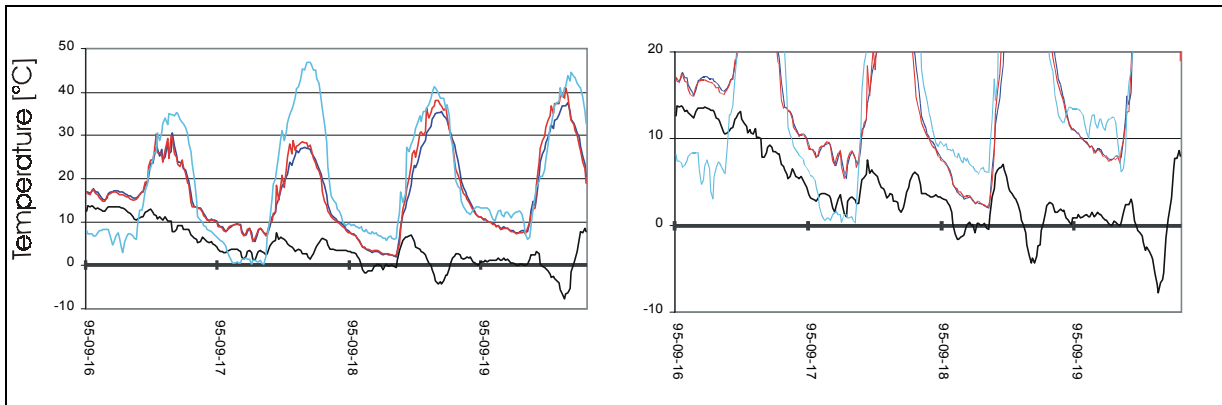


Figure 83. In situ surface temperatures of a quartz stone (dark blue line), temperatures (light blue line) and dew-point temperature (black line) near the ground of the quartz-field compared to a piece of shale (red line). Above: Diurnal course of temperatures. Below: Detail, showing the nocturnal minimum temperatures. Little Karoo, September 1995.

IV DISCUSSION

IV.1 The floral composition of the obligate quartz-field flora

The flora of the southern African quartz fields typically comprises a very narrow array of dwarf growth forms which differs considerably from the flora of the surrounding. This difference in structural and floral composition that indicates a high degree of specialisation on the quartz fields, is one of the starting-points and main issues of this study. Which taxa occur in the flora of the quartz fields? Does the spectrum of taxa differ among the regional quartz-field flora? And taking the occurrence of their next relatives into account: what is the phylogenetic and ecological background of this specialised flora?

Six main phytochoria for the QFF were defined by the occurrence of several endemic taxa. A comparative analysis of the regional quartz-field floras, revealed that the number of quartz-field species and the percentage of endemics deviated significantly from phytochorion to phytochorion, indicating different degrees of species overlap between the floras. The strongest separation of the Little Karoo from the remaining phytochoria, indicate a particularly low overlap of their species inventories. In fact, the only species that occurs in the entire area of distribution of the southern Africa quartz-fields is *Crassula columnaris* which, however, is represented by subspecies. This division can be attributed to a largely independent evolution within the two groups. The phytochoria of the Namaqualand (Knersvlakte, Riethuis-Wallekraal, Southern, and Northern Richtersveld Phytochorion) have the highest overlap in species inventory, among which the neighbouring phytochorion reveal the strongest overlap among each other.

IV.1.1 Major taxonomic groups

The southern African obligate QFF consists of angiosperms only. Algae, lichens, bryophytes, pteridophytes, and gymnosperms were not yet recorded as obligate quartz-field dwellers. The reason for this vary from group to group. Although not yet recorded as obligate quartz-field inhabitants, algae and lichens are very prominent on quartz fields. West-facing ridges and upper slopes of small hillocks with quartz layer are often covered with crust- and leaf-forming lichens. Algae are less obvious but they might be even more important. At least in terms of numbers of individuals they seem to surpass the vascular plants by far. The lower side of most of the middle sized quartz stones are covered with a dense layer of Chlorophyceae or Cyanobacteria. Due to lack of studies, only little is known about the species numbers and floristic spectrum of these algae (but see Vogel 1955, Rumrich *et. al.* 1989, 1992, and Büdel & Wessels 1991).

But according to the limited studies that have been conducted yet (Rumrich *et. al.* 1989, 1992) the algae (at least the Bacillariophyceae) show very little regional and ecological specialisation. Rumrich *et. al.* 1989, 1992 recorded Bacillariophyceae species which are also known from middle Europe where they occur in watercourses, standing waters as well as soils. If that is true for other taxonomic groups of algae as well, this contrasts considerably with the findings on vascular plants (see this study).

Pteridophyta are absent from the obligate QFF. Pteridophytes are generally poorly represented in the Succulent Karoo Flora where they represent 0.4 % of the species and infraspecific taxa (Hilton-Taylor 1996a). The absence of pteridophytes in the QFF can be attributed to the typical habitat ecology of this group. Pteridophytes are mainly restricted to hydrologically privileged

habitats. In the arid parts of southern Africa they are often found in gorges, rock crevices, and at sheltered rock faces. Quartz fields apparently, do not provide suitable growing conditions for pteridophytes.

Gymnosperms do not occur in the Succulent Karoo Flora at all (Hilton-Taylor 1996a). The arid areas of southern Africa in general, but the quartz-field habitats in particular, do not match with the ecological niches typically occupied by recent gymnosperms. Moreover, gymnosperms seem to be also excluded by their growth forms: gymnosperms never evolved other growth forms than phanerophytes which are lacking in the growth-form spectrum of the QFF (and are rare in the SKF). South Africa on total only comprises one indigenous gymnosperm genus which comprise three indigenous species (Leistner 2000).

Among the angiosperms, dicotyledonae represent the most important group within the obligate QFF. The extremely low species to family ratio within the monocotyledonae reveals poor speciation within this taxonomic group. In fact, as will be discussed below, there are only two monocotyledonous families that contribute more than two species to the QFF (Asphodelaceae: 7 species and Iridaceae: 3 species). The specialisation on quartz-field habitats of the few singular taxa within the remaining four monocotyledonous plant families seems rather to be due to random events than based on particular pre-adaptations of the respective families. Adaptive radiation on quartz fields - if it occurs at all (*Bulbine* in the Knersvlakte?) - seems to be very rare in the monocotyledonous families.

Summarising, dicotyledonae are strongly over represented in terms of numbers of species and genera compared to the entire Succulent Karoo Flora. The high percentage of closely related dicotyledonous species within the quartz-field flora indicate the occurrence of adaptive radiation on the quartz fields. The low number of monocotyledonous genera and species / subspecies and the random distribution of singular species within various monocotyledonous families, in return, indicate that monocotyledonae tend to be less successful on quartz fields than dicotyledonae. Their colonisation of quartz fields occurred rather randomly. The only monocotyledonae family that contributed more than two species to the QFF were Asphodelaceae (Chapter III.2.2).

IV.1.2 Family spectrum

The analysis of the family spectrum of the obligate QFF revealed that the Aizoaceae represent the most important family in terms of numbers of species/subspecies (> 65 % of the QFF). Crassulaceae, which represent the second highest number of species/subspecies comprise only 10 % of the obligate QFF. The remaining families (i.e., 11 families) contribute merely 5 % or less of the species/subspecies each. Compared to the flora of the Succulent Karoo (SKF), in general, the Aizoaceae, the Crassulaceae but also of Asphodelaceae and Portulacaceae are strongly over-represented in the obligate QFF. In the obligate QFF the percentage of the Aizoaceae is more than three times higher than in the SKF. Moreover, in the QFF the Aizoaceae are represented exclusively by the two subfamilies Mesembryanthemoideae Ihlenfeldt, Schwantes & Straka and the Ruschioideae Schwantes in Ihlenfeldt, Schwantes & Straka emend. Bittrich & Hartmann (Mesembryanthema, formerly acknowledged as Mesembryanthemaceae Fenzl). No member of the other subfamilies in Aizoaceae (Aizoaceae s.str.) belong to this flora. However, the figures given by Hilton-Taylor (1996a) for the SKF refers to the Aizoaceae s.l. Consequently, over-representation is even stronger for the Mesembryanthema whereas the remaining subfamilies of the Aizoaceae (Aizoaceae s.str.) are clearly under-represented within the QFF.

Besides the strong over-representation of the Mesembryanthema and the other families mentioned above, four families that belong to the most important families of the SKF in terms of numbers of species and infraspecific taxa are completely absent from the QFF: Fabaceae s.l. (incl.

Mimosoideae, Caesalpinioideae, Papilinoideae), Poaceae, Scrophulariaceae, and Oxalidaceae. The latter family is only represented in the SKF by the genus *Oxalis* L. (114 species, Hilton-Taylor 1996a). The absence of *Oxalis* species from the QFF may be also due to the general lack of knowledge about the genus, which - due to its geophytous life strategy - is strongly underrepresented in collections. Consequently, the occurrence of *Oxalis* species within the obligate QFF cannot be entirely excluded. Poaceae, Fabaceae, and Scrophulariaceae mainly comprise non-succulent species (Leistner 2000) which might be one reason for the absence from the quartz-field flora.

There are two different processes that might have been responsible for the high percentage of taxa of Mesembryanthema and Crassulaceae within the obligate QFF. For each of the two highly over-represented families, i.e., Aizoaceae (represented by Mesembryanthema) and Crassulaceae, one of the following processes seems to match.

(A) Taxa evolved at and in adaptation to the quartz fields with subsequent adaptive radiation:

This seemed to have happened in the **Mesembryanthema** which comprise a high number of genera that are largely or entirely restricted to quartz fields (Chapter III.2.3). Some of the quartz-field genera are considerably rich in species (*Argyroderma*, *Dicrocaulon*, *Dinteranthus*, *Gibbaeum*) others are monotypic (*Aspazoma*, *Muiria*) or nearly so (e.g., *Meyerophytum*, *Oophytum*, *Schlechteranthus*). These species-rich quartz-field genera often have a restricted range-size of distribution and are endemic or nearly endemic to one of the phytochoria of the QFF (Chapter III.2.4).

(B) The colonisation of quartz fields occurred several times convergently within particular taxonomic groups thus resulting in a few to several quartz-field species in generally specious genera:

The **Crassulaceae** family comprise only five indigenous genera in South Africa (*Adromischus*, *Crassula*, *Cotyledon*, *Tylecodon*, and *Kalanchoe*, Leistner 2000). All genera except *Kalanchoe* Adans. occur in the distribution area of the southern African quartz fields whereas only three genera contribute species to the obligate QFF. *Cotyledon* L., which does not contribute any species to the QFF. Also, there is only one species of *Adromischus* Lem. (*A. nanus*) that is restricted to the quartz fields. *Crassula* L. and *Tylecodon* Tölken, however, belong to the most species-rich genera within the obligate QFF (Table 23), providing ten species / subspecies (*Crassula*) or five species (*Tylecodon*) to the obligate QFF. The quartz-field taxa within *Crassula* L. are ascribed to three subsections of the subgenus *Crassula* (Tölken 1977a). A detailed phylogenetic analysis of the genus is not available yet (but see t'Hart 1995). Therefore, it cannot be determined whether the specialisation on quartz fields happened several times independently in each genus in Crassulaceae or whether there were merely three events, one in each section. The broadly scattered distributions of the quartz-field taxa of *Crassula* and *Tylecodon*, which are occur in several phytochoria indicate that a strong radiation within particular taxa did not take place but that the colonisation most probably happened several times independently.

Both hypothesised developments presume that there are particular abilities (pre-adaptations) within the families or at least within the genera that allow a frequent colonisation of the quartz fields or an adaptive radiation on this habitat. Moreover, both versions explain the same procedure at different stages of evolution. The singular species that enters the quartz fields in version B can theoretically be the initial stage of a radiating genera as described for A.

IV.1.3 State of taxonomy within Mesembryanthea and its implication for the floral analysis

Monotypic or nearly monotypic genera often represent unsolved taxonomic problems. Some monotypic genera of the quartz field flora have been sunk recently (*Maughaniella* in *Diplosoma*, Ihlenfeldt 1988 and *Dactyloopsis* in *Phyllobolus*, Gerbault 1995, *Muiria* in *Gibbaeum*, Thiede & Klak in Goldblatt & Manning 2000 - the latter recombination could not be considered for the floral analysis of the present study). Also the monotypic position of *Aspazoma* has been questioned: Gerbault (1995) suggests a close relation to the other stem-succulent genera of Mesembryanthea, *Brownanthus* in particular (Pierce & Gerbault 1997), whereas Klak & Linder (1998) stressed that the stem-succulence and other character states they have in common are plesiomorphies. Due to their ambiguous taxonomic status and the lack of knowledge about their next relatives, monotypic genera are difficult to interpret in terms of evolutionary tendency on quartz fields.

Moreover, there are several unsolved taxonomic problems within Mesembryanthea taxa. This applies in particular for the delimitation of certain genera (for instance the role of *Imitaria* N.E. Brown in *Gibbaeum* Haworth, J. Thiede, pers. comm.) and the state of monotypic genera (i.e., *Muiria*, *Aspazoma*). Moreover, those species which are interesting for laymen and succulent collectors (*Lithops* and *Conophytum* in particular) show a high number of infraspecific taxa. Also here thoroughly taxonomic studies based on additional, non-morphologic (molecular) characters seem to be needed. Due to the fact that vast parts of the Succulent Karoo were (compared to its species richness) poorly explored by botanists yet, the data on the distribution and habitat ecology of most of the species are incomplete.

It is evident that the analysis given above, only mirrors the present state of knowledge. Due to the species richness, the flora of the Succulent Karoo, the main distribution area of the quartz fields needs further studies. Within the Mesembryanthea, the most important taxonomic group of the Succulent Karoo in general (Hilton-Taylor 1996a) and of the flora of the quartz fields in particular, the inter- and infrageneric relationships still seem to be vague and unsolved: A number of monotypic or species-poor genera (e.g., *Aspazoma*, *Meyerophytum*, *Muiria*, *Oophytum*, *Schlechteranthus*) make the need for further taxonomic studies emerge. Several of the quartz species belong into such small genera.

Such uncertainties also influence the number of genera per family and thus have to be kept in mind when comparing and discussing the family spectra of QFF and the SKF.

IV.1.4 Outliers in the phytogeographical analysis

Eight taxa, all Mesembryanthea (Aizoaceae), were omitted from the ordination due to their deviant occurrence. *Diplosoma retroversum* is the only species that occurs on isolated quartz fields between Knersvlakte and Cape Town near the coast, in a far distance to the other phytochoria and with no obvious correspondence with any other quartz-field taxa. *Schwantesia borcherdsii* is found in the Bushmanland where it occurs on quartz fields with a very restricted range-size of distribution (QDS 2920AD only, Zimmermann & Hartmann 1995). It had to be omitted from the analysis since its distribution does not overlap with that of any other quartz-field species of the Bushmanland-Warmbad Phytochorion. However, due to its geographical vicinity to the other QDS of the Bushmanland-Warmbad Phytochorion, *Schwantesia borcherdsii* was included into the quartz-field flora of this phytochorion.

Acrodon quarvicola, *Gibbaeum esterhuyseniae*, and *Gibbaeum haagei* represent a particularly interesting group of quartz-field inhabitants that occur south of the Langeberge which form the southern borderline of the Little Karoo. This area receives markedly higher precipitation (459 mm /a, Weather Bureau 1988 for Riversdale) than the particularly dry Little Karoo (244 mm/a in Oudtshoorn or 318 mm/a in Montagu, Weather Bureau 1988). Due to the higher precipitation, the area south of the Langeberge is characterised by intensive agriculture. Most of the plains and valleys are ploughed and subjected to cattle and ostrich farming or cornfields. Only some isolated hillocks or shallow outcrops that are surrounded by extremely shallow soils are still undisturbed and fairly pristine. Several of these leftover hills consist of quartz veins. Such habitats are the to-date only and very isolated habitats of the three quartz-field taxa. *Gibbaeum esterhuyseniae* has been recently re-discovered near Stormsvlei but nevertheless considered as a very endangered taxon (Anonymous 1998; Hilton-Taylor 1996b). Also *G. haagei* is only known from very few restricted localities between Swellendam and Malgas (3420AA-BC) (Glen 1974). It occurs sympatrically with a still undescribed *Limonium* species (L. Mucina, pers. comm.), which is most probably also a quartz-field dweller. *Acrodon quarvicola* is recorded only from quartzitic slopes near the coast at Cape Agulhas (Hartmann 1996). It is quite likely that the former distribution of the taxa was far more widespread. However, even the present distribution may turn out to be less patchy and isolated if the isolated hills were searched intensively. The quartz fields south of the Langeberge can be regarded as (relict of) a fairly species-poor quartz-field phytochorion. The genus *Acrodon* occurs exclusively south of the Langeberge (Hartmann 1996) whereas *Gibbaeum* is largely restricted to the Little Karoo.

Glottiphyllum oligocarpum, *Glottiphyllum peersii*, and *Pleiospilos nelii* inhabit the southern fringe of the Great Karoo between the Little Karoo in the west and Steytlerville Karoo in the east. The density of quartz-field taxa is very low in this area, which can be attributed to the low density of quartz-field habitats.

Consequently, both the area South of the Langeberge and the area between the Little Karoo and the Steytlerville Karoo in the Eastern Cape can be acknowledged as species-poor phytochoria. In the area south of the Langeberge, agriculture seems to have a strong impact on the quartz-field habitats and hence the quartz-field flora. It is therefore hypothesised that not all quartz-field taxa of that area are known to science yet. The flora probably used to comprise more species and the populations had a denser and broader distribution than they are known today. The low density and number of quartz-field species in the Eastern Cape can be attributed to the poor state of knowledge about the area which has not been investigated within this study.

IV.2 Indications for the age and the history of the quartz-field flora

The contemporary distribution of the obligate QFF, – the phytogeographical pattern – can give insight into the genesis and history of the specialised flora (Cox & Moore 1993, Spellerberg & Sawyer 1999).

The major questions are: do the regional QFFs of the phytochoria differ from each other with respect to floristic and growth-form composition and what might be the reason for such a difference? Are there centres of origin from where the taxa spread into neighbouring phytochoria? Which are the putative ancestors of the quartz-field species?

To discuss the age and history of the quartz-field flora, first the formation of stone pavements and the palaeo-environmental conditions as the most important prerequisites for the evolution of the flora will be considered. Then a hypothesis on the history of the flora will be presented. Subsequently, the phytogeographical patterns are re-considered in order to test the hypothesis.

IV.2.1 The formation of stone pavements

Quartz fields as defined for this study are stone pavements. Such types of soil surface occur in different environments ranging from periglacial to mountain areas but is particularly common in hot deserts (Cooke *et. al.* 1993). Although named differently in different regions (e.g., *hamada* or *reg* in North Africa and Middle East, *gibber plains* or *stony mantles* in Australia, *desert pavements* in North America) and adopting a variety of different forms, they are largely comparable world wide. Stone pavements are mainly found in open, poorly vegetated areas where coarse and fine soil particles coexist in (mainly alluvial) deposits (Cooke & Warren 1973, Cooke *et. al.* 1993). Due to their frequent occurrence, there are numerous studies on their geomorphology. Since such studies give insight into the origin and the approximate age of desert pavements, a short review is given in the following.

There are three different processes that are discussed in literatures as being responsible for the formation of stone pavements, namely a) deflation, b) fluvatile erosion, and c) upward migration of stones.

- a) The role of deflation for the formation of desert pavements was discussed in the first half of the last century (Walther 1924, Free 1911, Moulden 1905). A high silt : clay ratio has been cited as an clear indicator for the deflation of the finest fraction (clay) by wind (e.g., Lustig 1965). In more recent publications, deflation is not entirely rejected as a possible agent of stone pavements but its dominating role has been questioned (Sharon 1962, Cooke & Warren 1973, Cooke *et. al.* 1993): it has been argued that visible signs of wind abrasion on the stones at the soil surface are scarce. Also, loose fine material is particularly unusual in arid areas; instead, the surface layer is often stabilised by thin soil crusts and underlying vesicular layers which effectively protect the surface from erosion. Bagnold (1953) showed that the smaller the particle (< 0.1 mm), the higher the wind velocity which is necessary to lift the particle up. Shrubby vegetation which occurs even in arid areas, however, may reduce winds to below the requisite threshold velocities.
- b) The role of fluvatile erosion for the development of stone pavements has been shown by more recent studies based on experimental removal of stone pavements such as those by Sharon (1962) and Lowdermilk & Sundling (1950, cited in Cooke & Warren 1973). Based on his experiments, Sharon (1962) suggests that surface runoff is the dominant process of pavement formation in Israel. He argues that due to the forming of surface crusts, wind erosion plays an important role only for a short period just after the removal of the stone cover, until newly formed crusts cover the soil surface again. Lowdermilk & Sundling (1950) removed stone pavement along a gradient of increasing inclination under identical rainfall conditions. They showed that the amount of fine-material removal increased directly with the gradient. As the experiment proceeded new stone pavements were re-established, first on steeper slopes and later on the gentle slopes. The impact of water erosion depends on various factors such as the intensity of rainfall (affecting the effect of raindrops on particle detachment) and the amount of runoff (which affects the removal of dislodged particles). The latter may be promoted by steeper slopes as well as by reduced infiltration of soil because of crusts.
- c) The upward migration of stones as one factor that promotes the formation of stone pavements has been shown by laboratory experiments (Springer 1958, Jessup 1960, Corte 1963, Inglis 1965). According to Inglis (1965) the following processes may take place: when frozen, the volume of the fine-material increases and lifts the coarse particles by adhesion of the ice to the coarse particle. Due to the rigidity of the coarse particle, a cavity would be left beneath it which - subsequently - will be filled by unfrozen fine-material. When thawing, the

volume of the fine-material decreases again, but coarse particle does not move back into its previous position which have been filled up by fine-material in the meanwhile. Consequently, the coarse particle will be lifted relatively to its surrounding fine material. The mechanism described by Cortes (1963) is more complex, taking the amount of water between the ice-water interface into account. Obviously, there is some disagreement on the precise mechanism. Comparative effects can be promoted by drying and wetting of soils as have been shown by Springer (1958).

It can be assumed that these three agents often operate together, simultaneously or in a sequence. In most cases it is impossible to determine which process played the major role and similar-looking pavements may be of totally different origin (Cooke & Warren 1973; a schematic flow diagram in Amit and Gerson (1986) gives an impression of the complexity of the processes of the development of the Reg soils).

IV.2.2 Age of the stone pavements

Corresponding to the various different mechanisms of formation, the ages of stone pavements differ considerably. One of the few quite precise datings of the age of desert pavements was published by Amit and Gerson (1986) for *Regs* from northeast Africa. A sequence of fifteen successive surfaces of alluvial fans were dated between 14000 years BP and recent (Holocene). Other pavements, however, seem to be comparatively old, having developed before the last glacial (Cooke *et al.* 1993). The re-establishment of pavements within a few years only after the experimental removal of the pavement by Sharon (1962) indicate that the formation of pavements can even be a very recent and short-term events. Sharon's experiment (Sharon 1962) also reveals that pavement formation can take place under present climatic conditions of the Northern Negev. The present climate in Israel does not differ considerably from that in the winter rainfall zone of southern Africa. Particularly the amount and seasonality of rainfall (about 100 mm/a, mainly in winter) corresponds well with the conditions of the regions with frequent occurrence of quartz fields in the Succulent Karoo (20-290 mm/a, Milton *et al.* 1997).

Desert pavements exert an important control on surface stability and protection from erosion and can therefore be seen as a substitute for vegetation cover which is usually low or entirely absent where desert pavements occur. The absence of plants may be caused by chemical and physical features of the pavement soils: comparative studies of soils inside and outside of pavements in Arizona by Musick (1975) have shown that the pavement soils have relatively high salinity, relatively high exchangeable sodium percentage (ESP) and consequently high alkalinity, high deflocculation of soil colloids and hence low infiltration capacity. According to Musick, the latter aspect is of highest importance for plants. The description of the chemical and physical soil conditions of the quartz fields (Chapter III.6) will show that also some of the quartz fields are characterised by high sodium contents and high salinity.

IV.2.3 Palaeo-environmental conditions in South Africa

The above review on the mechanisms of the formation and the age of stone pavements in general revealed that quartz fields could have either be developed recently, i.e., in the Holocene, or formed even during the last interglacial. The to-date distribution of stone pavements as well as the processes that may promote their formation indicate that the occurrence of open, unvegetated areas represents the most important preconditions for their formation. Lack of vegetation is either due to climatic conditions (aridity or very low temperatures / short growing seasons) and / or soil conditions (toxic or very saline soils). There is no doubt that the present

environmental conditions in the western part of southern Africa are suitable for the formation of quartz fields. However, if the quartz fields were older, there should have occurred similarly suitable climatic conditions in the past. Therefore, in the following section a short review on the present state of knowledge about the palaeo-climatic conditions of southern Africa since the late Tertiary will be given.

During the early and late Tertiary, subtropical conditions prevailed in the Karoo (Partridge 1993, Meadows & Watkeys 1999) supporting woody, mesic floras (Bamford & De Wit 1993, De Wit & Bamford 1993). At the late Tertiary (late Miocene) when the Antarctica ice sheet was formed the environmental conditions deteriorated drastically towards cooler and dryer conditions. As a consequence of the forming ice sheet the Benguela current offshore south-western Africa was intensified (Siesser 1980, Coetzee, 1978, Linder *et. al.* 1992, Dingle *et. al.* 1996, Scott *et. al.* 1997). At the same time the winter rainfall climate developed (Axelrod & Raven 1978). Most probably, the modern biomes were established during this time (Partridge 1993). Arid conditions seem to have prevailed in southern Africa since the end of the Tertiary.

During the Quaternary period southern Africa was not directly affected by ice sheets but the global glacial influenced the climate of the subcontinent significantly: dry and cool conditions (5-6°C lower than at present, Partridge 1993) occurred in the central and eastern parts of southern Africa during the glacial phases. This alternated with warmer and wetter interglacial phases (Partridge *et. al.* 1990, Partridge 1993, Meadows & Watkeys 1999). Such findings were mainly based on palynological analyses of dung middens of common rabbit-sized herbivore *Provacia capensis* (rock hyrax) (Scott 1994, Scott & Bousman 1990, Scott & Coorenmans 1992, Scott & Vogel 1992). In the west coast and adjacent interior the Last Glacial Maximum appears to have been associated with greater moisture availability. This has been shown by fossil pollen preserved in cave sediments at Elandsbay on the west coast (~23°S, Cowling *et. al.* 1999a, Parkington *et. al.* 2000) and in the Richtersveld mountains (~27° S) (Scott *et. al.* 1995). The fossil findings at both sites indicate the occurrence of relatively humid conditions during the Last Glacial Maximum which supported arid Fynbos vegetation in the Richtersveld. The Last Glacial Maximum (~21000 - 16000 years BP) was followed by a warming and a hypsithermal period between 7000 and 6500 years BP (Meadows & Watkeys 1999) providing temperatures of about 2°C higher than at present (Partridge 1993). Since then, the climate deteriorated slightly until today. This post-glacial climate change has major implications for the history of the Succulent Karoo vegetation in general and of the quartz field flora in particular.

Based on bioclimatic modelling (Rutherford *et. al.* 1996), well-founded palaeoecological information and current-day phytogeographic patterns, Midgley *et. al.* (2001) reconstructed the vegetation history of the western Succulent Karoo and the Fynbos Biome. They indicate that during the Last Glacial Maximum, under cool and wet conditions, the western part of the recent Succulent Karoo Biome was almost entirely covered by Fynbos vegetation whereas the Succulent Karoo vegetation was restricted to arid areas further north and to a few arid relictual islands. Such retreats were identified in parts of the Richtersveld mountains, the Knersvlakte, small areas along the west coast and of the northern Tanqua Karoo. With the climatic deterioration since 15000 years BP, the Fynbos vegetation retreated southwards to its present core area and the Succulent Karoo vegetation expanded from its glacial refugia to about its present distribution. Midgley *et. al.* (2001) argue that the interface between Fynbos and Succulent Karoo was thus repeatedly subject to latitudinal shifts (during glacial and interglacial changes). Midgley *et. al.* (2001) interpret the repeated expansion and contraction as the main mechanism as responsible for the unparalleled species richness of the Succulent Karoo and the Fynbos (Myers *et. al.* 2000).

According to the reconstruction of the palaeo-environments, quartz-field habitats could have been formed during the interglacials. They thus can be either of palaeo or recent origin. At the

present state, the question about the age of the quartz fields has to remain unsolved. However, if the model by Midgley and co-workers proves right and Fynbos vegetation covered the area of the present Succulent Karoo during the last glacial, the present distribution of the quartz-field flora must be of very recent origin. This would have been mirrored in its phytogeography and pattern of diversity.

Therefore, the hypothesis by Midgley and co-workers shall be tested by interpreting the floral correspondence between the quartz-field phytochoria (Chapter IV.2.4), the distribution of particular taxonomic lineages (Chapter IV.2.5), the patterns of diversity (Chapter IV.2.6), and the hypothetical floral history of the obligate QFF of the Knersvlakte (Chapter IV.2.7).

IV.2.4 Correspondence between the phytochoria

The floristic correspondence between the quartz-field phytochoria as a base for a floral historical reconstruction shall be focussed on the distribution of genera and infrageneric taxa within the quartz-field flora. With respect to the number and relative share of quartz-field species within the genus, four groups of genera can be distinguished:

- a) Genera with a high number of quartz-field species / subspecies which represent the majority of the entire genus (e.g., *Argyroderma*, *Dicrocaulon*, *Dinteranthus*, *Gibbaeum*, and *Monilaria*).
- b) Species-poor or monotypic genera which are entirely or largely restricted to quartz fields (e.g., *Aspazoma*, *Diplosoma*, *Ihlenfeldtia*, *Jacobsenia*, *Meyerophytum*, *Muiria*, *Oophytum*, *Polymita*, and *Schlechteranthus*).
- c) Genera with a high number of quartz-field species which, however, represent a small share of the entire genus only (e.g., *Bulbine*, *Conophytum*, *Crassula*, *Lithops*, and *Tylecodon*).
- d) Specious genera that were only represented with single species in the obligate QFF (e.g., *Adromischus*, *Androcymbium*, *Lasiopogon*, *Lachenalia*, *Oedera*, *Pentzia*, *Strumaria*, and *Zygophyllum*).

The genera with a high to very high share of quartz-field taxa, as in group a) and b) are particularly interesting with respect to the floral history of the obligate QFF. Monotypic or species poor genera (b), however, are often difficult to interpret. Genera that are compiled under group c) and d) are scattered broadly over the distribution area of the quartz fields in general (Chapter III.2.4). There is no indication for an adaptive radiation on the quartz fields within these genera nor any close relationships between the species. Obviously the colonisation of the quartz fields occurred several times independently in these groups.

Unfortunately, due to the present lack of knowledge on the phylogenetic relationship of most of the taxa (Chapter IV.1.3), a well-founded historical analysis is impossible. The following hypotheses are merely speculations that shall only be taken as working hypotheses for future phylogeographical studies.

1) The Knersvlakte / Riethuis-Wallekraal correspondence

The high correspondence on species and genus level between the obligate QFFs of the Knersvlakte and the Riethuis-Wallekraal Phytochorion may indicate both, a mutual influence of the two neighbouring floras or an unidirectional floral migration from one phytochorion into the other. The presumed phylogeny and distribution of *Monilaria*, *Dicrocaulon*, and *Jacobsenia*, which are the most species-rich genera within the quartz-field flora and which occur in both phytochoria give indications for the most possible direction of migration.

According to Ihlenfeldt & Jörgensen (1973) the presumably most basic *Monilaria* species (*M. pisiformis*) and its sister species (*M. chrysoleuca*) occur in the centre of the Knersvlakte (Chapter IV.2.7). This area has also been suggested as the centre of origin of the genus. From there the more derived taxa spread to the southern and western Knersvlakte (*M. moniliformis*) or to the north into the Riethuis-Wallekraal area and northern Namaqualand (*M. scutata* ssp. *scutata*, *M. scutata* ssp. *obovata*, *M. obconica*). If this proves right, *Monilaria* obviously migrated from the Knersvlakte to the north into the Riethuis-Wallekraal Phytochorion and Southern Richtersveld Phytochorion.

In *Jacobsenia* (Ihlenfeldt 1997) the only species that is not restricted to quartz fields and the possibly less derived species (*J. kolbei*) occurs in the Knersvlakte and along the west coast to the north where it is frequently found on the acid quartz fields (Chapter III.6.2). The two congeneric quartz-field species occur each in a small area of the north-western Knersvlakte (*J. hallii*) or further north in the Riethuis-Wallekraal Phytochorion and the southern fringe of the adjacent Southern Richtersveld Phytochorion (*J. vaginata*). In contrast to *J. kolbei*, the latter are both characterised by short stems and compact growth forms. Moreover, *J. vaginata* has very unusual bladder cell idioblasts which are unparalleled in the Mesembryanthema (Ihlenfeldt 1997). Both the compact growth forms and the unusual idioblasts may be interpreted as derived character states. Consequently, *Jacobsenia* might have migrated northwards from the Knersvlakte to the Riethuis-Wallekraal Phytochorion (and Southern Richtersveld Phytochorion).

The genus *Dicrocaulon* (H.-D. Ihlenfeldt, pers. comm.) is centred in the Knersvlakte. Ten of the twelve congeneric species are endemic to this area. They are found there on acid, non-saline quartz fields. Only two *Dicrocaulon* species (*D. spissum* and *D. ramulosum*) occur outside the Knersvlakte, in the Riethuis-Wallekraal Phytochorion where they inhabit saline quartz fields (Chapter III.6.3). The phylogeny of *Dicrocaulon* is very little understood yet. Thus, no unambiguous statement on the evolutionary trend within the genus can be made. However, the significant concentration of *Dicrocaulon* species in the Knersvlakte, the unusual habitat preferences of the two northern *Dicrocaulon* taxa, and the indication for a parallel development in *Monilaria* and *Jacobsenia* may indicate that the Knersvlakte is its centre of origin. Consequently, the two *Dicrocaulon* species might have migrated to the north. A hypothesis which needs to be proved by phylogenetic studies though.

Consequently, the hypothesis on the phylogeny of the respective genera indicate an unidirectional migration of some taxa from the Knersvlakte into the Riethuis-Wallekraal Phytochorion. Therefore, the Knersvlakte can be regarded as a centre of origin of the obligate QFF of the two phytochoria. The migration of the quartz-field taxa to the north, however, resulted in the differentiation into distinct species. None of the genera mentioned above comprise quartz-field taxa on species level that occur in both phytochoria. The other genera that have quartz-field species in the Riethuis-Wallekraal Phytochorion are widespread (*Conophytum*, *Crassula*, *Othonna*, and *Phyllobolus*) and - as have been discussed earlier (Chapter III.4.4) - they seem to have colonised the quartz fields several times independently by different infrageneric groups.

2) The Southern Richtersveld / Riethuis-Wallekraal correspondence

Due to the closer contact between the QFFs of the Riethuis-Wallekraal and the Southern Richtersveld Phytochorion, lineages that most probably originate from the Knersvlakte (*Jacobsenia* and *Monilaria*, see above: Knersvlakte/ Riethuis-Wallekraal correspondence) migrated into the Southern Richtersveld Phytochorion. Other taxa which occur in the Riethuis-Wallekraal and the Southern Richtersveld Phytochorion are *Aspazoma amplexens*, *Meyerophytum meyeri*, *Crassula grisea*, and *Phyllobolus prasinus*. Due to their broad distribution and lack of phylogeographical data a definite statement about the direction of their migration can hardly be given. However, the QFF

of the Riethuis-Wallekraal Phytochorion comprises no endemic genus, but - as has been hypothesised above - seems to have been repeatedly intruded by quartz-field taxa from the Knersvlakte. Also, the widespread taxa within the QFF of the Southern Richtersveld Phytochorion and the Riethuis-Wallekraal Phytochorion, i.e., *Aspazoma amplexans* and *Meyerophytum* spp., show similar distribution patterns as *Schlechteranthus*. The latter, however, does not reach the Riethuis-Wallekraal Phytochorion but seemed to be evolved in the Richtersveld. Therefore, it seems to be more likely to assume that *Aspazoma* and *Meyerophytum* did also not originate in the Riethuis-Wallekraal Phytochorion, but rather evolved somewhere in the Richtersveld and migrated southwards into the Riethuis-Wallekraal Phytochorion. Consequently, the exchange of quartz-field taxa among the Southern Richtersveld Phytochorion and the Riethuis-Wallekraal Phytochorion possibly happened in both directions. If that assumption proves right, this would also mean that the QFF of the Riethuis-Wallekraal Phytochorion comprises components from both, the QFF of the Knersvlakte and of the Richtersveld *sensu lato*.

Beyond the influence of the southerly adjacent QFFs, some locally restricted quartz-field species seem to derive from the area of the Southern Richtersveld Phytochorion. The endemic quartz-field taxa of the Southern Richtersveld Phytochorion, which separate the QFF of the Southern Richtersveld Phytochorion from those of the Northern Richtersveld Phytochorion are either members of widespread genera (i.e., *Bulbine*, *Conophytum*, and *Lithops*) or endemic to the Richtersveld *sensu lato* (*Mitrophyllum* and *Polymita*) and are generally poor in quartz-field species (*Polymita*: 1 species and *Mitrophyllum* 2 species within the QFF). There is thus no indication for a radiative speciation in this phytochorion.

3) The Southern Richtersveld / Northern Richtersveld correspondence

The Southern and the Northern Richtersveld phytochoria share five genera, i.e., *Aspazoma*, *Meyerophytum*, *Nelia*, *Schlechteranthus*, and *Mitrophyllum*. Whereas three of the genera are entirely restricted to quartz fields, the latter is only presented with one single species in the QFF. In contrast to the Knersvlakte and Riethuis-Wallekraal Phytochorion, the shared genera are particularly poor in species numbers: *Aspazoma* is monotypic and *Meyerophytum* and *Schlechteranthus* only comprise two congeneric species each. All of them are quartz-field dwellers. The infrageneric taxonomy of *Nelia*, however, is not solved yet. The number of recognised species varies between one (Hartmann 1991) and four species (Smith *et al.* 1998). For the present study only one species (*N. pillansii*) was recognised.

According to the present state of knowledge, the genera belong into very different taxonomic groups within two subfamilies of the Aizoaceae (Hartmann 1991) (Ruschioidea: *Schlechteranthus*: *Leipoldtia* Group, *Meyerophytum* = *Mitrophyllum* Group, *Nelia* = *Dracophilus* Group; Mesembryanthamoideae: *Aspazoma*). Hence, the colonisation of the quartz fields seems to have happened in several lineages independently. However, the genera show a distinct correspondence in their distribution. Those genera which are completely restricted to quartz fields cover most parts of both phytochoria with at least one of their species (i.e., *Aspazoma amplexans*, *Meyerophytum meyeri*, and *Schlechteranthus hallii*). *Aspazoma amplexans* even stretches into the Riethuis-Wallekraal Phytochorion. In *Schlechteranthus* and *Meyerophytum* the second congeneric species (*S. maximilianii* and *M. globosum*, respectively) has a particularly restricted distribution (*S. maximilianii* is restricted to a very small area in the north-west of the Northern Richtersveld Phytochorion (2816B). *M. globosum* is restricted to the quartz fields of the Riethuis-Wallekraal Phytochorion).

The difference between the two regions which resulted in separate phytochoria, is mainly due to the impact of the obligate QFF of other neighbouring phytochoria, i.e., the QFF of the Riethuis-Wallekraal Phytochorion intrudes in the Southern Richtersveld and the Bushmanland-Warmbad Phytochorion influences the Northern Richtersveld.

4) The Northern Richtersveld / Bushmanland-Warmbad correspondence

In correspondence to the Southern Richtersveld Phytochorion, the QFF of the Northern Richtersveld houses a similar array of endemic quartz-field species that belong to widespread genera (*Conophytum*, *Crassula*, and *Lithops*). Besides that, some odd genera (i.e., *Androcymbium*, *Cheiridopsis*, *Octopoma*, *Odontophorus*, *Strumaria*) which are not found on quartz fields elsewhere, contribute singular (or two in *Odontophorus*) endemic quartz-field taxa to the Northern Richtersveld Phytochorion and thus contribute considerably to the separation of the Northern Richtersveld Phytochorion as a phytochorion on its own.

The close connection between the QFFs of the Northern Richtersveld Phytochorion and of the Bushmanland-Warmbad Phytochorion on species level is mainly due to the genera *Anacampseros* (Portulacaceae), *Conophytum* (Aizoaceae), *Ihlenfeldtia* (Aizoaceae), and *Tridentea* (Asclepiadaceae). Their pattern of distribution may reveal driving forces such as palaeoclimatic oscillations (in correspondence to the hypothesis of Midgley and co-workers (Midgley *et al.* 2001) which might have been responsible for the generally close relationship between the quartz-field phytochoria of two completely distinct Floral Kingdoms.

All quartz-field species within *Anacampseros* belong into the section *Avonia* of the subgenus *Anacampseros* (Gerbaulet 1992a). They are largely restricted to the Little Karoo and Bushmanland-Warmbad Phytochorion which lie outside the strict winter rainfall zone. In the QFF of the Northern Richtersveld Phytochorion, however, *Anacampseros* is represented by three species, two of which (i.e., *A. papyracea* and *A. recurvata*) are also found in the Bushmanland-Warmbad Phytochorion. Besides in the quartz-field taxa, several species in *Anacampseros* (e.g., *A. albissima*, *A. baeseckii*, and *A. lanceolata*) occur under winter as well as under summer rainfall conditions (Gerbaulet 1992b).

The pattern of distribution in *Anacampseros* partly corresponds with that of the genus *Conophytum* (Hammer 1993b). The widespread and species-rich genus is mainly distributed in the winter rainfall zone but is also found in the transition zone and the western border of the summer rainfall zone. Most *Conophytum* species of the obligate QFF have an very restricted range size, several of them are only known from their type locality even (Hammer 1993b, Schmiedel 2001a). The highest number of quartz-field species within *Conophytum* occur at the western border of the winter rainfall zone and in the adjacent transition zone between Springbok and Pofadder where species of various sections (*sensu* Hammer 1993b, Schmiedel 2001a) colonised the quartz fields. In addition, two widespread *Conophytum* species of the obligate QFF (*C. lithopsoides* and *C. maughanii*) cover both the Bushmanland-Warmbad Phytochorion and the Northern Richtersveld Phytochorion. Consequently, the high number of *Conophytum* species that occur close to or in the transition zone may be attributed the oscillating borderlines between the winter and summer rainfall zone. However, since the phylogeny and infrageneric groups of *Conophytum* are still poorly understood. Little can be said about the presumable direction of migration within the genus. The occurrence of the highest number of *Conophytum* species in the winter rainfall zone does not necessarily indicate that the centre of origin of the genus is there as well.

In *Ihlenfeldtia*, a species-poor genus that is completely restricted to quartz fields, the presumably more derived taxon, i.e., *I. vanzylii* (Hartmann 1992), is endemic to the Bushmanland-Warmbad Phytochorion whereas *I. excavata* is more widespread and occurs in both, the Northern Richtersveld and the Bushmanland-Warmbad Phytochorion. Hence, *Ihlenfeldtia* occurs in the transition zone between the summer and winter rainfall zone, as does its presumable next relatives (i.e., *Tanquana* and *Vanbeerdea*) (Hartmann 1992). The centres of diversity of the group is located further east, in the Pofadder Centre and in the Griqualand (Hartmann 1991).

The 17 species of *Tridentea* are mainly distributed in the summer rainfall zone of the central plateau but also stretches into the winter rainfall zone (Leach 1980). Only the section *Caruncularia* to which *T. berrei* and *T. umdausensis* belong is largely restricted to the winter rainfall zone. Among them, *T. umdausensis*, however, occurs from the north-eastern Richtersveld (eastern border of the winter rainfall zone) to the Bushmanland-Warmbad Phytochorion.

The separation of widespread taxonomic groups on a comparatively low taxonomic level into winter and summer rainfall taxa has been found for several taxa of both tropical as well as temperate elements of the southern African flora (Gerbautet 1992b, Jürgens 1992, 1995, 1997). It is interpreted as an effect of the relatively young age (5 Mio years) of the winter rainfall zone. The occurrence of several taxa in the transition zone between summer and winter rainfall zone (as in *Ihlenfeldtia* and its next relatives and *Tridentea umdausensis*) as well as the strong diversification of some taxa (*Conophytum* Hammer 1993b, *Anacampseros*, Gerbautet 1992a) along the transition zone, can possibly be interpreted as a result of a oscillating borderline of the winter rainfall zone (Gerbautet (1992b). Gerbautet points out that within *Anacampseros* infrageneric taxa of different groups show the same pattern of distribution. This, in return, may indicate that the same area was colonised repeatedly during different climatic phases.

Unfortunately, beside Gerbautet's revision on *Anacampseros* (Gerbautet 1992a,b) there are no other studies that provide insight into the phylogenetic and biogeographical relationships of such groups. Therefore, little is understand about the direction of the migration of the taxa. However, preliminary data on *Ihlenfeldtia* (Hartmann (1992) revealed that the more derived and more drought-adapted species (*I. vanzylii*) occur in the east. This can either be interpreted as a result of a shifting interface between rainfall regimes and subsequent specialisation and speciation of the eastern-most populations of *Ihlenfeldtia excavata* or of its migrating into a new, more arid habitat.

5) The Bushmanland-Warmbad Phytochorion

The obligate QFF of the Bushmanland-Warmbad Phytochorion is very poor with respect to genera of their own. Only *Dinteranthus* and *Lapidaria* are endemic to the phytochorion whereas *Ihlenfeldtia* is also found on the western border of the Northern Richtersveld Phytochorion. These three genera form part of the *Titanopsis* Group within the Ruschioideae which is restricted to the continental plateau of the subcontinent (Hartmann 1991). Besides, the *Titanopsis* Group also comprises *Lithops* and *Schwantesia*, two genera that also contribute species to the QFF. Provided that *Dinteranthus*, *Ihlenfeldtia* and *Lapidaria* are monophyletic taxa, the Bushmanland-Warmbad Phytochorion can be interpreted as a third centre of origin of the obligate QFF which is relatively poor in endemic genera though. However, the majority of the obligate QFF of the Bushmanland-Warmbad Phytochorion form part of the widespread, non-endemic genera that contribute several (*Lithops*, *Conophytum*) or a few species (*Adromischus*, *Tridentea*) to the QFF.

6) The Little Karoo Phytochorion

The Little Karoo only comprises two largely endemic genera in the local QFF, *Gibbaeum* and *Muiria*. The close relationship between *Gibbaeum* and the monotypic genus *Muiria* which will be sunk into *Gibbaeum*. Both genera form part of the Delosperma group *sensu* Hartmann (1991) which comprises no further genus of the obligate QFF. Due to the geographical and taxonomic isolation of the *Gibbaeum* (incl. *Muiria*, Thiede & Klak in Goldblatt & Manning 2000) within the entire QFF, the Little Karoo has to be recognised as a fourth centre of origin of the QFF. Although this centre is particularly poor in species and genera.

7) The spectrum of non-endemic taxa

The spectrum of non-endemic taxa comprise comparatively few Aizoaceae (Mesembryanthema) species whereas the Crassulaceae, Asteraceae, Portulacaceae, and Asclepiadaceae are over-represented. The members of Asteraceae (*Othonna*, *Senecio*), Crassulaceae (*Crassula*), and Portulacaceae (*Anacampseros*) are also these taxa which are typically found on non-saline quartz fields whereas Mesembryanthema (Aizoaceae) contribute largely to the halophytic quartz-field flora.

The non-endemic QFF also comprises a higher percentage of the less derived growth from groups, i.e., micro-chamaephytes, compact nano-chamaephytes, and “other” nano-chamaephytes, whereas subglobose and subterraneous nano-chamaephytes were under-represented in the non-endemic QFF.

8) The quartz-field phytochoria and general centres of phytodiversity

The entire quartz-field flora has been assorted into six centres of diversity and endemism which were defined as phytochoria (Chapter III.1.1). Four of them, the two Richtersveld Phytochoria, the Knersvlakte Phytochorion, and the Little Karoo Phytochorion correspond strongly with general centres of endemism (Nordenstam 1969; Werger 1978; Jürgens 1986; 1991; Hartmann 1991; Hilton-Taylor 1994; 1996a). The contribution of the regional quartz-field flora to these centres of endemism varies strongly. The Knersvlakte, for instance, which Nordenstam (1969) named Vanrhynsdorp Centre, houses more than 150 endemic taxa (Hilton-Taylor 1994) of which 63 taxa (Figure 5) - that is about 40 % - are restricted to quartz fields. All endemic genera of the Knersvlakte (*Argyroderma*, *Oophytum*) are largely or entirely restricted to the quartz fields.

The Southern and Northern Richtersveld phytochoria largely cover the Gariep Centre of endemism (Garip is the Koi-San word for Orange River, Hilton-Taylor 1994). According to Hilton-Taylor's (1994) estimates, this centre houses more than 350 endemic taxa. The contribution of the quartz-field flora (ca. 30 endemic taxa) to this centre of endemism is comparatively poor. In contrast to the Knersvlakte, the two endemic plant genera (*Dracophilus* and *Juttadinteria*, Hilton-Taylor 1994), do not form part of the quartz-field flora.

For the Little Karoo Centre of endemism the exact number of endemic plant taxa are poorly known. Hilton-Taylor (1994) estimates between 200 and 300 and assumes that this is a major centre of plant endemism and species richness. The obligate quartz-field flora (8 endemic taxa) only contributes a very small share to this high endemism. Among the endemic plant genera (*Cerochlamys*, *Gibbaeum*, and *Zeuktophyllum*) only *Gibbaeum* forms part of the quartz-field flora.

IV.2.5 Hypothetical trends in the floral history of the QFF

The six regional QFFs derived from four largely isolated centres of origin (i.e., Little Karoo, Knersvlakte, Richtersveld s.l., and Bushmanland-Warmbad area). Each of the centre is dominated by different taxonomic groups of the Mesembryanthema.

In the Knersvlakte, two subtribes, i.e., the Leipoldtiinae (comprising *Argyroderma* but also *Cephalophyllum*, Hartmann 1987) and the Mitrophyllinae (*Dicrocaulon*, *Diplosoma*, *Jacobsenia*, *Monilaria*, and *Oophytum*, Ihlenfeldt 1971b), contribute the highest number of species to the obligate QFF. Among them, Mitrophyllinae are of highest importance in the Knersvlakte which also represents the centre of diversity within the group. The most primitive taxa within the

Mitrophyllinae (*Mitrophyllum* and *Meyerophytum*, Ihlenfeldt 1971b), however, are found in the Richtersveld. It seems that the formerly widespread ancestors of the group experienced strong radiation in the south (Knersvlakte) whereas the northern taxa remained more primitive. From the Knersvlakte, several genera of the Mitrophyllinae spread to the north into the Riethuis-Wallekraal Phytochorion (*Dicrocaulon*, *Jacobsenia*, *Monilaria*) or even beyond that (*Jacobsenia*, *Monilaria*) where they differentiated into separate species or subspecies.

The largely endemic genera of the QFF of the Richtersveld form part of various different Mesembryanthema groups or subtribes: the Leipoldtiinae (*Schlechteranthus*), the Mitrophyllinae (*Meyerophytum*, *Mitrophyllum*), the Dracophilus group (*Nelia*), and the Ruschia group (*Polymita*) contribute (largely) endemic genera to the quartz-field flora. None of them conducted a similar radiation as the Mitrophyllinae in the Knersvlakte. The singular colonisation of the quartz fields by only one or two species within the *Dracophilus* and *Ruschia* Group seems to be rather due to random events than to particular pre-adaptations. In contrast to the other centres of origin, the Richtersveld area lacks particular taxonomic groups that dominate the regional QFF.

Ihlenfeldtia is closely related to *Tanquana* and *Vanbeerdea* (Hartmann 1992) which both form part of the *Titanopsis* Group *sensu* Hartmann (1991). The *Titanopsis* Group that also comprises other important quartz-field taxa (*Dinteranthus*, *Lapidaria*, *Lithops*) is mainly distributed in the central plateau of the southern African sub-continent (Hartmann 1991) in the proper summer rainfall zone. In the QFF of the Bushmanland-Warmbad Phytochorion the *Titanopsis* Group plays the most important role since all Aizoaceae species except *Conophytum* (*Dracophilus* Group) of the QFF of the Bushmanland-Warmbad Phytochorion, belong into this group (i.e., the genera *Dinteranthus*, *Ihlenfeldtia*, *Lithops*, *Schwantesia*). Which is centred in the summer rainfall zone of southern Africa (Hartmann 1991).

The two endemic genera of the Little Karoo, *Gibbaeum* and *Muiria* that contribute the majority of the obligate QFF form part of the *Delosperma* Group. The Little Karoo also represents the centre of highest density of genera of the group (Hartmann 1994). From there most of the genera spread to the east, from the Southern Karoo into to the Eastern Cape along the southern escarpment. Hence, the *Delosperma* Group occurs mainly outside the winter rainfall zone.

Summarising, the diversification in the four centres of origin of the quartz-field flora derives from completely different lineages which are centred in the respective phytochorion and hardly overlap with each other. The Mitrophyllinae and the Leipoldtiinae which are most important in the Knersvlakte but also occur in the Richtersveld, are mainly centred in the winter rainfall zone. The *Titanopsis* Group that gave rise to several quartz-field taxa in the Bushmanland-Warmbad Phytochorion are centred in the central plateau whereas the *Delosperma* Group mainly occurs south and east of the *Titanopsis* Group, outside the winter rainfall zone. This, again, stresses the low correspondence between the regional QFF. The only correspondence between the floras on genus level is based on the widespread genera that mainly occur outside the quartz fields but repeatedly colonised the quartz fields of different phytochoria (mainly *Anacampseros*, *Conophytum*, *Crassula* but also *Bulbine*, *Othonna*, and *Tylecodon*).

Consequently, the obligate quartz-field flora largely mirrors a general pattern of southern African phytogeography but only in the Knersvlakte, which houses the highest number of endemic quartz-field taxa, the quartz-field flora contributes significantly to the high number of endemics of the area. The distribution of the Knersvlakte and Richtersveld general centres of diversity correspond well with the hypothesised glacial refugia of the Succulent Karoo taxa (Midgley *et al.* 2001). In correspondence to the putative oscillation of the biome interface during the Quaternary, the origin of the Little Karoo Centre has been explained by the invasion of different taxa in subsequent waves (Hartmann 1994).

Riethuis-Wallekraal Phytochorion which does not correspond with any general centre of diversity can be interpreted as a secondary centre of endemism. This centre evolved due the post-glacial colonisation of the quartz fields by northwards migrating quartz-field taxa from the Knersvlakte.

The endemism and diversity of the Bushmanland-Warmbad Phytochorion is not mirrored by any general phytogeographical pattern and not explained by the palaeoenvironmental reconstruction. It can thus be concluded that this endemism is largely restricted to the quartz-field taxa, due to the adaptation of particular lineages to these spatial isolated and edaphically special quartz-field habitats.

It can thus be concluded that the hypothesised expansion of the Succulent Karoo flora in the post-glacial phase is supported by the reconstructed floral history of the quartz fields. The Richtersveld s.l. and the Knersvlakte, the putative glacial refugia *sensu* Midgley *et al.* (2001) are the identified as two centres of origin of the quartz-field flora. From there several quartz-field taxa spread southwards respectively northwards. The majority of the present endemics of the Riethuis-Wallekraal Phytochorion are derived from lineages that are centred in the Knersvlakte. The close relationship between the Northern Richtersveld and the Bushmanland-Warmbad Phytochorion has also to be interpreted as a result of the glacial-interglacial shifting of the interface between different rainfall regimes.

IV.2.6 Difference in diversity between the phytochoria

The floral analysis of the phytochoria revealed strong differences in species and growth-form richness between the five quartz-field phytochoria (Chapter III.3). The Knersvlakte houses the highest number of quartz-field taxa (67 taxa) and quartz-field endemics (63 taxa). The Northern Richtersveld Phytochorion has 40 quartz-field taxa of which 22 are endemic to the region. In the Bushmanland-Warmbad Phytochorion 24 quartz-field taxa occur of which 16 are regional endemics. The remaining three regional QFF merely comprise less than 20 taxa each (Chapter III.3).

Five factors can be considered to be responsible for the differences in diversity between the phytochoria: differences in age and origin of the quartz-field flora (1), differences in size (2) and density (3) of the quartz-field archipelagos as well as in their habitat diversity (4), and particular preconditions within taxonomic groups (5) that result in comparably fast adaptation and speciation. In this chapter the possible factors shall be discussed in order to conclude whether other factors than the location of the glacial refugia of the Succulent Karoo flora are rather responsible for the differences in diversity.

- 1) Differences in history: As has been stated above, very little is known about the age of the quartz-field habitats. The reconstruction of the palaeo-environment (Chapter IV.2.3) indicate that the mountainous (i.e., northern) Richtersveld and the Knersvlakte formed refugia and the resources for re-colonisation of the present Succulent Karoo Biome. Consequently, their generally high endemism and high degree of quartz-field endemics of the Knersvlakte Phytochorion and the Northern Richtersveld Phytochorion can be attributed to this historical pattern. The Riethuis-Wallekraal Phytochorion and the Southern Richtersveld Phytochorion which have been interpreted as a secondary centre of endemism (Chapter IV.2.5) are comparatively poor in quartz-field endemic. The moderately high number of quartz-field endemics in the Bushmanland-Warmbad Phytochorion are partly due to the occurrence of taxa which it has in common with the Northern Richtersveld Phytochorion. This floristic correspondence can partly be attributed to the Quaternary climatic oscillations. It can thus be summarised that the differences in diversity and level of endemism between the regional

quartz-field floras can be explained by the floral historical patterns hypothesised above (Chapter IV.2.5).

- 2) Different size of the quartz-field archipelagos. Quartz fields present island-like habitats which are grouped together to inland archipelagos surrounded by zonal soil types. The equilibrium theory of islands which have been developed by MacArthur & Wilson (1963, 1967) and subsequently discussed and elaborated by numerous authors (e.g., Whitehead & Jones 1968, Brown & Kodric-Brown 1977, Whittaker 1998) draws attention to the fact that the species-area relationship observed for biota on mainland (Preston 1962) is true for islands as well. MacArthur & Wilson also indicated a relationship between species richness of islands and their distance to the source of immigrating species. Since quartz fields often form dense patterns of smaller or larger patches and the borders of the single patches might not always be possible to determine, the theory cannot be applied to single quartz fields. But analogously with the study of Adler (1992) as well as Adler & Rosenzweig (in Rosenzweig 1995) on species richness of birds on Pacific archipelagos, the size and species richness of quartz-field archipelagos have been analysed (Figure 28). The plotting of numbers of total and endemic quartz-field taxa against the number of quarter-degree squares covered by the phytochorion revealed no linear relationship (Chapter III.3.2). The phytochoria with the largest extension (Bushmanland-Warmbad and Little Karoo Phytochoria) comprise far less total as well as endemic quartz-field species than the much smaller Northern Richtersveld and the Knersvlakte Phytochoria.

Consequently, the equilibrium theory of islands by MacArthur and Wilson does not hold for the quartz-field archipelagos.

- 3) Difference in density of quartz fields. In the relatively species-poor Bushmanland-Warmbad Phytochorion only the area around Pofadder (2919AB) and Aggeneys (2918BB) has a high density of quartz fields (and thus a higher species richness, Figure 22), whereas in the eastern sections of the phytochorion quartz fields and quartz-field taxa are extremely sparse. The Little Karoo Phytochorion comprises sections with low density of quartz fields. In return, the Knersvlakte Phytochorion which comprises the most species-rich quartz-field flora and the highest number of quartz-field species per QDS, also has the highest density of quartz fields: they almost cover the entire phytochorion. The same holds true for the Riethuis-Wallekraal Phytochorion which comprises a very small area but has a high density of quartz fields.

The number of quarter-degree squares covered by the phytochorion does not mirror the density of the quartz fields within the area.

- 4) Difference in habitat diversity. The equilibrium theory of island indicates (although not explicitly expressed by MacArthur & Wilson 1963) that one reason for the increase of species diversity is the increase of habitat diversity which increases with the size of the island. However, the increase of habitat diversity of quartz fields depends on more than the size of its area. The heterogeneity of the geology, geomorphology, and of the soil conditions are the main factors that influence the diversity of the quartz-field habitats. The geomorphology and the soil conditions strongly depend on climatic conditions. The strongest impact on the variance of species data of the quartz fields has been revealed for the variables electrical conductivity and H^+ concentration. Both variables showed the lowest mean values and lowest variance (expressed in weighted standard deviation) for the data from the Bushmanland-Warmbad Phytochorion (Table 61). This low variance can be attributed to the summer rainfall conditions of the area which are characterised by local but strong rainfall events. This kind of precipitation promotes runoff, erosion, leaching of the soils, and results in more geomorphological and soil chemical equalisation of the quartz-field habitats than in the winter rainfall zone.

Consequently, the spatial extension of the phytochorion does not mirror its environment and habitat diversity as it is implied

- 5) Accelerated radiation in geographically restricted taxonomic groups. Among the quartz-field taxa, the subtribe Mitrophyllinae (Ruschioideae, Aizoaceae) contributes the highest numbers of genera and species. They are generally found in the winter rainfall zone (Hartmann 1994), but have the highest density of quartz-field taxa in the Knersvlakte Phytochorion. The majority of the genera is largely or exclusively restricted to quartz fields. Other subtribes or taxonomic groups (*sensu* Hartmann 1991) are either represented by a single genus or a few species only. Ihlenfeldt (1971a,b, 1975, 1994) repeatedly pointed out that the phenological variance within the Mitrophyllinae is due to ontogenetic abbreviation and changes of ontogenetic sequences that can be studied within this subtribe. Ihlenfeldt (1994) hypothesises that the performance of ontogenetic abbreviation can be attributed to the occurrence of homoeotic genes, i.e., high-ranking regulatory genes, which are responsible for the ontogenetic program and thus can promote changes of the general phenotypic architecture by altering the sequence of ontogenetic processes (Kubitzki *et al.* 1991). Such genes have first been identified for various animals where they turned out to be widespread and highly conserved (McGinnis *et al.* 1984, Carrasco *et al.* 1984). Due to this ability, reduction of internodes and numbers of leaves have been performed in different genera, leading to an increase of compactness (dwarfism) of the plant's architecture. Although similar abilities can also be assumed for other groups (in the subtribe Leipoldtiinae, for instance, where the stemless and unbranched *Argyroderma* might represent the juvenile stage of fruticose taxa such as of *Leipoldtia*), they are less prominent and less successful on quartz fields. No other taxonomic group contributed comparatively numerous taxa to the QFF as the Mitrophyllinae. It can therefore be argued that the unparalleled success of the Mitrophyllinae contributes significantly to the particularly high species richness of the quartz fields of the Knersvlakte

Consequently, the species richness of the quartz-field phytochoria does not depend on the total size of the phytochoria but rather on the density of quartz-field habitats within this area as well as on the habitat diversity. The low species richness of areas with a low density of quartz fields (as in the western Bushmanland-Warmbad Phytochorion) can be explained by the same rules as shown for remote islands (Diamond 1972). However, only a study on the relationship of species richness and the distance of single quartz-field islands from the next group of such habitats of all phytochoria could reveal whether the low species richness is controlled by the distance to the next group of quartz fields or other factors, such as diversity of soil conditions or climate (e.g., increasing impact of summer rainfall conditions). Ontogenetic abbreviations and changes of ontogenetic sequences within the Mitrophyllinae can be interpreted as a key innovation which facilitate the evolution of structural adaptations to the quartz fields and result in a high density of quartz-field species within this particular subtribe which mainly occurs in the Namaqualand *sensu lato*. Such a radiation is unparalleled in other groups and might be additionally speeded up by the speciation mechanisms associated with the refugial phase in the central Knersvlakte. This phase would have promoted speciation in isolated populations on separated island-like refugia which leads to genetic isolations, vicariance and allopatric speciation supported by strong founder effects.

The pattern of distribution of quartz-field taxa in the Knersvlakte and resulting hypothesis on their history and migration is discussed in the following section.

IV.2.7 Hypotheses on the floral history of the Knersvlakte

Due to the high number of quartz-field species and the high percentage of endemism, the Knersvlakte can be regarded as the main centre of diversity and endemism of the QFF. It could be assumed that the high species diversity of the area can partly be attributed to the occurrence of arid glacial refugia in the Knersvlakte as they have been hypothesised by Midgley and co-workers (Midgley *et al.* 2001, see also the previous chapters). This should, however, be mirrored in the distribution and phylogeny of the recent taxa. Therefore, a discussion about the hypothesised glacial refugia in the Knersvlakte shall be based on the reconstruction of the history of the regional quartz-field flora. Due to the research activities in the Knersvlakte during the present study, the distribution of the taxa is well known. In this context, the phylogeny of those genera which are either endemic to the area (*Argyroderma*, *Oophytum*) or have their centre of diversity there (*Dicrocaulon*, *Monilaria*) are particularly interesting. However, no phylogenetic studies have been conducted so far on these taxa. Preliminary phylogenies, which are derived from morphologic and anatomical features, are available for *Argyroderma* (Hartmann 1973, 1977), *Oophytum* (Ihlenfeldt 1978), *Diplosoma* (Ihlenfeldt 1988), and *Dicrocaulon* (H.-D. Ihlenfeldt, pers. comm.). All these species belong to the Mesembryanthema (Aizoaceae). Based on these preliminary phylogenies and on the interpretation of some pairs of putatively closely related taxa (*Jacobsenia hallii* and *J. kolbei*, *Phyllobolus digitatus* ssp. *digitatus* and *P. d.* ssp. *littlewoodii*, Aizoaceae; *Leucoptera* spp., Asteraceae), hypotheses on the floral history of the quartz-field flora of the Knersvlakte shall be discussed.

The phytogeographical analysis of the Knersvlakte revealed three phytogeographical sub-centres of the Knersvlakte, the Central Knersvlakte, the Northern Knersvlakte, and the Western Knersvlakte (Chapter III.1.2).

The quarter-degree square 3118BC of the Central Knersvlakte (comprising the farms Luiperskop, Quaggas Kop, Arizona, Wolvenest, Rooiberg, Bergplaas) houses by far the highest number of quartz-field species and subspecies (Chapter III.3). Five species / subspecies are entirely restricted to this QDS (*Argyroderma framesii* ssp. *framesii*, *A. patens*, *Bulbine louwii*, *B. margarethae*, *B. wieseii*). Other taxa also occur in the adjacent QDS to the west (*A. pearsonii*, *Cephalophyllum spissum*, *Dicrocaulon humile*, *D. neglectum*, *Tylecodon tenuis*). Nine taxa stretch further to the east into the QDS 3118BD and/or to the south (3118CB). The high number of quartz-field taxa within the Central Knersvlakte may indicate either the occurrence of a centre of origin or a centre of secondary diversification of the present quartz-field flora.

The preliminary phylogeography of the quartz-field taxa of the Knersvlakte (a) as well as the distribution of the quartz-fields of the area (b) seem to support the first explanation.

a) The phylogeographical interpretation of the to-date patterns of distribution

The Central Knersvlakte not only comprises the highest species richness but also a significant number of presumably basal quartz-field taxa. Their (presumably more derived) next relatives are either restricted to the Northern Knersvlakte or they extended their distribution into all three sub-units of the Knersvlakte (Central, Northern and Western Knersvlakte).

According to Ihlenfeldt and Jørgensen (1973), *Monilaria pisiformis* which has the least succulent axes is the most primitive taxon within the genus. He suggests that *M. pisiformis* is the possible ancestor of *M. chrysoleuca* and *M. moniliformis*. *M. pisiformis* is restricted to the Central Knersvlakte, whereas *M. chrysoleuca* is restricted to the Northern Knersvlakte. *M. moniliformis* is widespread in

the Knersvlakte, covering all three phytogeographical sub-centres and some QDSs at the fringe of the Knersvlakte.

In the genus *Argyroderma*, *A. congregatum* and *A. framesii* which are both supposed to be less derived quartz-field taxa within the genus are restricted to the Central Knersvlakte. According to Hartmann (1973, 1977) *A. congregatum* derived from *A. fissum*, which is the only *Argyroderma* species that is not restricted to quartz fields. *A. congregatum* again, is the presumed ancestor of *A. crateriforme* and *A. delaetii* which either occur in the Central and Northern Knersvlakte (*A. delaetii*) or cover all three sub-centres of the Knersvlakte.

The phylogeny of *Dicrocaulon* is little understood. But based on his taxonomic investigations in *Dicrocaulon*, H.-D. Ihlenfeldt (pers. comm.) points out the existence of pairs of closely related species: e.g., *D. brevifolium* and *D. humile* as well as *D. microstigma* and *D. prostratum*. Within the first pair, *D. humile* which is presumably more derived than *D. brevifolium* (H.-D. Ihlenfeldt, pers. comm.), inhabits a very small area in the most species-rich QDS of the Central Knersvlakte (3118BC) as well as adjacent QDS to the west (3118AD). *D. brevifolium*, in return is widespread in the Central Knersvlakte and stretches even into the Northern Knersvlakte (3118BA). The species pair *D. microstigma* and *D. prostratum*, however, deviate from the pattern found in most of the other groups: *D. microstigma* occurs south of the Central Knersvlakte in the area between Vredendal and Klawer which is particularly poor in quartz-field taxa and does not belong to any of the zones defined above. *D. prostratum* is restricted to the eastern fringe of the Central Knersvlakte.

Oophytum oviforme and *O. nanum* are the only species of the genus (Ihlenfeldt 1978) and are thus closely related. Both species are found in the Central Knersvlakte but they show two different patterns of distribution, which partly overlap though. *Oophytum oviforme* is restricted to the Central Knersvlakte whereas the distribution of *O. nanum* stretches further to the north into the Northern Knersvlakte. In the north-western part of the Central Knersvlakte (QDS 3118AD,BC) both species are found in neighbouring habitats - but never occur sympatrically.

For *Phyllobolus digitatus* little is known about its next relatives. It has been sunk into *Phyllobolus* only recently by Gerbault (1997) who also recognised *Dactyloopsis littlewoodii* as a subspecies of *P. digitatus*. Due to its unusual, bizarre habit (Hammer 1996), the re-combination of Gerbault yet met very little acceptance among ecologists and the status of the taxon seems to require more attention still. The phylogeny of the genus is unsolved still, but Gerbault presumes that the next relative of *P. digitatus* is *P. resurgens* (Gerbault 1995, 1997). She does not indicate which of the two subspecies in *P. digitatus* might be more derived. Provided that the hypothesis proves right that increasing specialisation on quartz fields tends to go along with reduction of size and number of leaves, the smaller and more compact sub-species, i.e., *P. d. ssp. littlewoodii*, would be the putative more derived taxon. *P. d. ssp. littlewoodii* occurs in the Northern Knersvlakte whereas *P. d. ssp. digitatus* is largely restricted to the Central Knersvlakte.

Another pair of closely related taxa are *Cephalophyllum spissum* and *Cephalophyllum caespitosum* which were arranged together with *C. rostellum* and *C. curtophyllum* to the *C. spissum*-group (Hartmann 1988). *C. spissum* is restricted to the Central Knersvlakte whereas *C. caespitosum* is widespread and covers all three phytogeographical sub-centres of the Knersvlakte. Hartmann (1988) does not state which of the two species is putative more derived. However, based on the distribution data of the genus *Cephalophyllum* Hartmann (1988) hypothesises a possible centre of origin in the Central Knersvlakte to which *C. spissum* is restricted.

For the *Leucoptera* species (Asteraceae) within the obligate QFF, a completely different origin has to be considered. *Leucoptera oppositifolia* (Asteraceae) which is restricted to the Western Knersvlakte, seems to be derived from the coastal flora where one of the three congeneric

species, *Leucoptera nodosa* (Nordenstam 1976) inhabits the coastal Strandveld between Hondeklip Bay and Clanwilliam. *L. nodosa* and *L. oppositifolia* both represent narrow-leaved, non-succulent frutescent shrubs of up to 50 cm height. The only other species of the genus known so far, i.e., *L. subcarnosa*, colonises the quartz fields of the Central and Northern Knersvlakte. Due to its short and often decumbent stems as well as sub-succulent leaves, *L. subcarnosa* seems to be morphologically better adapted to quartz-field habitats than *L. oppositifolia*. It can therefore be hypothesised that these two quartz-field taxa might have been derived from the coastal flora and have subsequently colonised the inland quartz fields. The general pattern of distribution within this lineage is not in line with the patterns presented above for the Mesembryanthema. The development within this genus seems to deviate from the others.

Further quartz-field taxa that are restricted to the Central Knersvlakte or even to the most species-rich quarter-degree square (3118BC), i.e., *Bulbine* spp., *Phyllobolus abbreviatus*, *Tylecodon* spp., *Zygophyllum teretifolium*, represent either the only quartz-field taxon within their group (*Zygophyllum*) or their infrageneric relationship and thus their next relatives are fairly unknown (*Bulbine*, *Phyllobolus*, *Tylecodon*). Consequently, these taxa can not be considered for this issue.

Summarising, according to the interpretation of the distribution and hypothesised phylogeny of the taxa, the rather primitive members and putative ancestors of more derived quartz-field taxa are typically restricted to the Central Knersvlakte. Most of their more derived relatives are more widespread and either cover all three sub-units of the Knersvlakte or are restricted to the Northern Knersvlakte. This indicates that the quartz-field flora of the Knersvlakte has their centre of origin in the Central Knersvlakte. From there the taxa may have spread into the Northern and Western Knersvlakte. Some of them even migrated up to the Riethuis-Wallekraal area (*Dicrocaulon*, *Monilaria*, compare Chapter IV.2.4). If the hypothesis proves right that during the Last Glacial Maximum cooler and wetter conditions prevailed in present area of the western Succulent Karoo and the Succulent Karoo flora was restriction to arid refugia (Midgley *et al.* 2001), one of these refugia might have been in the Central Knersvlakte.

b) The distribution of quartz fields in the Knersvlakte and its impact on the migration of quartz field taxa

The majority of quartz fields in the Knersvlakte are associated with extended drainage systems. Along the (nearly) uninterrupted sequence of quartz fields along drainage systems, the quartz-field taxa would have migrated during the post-glacial phase. Three major drainage systems can be distinguished for the distribution area of quartz fields in the Knersvlakte (Figure 84):

The largest and longest drainage system, the Sout Rivier (Salt River), intersects the Knersvlakte from north-east to south-west. It starts at the escarpment in the most north-eastern corner of the Knersvlakte and flows to the southwestern border of the quartz-field area of the Knersvlakte (3118CB) where it conflues with the Vars Rivier to the Hol Rivier which flows into the Olifants Rivier. For the longest part of its course, that is, from its start to where the Geelbeks Rivier flows into the Sout Rivier, the Sout Rivier runs through terrace deposits (Gresse 1992) or dark shale bands. Along this section, quartz fields are absent or poorly developed (for instance at the farm Bokkraal). From the Geelbeks Rivier mouth downstream to the confluence of the Sout Rivier and the Vars Rivier into the Hol Rivier, quartz fields are most prominent.

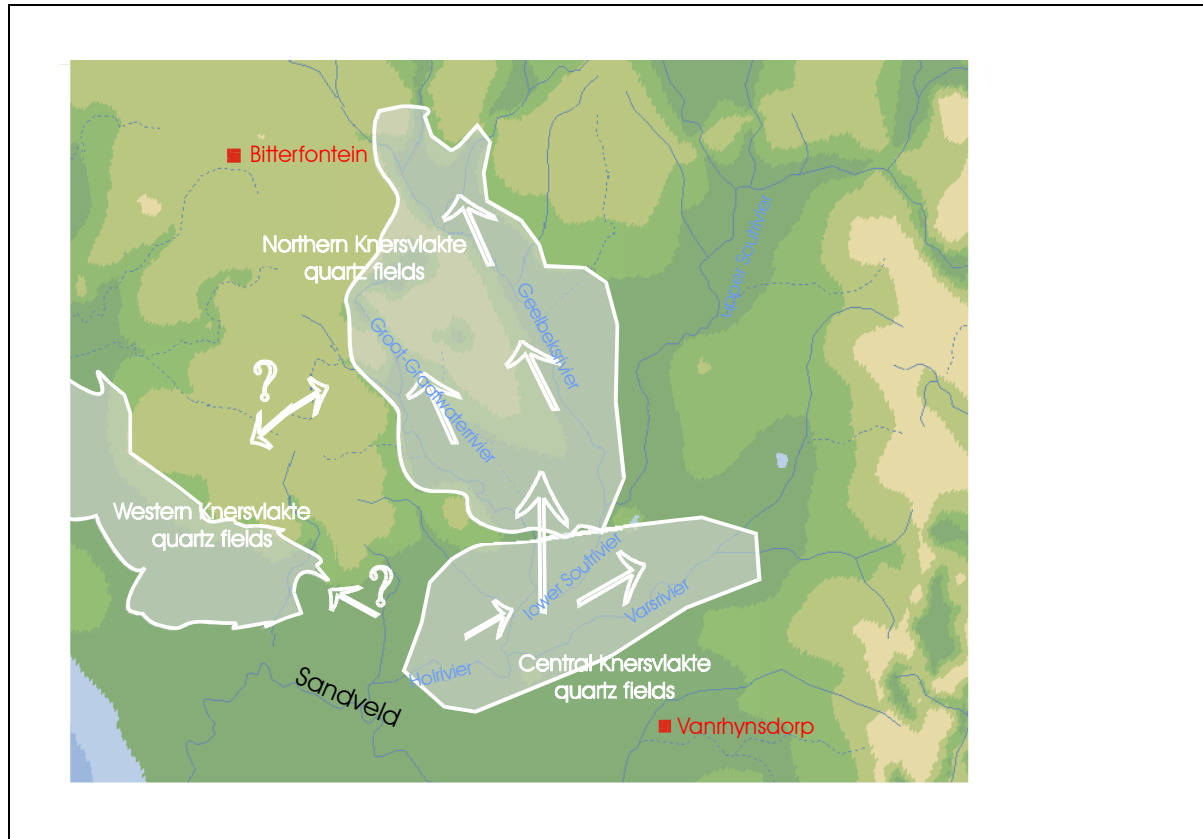


Figure 84. Map of the Knersvlakte showing the major drainage systems and hypothetical migration of the QFF of the Knersvlakte.

The second drainage system (Geelbeks Rivier) runs in north-south direction from the uplands of the Namaqualand (Hardeveld) to the south where it flows into the Sout Rivier. For most parts of its course the Geelbeks Rivier runs through soft rocks (phyllite, mudstones) which are rich in quartz veins. Therefore, the drainage system of the Geelbeks Rivier is densely covered with quartz patches which stretch from the farms Koulei, Toontjieskop, Strykloof, and Breektand in the north (3018CD) to the farm Arizona in the south (3118BC). The sequence of quartz fields is interrupted for some kilometres near the border between the farms Flaminkvlakte and Kareeberg (about $31^{\circ}13'S$, $18^{\circ}32'E$). West of the lower section of the Geelbeks Rivier (from the Flaminkvlakte southwards) another drainage system which comprises the Kraalboskolklaagte, the Groot-Graafwater Rivier, and the Rooiberg Rivier runs parallel to the Geelbeks Rivier. Both drainage systems form part of a continuous quartz-field area.

The third drainage system (Vars Rivier) extends from the escarpment in the east of the Knersvlakte to the west where it conflues with the Sout Rivier to the Hol Rivier. From east to west the frequency of quartz veins and the undulation of the landscape increases. Compared to the Geelbeks Rivier and the lower course of the Sout Rivier, the Vars Rivier system is less diverse with respect to quartz-field habitats.

All three drainage systems conflow in the Central Knersvlakte (QDS 3118BC), which has been pointed out as being the putative centre of origin of the quartz-field flora. If the quartz-field flora spread from there towards north, they must have migrated along the quartz-field habitats parallel to the Geelbeks Rivier / Grootgraafwater Rivier and Vars Rivier.

The short-range dispersal of seeds due to the hygrochastic capsules which are typical for the Mesembryanthema (Ihlenfeldt 1983, 1994, Parolin 2001) enhance genetic isolation of the single

populations. Moreover, the hydrochastic fruits make downstream dispersal of seeds more likely than upstream dispersal*. This would result in: a) stronger genetic isolation with subsequent speciation of the upstream, marginal populations and b) genetic heterogeneity on population level and the species richness of the downstream population (Ellis 1999). This hypothesis is supported by the fact that the more derived species are either restricted to the Northern Knersvlakte (e.g., *Monilaria chrysoleuca*, *Phyllobolus digitatus* ssp. *littlewoodii*) or they cover both the Central and the Northern Knersvlakte (e.g., *Argyroderma delaetii*, *Dicrocaulon brevifolium*, *Monilaria moniliformis*). The restriction of the more basal taxa within the genera to the Central Knersvlakte which has been described above correspond well with these hypothesised processes.

Based on this hypothesis of population dynamics in the quartz fields flora of the Knersvlakte, Ellis (1999) commenced a population genetic study on some selected species of *Argyroderma*. This study shall give first evidence whether this hypothesis holds true.

No drainage system connects the Western Knersvlakte with the Central and the Northern Knersvlakte. The Northern and the Western Knersvlakte are separated by the Namaqualand mountains (Hardeveld) which stretch far to the south between the two sub-centres. The Western Knersvlakte borders to the Central Knersvlakte but both sub-centres are separated by an area of low occurrence of quartz veins as well as a watershed which is formed by a low, east-west stretching elevation (at about 31° 20' S). Despite these topographically induced separations of the Western Knersvlakte from the rest, this phytogeographical sub-centre shares several quartz-field taxa with the Western and Northern Knersvlakte. These taxa, however, are generally widespread in the Knersvlakte. It is therefore hard to deduce from their pattern of distribution, what the main direction of migration might have been. Considering the topography, it seems to be more likely that the QFF of the Western Knersvlakte derived from western populations of the QFF, from the quartz fields at Moedverlor and Kliphoeck (north of Koekenaap, 3118AD) of the Central Knersvlakte. In that case, the taxa would have migrated along the coastal plains from the quartz fields at Moedverlor and Kliphoeck to the northwest. This seems to be more likely than the crossing of the Namaqualand mountains by the quartz field taxa. This hypothesis gets some support from the patterns of distribution of some quartz-field taxa: three widespread species that occur in all three sub-centres of the Knersvlakte are only found in the western part of the Western Knersvlakte (QDS 3118AA) but are absent in the eastern part (QDS 3117BB) which borders to the Northern Knersvlakte. However, this gap in the distribution may also be due to incomplete collection since three respective species, i.e., *Diplosoma luckhoffii*, *Phyllobolus herbertii*, and *Tylecodon occultans*, are particularly hard to spot since they are extremely small and their aboveground parts dye back during the dry season.

It is not self-explanatory that the presumably basal taxa within the quartz-field flora are restricted to the Central Knersvlakte whereas the more derived species have a broader distribution and often stretch into the Northern Knersvlakte. If the more derived species, which are typically more compact (as in *Argyroderma* Hartmann 1977; *Phyllobolus digitatus*, Gerbaulet 1997; *Dicrocaulon*, H.-D. Ihlenfeldt, pers. comm.) and often more succulent (as in *Monilaria*, Ihlenfeldt & Jörgensen 1973; *Leucoptera*, Nordenstam 1976) are generally better adapted to the adverse habitat conditions of the quartz fields, their ancestors should have been extinguished by competition. This, however, did not happen in the Central Knersvlakte. There, the putative more primitive taxa

*It shall be noted that seed dispersal by other vectors than splashing and flowing cannot be excluded. Particularly during hot and dry easterly winds (so called bergwinds) dust, sand, seeds, and even fruit capsules can be transported for long distances. But there is a relative small chance of the diaspores which are transported like that to meet an adequate habitat. This mechanism seems to be rather of secondary importance.

seem to be as successful as their descendants whereas they do not occur in the Northern Knersvlakte. Why do the basal taxa still occur in the Central Knersvlakte? Maybe because of the relatively less adverse conditions which prevail there. The Central Knersvlakte is less arid than the Northern Knersvlakte, due to the higher precipitation (compare Figure 39) and the impact of fog. According to the experiences during the field campaigns, the fog which comes in from the west coast occurs in the western Central Knersvlakte (Moedverlor) with highest frequency and longest duration per day but also intrudes further inland to the central section of the Central Knersvlakte. But due to the mountain ridge that runs from Nuwerus in the north to the Moedverlorberg in the south, the fog hardly reaches the Northern Knersvlakte. The highest frequency of fog has to be expected for the Western Knersvlakte, due to its close vicinity to the coast (app. 30 km).

The low impact of fog in the Northern Knersvlakte increases the edaphic aridity of the quartz fields which, in return, promotes morphologic-anatomical adaptations of the quartz-field inhabitants. Such increase of xeromorphic structures which corresponds with the increase in distance to the coast can be observed in several taxa within the quartz-field flora as described above.

Summarising, the present pattern of distribution of closely related taxa indicates that the flora of the quartz fields in the Knersvlakte have their centre of origin in the Central Knersvlakte and spread from there to the north and west. The genetic isolation of the marginal populations could have resulted in the differentiation of distinct taxa in three phytogeographical sub-centres. The higher number of putatively more basal taxa in the presumed centre of origin (Central Knersvlakte) can be explained by the higher impact of fog in that part of the Knersvlakte which eases the edaphically arid conditions of the quartz fields (Chapter IV.6). Current molecular phylogenetic (by G. Bertram, University of Hamburg) and population genetic studies (A. Ellis, University of California Irvine) of selected taxonomic groups can give evidence for this hypothesised phylogeography of the quartz-field taxa of the Knersvlakte and other phytocoria.

IV.3 The ecological background of the quartz-field flora

The analysis of the habitat conditions on quartz fields revealed (Chapter III.6) that the habitat conditions of non-saline quartz fields are characterised by shallow and skeletal soils and low soil pH and are thus similar to that of rocky habitats and outcrops. Therefore, the vegetation of non-saline quartz fields has a high species overlap with rocky outcrops which particularly prominent in the *Conophytum* (Mesembryanthema), *Crassula* (Crassulaceae), and *Anacampseros* (Asclepiadaceae), as well as *Senecio* and *Othonna* (Asteraceae). The species overlap decreases strongly with increase of salinity and the more the outcrop character and the rockiness diminish. The strong ecological and floristic correspondence between non-saline quartz fields and rocky outcrops may indicate that the flora of the non-saline quartz fields originated from the flora of rocky outcrops. This hypothesis, which has also been discussed by Desmet *et al.* 1998, can only be verified by employing phylogenetic and autecological data of congeneric taxa which are found outside quartz fields on rocky outcrops and on non-saline quartz-fields or - alternatively - on non-saline and saline quartz fields. If the hypothesis proves right, the taxa that are restricted to saline quartz fields would be furthest derived and those on the rocky outcrops most basal, whereas the inhabitants of the non-saline quartz fields were intermediate. In the following, this hypothesis was tested by analysing the preliminary phylogenies of some specious genera of the obligate QFF as they were discussed in Chapter IV.2.5.

In *Argyroderma* (Mesembryanthema) the presumable ancestor of all species of the subgenus *Argyroderma* which also present the quartz-field taxa within the genera, is *A. fissum*, Subgenus *Roodia* (Hartmann 1977). *A. fissum*, however, is no outcrop dweller but mainly occurs on saline

quartz fields and zonal soils outside the quartz fields. Within the subgenus *Argyroderma*, however, the putatively more derived species (*A. pearsonii*, *A. delaetii*) are typical inhabitants of saline quartz fields whereas the more basic species (e.g., *A. congregatum*, *A. framesii*, *A. subalbum*) are largely restricted to non-saline quartz fields (U. Schmiedel, unpublished data).

The majority of *Dicrocaulon* species (Mesembryanthema) inhabit non-saline, acid quartz fields. Only *D. ramulosum* which is restricted to the quartz fields of the Riethuis-Wallekraal Phytochorion inhabits saline quartz fields. If, as have been discussed above (Chapter IV.2.5), the centre of origin of the genus *Dicrocaulon* lies in the Knersvlakte, *D. ramulosum* were a phylogenetically younger species. If this hypothesis on the phylogeny of *Dicrocaulon* proves right, it would support the hypothesised origin of the quartz-field flora from saxicolous taxa.

In *Monilaria* (Mesembryanthema), however, the presumable basic taxon (*M. pisiformis*) is the only taxon within the genus that partly occur on saline quartz fields. The monodominant *Monilaria pisiformis* Community (# 30) even represents the transition between the saline and non-saline quartz fields. The other, putatively more derived infrageneric taxa are restricted to non-saline, rocky quartz-field habitats. For *Monilaria*, thus, the reverse process (migration from saline to non-saline habitats) seems to apply.

Most of the numerous *Conophytum* species occur on rocky habitats and in rock crevices. Within the quartz-field flora, *Conophytum* species are mainly restricted to non-saline, acid quartz fields with the only exception of *Conophytum concavum*, *C. obscurum* ssp. *vitreopapillum*, and *C. subfenestratum* (Schmiedel 2001a). Since the phylogeny of the genus is unsolved still, it can only be speculated whether these taxa are more derived than the other congeneric species.

Consequently, the hypothesised origin of quartz-field taxa from rocky outcrops does not apply to all genera considered. Besides *Monilaria*, none of the genera indicate the opposite evolutionary direction, i.e., from saline quartz-fields to non-saline quartz fields. The only genus that is completely restricted to saline quartz fields, is *Oophytum* (Aizoaceae) from the Knersvlakte. With respect to its next relatives within the subtribe Mitrophyllinae, the *Oophytum* can be regarded as a highly derived Mitrophyllinae taxon (Ihlenfeldt 1971b) the next relatives of which are largely restricted to non-saline quartz fields. It can thus be argued that the quartz-field flora derived from the saxicolous lineages as it is still obvious in genera like *Conophytum* (Mesembryanthema) and *Crassula* (Crassulaceae) which are typically found on rock outcrops and only a few taxa also colonised the saline quartz fields.

IV.4 Vegetation classification

IV.4.1 Little Karoo

Within the quartz-field vegetation of the Little Karoo, the near endemic genus *Gibbaeum* is of particular importance: it represents the diagnostic as well as the dominating species of most of the communities. However, the genus *Gibbaeum* is not completely restricted to quartz fields but occurs on other edaphically induced special habitats such as desert pavements of other lithology than quartz. *Gibbaeum* seems to have conducted an adaptive radiation on quartz fields and related habitats. In order to understand the vegetation of the quartz fields of the Little Karoo and to get insight into the major role of *Gibbaeum* taxa within the vegetation of quartz fields and related habitats, communities and habitat conditions of all *Gibbaeum* taxa (except *G. johnstonii* and *G. esterhuyseniae*, two very rare species) have been included into the study. The genus *Gibbaeum* is largely restricted to the Little Karoo. Only *Gibbaeum gibbosum* is also found north of the

Swartberge in the southern Ceres Karoo whereas *G. haagei* and *G. esterhuyseniae* are restricted to a small area south of the Langeberge.

The zonal vegetation of the Little Karoo is very heterogeneous and comprises a broad array of major vegetation types, such as fynbos and renosterveld in the mountains and the Succulent Karoo at lower altitudes and valleys bottoms. Since the present focuses on the vegetation of quartz fields and related habitats, the zonal vegetation was included only for comparison purposes and was therefore focused on Succulent Karoo vegetation in the vicinity of the quartz fields.

Cover values and species richness

The total cover values were low for most of the communities under investigation (mean values < 20 %). Only the *Psilocaulon junceum* Community (# 16) showed considerably high mean values for total cover (app. 60 %, Figure 38). The sparse coverage is characteristic for the vegetation of the quartz fields. Average values for total cover of the quartz fields vegetation of the Knersvlakte (average total cover value = 8.6 %) and the Little Karoo (average total cover value = 7.7 %) were generally low whereas the zonal vegetation in the Knersvlakte had higher total values (average = 23 %) than in the Little Karoo (average = 12.7 %) (Schmiedel & Jürgens 1999). The relatively low cover values of the quartz fields vegetation and of these relevés sampled for the zonal vegetation of the Little Karoo in this study (*Pteronia pallens*-*Aridaria noctiflora* ssp. *defoliata* Community # 10) can be attributed to the arid growing conditions due to shallow, stony soils and relatively low rainfall (240 mm/a). Similarly low plant cover (average = 18 %, range 11-30 %) has been recorded for the zonal, allied vegetation near Prince Albert on the southern edge of the Great Karoo, north of the Swartberg mountain range with similarly low rainfall (167 mm/a) (Milton *et al.* 1992).

In return, the higher cover values of zonal vegetation of the Knersvlakte might be due to the relatively more favourable conditions regarding water supply which is positively influenced by the regular occurrence of fog (Desmet & Cowling 1999b) but associated with low average annual rainfall (120 - 150 mm/a, Weather Bureau 1988) though.

Correspondingly, the extraordinarily high cover values of the *Psilocaulon junceum* Community (# 16) of the Little Karoo can be attributed to the special conditions of its habitat: *Psilocaulon junceum* is typically associated with earth mounds (termitaria, locally known as *beuweltjies*) which are of zoogenic origin and inhabited by termites, ants, and borrowing small mammals (Lovegrove & Siegfried 1986, Dean & Yeaton 1993). Due to the accumulation of organic matter by ants and termites, the status of soil nutrients and soil organic matter is about double as high as in the soils of their surroundings (Dean & Yeaton 1993, Midgley & Musil 1990). The soils of the termitaria are also soft and well-drained (Lovegrove & Siegfried 1986). These conditions promote a vegetation of its own, typically dominated by species of vigorous growth with a higher nutrient requirement (Midgley & Musil 1990) and tolerance for pedoturbation and other disturbances.

Regarding the species richness, quartz fields and related habitats generally did not differ from the surrounding vegetation (≤ 11 spp./relevé). Merely the *Zeuktophyllum suppositum* Community (# 6) showed a considerably high species richness (17 spp./relevé). This can be attributed to the habitat conditions which are typical for the community: rocky, steep slopes, low electrical conductivity, and slightly acid soil pH. Such conditions are typical for the Upland Succulent Karoo (Hoffman 1996b) of the central Namaqualand and the Richtersveld (Jürgens 1986). They provide a small scale mosaic of substrate subdivided by bedrocks and which subdivide the habitat into small units like in a rock garden and therefore may reduce the competition and allow the coexistence of different species in a small area (Hanski 1995). Such miniature habitats can only be

used by plants of dwarf size, each having a very restricted root volume and clearly depicting the small scale patterns of soil conditions (Desmet *et al.* 1998). The other communities are found on more homogeneous soils the majority of which even provided extreme growing conditions (i.e., high salinity, low soil pH, low soil depth). These extreme conditions restrict the species spectrum of the community to a small number of specialists.

The majority of the communities are defined by one diagnostic species only which also dominates the vegetation. Such monodominant vegetation units are typical for quartz-field vegetation and has been shown for the communities of other area as well (Schmiedel 1994, Schmiedel & Jürgens 1999. This phenomenon is discussed separately in Chapter IV.5.

Geographical distribution of the communities

Most of the obligate quartz-field taxa have a very restricted range size of distribution (Chapter III.1.1). This is also true for several *Gibbaeum* taxa and other Mesembryanthema recorded in this study. In particular, the small area between Barrydale, Vanwyksdorp and Ockertskraal (3320DC, 3321CC, CD, DA) in the southern section of the Little Karoo, houses a high number of local endemics *G. album*, *G. angulipes*, *G. dispar*, *G. hortenseae*, *G. pachypodium*, *G. petrense*, and *G. velutinum* as well as *Zeuktophyllum suppositum*. This area (corresponding with the half-degree squares 3320D, 3321C) comprises generally very high numbers of endemic (# 6-7), near endemic (# 4-6) as well as widespread genera (# 21-25) of Mesembryanthema within the Little Karoo Centre (Hartmann 1994). The high endemism can thus not only be accounted to the occurrence of quartz fields (Chapter III.3.1).

G. haagei, in contrast, is confined to the Swellendam area south of the Langeberge.

The very locally restricted occurrence of several *Gibbaeum* taxa which represent diagnostic and dominating species of communities results in the restricted range size of distribution of several syntaxa and therefore - in direct correspondence to the local centre of endemism of species - in a centre of endemism of vegetation units in the southern section of the Little Karoo. Obviously, the distribution of the quartz-field communities is closely associated with the discontinuous distribution of quartz-field habitats. However, not all locally endemic communities given above are restricted to quartz fields but some of them are preferably found on other habitats such as shale bands (*G. dispar* C. # 5 and *G. velutinum* Community # 2), sandstone gravel (*G. pachypodium* Community # 15), rocky habitats (*Z. suppositum* Community # 7).

Other communities, such as the *G. cryptopodium*, *G. geminum*, *G. gibbosum*, *G. heathii*, *G. pubescens*, *G. shandii*, the *Pteronia pallens*-*Aridaria noctiflora* ssp. *defoliata* Community (# 8-14) as well as the *Psilocaulon junceum* Community (# 16) are widespread in the western section of the Little Karoo or stretch into adjacent areas even (*G. gibbosum* Community # 11). The majority of the widespread communities are therefore phytosociologically related and associated in Community Group D, defined by Species Group J which comprises several common and widespread, succulent and non-succulent Karoo shrubs which are not found in the Communities # 1-7. Local endemism as has been described for the southern fringe of the Little Karoo has not been found for communities of the western section of the Little Karoo. The *Gibbaeum pachypodium* C. # 15 is the only community in Group D although which is geographically restricted to a small area near Ockertskraal. This area, however, largely overlaps with the small centre of endemism in the southern section of the Little Karoo.

The southern sub-centre of endemism of the Little Karoo has not been recognised by for the taxonomic groups by phytogeographical studies on the succulent flora (Nordenstam 1969, Jürgens 1992, Hartmann 1994) which might mainly due to the comparatively rough scale

(Nordenstam 1969, Jürgens 1992) or the focus on genus level (Hartmann 1994). So far, this sub-centre seems to be fairly restricted to some infrageneric taxa of *Gibbaeum*, *Muiria*, and *Zeuktophyllum*). It can be argued that this centre is due to temporal isolation of the southern populations during the palaeoclimatic oscillations in the glacial and interglacial phases. The impact of such oscillations on the vegetation of the Namaqualand *sensu lato* (Chapter palaeoclimate) is supported by the present phytogeographical pattern of the quartz-field flora. The molecular phylogenetic studies on *Gibbaeum* which are presently conducted by Gisela Bertram (Botany Department of the University of Hamburg) might give insight into the factors that were responsible for this sub-centre. Future phytogeographic studies should further reveal whether this centre of endemism is mirrored in other taxonomic groups as well.

IV.4.2 Knersvlakte

For the Knersvlakte, five Major Habitat Units (MHUs) were described which were characterised by geomorphological and edaphic features (Chapter III.5.3). Each of the MHUs comprised a certain array of plant communities. The vegetation of the quartz fields showed the lowest overlap of the inventory of communities and species with the other MHUs.

Also, the vegetation of the quartz fields comprises a very high number of different communities. Particularly the communities of the saline quartz fields are mainly defined by the clear dominance of a singular species (monodominant communities) as they were also found for the quartz-field vegetation of the other regions. The differentiation into various communities which are defined by a few species only present a special feature of the quartz-field vegetation and will be discussed later in more detail.

The quartz-field communities of the Knersvlakte are clearly separated into two main groups (Chapter III.5.3), i.e., communities that mainly occur on saline quartz fields and those that are largely restricted to non-saline, acid quartz fields. The Phytosociological Table II of the Namaqualand Communities (Appendix 9 and Appendix 10) revealed that the two main community groups of quartz-field communities of the Knersvlakte have a stronger association with other communities outside the quartz fields of the Knersvlakte, than with each other. The first group shares several species with the communities which typically occur outside the quartz fields but within the mosaic of quartz fields and zonal soils (Communities # 10-20) whereas the communities of the non-saline, acid quartz fields of the Knersvlakte have a higher overlap in species inventories with the quartz-field communities of the Riethuis-Wallekraal area but also of the Richtersveld.

This result is in line with the findings of the phytogeographical analysis of the obligate QFF (Chapter III.1). Halophytic taxa of the obligate QFF tend to have a very restricted range size of distribution whereas those that inhabit non-saline, rocky quartz fields have a broader distribution and cover more often more than one phytochorion. This has been ascribed to the broader distribution of related habits, such as rock outcrops which may also be used as substitute habitats. The close relationship of the communities of the non-saline quartz-field of the Knersvlakte with that of the quartz fields of other regions can also be attributed to the frequent occurrence of generally saxicolous taxa (e.g., *Crassula capitella* ssp. *thyrsiflora*, *Euphorbia hamata*, *Gazania krebsiana*, *Hirpicium alienatum*, *Pelargonium crithmifolium*, and *Pteronia ciliata*, compare SGs EF, AG in Phytosociological Table II (Appendix 10) on these quartz-field habitats.

IV.4.3 Riethuis-Wallekraal area

The quartz fields of the Riethuis-Wallekraal area are very restricted in size and distribution and thus comprise a relatively small array of habitat types and plant communities. Also, the number and constancy of the joint species that combine communities of the Riethuis-Wallekraal area to a major Community Group, i.e., Species Group AR in the Phytosociological Table II (Appendix 10) is relatively low. Therefore, the correspondence between the communities is mainly based on the occurrence of *Dicrocaulon spissum* and *Monilaria scutata* ssp. *obovata* which are diagnostic species of certain communities but also occur in other communities with low constancy.

Beyond the saxicolous and rocky soils inhabiting taxa of SGs AF and AG which combine the communities of the non-saline, acid quartz fields of the Knersvlakte with those of the Riethuis-Wallekraal area (SG AF and AG) and the Richtersveld (SG AF only), there is no further overlap of species inventories between the Riethuis-Wallekraal area and the Richtersveld.

They also consist of saline and non-saline quartz fields, however, the differences are less significant and therefore, the subdivision is less strict. The trend that communities that inhabit more extreme habit conditions (i.e., highly saline quartz fields, *Jacobsenia vaginata* C. # 41, *Dicrocaulon spissum* C. # 42, and *D. ramulosum* C. # 43) are defined by only one or two species, whereas the *Monilaria scutata* ssp. *obovata* (# 40) and the *M. s.* ssp. *scutata* Community (# 45), which are confined to non-saline quartz fields comprise three and more diagnostic species. The role of the monodominant communities will be discussed below (Chapter IV.5).

IV.4.4 Richtersveld

For the quartz-field vegetation of the Richtersveld six communities were described among which two communities (*Ruschia leucosperma* C. # 46 and *Eberlanzia cyathiformis* Community # 49) are not even restricted to quartz fields. The *Brownanthus pubescens* Community (# 51) is the only community of the Richtersveld which has been exclusively recorded for very saline quartz fields. Hence, although covering a broader the same number of communities have been recorded for the Richtersveld as have been described for the Riethuis-Wallekraal area. The difference in number of communities is not attributed to a lower intensity of research activities in this area, since far more relevés were included in the table for the Richtersveld (66 relevés) compared to the Riethuis-Wallekraal area (33 relevés). In contrast, the poor phytosociological separation of the *Ruschia leucosperma* C (# 46), the *Cephalophyllum regale* C. (# 47), and the *Aspazoma amplexens* C. (# 48) as well as the comparatively high number of accompanying species which occur with low constancy values only in the *Eberlanzia cyathiforme* C. (# 49) and the *Schlechteranthus ballii* Community (# 50) (Phytosociological Table II Appendix 10), rather indicate a low degree of habitat specialisation within the non-saline quartz-field vegetation of the Richtersveld. This can also be deduced from the species composition and the habitat conditions which are characteristic for the respective communities: most of the accompanying taxa of the communities (e.g., SG AY as well as *Ceraria fruticulosa*, *Euphorbia gummifera*, *Galenia dregeana*, and *Ruschia atrata*) are not restricted to quartz fields but have a broader distribution and ecological amplitude.

IV.4.5 Bushmanland-Warmbad area

The diversity of plant communities in the Bushmanland-Warmbad area is comparatively poor. Four communities have been defined of which one (*Oropetium capense* Community # 3 B-W), however, comprises four sub-communities. In contrast to the quartz-field communities of the Namaqualand *sensu lato* as well as the Little Karoo, most of the quartz-field communities of the

Bushmanland-Warmbad area are particularly rich in species. Only the *Zygophyllum decumbens*- (# 1 B-W) and the *Lithops julii* Community (# 2 B-W) reveal the characteristic monodominance which has been pointed out for most of the quartz-field communities of the other regions (Chapter IV.5).

The most important species in terms of both constancy or cover values of the communities are generally not restricted to quartz fields (compare Table 31) but have a broader ecological amplitude and geographical distribution. *Oropetium capense*, for instance, occurs in the entire summer rainfall zone of southern Africa and in the tropical east Africa (van Oudtshoorn 1991). The Bushmanland-Warmbad area presents thus its most arid border of its distribution. *Ruschia odontocalyx* is found from the Namaland in Southern Namibia into the Richtersveld (P. Chesselet, pers. comm.). *Zygophyllum decumbens* occurs from the summer rainfall part of the Richtersveld along the Orange River into the Bushmanland (N. Jürgens and U. Schmiedel, unpubl. data). The obligate quartz-field taxa (*Conophytum friedrichiae*, *Dinteranthus wilmotianus*, *Lapidaria margaretae*), in contrast, occur with relatively low constancy in the communities.

The quartz-field vegetation of the Bushmanland-Warmbad area, is thus characterised by the summer rainfall regime. In contrast to the quartz fields of the other phytochoria, the quartz-field vegetation is dominated by grass and the obligate quartz-field taxa occur with very low cover values. These taxa are restricted to quartz fields but are of low importance for their vegetation.

IV.5 Monodominance in the quartz-field vegetation

The monodominance of certain taxa in vegetation communities is a characteristic feature of the southern African quartz fields. This phenomenon is not evenly distributed among the communities but seems to be more frequent in the communities that occur under most edaphically arid habitat conditions, whereas rocky, non-saline quartz fields with a moderate soil depth are typically inhabited by communities which comprise several diagnostic species with a high fidelity (Chapter IV.4). Special growing conditions can either be caused by high salinity (e.g., *Argyroderma pearsonii* C. # 25, *A. delaetii* C. # 23), very shallow, skeletal soils (e.g., *Conophytum minutum* ssp. *minutum* Community # 31) or other special habitat conditions such as fog exposed edges (*Oophytum oviforme* Community # 29) and extremely silty, soft soils on slopes (*Phyllobolus digitatus* ssp. *digitatus* Community # 28). The occurrence of monodominant communities on extreme habitats can be interpreted as the result of morphological-anatomical and physiological adaptations of the taxa to the particular habitat conditions.

However, the species which form monodominant communities typically also occur in other plant communities but with low cover values. Their occurrence on other quartz-field communities as well as the successful horticultural cultivation of the plants in uniform substrates reveal that these taxa are not necessarily dependent on the particular habitat conditions. Their adaptations on the one hand enable the taxa to cope with the adverse growing conditions (e.g., low water storage capacity or very negative osmolarity due to high salt concentration), on the other hand they reduce the compatibility of the taxa due to relatively lower growing rate or high investment in protection against transpiration etc. Due to their low compatibility, edaphic specialised plants are restricted to habitats where potential competitors are excluded and which comprise such adverse conditions they can cope with (Gankin & Major 1964, Proctor & Woodell 1975, Kruckeberg & Rabinowitz 1985, Baskin & Baskin 1988, Ware 1990).

Salt marshes which are also characterised by high salinity house similarly species-poor and monodominant communities (Adam 1981, Adam *et al.* 1988, Ellenberg 1996). The restriction of halo-tolerant species to extremely saline soils due to their reduced compatibility compared to less salt-tolerant taxa have been pointed out by Chapman (1975).

Among the monodominant communities of the saline quartz fields, the differences with respect to habitat conditions are generally vague and hence the constrained scores of the CCA analyses (Chapter IV.6) never separated these communities completely. Consequently, the habitat conditions cannot explain comprehensively the presence or absence of a community at a particular site. It can therefore be assumed that also historical events (the question which population was the first to colonise the particular quartz fields) or historical processes which influenced the growing conditions during the colonisation (e.g., wetter or dryer phases) also play a role for the decision, which population dominates the quartz fields.

IV.6 Vegetation ecology of the quartz fields

Quartz fields represent special habitat types which occur in different sections of southern African arid regions. Each area comprises a largely independent quartz-field flora (Chapter III.1) and a distinct array of plant communities (Chapter IV.4). Due to the strong correspondence with respect to the vegetation structure it has been hypothesised (Jürgens 1986, Schmiedel & Jürgens 1999) that the similarity in growth form spectrum can be attributed to convergent evolution in adaptation to identical habitat conditions. Since quartz-field habitats are defined by their soil (surface) conditions (Chapter I.4), topographic and edaphic variables were employed to analyse and interpret the main gradients within the quartz field vegetation.

IV.6.1 Little Karoo and adjacent areas

Gradient analysis

The multivariate direct gradient analysis of the data set of the communities of the Little Karoo and adjacent areas revealed a strong negative association of quartz-field habitats with soil depth and carbonate content in soil and a positive association with salinity, low soil pH and stone content in soil. Low soil pH and high electrical conductivity, seem to be two characteristics of quartz fields which largely occur vicariously, each supporting different quartz-field communities.

Within the defined communities of quartz-field and related habitats of the Little Karoo and adjacent areas, four communities (i.e., # 1-4: *Gibbaeum haagei*-*Delosperma asperulum* C., *G. velutinum* C., the *Gibbaeum angulipes* C., and the *G. album* C.) deviate strongly from the remaining 12 communities (i.e., # 5-16). This difference emerged at three levels. Within the vegetation classification (a) they represent two Community Groups (A and B) of their own and the correspondence analysis of the synoptic data (b) separated them from the rest as did the ordinations of the correspondence analyses (c) where they were revealed as outliers compared to the rest. The CCA ordinations revealed that the environmental variables employed do not thoroughly explain the separation. Communities # 1-3 are typically associated with extremely low soil pH and high quartz cover whereas Community # 4 has a moderate soil pH and high quartz cover. These edaphic conditions, however, are not entirely restricted to the three communities. Also the content and composition of ions in soil did not reveal any correspondence between these communities and particular ion compositions.

Consequently, other factors have to be taken into account. Geographical isolation as a possible factor that might induce phytosociological isolation, only applies to the *G. haagei*-*Delosperma asperulum* Community (# 1, Community Group A). This community occurs south of the Little Karoo in the Swellendam area in the South & South-west Coast Renosterveld vegetation of the Fynbos Biome (Rebello 1996). The species associated with this community (*Pentaschistes eriostoma*, *Delosperma asperulum*) are thus largely absent from most of the other communities. However, they

do occur in Communities # 2 and # 4 of the Community Group B which causes the strong relationship between Community Group A (Community # 1) and Community Group B (Communities # 2-4). In contrast to Community Group A, Community Group B occurs north of the Langeberge in the Little Karoo. It is, however, devoid of the quartz-field taxa of central and northern Little Karoo (Community Group D) and of the ubiquitously occurring Karoo species (Species Group E) that are frequently found in Community Group C & D (Community # 5-7 and # 8-15). Community Group C is also restricted to the southern fringe of the Little Karoo (between Barrydale, Vanwyksdorp, and Ockertskraal) and to the same geographical area as Community Group B. In contrast to the latter, Community Group C is phytosociologically less isolated but comprises numerous common Karoo species (SG E). The defined communities of the south-eastern fringe of the Little Karoo can be consequently subdivided into two Community Groups (B and C) of which the first is related to the vegetation of the quartz fields of the Swellendam area and the second to the vegetation of the central and northern Little Karoo. This subdivision is not solely explained by one of the environmental variables which have been employed.

The Community Groups D (Community # 8-15) and E (Community # 16) which comprise the communities of the central and northern Little Karoo have a broad overlap in species composition (SGs E and J, Table 75) and are thus plotted next to each other in the ordination of the unconstrained relevé scores of the CCA. However, all communities except the *Gibbaeum cryptopodium* Community (# 8) were nevertheless plotted in distinct groups. Since the unconstrained relevé scores are reciprocally derived from the species scores, this pattern reveals a distinct relationship between the dominant (and diagnostic) species of the community and the environmental variables employed. Due to the monodominant structure of the communities, these preferences can be attributed to the dominant species of each community. Particularly among Communities # 8-15 the habitat preferences overlap broadly with each other.

This result was supported by the constrained relevé scores which are derived by regressing the relevés on the environmental variables (ter Braak & Smilauer 1998). This ordination revealed certain habitat preferences for most of the communities, which nevertheless overlapped broadly with those of others. The far lower separation of the communities along the gradients in the constrained ordination compared to the unconstrained ordination can be attributed to the much higher sensitivity to the noise of environmental data and thus lower reliability of the first (McCune 1997b).

Consequently, the comparatively clear separation of communities along the gradients based on the unconstrained relevé scores reveals the association of the dominant species of each Community with particular habitat conditions. The strong deviation of the Community Groups # 1-4 which has been shown by the CA ordination was not mirrored thoroughly by the CCA ordinations. The significant phytosociological isolation of these Communities can only partly be explained by their preference of particularly acid soils and by their geographical isolation at the southern fringe of the Little Karoo. The constrained relevé scores in return, seem partly to be biased by the noise in environmental data.

Difference in habitat preferences between local endemic and broadly scattered communities

The broader geographical distribution of the Communities # 8-14 is associated with a higher ecological amplitude regarding soil conditions compared to the Communities # 1-7, and # 15 which have a restricted range size of distribution (Figure 46). The mean soil pH of the latter group is slightly or extremely acid and generally lower than in the widespread communities (# 8-14), which is about neutral. The variance among the soil pH values is < 2 pH for most of the

locally restricted communities, whereas it is ≥ 2 pH for the majority of the widespread communities. Only the *Gibbaeum geminum* Community (# 12) shows a narrow range of soil pH (variance = 1.3 pH). Also regarding the electrical conductivity, the locally restricted communities show generally higher mean values and a narrower ecological amplitude (variance > 3 mS/cm), which contrasts to the very broad amplitude of > 5 mS/cm for most of the widespread communities. Only the zonal vegetation, represented by the *Pteronia pallens-Aridaria noctiflora* ssp. *defoliata* Community (# 10), as well as the *G. gibbosum* Community generally prefer soils with low salt content and show relatively low variance (< 3 mS/cm). The widespread communities also show high tolerance regarding carbonate content in soil. In return, carbonate has not been recorded for any of the locally restricted communities. Soil depth, stone cover of quartz stones and of stones of other lithology also have a lower variance in the localised communities than in the widespread communities. The differences are less pronounced though.

The very narrow amplitude of soil conditions of Community # 1-7, and # 15 is interpreted as the result of a strong ecological specialisation of the diagnostic and dominating species to edaphically arid, often extremely saline and consequently adverse habitat conditions. Such specialisation and its subsequent structural adaptations obviously go along with decreased competitive capacity. This low competitiveness excludes these communities from habitats with deviating conditions and therefore impede the extension of their distribution beyond the archipelago-like habitat islands of a small area.

IV.6.2 Knersvlakte area

The CA and CCA ordinations of the quartz-field vegetation of the Knersvlakte revealed that salinity and H^+ concentration have the strongest impact on the species composition of the vegetation of the quartz fields. The two environmental variables are diametrically opposed and consequently divide the quartz-field vegetation of the Knersvlakte into the halophytic quartz-field vegetation and the quartz-field vegetation of the non-saline, rocky quartz fields. This subdivision was not only mirrored in the canonical analysis, which was based on species and environmental variable data, but also emerged significantly when analysing merely the species data (CA). Consequently, the two groups of quartz-field habitats house two largely separated species inventories and plant communities. This finding is in line with the results of the vegetation classification (Chapter III.5) which showed very little overlap in species inventory between communities of saline and acid quartz fields.

Among the quartz fields the variance in density of quartz cover (of medium size, < 60 mm in diameter) does not play a very important role for the species composition in the Knersvlakte. However, the CA and CCA ordinations revealed that saline quartz fields have a generally higher density of quartz cover than acid quartz fields which more frequently have higher percentage of coarse quartz cover (> 60 mm in diameter). The Knersvlakte is comparatively poor in carbonate in soil. Carbonate is only frequently found on limestone dominated areas such as on the farm Aties (MHU 5) or on heuweltjies (i.e., termitaria, which characterised by biogenic disturbance) and their immediate surrounding. On quartz fields, in return, carbonate content has only been recorded for the habitats of the *Drosanthemum diversifolium* Community (# 21).

In the **saline quartz fields in the Knersvlakte**, besides the environmental variable electrical conductivity also the occurrence of carbonate in soil explains the variance of species data. The communities have a principally lower turnover in species data which results in a less distinct separation of the communities within both the CA and the CCA ordination than has been found for the non-saline quartz fields. This corresponds with the strong overlap of species inventories of the communities of the saline quartz fields as it is shown by classification of the vegetation

(Synoptic Table II, Appendix 9). The unconstrained relevé scores revealed clusters representing the communities defined in the phytosociologic table. These clusters, however, are poorly separated and thus indicate relatively low difference in habitat preferences which overlap broadly. The habitat preferences of the different communities of the saline quartz-field of the Knersvlakte are given below.

Only the *Oophytum oviforme* Community (# 29) was clearly separated from the rest. This separation is not explained by any of the environmental variables employed for the analysis, except a generally positive association with salinity, which it has in common with the other communities of the saline quartz fields. However, the *Oophytum oviforme* Community has particular habitat preferences which were given in the description of the community (Chapter IX.1.3 # 29) but which are not sufficiently characterised by any of the environmental variables employed for the CCA. The community is largely restricted to upper slopes and ridges of plateaux which are exposed to south or south-west from where the fog comes in from the sea (Chapter IX.1.3 # 29). This habitat preference of the characteristic species of the community, *Oophytum oviforme*, has been mentioned by Ihlenfeldt already in the revision the genus *Oophytum* (Ihlenfeldt 1978).

Among the communities of the saline quartz fields the *Oophytum nanum* Community (# 27) is an outlier. Its strong separation can mainly be explained by its association with both relatively low soil pH and high salinity in soil. Such low soil pH has hardly been recorded for other communities of the saline quartz fields. The combination of high salinity and low soil pH is comparatively rare since the majority of the salt content mainly comprise sodium-chloride which dissolves in water with a neutral pH (Chapter IV.7), thus rising the soil pH of acid quartz fields considerably.

According to the unconstrained relevé scores of the CCA of the saline quartz fields, the three communities which are each dominated by a different *Argyroderma* species, show different habitat preferences. The *Argyroderma fissum* Community (# 22) revealed the broadest ecological amplitude among the communities of the saline quartz fields. This corresponds with the fact, *A. fissum* that the diagnostic species of the community is not restricted to quartz fields but is also found in other communities outside the quartz fields (Community # 10-20, see Synoptic Table II, Appendix 9). The *Cephalophyllum spissum* Community (# 24) has several species in common with the *Argyroderma fissum* C. They merely differ in regard to the dominating species which are *C. spissum*, an obligate quartz-field taxon in the first and *A. fissum* in the second community (IX.1.3, # 22, # 24). Yet, both communities differ regarding their habitat preferences. The results of the CCA analysis of the saline quartz fields of the Knersvlakte reveal that the *C. spissum* Community occurs on less saline but more sloping quartz fields which may also comprise an increasing amount of coarse quartz cover and cover of other lithology than quartz and is thus restricted to more particular habitat conditions than the *A. fissum* Community.

The dominating and diagnostic species of the *Argyroderma pearsonii* C. (# 25) and the *A. delaetii* Community (# 23) belong in the same genus as that of the *A. fissum* Community (# 22). The detailed analyses of the saline quartz fields make the differences between the three communities emerge. The *A. fissum* Community has a comparatively broad ecological amplitude. This is in contrast to the *A. pearsonii* Community, typically found on extremely saline quartz fields, which mainly present run-on areas along river beds as they are often found along the Soutrivier of the Knersvlakte. The *A. delaetii* Community prefers the less saline but slightly acid soils of quartz fields.

The typical habitat conditions of the *Phyllobolus digitatus* ssp. *digitatus* Community (# 28) ranges between high salinity in soil and high inclination of slopes which are contradictory variables within the data set. The relevés of the community are hence scattered along both variables according to the constrained relevé scores of the CCA ordination. This pattern reveals that the

typical habitat of the community is often found on slopes which are covered by quartz gravel (Chapter IX.1.3, # 28). Depending on where along the topo-sequence of the slope the population occurs, the salinity may increase due to the subterraneously percolating water which comes to the surface somewhere along the slope and causes accumulation of easily soluble salts such as sodium chloride.

The soil conditions which are typical for the *Drosanthemum diversifolium* Community are fairly atypical for quartz fields in general. According to the CA and the CCA ordination, the community is strongly associated with comparatively deep, soils with high carbonate content. Both environmental variables, however, are typically not associated with quartz fields. This is in line with the fact that the diagnostic and dominating species of the community, *D. diversifolium*, is not restricted to quartz fields but mainly found within the zonal vegetation on loamy soils in the vicinity of quartz fields (MHU 3.1-4).

The direct and indirect gradient analysis revealed a stronger turnover in species inventory and variance in environmental variable data of the **non-saline, acid quartz fields of the Knersvlakte** compared to the communities of the saline quartz fields. Six of the eight environmental variables which were employed for the ordinations explained the variances of species on the non-saline, acid quartz fields. Only two of them explained the variance on the saline quartz fields. However, the clear separation of the communities according to the CA and to the unconstrained relevé scores of the CCA was not completely mirrored by the constrained relevé scores though. This clear separation is mainly based on the species data. Also the classification of the vegetation (Chapter III.5.3) revealed that all communities of the non-saline, acid quartz fields of the Knersvlakte are defined by one or more proper diagnostic species which occurs exclusively in that community. The majority of the communities of the saline quartz fields are only based on the significant dominance of a species which may also be found in other communities of the quartz fields.

The communities of the non-saline quartz fields can be grouped according to their distribution within the CCA ordination and thus to their habitat preferences. Most of the communities dominated and defined by *Dicrocaulon* species (i.e., *D. longifolium*, *D. nodosum*, and *D. pseudonodosum*) are positively associated with three environmental variables: coarse quartz cover, inclination of slope, and soil depth. The communities dominated and defined by *Monilaria* species (*M. chrysoleuca*, *M. moniliformis*, *M. pisiformis*) as well as the *Brownanthus corallinus* Community (# 32) do not show strong preferences regarding any of the variables employed. They are plotted near the centre of the ordinations. The *Conophytum minutum* var. *minutum* Community is the only community that is strongly positively associated with low soil pH (H^+ concentration) and stone cover in soil. The *Ruschia burtoniae* C. (# 33) and *Dicrocaulon brevifolium* C. (# 36) cover a broad range of acid quartz fields. The similarity in habitat preferences of communities with closely related diagnostic species indicates a preadaptation of certain taxa for particular habitat conditions.

Due to their habitat ecology on quartz fields, the *Dicrocaulon* species can be characterised as typical inhabitants of rocky, sloping sites whereas *Monilaria* species seem to cover the interface between saline and non-saline quartz fields. This is most obvious for the putatively basic taxon *M. pisiformis* but is also revealed by the constrained relevé scores for the communities dominated by the other *Monilaria* species. Communities of acid quartz fields of the Knersvlakte which are dominated by closely related taxa (*Dicrocaulon* or *Monilaria* species) thus show a lower habitat differentiation than within comparative communities of the saline quartz fields (dominated by *Argyroderma* species). This lower habitat differentiation might be attributed to a stronger geographical separation within the genera *Monilaria* (Ihlenfeldt & Jörgensen 1973) and *Dicrocaulon*

(H.-D. Ihlenfeldt, pers. comm.) which both cover a broader area than the *Argyroderma* species (Hartmann 1977).

The joint plot of the constrained relevé scores which are linear combinations of the environmental variables point to distribution patterns of the communities in the CA ordination which are not completely explained by the environmental variables employed. According to the unconstrained relevé scores, only a few communities are strictly associated with particular environmental variables. Others have a generally positive but broad association with several environmental variables. This divergence between CA and CCA ordinations can be attributed to three factors:

- Noises in the environmental data set (McCune 1997b).
- Occurrence of geographically vicarious species *Dicrocaulon pseudonodosum*, *D. nodosum*, *D. longifolium* or *Monilaria moniliformis*, *M. chrysoleuca*, which inhabit similar habitats but in different parts of the Knersvlakte.
- The low separation of the communities by the constrained relevé scores mirrors the *de facto* high correspondence of habitat preferences of the communities which is also depicted by the broad overlap in species inventories among the communities of the saline quartz fields.

At saline quartz fields the ecological correspondence and broad overlap of habitat preferences between the quartz-field communities allows a broad overlap of their species inventories. However, the existence of distinct communities which are based on the monodominance of particular species indicates that each species has its optimum along the broad gradients at which it is able to dominate (Chapter IV.5). At the non-saline, acid quartz fields of the Knersvlakte the separation of the communities might be due to the vicarious occurrence of species, the ecological similarity of which thus seems to bias the separation of communities based on constrained relevé scores.

IV.6.3 Riethuis-Wallekraal area

The multivariate gradient analyses (CA and CCA) of the species and habitat data of relevés of the Riethuis-Wallekraal area reveal a strong differentiation into saline and non-saline quartz-field relevés as well as relevés outside the quartz fields. Thus, as in the Knersvlakte, the quartz fields of the Riethuis-Wallekraal area comprise two contrasting habitat types. In correspondence with the non-saline quartz fields of the Knersvlakte (Chapter III.6.2), the non-saline quartz fields of the Riethuis-Wallekraal area are positively associated with coarse quartz cover (> 60 mm) and H⁺ concentration. The saline quartz fields of the Riethuis-Wallekraal area are positively associated with small to medium sized quartz cover (< 60 mm) on soil surface, stone content in soil, inclination of slope and soil depth. They thus differ from the saline quartz fields of the Knersvlakte by the generally positive association with stone content in soil and inclination. In the Knersvlakte, both variables are rather associated with non-saline quartz fields.

The unconstrained and constrained relevé scores CCA were largely identical and the distortion of the community patterns defined by the Phytosociological Table II (Appendix 10) was moderate, thus indicating low noise in the environmental data set (McCune 1997b).

In the CA ordination which is solely based on the vegetation data, the vegetation of the saline quartz-field is again subdivided into two major groups each comprising two to three plant communities (Synoptic and Phytosociological Table II, Appendix 9 and Appendix 10). This separation, however, is not mirrored by the environmental gradients in the CCA ordinations where the communities of the saline quartz fields are plotted together in a diffuse group. The differentiation among the communities of the saline quartz fields is thus not entirely explained by

the environmental variables employed although the cumulative percentage of variance of species-environment relation is comparatively high for the CCA ordination (44 %).

The comparatively high variety of quartz-field communities that are restricted to saline quartz fields compared to only two communities that are found on non-saline quartz fields in the Riethuis-Wallekraal area indicate a high variety and frequency of saline quartz field habitats. The variety of habitat conditions on saline quartz fields is also shown by the high number of environmental variables that explain the variance of species data among the group of saline quartz fields, whereas only two variables explain the variances of species data of the non-saline quartz-field relevés. Also, taxa within lineages, which are generally restricted to non-saline quartz fields (*Conophytum*, *Dicrocaulon*, *Jacobsenia*, and *Monilaria*, all Mesembryanthema) inhabit saline quartz fields in the Riethuis-Wallekraal area (*Conophytum concavum*, *C. obscurum* ssp. *vitreopapillum*, *C. Dicrocaulon ramulosum*, *D. spissum*, *Jacobsenia vaginata*, and *Monilaria scutata* ssp. *obovata*) and are largely restricted to this area (Chapter III.2.4). Among these lineages only *Monilaria scutata* var. *scutata* occurs on non-saline quartz fields of the Riethuis-Wallekraal area. If the hypothesis proves true that *Dicrocaulon*, *Jacobsenia* and *Monilaria* have their centre of origin in the Knersvlakte (Chapter IV.2.5), the taxa colonised the saline quartz fields only after having arrived in the Riethuis-Wallekraal area which is particularly rich and diverse in saline quartz fields. In the frame of this hypothesis, *Monilaria sc.* ssp. *scutata* can be interpreted as the relatively basal infraspecific taxon which also covers the southern sub-area of the species (Ihlenfeldt & Jörgensen 1973). *M. sc.* ssp. *obovata* can be interpreted as the more derived taxon which covers the northern sub-area of the distribution area of the species. *M. s.* ssp. *obovata* might have split in adaptation to the newly colonised habitats in the north. This is also in line with Ihlenfeldt & Jörgensen's hypothesis on the phylogeny of the genus *Monilaria* (Ihlenfeldt & Jörgensen 1973, Ihlenfeldt 1994). Due to the lack of understanding of the phylogeny of the respective taxa, the next relatives of the other halophytic quartz-field taxa of the quartz fields are not yet known.

IV.6.4 Richtersveld

The ordinations of the vegetation relevés of the Richtersveld reveal three main groups of communities, each positively associated with one of three most important environmental variables: communities that occur outside (associated with carbonate), the quartz fields, communities of the saline quartz fields (associated with electrical conductivity), and those of the non-saline quartz fields (associated with H⁺ concentration). The division of the quartz-field relevés into two main groups, saline and non-saline but acid quartz fields, is in line with the findings for the Knersvlakte and Riethuis-Wallekraal area (Chapters IV.6.2 and IV.6.3). In agreement with the latter, saline quartz fields of the Richtersveld are associated with dense quartz cover of small to medium-sized quartz debris (< 60 mm) whereas the non-saline quartz fields are positively associated with coarse fraction of quartz cover (> 60 mm). The saline quartz-fields of the Richtersveld, however, deviate from those in the Knersvlakte by being positively associated with inclination of slope and from those in the Riethuis-Wallekraal area by being positively associated with soil depth (Chapter IV.7).

The CA ordination shows a strong species overlap between the communities of the non-saline quartz fields and the *Ruschia leucosperma* C. (# 46) as well as the *Eberlanzia cyathiforme* Community (# 49) which are both mainly found outside quartz fields. Only the *Brownanthus pseudoschlichtianus* Community (# 52) was clearly separated from the quartz-field communities. The CCA ordinations showed that the *R. leucosperma* C. and the *E. cyathiforme* C. are both associated with edaphic habitat conditions (carbonate content and soil depth), which are typical for zonal soils outside the quartz fields.

The constrained and unconstrained relevé scores of the CCA ordination are largely identical. Community patterns which are revealed in the Phytosociological Table II (Appendix 10) and the CA are clearly grouped thus indicating relatively low noise in the environmental variable data (McCune 1997b).

In contrast to the communities of the Riethuis-Wallekraal area (Chapter III.6.3), most of communities and relevés of the quartz fields in the Richtersveld are associated with non-saline, acid quartz fields rather than with saline quartz-fields (one community with two sub-communities only), which also comprise a far higher number of species within the communities. The dominance of non-saline, acid quartz fields indicate that saline quartz fields are less extensive and less diverse due to the mountainous and rocky nature of the Richtersveld (Jürgens 1986). The more frequent association of quartz fields to rocky habitats in the Richtersveld and thus a great variance in altitude, might result in an increase of drainage and leaching of soils of the upper sequences of the soil catena. This is also in line with the generally lower values (> 1 mS/cm) and lower standard deviations of electrical conductivity among all quartz fields of the Richtersveld than of the Knersvlakte (> 3 mS/cm, compare Table 63). The Knersvlakte and the Riethuis-Wallekraal area, in return, are poorly undulated lowland areas which can be interpreted as extensions of the coastal plains.

IV.6.5 Bushmanland-Warmbad area

In the Bushmanland-Warmbad area, quartz fields do not comprise the two main groups, i.e., saline and non-saline, acid quartz fields which have been revealed for the quartz fields of all other areas (Chapter III.6.1-4). In contrast, the quartz fields of the Bushmanland-Warmbad area are subdivided into level quartz fields with deep soils on the one hand and in sloping quartz fields with high stone content in soil, low soil pH, and high electrical conductivity on the other hand. Thus, skeletal, acid quartz fields are positively associated with salinity. However, the salinity value ($\ll 1$ mS/cm) and its variance of these quartz fields are very low compared to the quartz fields of all other areas and can thus not be addressed as saline habitats. It can therefore be concluded that soil salinity does not play a role as habitat factor on these quartz fields. Also, the variance in H^+ concentration (most soil pH values range between pH 6 and 8; compare table Appendix 13) is relatively low and thus can hardly have an impact on the species turnover on the quartz fields. The low importance of H^+ concentration and electrical conductivity for the species composition is mirrored by the relatively short arrows representing these variables in the CCA ordination.

The low soil-chemical differentiation of the quartz-field habitats in the Bushmanland-Warmbad area can be attributed to the summer-rainfall conditions. These are characterised by short but very heavy rainfall events, which generally have a very patch character. Such heavy rainfalls can facilitate fluvial transport of soil material. By causing vast flood plains the summer rainfall may thus be able to level out landscape variation with respect also to chemical soil properties. By this and due to the dominance of coarse and freely drained soil texture (Watkeys 1999), small scale differences in soil conditions (which are due to in situ weathering of different lithology as well as by small scale dislocation and accumulation of salts) might be diminished.

Whereas on the quartz fields of other areas, the major differentiation of taxa and syntaxa is mainly conducted along the strong gradients of salinity and soil pH, for the Bushmanland-Warmbad area it can be hypothesised that the comparatively low diversity on obligate quartz-field taxa and quartz-field communities is attributed to the low diversity of quartz-field habitats. This hypothesis is supported by the fact that in the genus *Dinteranthus* the main differentiation on species level occurred by geographical separation, rather than by ecological specialisation to

edaphic particularities in a small-scale mosaic, as it has been shown for other quartz-field taxa (e.g., *Gibbaeum*) (Chapter III.6.1).

IV.6.6 Summary and conclusions

The multivariate analyses of the vegetation ecology of the quartz fields and adjacent zonal vegetation of five different areas revealed a clear differentiation between quartz fields and their surrounding. Quartz fields are typically positively associated with low soil depth, high salinity, high stone content, and/or low soil pH, respectively. In all areas, except in the Bushmanland-Warmbad area, quartz fields were separated into two contrasting habitat types: saline quartz fields and non-saline quartz fields (Table 68). The latter are often associated with very low soil pH and high stone content whereas the saline quartz fields are typically less skeletal and have an approximately neutral soil pH. In the Bushmanland-Warmbad area, this differentiation is less pronounced due to the generally low electrical conductivity on these quartz fields (< 1 mS/cm) (compare Table 61).

Both types of quartz-field habitats provide adverse growing conditions, which is caused by extreme edaphic aridity. They are either extremely saline which causes high osmolarity in soil, or they are non-saline but then characterised by shallow soils and/or high stone content, which causes low ability to store water.

Table 68. Characteristic range of edaphic variables for the two main groups of quartz fields in the Little Karoo, Knersvlakte, Riethuis-Wallekraal, Richtersveld.

Area	Habitat type	Soil depth [cm]	Stone content in soil [% weight]	Electr. conductivity [mS/cm]	Soil pH	Carbonate content in soil [Class 1-5]
Little Karoo	saline	0-25	40-80	1.5-7.5	7.0-8.5	0-3.2
	non-saline	0-20	30-50	0.1-2.0	4.4-7.0	0
Knersvlakte	saline	0-30	< 40	1.5-10.0	5.5-7.5	0
	non-saline	0-25	40-70	0.1-2.0	3.5-6.5	0
Riethuis-Wallekraal	saline	5-35	8-60	0.3-7.0	4.5-7.7	0
	non-saline	5-37	15-80	0.2-3.0	3.8-5.7	0
Richtersveld	saline	5-40	5-70	1.0-5.0	6.9-8.3	0-3
	non-saline	0-50	5-70	0.05-3	4.5-8.2	0-3

The indirect (CA) and direct (CCA) multivariate gradient analyses of the vegetation of different areas revealed a clear separation of the vegetation outside and inside the quartz fields as well as the differentiation within the quartz fields. This indicates particular habitat specialisation in species along edaphic gradients which has a strong impact on the species turnover on community level. Saline and non-saline quartz fields, house a completely different flora as has been shown by the vegetation classification as well (Chapter III.5 and IX.1).

These gradients can be quite subtle as has been shown for most of the communities of the saline quartz fields which revealed a broad overlap of species inventories and were typically defined by differences in species abundance. The constrained relevé scores of the direct gradient analyses showed, that very fine variances in habitat conditions determine which of the taxa dominates the particular quartz-field. This has been shown for *Argyroderma pearsonii* (# 25) and *Argyroderma delaetii* Community (# 23) in the Knersvlakte, for instance (Chapter IX.1.3). However, it can be assumed that also historical events (the question which population was the first to colonise the particular quartz fields) or historical processes which influenced the growing conditions during the colonisation (e.g., wetter or dryer phases) also play a role for the decision, which population dominates the quartz fields.

Communities on non-saline quartz-field, in return, typically have a strong species turnover and are thus defined by species with high fidelity. This can be attributed to the stronger ecological gradients within these quartz fields. They are characterised by inclination of slope, soil depth, stone content, and soil pH.

Consequently, there is not a single quartz-field habitat but quartz fields comprise at least two completely different types of habitats which provide contrasting growing conditions. Both habitat types house their own flora and vegetation which derive from contrasting ecological background. The saline quartz fields require halo-tolerance whereas the non-saline quartz fields are inhabited by generally saxicolous taxa. Further speciation and ecological specialisation by fine-scale discrimination of habitats resulted in the existence of many related species occurring in similar quartz-field habitats within a relatively small area. This is particularly obvious for lineages in Mesembryanthema. Similar processes, however, have been observed outside the quartz fields for other lineages as well, e.g., for geophytes (Goldblatt & Manning 1996) and in *Conophytum* (Hammer 1993b).

A strong relationship between particular soil conditions and vegetation is well known for various semi-arid systems (Zohary 1942, Box 1961, Greig-Smith & Chadwick 1965, Brown 1971, Jenny *et al.* 1990, Montana 1990). On edaphically extreme habitats this relationship reveals to be particularly strong and may result in species turnover on a small scale due to specialisation to adverse soil conditions. This has been shown for saline (e.g., Gates *et al.* 1956, Waisel 1972, Chapman 1975, Cantero *et al.* 1998, Daiyuan *et al.* 1998) and gypsum environments (Meyer *et al.* 1992, Guerra-Campo *et al.* 1999, Rubio & Escudero 2000).

For the Succulent Karoo Biome, such strong plant-soil relationship seems to be a common phenomenon in particular on mountainous (Jürgens 1986) and on edaphically special habitats (Schieferstein & Loris 1992, Schmiedel & Jürgens 1999, this study). The strong variances of edaphic properties on a small scale have a major impact on the species turnover and contribute considerably to the very high beta-diversity of the Succulent Karoo (Jürgens 1986, Ihlenfeldt 1994, Schmiedel & Jürgens 1999, Desmet *et al.* 1998, Desmet & Cowling 1999a, this study). So far, comparatively few studies has been conducted on the pattering of vegetation due to the patterns of different soil and geological conditions (but see Jürgens 1986). Most of the studies which investigate the relationship between vegetation pattern and physio-chemical soil features in the southern African Karoo are focussed on the biogenic patterns of soils. Such patterns can be induced by animals, known as heuweltjies and fairy rings (Midgley & Musil 1990, Milton 1990, Dean & Yeaton 1993, Milton & Yeaton 1993, Smith & Yeaton 1998, Becker & Getzin 2000), or plants (Palmer *et al.* 1988, Dean *et al.* 1999, Stock *et al.* 1999).

Considering the strong control of species composition and alpha and beta diversity of the Succulent Karoo vegetation by topographic and soil features, this aspect deserves more attention in future.

IV.7 Soil conditions of the quartz fields

The multivariate analyses (Chapter III.6) and the habitat description of the plant communities (Appendix IX.1) revealed following characteristic properties of quartz-field soils. They are shallower than the zonal soils and often skeletal. The fine material derived from shale or phyllite bedrock which are the dominating lithology and have a fine soil texture (fine-grained sand with varying portions of clay, loam, or silt). They are typically free of carbonate content. The quartz cover on soil surface varies in density and the size of the quartz fractions varies depending on the distance to the quartz veins. Beyond these general characteristics, two contrasting habitat conditions prevail on quartz fields. Quartz fields are either very saline but comparatively poor in stone content but densely covered by small- to medium-sized quartz debris. Or they are characterised by skeletal soil, high percentage of coarse quartz fractions on soil surface, low soils pH, and low salinity values. Although the detailed characteristics the two types may vary slightly from area to area (Table 68), the differentiation of saline and non-saline habitats is generally consistent for quartz fields in all southern Africa. Only in the Bushmanland-Warmbad area, where the salinity on quartz-field soil was generally very low (< 1 mS/cm), the differentiation into non-saline and saline quartz fields does not exist.

For the Namaqualand in general and the Knersvlakte in particular the differentiation in saline and non-saline quartz fields is most prominent. To date, little is known about the origin and age of the quartz fields (Chapter IV.2). Based on their position along the topo-sequence in the landscape and on physical and chemical soil properties, it can be hypothesised, that in the Namaqualand *sensu lato* the two quartz-field habitats are derived from different geomorphological processes. The majority of the saline quartz fields are found in plains, on foothills, or on broad valley floors along the drainage lines. Their soils seem mainly consists of allochthonic material, i.e., deposits of fluvial erosion from the surrounding elevations. The levelled and homogeneous soil surface, the poorly structured and relatively deep layer of substrate above bedrock (up to 30 cm) and the low stone content in soil (< 40 % weight) support this hypothesis. The stone content in soil consists mainly of (small- to medium-sized) quartz debris which were transported and deposited together with the fine material. The stone pavement would thus be a secondary development due to deflation and other processes that promote the formation of stone pavements (Chapter IV.2.1). Their position at run-on sites also influences the soil chemical properties of these quartz fields. Here the superficially or subterraneously flowing water accumulates, partly percolates, and evaporates over time which causes salinisation in the topsoil. The soil pH of the saline quartz fields is typically about neutral.

The soils of non-saline quartz fields, in return, apparently derived from *in situ* weathered bedrock material (mainly phyllite or shale) and are thus autochthonic. The majority of the stone content comprises coarse fractions of the poorly weathered bedrock (phyllite or shale) as well as quartz. In the direct vicinity of quartz veins, quartz may dominate the stone content. The accumulation of quartz stones on soil surface seems to be due to the same processes as for the saline quartz fields (compare also Chapter IV.2.1).

In the Namaqualand *sensu lato* these non-saline quartz fields are typically associated with extremely low soil pH (pH 3-4). This can partly explained by the occurrence of magnesium sulphate or other sulphatic salts (Schachtschabel *et al.* 1992). According to the ion spectra (Chapter III.6), sulphate and magnesium occur with largely the same absolute amount on saline and non-saline quartz fields. However, the proportional representation of ions showed, that sulphate occur with a higher proportion on non-saline (~ 20 -30 % of the anions) than on saline quartz fields ($\sim < 10$ -20 % of the anions). Also the proportion of magnesium was higher on non-saline quartz fields. Therefore, the low soil pH of the non-saline quartz fields can be attributed to

the increased proportion of sulphate in these soils. It can be assumed, that the majority of the sulphate occur in soil as magnesium sulphate.

Another possible reason for the extremely low soil pH is the occurrence of aluminium (Al^{3+}). Aluminium causes and is promoted by low soil pH (Schachtschabel *et al.* 1992, G. Miehlisch, pers. comm.). It is worth noticing, that also Vogel (1955) claimed in his descriptive paper on the algae underneath quartz stones, that the soils of quartz fields in the Knersvlakte comprise aluminium sulphate (“*Alaum*”), without giving any references or details though. The aluminium content determined by Jähnig (1994) for four soil profiles of quartz fields in the Knersvlakte revealed an aluminium content of 2.3-7.7 mg/kg. This is very much in line with the values for the 39 other soil profiles from the Namaqualand (1.7-8.0 mg/kg). The soil profiles sampled by Jähnig (1994), however, were saline quartz fields with electrical conductivity of 1.3-12 mS/cm and soil pH between pH ($CaCl_2$) 6.5-8.5. Future soil studies on the detailed chemical composition of quartz-field soils with special focus on the acid quartz fields seems to extremely rewarding.

In some patches, autochthonic soils with high salinity values (up to 6.8 mS/cm) occur. This result in an increase of the soil pH (5-6.2) compared to the non-saline quartz fields, which is still below the pH values common for the saline quartz fields (pH ~6.5-7.5). Such soils are far less frequent than non-saline acid soils but provides the typical habitat of *Oophytum oviforme* Community (# 29) in the Knersvlakte. In the CCA ordinations this community was grouped among the saline quartz fields but had an outlying position there (Chapter III.6.2).

Due to their topography and geomorphology, non-saline quartz fields comprise a higher variance in habitat conditions which typically occur in small-scale mosaics. These mosaics mirror the differences in bedrock lithology, in inclination of slope, exposition, percentage of run-on and run-off etc. The saline quartz fields in the plains (or salt pans), in return, are equalised by the homogenous topography, the uniform deposition of fine material and the impact of the extremely high salinity. For the plants, the extremely high salinity with its physiological implications seems to be most important and overrule other factors. Consequently, non-saline quartz fields are characterised by a high variety of habitats which form small-scale patterns, whereas saline quartz fields tend to be more extensive and homogeneous. In between these two extremes ranges a broad array of intermediate habitats, such as gently sloping quartz fields with influence of both in situ weathered soils and deposited salts, patches of saline quartz fields in shallow depressions among rocky, non-saline quartz fields, non-saline elevations in broad saline salt pans, etc. These gradients, specialisation and speciation of quartz fields taxa takes place.

IV.8 Structural composition of flora and vegetation

IV.8.1 The selection of functional traits

Morphological structures and phenological features represent an adaptive answer of plants to the conditions of their biotic and abiotic surrounding. Hence, edaphically and climatically similar conditions support an identical array of plant growth forms. Identical growth forms in non-related taxa have often been interpreted as a result of convergent evolution due to similar environmental conditions (Cody 1973, Orians & Solbrig 1977, Cody & Mooney 1978, Shmida 1981, Orshan *et al.* 1984, Orshan 1989).

The strong dominance of dwarf and leaf-succulent plants on quartz fields is striking and becomes evident at the first glance, as descriptive approaches reveal (Maneveldt 1995, Struck 1995, Schmiedel 1997, 2001b). One aim of this study is to understand the significance of the particular

array of growth forms on quartz fields and the ecological constraints that are responsible for them.

A prerequisite of the analysis of the relationship between structural features and ecological growing conditions is the selection of structural and functional traits which are most relevant for the response of a species to its surrounding. Numerous systems of classification have been suggested resulting in an endless series of terms and definitions: e.g., strategy types (Grime 1974, 1979a,b), plant functional types (Smith *et al.* 1997), “vital attributes” (Noble & Slatyer 1980), or life-form types (Raunkiaer 1934, Danserau 1951). A summary of the number of approaches is given by Duckworth *et al.* 2000. The literature on such non-taxonomic approaches and their application increased rapidly during the last three decades. This increase can be attributed to (a) the need to compare taxonomically distinct floras (Cody & Mooney 1978, Orloci & Stofella 1986, Shmida 1981, Orshan *et al.* 1984, Orshan 1989), (b) the assessment of overwhelming biodiversity of natural systems (Grime 1997, Gitay & Noble 1997, McIntyre *et al.* 1999), (c) investigation in the functional impact of the rapid decrease of species numbers (Walker 1992, Tilman *et al.* 1997), and (d) the needs of global change research (Diaz & Cabido 1997, Leemans 1997) as well as predictive modelling (Lavorel *et al.* 1997, Campbell *et al.* 1999).

To analyse vegetation ecology across regions and biomes, structural and functional traits need to be aligned and reduced to receive a manageable number of consistent characters to work with (Weiher *et al.* 1999). The selection on the one hand and lumping of characters at the other hand, can be done either deductively, i.e., based on an intimate knowledge of the role of different species in a particular ecosystem, or inductively by a statistical analysis of single character states and their particular response to the biotic and abiotic surrounding, as it has been suggested by Pillar (1999).

The present study aims at an understanding of the role of particular structural features (i.e., dwarf growth forms) which obviously dominate the vegetation of the quartz fields. Therefore, a deductive approach has been chosen, thus testing the null hypothesis that the dwarf growth forms have no ecological significance for the flora and vegetation of the quartz fields. For this purpose, the plants occurring on quartz fields were classified into groups according to their architectural and partly phenological features by employing Raunkiaer’s system of plant life forms (Raunkiaer 1934, modified by Ellenberg & Mueller-Dombois 1966, and Jürgens 1986). The life-form system by Raunkiaer, in addition to the modifications by Ellenberg & Mueller-Dombois (1966) and Jürgens (1986) which both aim to adjust the system to tropical and subtropical biomes, comprise a reasonable amount of groups.

Several other studies applied Raunkiaer’s life-form system for a non-taxonomic, structural approach to vegetation or flora (e.g., Whittaker & Niering 1965, Jürgens 1986, Danin & Orshan 1990, van Rooyen *et al.* 1990, Esler *et al.* 1999). However, the universal applicability of the system, which is based on the height of the renewal buds and was mainly developed for temperate to arctic biomes, has been questioned by some authors (Schulze 1982, Hoffman & Cowling 1987). Midgley & van der Heyden (1999), in return, point out that the Raunkiaer’s system recognises the plant’s investment in woody tissue relative to photosynthetic tissue and thus reflect very important aspects of life strategies.

The terms growth forms and life forms were often used synonymously although they cover different aspects (Hoffman & Cowling 1987, Midgley & van der Heyden 1999). The term “growth form” refers to the morphological architecture and general habit of the plant while “life form” refers specifically to the adaptive morphology or phenology in terms of its ability to survive the unfavourable season (Barkman 1988). Since this study is focussed on the architecture of the plants (i.e., mainly distinguishing between various types of chamaephytes) the term “growth form” was used throughout. The analyses conducted in the study shall reveal whether

these growth forms also form part of a life form, i.e., an adaptation to this particular habitat and its constraints. The role of growth forms will be discussed on two levels: with respect to phytogeographical distribution and composition (Chapter IV.8.2-6) as well as vegetation ecology (Chapter IV.8.7).

IV.8.2 The growth-form composition of the quartz-field flora

The growth-form spectrum of the obligate QFF is strongly dominated by chamaephytes among which the nano-chamaephytes (Chapter II.2.1) represent the most important growth-form group. All non-chamaephyteous growth forms are represented by very low percentages.

Unfortunately, the data available for the growth-form spectrum of the entire Succulent Karoo Flora (SKF) are patchy and incomplete, making a more detailed comparison difficult. The data by Orshan *et al.* (1984) that represents a growth-form spectrum of the SKF within their comparative study is based on two single relevés only and were therefore rejected as comparative data here. The most comprehensive figures are given by Milton *et al.* (1997). However, they are based on unpublished data by Acocks which comprise merely 863 species (Milton *et al.* 1997). This is less than 20 % of the 4850 plant species recorded for the SKF according to Hilton-Taylor (1996a). Due to this incompleteness, the data for the growth-form spectrum of the Goegap Nature Reserve (formally Hester Malan Nature Reserve, data taken from van Rooyen *et al.* 1990) were also included. The well investigated Goegap Nature Reserve (Le Roux 1984, van Rooyen *et al.* 1979a,b) is located in the Western Mountain or Upland Succulent Karoo (Hoffman 1996b) and, hence, represents a special section of the SKF. Both data sets of the Succulent Karoo show a high correspondence with respect to the growth-form spectra. They both differed considerably from that of the obligate QFF. Chamaephytes are generally over represented in the obligate QFF. In the Bushmanland-Warmbad Phytochorion and the Little Karoo Phytochorion, they even represent the only growth-form type within the obligate QFF. Phanerophytes and therophytes are underrepresented in the obligate QFF of all phytochoria. Geophytes and hemicryptophytes occur with largely the same percentage in the total SKF as in the obligate QFFs of the Knersvlakte, Northern and Southern Richtersveld Phytochoria.

Besides the above-ground parts of a plant the root systems are of high importance for the adaptation to habitats (Rundel & Nobel 1991). Unfortunately, despite of some early preliminary studies by Scott & van Breda (1937a,b, 1938, 1939) the root architecture of the Succulent Karoo vegetation is very little known (Midgley & van der Heyden 1999). But in contrast to floras of other winter rainfall zones (e.g., Mohave desert) where competition for soil water resources has led to the evolution of shrubs with divergent patterns of rooting depths (Cody 1989, 1991, Esler *et al.* 1999) the structural diversity of roots in the SKF seems to be comparatively low. The majority of the leaf-succulent shrubs of the biome have shallow roots that reach 10 to 20 cm (maximally 30 cm) in soil depth (Esler & Rundel 1999). The roots of the dwarf shrubs as they are typical for the QFF in particular, in most cases reach even less than 10 cm below soil surface. Hence, in terms of root growth forms the QFF does not seem to show significant variation. The root system was therefore excluded from the analysis.

IV.8.3 Correspondence in growth forms between the phytochoria

The comparative analysis of the regional fractions of the obligate QFF revealed a strong correspondence between their growth-form spectra. All regional quartz-field floras share the same dominance of chamaephytes. Among them, nano-chamaephytes are represented by the

highest number of species in all regional QFF. The similarity in growth-form spectra in the taxonomically distinct floras supports the hypothesis of the convergent evolution of growth forms.

This similarity is even more striking when taking in account that the six quartz-field phytochoria occur in two different Floristic Regions i.e., the Cape Floristic Region (i.e., the Richtersveld, central Namaqualand, Knersvlakte, and Little Karoo) and the Palaeotropis (i.e., Bushmanland-Warmbad area) (Jürgens 1991). The Floristic Regions are associated with different rainfall seasonalities. The Cape Floristic Region lies in the proper winter rainfall zone (rainfall peaks between May and August) whereas the Palaeotropis receives rainfall mainly in summer (compare Figure 2). The Little Karoo Phytochorion, however, ranges from the proper winter rainfall zone into the late summer rainfall zone: rainfall peaks occur from May to August in the western Little Karoo (weather station at Montagu) but shifts to November and March in the east (weather station at Oudtshoorn). The different rainfall regimes also support different biomes. The semi-arid winter rainfall zone of the Cape Floristic Region houses the Succulent Karoo Biome, which is dominated by leaf-succulent shrubs (Hilton-Taylor 1996a, Milton *et al.* 1997). The semi-arid summer rainfall zone houses the Nama Karoo Biome where the vegetation mainly comprises annuals, geophytes, grasses, and non-succulent small shrubs (< 1 m) (Palmer & Hoffman 1997). The occurrence of succulents increases in the southeast of the Nama Karoo (Cowling *et al.* 1994).

The difference in growth-form composition between the zonal vegetation of the Succulent Karoo Biome and the Nama Karoo Biome is not mirrored in the regional QFFs which are all dominated by leaf-succulents dwarf plants irrespective of their distribution. The special habitat conditions of the quartz fields obviously overrule the regional differences in rainfall regime and promote convergent evolution of largely identical growth forms in entirely separate floras.

However, besides the general correspondence, particular similarities and dissimilarities with respect to the growth-form types were detected between certain QFFs, thus resulting in two main groups: the Bushmanland-Warmbad Phytochorion as well as the Little Karoo Phytochorion on the one hand and the Phytochoria of the Namaqualand *sensu lato* on the other hand.

The **Bushmanland-Warmbad Phytochorion** and the **Little Karoo** differed from the other four QFF due to their high percentage of nano-chamaephytes and - hence - under-representation of all other growth-form groups. The nano-chamaephytes again, mainly consisted of the subglobose subgroup (they comprise 50 % or more of the taxa) whereas the other three nano-chamaephyteous subgroups were represented by comparatively low percentages only.

In the QFF of the **Namaqualand *sensu lato***, i.e., the Knersvlakte Phytochorion, the Riethuis-Wallekraal Phytochorion, the Southern and the Northern Richtersveld Phytochorion nano-chamaephytes were the most important group. In contrast to the Bushmanland-Warmbad and the Riethuis-Wallekraal Phytochorion also the other growth-form groups occur with a high frequency but low percentage. Among the nano-chamaephyteous subgroups the “other” nano-chamaephytes (Chapter II.2.1) comprise the most important groups except in the Knersvlakte Phytochorion where the subglobose nano-chamaephytes were slightly richer in species numbers.

In general, the very narrow array of growth forms within the eastern QFFs (Bushmanland-Warmbad and Little Karoo Phytochorion) deviate strongest from the growth-form spectrum of the general SKF by pronouncing the unique features of the obligate QFF most: chamaephytes, which represent the most important growth-form group of the QFF in general, represent 100 % of the growth forms within these QFFs. Moreover, most of the nano-chamaephytes within the eastern QFFs belong to the subglobose subgroup and consequently represent one of the most important nano-chamaephyteous subgroups of the total QFF. In contrast, in the QFFs of the Namaqualand *sensu lato* the most numerous subgroup of nano-chamaephytes is presented by the

“other” nano-chamaephytes, that is, by growth forms which do not meet the three main subgroups of growth forms of the obligate QFF (compact, subglobose, subterraneous). Consequently, the deviation of the growth-form spectrum of the obligate QFFs of the Bushmanland-Warmbad Phytochorion and the Little Karoo Phytochorion can be interpreted as an overemphasis of the generally observed trend within the obligate QFF.

This deviation could be attributed to the bias of data due to the low total number of obligate quartz-field taxa (11 taxa) within this phytochorion. However, this would not apply to the spectrum of the Bushmanland-Warmbad Phytochorion which comprises 24 taxa and has a higher number of species than the Riethuis-Wallekraal Phytochorion and the Southern Richtersveld Phytochorion. Therefore, these differences are interpreted in terms of adaptation to regional particularities of habitat conditions on quartz fields. Being part of two different Floral Regions and biomes (Chapter I.6) the Bushmanland-Warmbad Phytochorion and the Little Karoo Phytochorion correspond in their distance to the coast (a) and the increase of summer rainfall influence (b).

a) The Namaqualand *sensu lato* extends in south-north direction parallel to the west coast of the subcontinent (see Figure 1) whereas the Little Karoo and the Bushmanland-Warmbad Phytochorion lie further inland, in a distance of a minimum of 100km (Bushmanland-Warmbad Phytochorion) or 150km (Little Karoo Phytochorion) from the west coast. Generally, the increasing distance to the coast is correlated with the increasing continentality of the climate (more extreme temperatures and lower air humidity). The cold Benguela current along the southern African west coast regularly induces fog occurrences along the coast (Desmet & Cowling 1999b, Hachfeld & Jürgens 2000). The importance of the fog is generally acknowledged by ecologists (Jürgens 1986, von Willert *et al.* 1992, Desmet 1996, Cowling *et al.* 1999b, Desmet & Cowling 1999b) although only little is really understood about its physiological relevance for the plants (but see Hachfeld & Jürgens 2000, and unpublished data by K. Loris). The geographical vicinity of the Indian Ocean to the south of the Little Karoo has no influence on the climate since the Langeberge form a barrier for rain clouds and humid air coming from the south.

b) Although the differences between growth-form spectra of the Bushmanland-Warmbad Phytochorion and the Little Karoo Phytochorion on the one side and the phytochoria of the Namaqualand *sensu lato* on the other side is not purely in line with the delimitation of the rainfall zones (Figure 2), the impact of summer rainfall conditions increases with increasing distance to the west coast. The Bushmanland-Warmbad Phytochorion lies in the summer rainfall zone whereas in the Little Karoo Phytochorion the impact of summer rainfall increases with the distance to the west coast.

It seems that the increase of continentality and summer rainfall conditions resulted in a moderately different growth-form composition of the respective QFFs. However, in contrast to the zonal vegetation, in the obligate QFF they seem to even overemphasise those structural features, which are generally typical for winter rainfall conditions (leaf-succulence) but do not support the growth-form spectra of the summer rainfall zone. The particular edaphic and microclimatic habitat conditions of the quartz fields which might be responsible for these structures will be discussed in Chapters IV.8.7 and IV.9.4.

IV.8.4 The dominance of leaf-succulence

The overwhelming majority (97.4 %) of the QFF are succulents. Within this group leaf-succulents dominate clearly (only 4.5 % of the succulents were purely stem-succulent). The flora of the arid parts of southern Africa is generally acknowledged for its very high number of succulents which outranks most of the other regions world wide (Stock *et al.* 1997). However,

comprehensive, comparable data for the entire SKF hardly exist. The PRECIS data compiled by Gibbs Russell (1987) for instance, seem to be misleading with respect to number of succulents within the Succulent Karoo. Very little succulent taxa are recorded for this biome. This disproportion is probably due to the lack of Succulent Karoo data in the PRECIS data base in Pretoria at the time when the study by Gibbs Russell was conducted. Such incompleteness of the data set is also indicated by the obviously strong under-representation of the most important Mesembryanthema genera (such as *Ruschia*) in her compilation. Also other figures that can be drawn from literature are probably not complete but shall allow a preliminary approach. According to Werger and Ellis (1981) only 32 % of succulent taxa recorded for the SKF are succulents and van Rooyen *et al.* 1990 calculated 45 % of succulents for the Goegap Nature Reserve (in the Western Mountain or Upland Succulent Karoo (Hoffman 1996b). The figures given by Acocks (unpublished, cited in Milton *et al.* 1997) for the Western Mountain or Upland Succulent Karoo (Hoffman 1996b) and Jürgens (1986) for the western Richtersveld (Numees Valley) are significantly higher (82 % and 90 %, respectively). Irrespective which regional section or calculation is taken into account, in the obligate QFF succulents are clearly over-represented (~97 %) compared to the general SKF.

In order to understand the ecological background of succulent richness in various regions, several analyses of the relation between abiotic features (climate in particular) and succulent abundance have been conducted (Nobel 1980, Ellenberg 1981, Burgess & Shmida 1988, Hoffman & Cowling 1987, von Willert *et al.* 1992, Cowling *et al.* 1994, van Coller & Stock 1994). The deductive cognition of these syntheses is that a high abundance of succulence is mainly associated with areas of low but highly predictable rainfall. The occurrence of winter rainfall, which is characterised by high predictability (Hoffman & Cowling 1987) was the strongest predictor of the total number of succulents per sites in the Karoo (Cowling *et al.* 1994). The possible reasons for this relationship between succulents and rainfall has been summarised by Burgess and Shmida (1988) as follows: low rainfall is the necessary precondition for the succulents to be successful against their non-succulent competitors. Therefore, drought periods must be frequent and long enough to make obligate daytime carbonate fixation (C_3 and C_4 pathway) too risky for perennials.

Besides the rainfall regime, maximum temperatures seem also to delimit the distribution of succulents (von Willert *et al.* 1991). According to Jürgens' phytogeographic analysis of the southern African flora succulents are absent or rare in regions with maximum temperatures above 32° and minimum temperatures below 0°C, respectively (Jürgens 1991). Although relatively little is known about the thermal budget of succulents, it is likely that this restriction of the leaf-succulent growth forms is due to the leaf size. The larger the leaves the thicker are the leaf boundary layers. Consequently, larger leaves have a longer conduction distance and therefore, lower heat conduction (Nobel 1988). In case of a crassulacean acid metabolism, (CAM) cooling by transpiration via open stomata does not take place. Therefore, self shading (Nobel 1981) as well as highly reflecting cuticulas and cytoplasmatic tolerance (Steponkus 1981) are common in succulent plants.

Jürgens (1986) analysed the ecology and distribution of leaf- and stem-succulent growth forms in southern Africa. He interpreted the dominance of leaf-succulence in the winter rainfall zone as controlled by the coincidence of the rainfall period and growing season with low average temperatures. Stem-succulents, in return, are largely associated with areas where the rainfall period and growing season occurs during the hot months of the year. It can thus be hypothesised that the quartz fields provide special growing conditions which are compatible with regional conditions which generally seem to support leaf-succulent growth forms, such as low but predictable rainfall, moderate minimum and maximum temperatures, low evapotranspiration, and low competition. This hypothesis has been strongly supported by the data on the edaphic and microclimatic conditions of the quartz fields (Chapters IV.6, IV.8.7, and IV.9.4).

IV.8.5 The occurrence of leaf-deciduous plants

Drought-deciduous plants were under-represented within the obligate QFF. About 56 % of the taxa had drought-deciduous leaves (Table 11). According to Milton (1990), in the proper winter-rainfall zone of the Succulent Karoo the flora comprises 80 % of drought-deciduous species. The percentage of drought-deciduous plants also included all those taxa, in which the leaves were either dropped during the dry period or they remain on the plants but as dry papery sheaths, often providing shelter and shade for the newly formed leaves. The latter type is particularly typical for several Mesembryanthema of the *Mitrophyllum*-group (Ihlenfeldt 1971b) but also for other taxonomic groups within Mesembryanthema such as *Conophytum* spp., *Gibbaeum cryptopodium*, and *Muiria*.

In the eastern QFFs (Bushmanland-Warmbad Phytochorion and the Little Karoo Phytochorion) the percentage of drought-deciduous plants are even lower (20-35 %) than in the western QFFs (Namaqualand *sensu lato* 33-53 %, Table 12) and thus they deviate even stronger from the spectrum of the general SKF. Hence, the eastern QFFs seem to pronounce the characteristic features of the total QFF even more than the western QFFs. However, the decreasing percentage of drought-deciduous leaves towards the east corresponds with the findings of Milton (1990) that the percentage of drought-deciduous plants decrease with increasing influence of (additional!) summer rainfall. Whereas in the proper winter rainfall zone about 80 % of the species are drought-deciduous, the percentage is considerably lower in Worcester (16 %) and Prince Albert (10 %) (Milton 1990). This decrease of drought-deciduous plants has been attributed to the higher probability of receiving some rainfall outside the main rainfall season (Le Roux *et al.* 1989, Milton 1990).

The situation found for the regional QFFs can be explained in the same way. The lowest percentage of plants with drought-deciduous leaves were found in the QFF of the Little Karoo (20 %) and in the Bushmanland-Warmbad Phytochorion which both lie outside the the proper winter rainfall zone. The western part of the Little Karoo receives about 30 % of summer rainfall whereas the eastern part of the Little Karoo gets about 50-60 % of summer rainfall. The Bushmanland-Warmbad Phytochorion receives 50-80 % summer rainfall. Consequently, the low percentage of drought-deciduous plants in these Phytochoria can be attributed to the (additional) impact of summer rainfall there. The Phytochoria in the proper winter rainfall zones (Knersvlakte, Riethuis-Wallekraal Phytochorion, and Southern Richtersveld Phytochorion) showed a higher percentage of drought-deciduous plants. The relative lower percentage for the QFF of the Northern Richtersveld flora might be attributed to the floristic relationship to the Bushmanland-Warmbad Phytochorion (Chapter IV.2.4).

IV.8.6 Correspondence between growth-form and species richness

The relationship between the number of taxa and growth-form types per quarter-degree square varied strongly among the phytochoria (Chapter III.3). The Knersvlakte phytochorion, for instance, which is particularly rich in quartz-field species has a relatively low growth form-taxa-coefficient whereas for the Northern Richtersveld Phytochorion the coefficient is comparably high. In the case of the Knersvlakte, the low coefficient is obviously due to the very high number of obligate quartz-field taxa per quarter-degree square. The Knersvlakte flora showed a steep increase of growth forms with increasing number of taxa up to 15 taxa per quarter-degree square. The quarter-degree squares that housed about 15 quartz-field species comprised about seven different growth forms. With further increase of taxa, the number of growth forms increased

merely very little. Obviously, there was a non-linear relationship between species and growth-form richness at species numbers of > 15 per QDS.

Consequently, in particularly species-rich quarter-degree squares a redundancy of growth forms occurs. The occurrence of a greater degree of redundancy of growth forms in the SKF (compared to the Nama Karoo) has been discussed by Cowling *et al.* (1994). This seems to apply in particular to the narrow array of growth forms of the obligate QFF. Such growth-form redundancy, which is associated with a high species diversity, may indicate a functional redundancy which makes a certain portion of the flora dispensable for the functioning of ecologically important processes (Chapin *et al.* 1992, Walker 1992). However, the results of the analysis of the habitat ecology of growth forms (Chapter III.7) indicate that identical growth-form types may colonise different habitat types. Growth-form groups as defined for this study thus do not explain completely the functional role of the species within the ecologically important processes. Instead, other biological aspects such as the physiological adaptation of the species to certain abiotic conditions (von Willert *et al.* 1990, 1992, Veste *et al.* 2001) may influence the ecology of the taxa significantly.

IV.8.7 Edaphic control of the growth-form composition of the quartz-field vegetation

The growth-form spectrum of the quartz-field flora is characterised by a high importance of unusual growth forms with very specific morphological structures. Species confined to quartz fields tend to have reduced body size (dwarfism) and leaf number (Chapter III.7.2).

According to the distribution of different growth-form types along a gradient of increased density of quartz cover, mega-chamaephytes are generally negatively associated with quartz cover. The occurrence of nano- and micro-chamaephytes was largely independent from quartz cover. This has been shown for the quartz-field vegetation for different areas in the Succulent Karoo. For the vegetation of the Bushmanland-Warmbad area, in turn, this correspondence does not exist. The distribution of growth-form types along a gradient of increased salinity also did not show a significant correspondence for the different growth forms of all regions. This indicates, that there is no univariate relationship between growth-form distribution and quartz cover or salinity. The growth-form distribution inside and outside of quartz fields has to be analysed by employing multivariate statistics.

The growth-form types employed in the multivariate analyses of growth-form distribution along edaphic gradients for five different regional quartz-field landscapes showed distinct habitat preferences (Chapter III.7.3). Phanerophytes were generally absent from quartz fields. Mega-chamaephytes are positive associated with comparatively deep soils and high carbonate content and negatively associated with skeletal and saline quartz fields. Micro-chamaephytes revealed a broad distribution but are less abundant outside than inside the quartz fields where they may inhabit saline and non-saline habitats. Compact nano-chamaephytes have a generally similar habitat ecology like micro-chamaephytes but they are more positively associated with quartz cover than the first. Subglobose and subterranean nano-chamaephytes, the putatively most derived growth forms, in return, reveal the strongest association with particular habitat conditions. Where subglobose nano-chamaephytes reach high cover values (i.e., in the Knersvlakte, Little Karoo and Bushmanland-Warmbad area), they are largely restricted to skeletal, non-saline quartz fields which are often correlated with inclination of slope and low soil pH. Subglobose nano-chamaephytes typically occur with high cover values on saline quartz-field habitats with low stone content in soil.

Thus, the growth-form composition of quartz fields in all studied areas – a response to analogous gradients in edaphic aridity – is strikingly similar. Relative to surrounding zonal habitats, quartz-field soils are either shallower and their pore volume is further reduced by a dense packing of quartz debris (non-saline quartz fields), or aridity is exacerbated by high soil salinity (saline quartz fields). The relatively low cover of taller chamaephytes and the absence of phanerophytes on quartz patches has enabled their colonisation by nano-chamaephytes. Within the regional landscapes they are the exclusive habitat for subglobose and subterranean nano-chamaephytes. These tiny succulent growth forms are a unique and charismatic component of the SKF (Van Jaarsveld 1987; Hammer 1993b).

Within the quartz-field vegetation of all studied areas, the overall trend with regard to growth-form distribution is for larger forms to have less specialised habitat preferences and smaller forms to be more specialised. This is clearly evident among the subgroups of nano-chamaephytes: whereas the compact forms occur under more diverse habitat conditions, the smaller, subglobose nano-chamaephytes and especially the subterranean nano-chamaephytes are confined to more specific habitats. These trends are evident in independent lineages, within and among quartz-fields phytochoria. They are the result of convergent evolution in response to the strong selective regime associated with the unusual edaphic environments of quartz fields.

The non-saline quartz fields are similar to other stone fields or desert pavements of the Succulent Karoo (cf. Desmet & Cowling 1999a). Among the nano-chamaephyteous flora, they are home to subglobose members of *Conophytum*. This genus is associated with a wide range of rocky and shallow-soil habitats throughout the Succulent Karoo (Hammer 1993b). However, the saline quartz fields, which probably represent the most edaphically extreme habitats, are the exclusive home of most of the subglobose and particularly the subterranean forms.

These unusual growth forms are not exclusively confined to quartz fields. Locally endemic, contracted succulent shrubs are associated with many other shallow-soil habitats in the Succulent Karoo and its margins, including quartz and shale outcrops, fissures in granitic bedrock and other desert pavements (e.g., Hammer 1993b; Desmet & Cowling 1999a). For example, the three species of the genus *Tanquana* H.E.K. Hartmann & Liede (Mesembryanthema), a typical contracted succulent, are endemic to the Tanqua Karoo and the Little Karoo and never occur on quartz fields (Hartmann & Liede 1986). Nevertheless, species of this genus show the same growth forms (compact, subglobose and nano-chamaephytes) as found in the quartz-field flora. Most of the app. 120 species and sub-specific taxa of the genus *Conophytum* N. E. Brown (Mesembryanthema) are compact, subglobose, or even subterranean nano-chamaephytes (Hammer 1993b), whereas only 14 species (21 species and subspecies) of *Conophytum* are restricted to quartz fields (Chapter , Schmiedel 2001a).

The major difference between quartz fields and other shallow-soil habitats in the Succulent Karoo and its margins, is that contracted shrubs are the principal growth form on the former, whereas a greater diversity of growth forms coexist on the latter (Jürgens 1986; Cowling *et al.* 1994). Therefore, the question of interest remains: why are nano-chamaephytes the dominant growth form on quartz-field habitats? The microclimatic measurements on quartz fields and neighbouring habitats indicate that besides the edaphic conditions the microclimate of the quartz fields seems to play an important role (Chapter IV.10).

IV.9 Microclimatic conditions of quartz fields

Various authors considered southern African quartz fields as habitats that provide special microclimatic conditions (Vogel 1955, Hartmann 1981, Jürgens 1986). This hypothesis is mainly based on the striking experience of the strong reflection of visual light by quartz fields: during

clear, bright days quartz fields can appear as glaring and dazzling as new snow. Up to date, very few studies on the microclimatic conditions of quartz fields have been conducted. Von Willert *et al.* (1992) showed the thermal properties inside and outside quartz fields during a late summer day in the Knersvlakte (March 1977) but the thermal impact on dwarf plants at both habitat types has not been studied so far. However, the ecological advantage of submerged growth forms as they are typical for *Lithops* N.E.Br. (Aizoaceae) and several quartz-field taxa has been questioned repeatedly (Eller & Nipkow 1983, Eller & Grobbelaar 1986, Turner & Picker 1993) with controversial results. According to Eller & Nipkow (1983) and Eller & Grobbelaar (1986) the embedded growth form has no positive effect on the thermal properties of the plant and can merely be interpreted as a structural adaptation to reduce transpirational water-loss as has been shown by Eller & Ruess 1982 or even as a mechanism to protect the plant from browsing and trampling by larger herbivores. Turner and Picker (1993), in return, show evidence that the temperatures of submerged leaves and surrounding soils are strongly coupled and result in a heat flux from the leaf to the cooler soil. This, however, denies the existence of isolation by the old leaves which under natural conditions comprise several layers. In order get insight into microclimate of quartz fields and its possible impact on its dwarf inhabitants, microclimatic measurements were carried out.

IV.9.1 Radiation

The measurements of incoming global solar radiation and reflected radiation above quartz fields and above soils without quartz cover revealed an impinging global solar radiation of about 950 to 1100W/m² and a 5 % higher reflection by soils with quartz cover than neighbouring soils without quartz cover.

The maximum impinging global solar radiation of about 900 to 1100W/m² is in line with the value of 950-1200W/m² given for deserts by von Willert (von Willert *et al.* 1992). The 5 % higher reflection by quartz fields seems to contrast with the results by Eller who determined the optical properties in the wavelength range between 300 and 1300nm of a quartz stone from the southern African quartz fields. Eller (in von Willert *et al.* 1992) shows that the reflectivity of the quartz stone in the visible spectrum (300-700nm) is far higher than the reflectivity of a brown shale stone but does not differ considerably from that of red desert soil, whereas in the range of wavelength of the sun's infrared radiation (750-1350nm) the quartz stone reflects about 15 to 20 % less radiation than the red desert soil.

The data given by Eller (in von Willert *et al.* 1992) are difficult to compare with the data gathered in this study: the soil without quartz cover in the present study derived from weathered phyllite and was neither brown shale nor red desert soil. Also, the spectrum measured was broader (300-3000nm) than that employed by Eller (300-1350nm) and did not differentiate between different ranges of wavelength as has been done by Eller. However, the results by Eller that quartz fields have the same reflectivity for visible radiation as red desert soil contradicts the dazzling shine of the white quartz fields which indicate high reflectivity of the quartz fields in the visible spectrum. Von Willert *et al.* (1992) do not give a solution to that problem. Instead, they assume that, due to the reduced reflectivity, the radiation input on the plant by solar radiation reflected from the soils is reduced for plants growing on quartz fields compared to those that grow on red desert soils. Maybe, this obvious contradiction between measured data and experience in nature has methodical reasons. Since Eller's measurements were carried out on a single stone in an integrating sphere (von Willert *et al.* 1995), they may not represent the situation *in situ*. The reflectivity of a dense layer of quartz stones may differ from that of a single stone because of multiple reflection of neighbouring stones (D. J. von Willert, pers. comm.).

The measurements of radiation properties of quartz fields within this study were restricted to a short period during winter time (September and October 1996). Future measurements of global

and reflected radiation should differentiate between visible and sun's infrared radiation and should be carried out during summer and winter time and under various different weather conditions, i.e., clear, overcast or cloudy sky.

IV.9.2 Thermal regime on quartz fields

During hot summer days, the daily maximum temperatures of the air near the ground exceed 60°C. These temperatures surpass the air temperature at 2 m height by up to 20°C. Quartz fields have considerably lower maximum air temperatures (differences of up to 10°C) than neighbouring soils without quartz cover for most days of the year. The maximum temperatures of the soil surface of quartz fields are lower only during the hot season whereas the relationship is inverse during winter.

The results are in line with the only comparative studies of surface temperature of soils with and without quartz cover during a summer day (5 March 1977) in the Knersvlakte carried out by von Willert *et al.* (1992). The soil surface of the quartz field showed a far lower maximum temperature (about 40°C) than the soil surface with quartz cover (about 48°C).

The relatively lower temperatures may be partly attributed to the higher reflection of the quartz fields, indicated by the 5 % higher reflection determined in the present study. However, besides reflectivity, heat capacity, heat conductivity, and evaporation influence the energy budget of a body. Since the determination of the energy budget of the quartz fields was not the objective of the study, the latter three variables have not been determined within the present study.

In warm desert environments temperatures of soil surface can reach 70°C (Nobel 1984, von Willert *et al.* 1992). The thermal impact on the plants can be extreme (Nobel *et al.* 1986; Nobel 1989), especially for dwarf plants growing near the soil surface. This even may surpass the extreme heat tolerance of some desert plants (> 60°C for *Haworthia* Duval and *Lithops*, Nobel 1989). Dwarf plants live near the ground and - if not shaded by surrounding plants or rocks - are therefore fully subject to these temperatures. The impact on the seedlings' survival by high maximum temperatures has been shown by Nobel (1984). Therefore, the occurrence of dwarf growth forms at open and exposed sites is supposed to be limited by the maximum temperatures on the soil surface. The relatively milder temperatures on quartz fields relatively reduce the thermal impact on the plants near the ground and thus cause less adverse growing conditions.

Quartz fields seem to be the only habitat type in southern Africa where dwarf growth forms occur exclusively and in high densities on level and open (i.e., not shaded) sites. Due to the fact that shrubby growth forms only occur with very low abundance and, consequently, shade provided by such plants is rare, dwarf growth forms on quartz fields are fully exposed to the incoming solar radiation.

Regarding the extreme temperature prevailing near the ground, the relatively lower maximum temperatures on quartz fields can possibly be relevant for the survival of dwarf plants near the ground. This presumption can be supported by the lower maximum temperatures of leaf surface of dwarf plants growing inside compared to the same species growing outside the quartz fields.

Beside the present study, no data have been published yet on leaf surface temperatures of comparable plants inside and outside of quartz fields. Von Willert *et al.* (1992) compare the leaf surface temperature of a dwarf *Argyroderma* plant inside quartz fields with that of a shrubby *Ruschia* Schwantes (Aizoaceae) plant outside quartz fields. They show that the leaf-surface temperatures of the latter exceed that of the ambient air by > 10°C thus reaching surface temperatures of > 45°C, whereas the leaf-surface temperature of the *Argyroderma* plant was close to that of the ambient air (ca. 35°C). This data does not properly compare the microclimatic conditions inside and outside the quartz fields, since the comparison refers to different growth forms which were measured at different heights above soil surface.

IV.9.3 Water supply

Another factor that seems to be important for the occurrence of succulents is a reliable water supply: The interdependence of low but predictable winter rainfall and high diversity of succulents has been stressed by numerous authors (Ellenberg 1981, Jürgens 1986, Hoffman & Cowling 1987, von Willert *et al.* 1992, Cowling *et al.* 1994, Stock *et al.* 1997).

In the western Succulent Karoo (the Namaqualand) fog plays an important role (Schulze & McGee 1978, Werger 1986, Weather Bureau 1988, Schulze 1997) and its impact on the Karoo vegetation has been discussed by various authors (Hoffman & Cowling 1987, Stock *et al.* 1997, Cowling & Hilton-Taylor 1999, Midgley & van der Heyden 1999). Dew, which can be recorded regularly for clear nights after hot days, occurs with even higher frequency (Desmet & Cowling 1999b). Stones and plants which practically represent a black body (von Willert *et al.* 1992, Geiger *et al.* 1995) often reach predawn minimum temperatures below the dew-point temperature of the ambient air, which results in a considerable amount of dew deposited on their surface.

The surface temperatures of a quartz stone and a brown shale stone, however, showed almost identical nocturnal minima. They both do not necessarily drop below the dew-point temperature of the ambient air; at some nights they are even several degrees above. This indicates no particular thermal conditions of quartz stones during night. If that holds true for other weather conditions (e.g., summer) and stones of other lithology than brown shale, quartz stones do not provide a better source for additional water supply by dew than other desert pavements.

However, desert pavements can generally be considered as having a positive effect on water supply. The roughness of the soil surface caused by the dense stone layer decreases the runoff and therefore increases the infiltration by water. The precipitation runs off the stones and concentrates in the gaps between them where it can penetrate deeper into the soils than when evenly distributed (Vogel 1955). Also, on desert pavements the total surface area at which condensation of water vapour can take place is increased by the stone layer. This may result in an increase of water input by dew or fog. The evaporation of the soil moisture is reduced by the stone layer on soil surface which seals large parts of the of the surface. On quartz fields this may result in the occurrence of green algae and cyanobacteria underneath semi-translucent quartz stones (Vogel 1955, Büdel & Wessels 1991, Rumrich *et al.* 1989, 1992). It seems to be likely that only shallow rooting dwarf succulents or cryptogams can benefit from such small amounts of water.

Consequently, it can be hypothesised that the relatively higher amount of dew deposited on desert pavements compared to other soil surfaces, might increase the predictability of humidity for their vegetation and has a positive effect on the succulent vegetation growing in such habitats. This might also promote the occurrence of dwarf succulents on quartz fields even outside the proper winter rainfall zone (i.e., the Bushmanland-Warmbad and Little Karoo Phytochorion). Perhaps, the regular dew fall replaces the predictable winter rainfall in this area. Also other dwarf plants that mainly occur on open plains, such as *Lithops* and *Tanquana* H.E.K Hartmann & Liede species both Aizoaceae, are also typically found on desert pavements - mainly of different lithology though, i.e., marble, feldspar (*Lithops*, Cole 1988, Hammer 1999) or shale (*Tanquana*, Hartmann & Liede 1986). This hypothesis, however, needs to be proven by measurements of the relative humidity of soils inside and outside the various desert pavements under different ranges of temperatures (summer and winter) and weather conditions.

IV.9.4 The possible impact of the microclimate on the vegetation of the quartz fields

Unshaded dwarf growth forms in warm deserts are exposed to extreme air temperatures near the ground. This is also true for the inhabitants of the quartz fields. However, quartz fields provide

relatively lower maximum air temperatures than surrounding soils. This results in lower maximum temperatures of the plants compared to similar plants growing outside quartz fields. These relatively less adverse growing conditions for dwarf plants on quartz fields alone cannot explain the dwarfism of their inhabitants: even on quartz fields, the maximum air temperatures near the ground are still far above the maximum air temperatures in 2 m height. Rather the dwarfism within the quartz-field vegetation seems to be controlled by soil chemical and physical conditions (Chapter IV.7). The microclimatic conditions on quartz fields might reduce the heat stress of the dwarf plants on quartz fields relative to other habitats and therefore facilitate the occurrence on such open and exposed habitats.

However, in southern Africa dwarf growth forms are not restricted to quartz fields. Numerous species (e.g., *Crassula* L. and *Conophytum* N.E. Brown species) are specialised on rocky habitats, e.g., outcrops and soil pockets in rock crevices (Hammer 1993b, Hammer *et al.* 2001). Until now little is known about their thermal properties. But in contrast to open and plain habitats like quartz fields, rocky habitats may provide shade due to surrounding rocks for at least parts of the day. Such shade combined with a clear sky (open shade) can result in a negative net thermal radiation flux, i.e., energy loss by the plant (von Willert *et al.* 1992).

Thus, the combination of shallow, quartz debris-covered, and fine-grained soils, with a clear gradient of decreasing stone content by volume and increasing salinity, explains the gradients in growth-form composition in quartz-field landscapes. The question remains: how do these dwarf growth forms persist in an arid environment? An explanation, fundamental to the existence of dwarf succulents throughout the Succulent Karoo, is that the unusual reliability of seasonal rains (Hoffman & Cowling 1987; Desmet & Cowling 1999b; Esler & Rundel 1999) enables the persistence of these small bodied plants. The low water storage capacity in their contracted leaves and stems would not be adequate for enduring severe and prolonged droughts (von Willert *et al.* 1992). However, this argument applies generally to subglobose and subterranean nanochamaephytes in the Succulent Karoo. Quartz patches, especially saline ones, represent an extreme case. Midgley & van der Heyden (1999) point out the importance of the regular fog precipitation in the western part of the Succulent Karoo (Knersvlakte to Richtersveld) for shallow rooting miniaturised plants on quartz fields. Again, this argument applies generally to dwarf plants and not to the quartz-field flora only. In contrast, the quartz fields outside the influence of fog (Little Karoo, Warmbad area and Bushmanland) show the same dominance of dwarf plants as in the western part of the Succulent Karoo.

It is therefore proposed that the high importance of ground-level growth forms on quartz fields is enabled by a decrease of thermal impact, owing to the specific properties of quartz. This might be relevant for subterranean growth forms as well, although the thermal advantage of growing under the soil surface is still a controversy (Eller & Nipkow 1983; Eller & Grobbelaar 1986; Turner & Picker 1993). In contrast, taxa like most of the *Conophytum* species which are not restricted to quartz fields, but comprise various ground-level or subterranean growth forms, generally inhabit micro-sites like rock crevices which are edaphically arid but are shaded for part of the day. More research is required on the comparative microclimatology of quartz fields and adjacent habitats as well as other habitats that support subglobose and subterranean nanochamaephytes.

IV.10 Synthesis and prospects

The gradient analyses of the vegetation of different regions showed a strong separation into two types of quartz fields. Both quartz-field habitats provide adverse growing conditions. They are either extremely saline which causes high osmolarity in soil, or they are non-saline but then characterised by shallow soils or high stone content, which limits the ability to store water. The growth-form distribution on quartz fields of different areas revealed an increase in growth-form

reduction and in habitat specialisation with increasing edaphic aridity. This is clearly evident among the more reduced subgroups of nano-chamaephytes: while the compact forms occur under more diverse habitat conditions, the subglobose and subterraneous nano-chamaephytes are confined to more specific habitats. The dwarfism on quartz fields can thus be interpreted as an adaptation to edaphically arid habitat conditions. The dwarf growth forms on quartz fields optimise the surface-volume ratio of the leaves (Ihlenfeldt 1978). The reduction of internodes decreases the investigations in the axes. Their low growing rate and small size restrict these plants to habitats with low competition such as habitats with adverse growing conditions (Gankin & Major 1964, Kruckeberg & Rabinowitz 1985, Ware 1990).

In hot deserts, temperatures on soil surfaces may reach extreme maximum temperatures (Nobel 1984, Nobel *et al.* 1986). This can have a severe impact on plants near the soil surface (Nobel *et al.* 1989, von Willert *et al.* 1992). Growth-form reduction, even though it is a successful plant strategy to cope with edaphic aridity, can have a severe impact on the plant's thermal regime. This is particularly relevant for open habitats - like quartz fields - where the plants are fully exposed to the impinging radiation without being shaded by surrounding shrubs or rocks. In return, in less open habitats like crevices of rocky outcrops dwarf plants may take advantage of being shaded for at least parts of the day. Such shade combined with a clear sky ("open shade") can result in a negative net thermal radiation flux, i.e., energy loss by the plant (von Willert *et al.* 1992). Quartz fields, as has been shown in this study, have relatively mild microclimatic conditions which measurably decrease the thermal impact on the plants. These conditions can possibly facilitate the occurrence of dwarf growth forms on quartz fields. Moreover, the roughness of the soil surface and the decrease of evaporation due to the stone cover, may improve the reliability of water supply for the dwarf plants on quartz fields (Chapter IV.9.3).

Summarising, quartz fields are on the one hand extremely adverse, i.e., edaphically arid, plant habitats. They require particular morphological and physiological adaptations. On the other hand they seem to provide mitigation due to their relatively milder microclimate and additional water supply on a small scale. This mitigation, however, can only be beneficial for dwarf plants.

With respect to both, relatively mild thermal regime and low but reliable water supply, quartz-fields seem to overemphasise southern African winter-rainfall conditions which - compared to summer-rainfall conditions - are characterised by relatively high rainfall reliability and tempered temperature regime (Cowling *et al.* 1999b, Esler *et al.* 1999). These ecological conditions are mirrored in the floristic and growth-form spectrum of the quartz-field flora (Chapter 0). The flora of the quartz fields overemphasises the typical features of the Succulent Karoo Flora in general, i.e., high degree of leaf-succulents, high percentage of Mesembryanthema and Crassulaceae taxa. Until now the microclimatic measurements on quartz fields were restricted to the winter rainfall zone. Comparative measurements under summer rainfall conditions (i.e., in the Bushmanland-Warmbad area) would be desirable. They should reveal whether the special microclimatic conditions on quartz fields in the winter rainfall zone also apply to those of the summer rainfall zone. Additional microclimatic studies should also include the thermal regime of rock-dwelling plants. To prove the hypothesised mitigation by the microclimatic conditions of quartz fields, its physiological effect (referring to heat stress and water budget) needs to be investigated by physiological studies. Such studies should also comprise the comparative investigations on the thermal regime of dwarf plants on rocky outcrops and in crevices.

Dwarf growth forms are also a common phenomenon in other arid ecosystems. In the Chihuahuan Desert and in the Sonoran Desert 78 % and 46 %, respectively, of the cactus species have small globular forms (Nobel *et al.* 1986). Many of these taxa may have special morphological and thermal properties that permit them to tolerate 70°C or more that can occur near the soil surface (Nobel *et al.* 1986). A comparison of the habitat ecology of dwarf succulents in the

northern American and southern African hot deserts could reveal whether the findings within this study are transferable to dwarf growth forms in general.

The examination of the obligate quartz-field flora revealed that several distantly related lineages conducted adaptive radiation on quartz fields which resulted in the convergent evolution of growth forms (Chapter IV.8.3). The occurrence of multiple adaptive radiation indicates that at one stage in the past quartz fields were opened up for (re-)colonisation. They provided new environments and release of competition which facilitate the rapid speciation of pre-adapted taxa, most probably saxicolous succulents. The reconstruction of the palaeo-environmental conditions of the South African west coast and adjacent interior by Midgley and co-workers (Midgley *et al.* 2001) indicates that this colonisation of quartz fields might have happened only after the Last Glacial Maximum (i.e., 15000 years BP) (Chapter IV.2.3). This implies that the highly specialised quartz-field flora, but also the majority of the Succulent Karoo species must have evolved very recently. This finding is supported by the molecular phylogenetic studies on more derived lineages in Mesembryanthema (Ruschioideae) by employing ITS sequences. They revealed very poor resolution on the species level (C. Klak and J. Thiede, pers. comm.). This indicates that the enormous speciation within the Mesembryanthema is a very recent and still ongoing process.

This process shows correspondence to the explosive radiation in the post-glacial phase in the cichlids of the east African lakes (compare Meyer 1993, McCune 1997a, Sturmbauer 1998, and others). In analogy to the varying water-levels of the east African lakes, climatic oscillation in southern Africa might have contributed to the repeated fragmentation of populations in the Succulent Karoo. The subsequent genetic isolation of local populations could have possibly been enhanced by the dominance of short-distance dispersal of the hygrochastic capsules in the Mesembryanthema (Ihlenfeldt 1983, Parolin 2001). Such isolation can result in disruptive speciation. In addition to the environmental conditions, key innovation as intrinsic factors can play a role for strong adaptive radiation in certain taxa. Such innovation allows a taxon to utilise an existing niche which is hardly accessible by other taxa. A key innovation, which might have accelerated the colonisation of quartz fields might have been the ontogenetic abbreviation (neoteny, Ihlenfeldt 1971a, 1994). It allows a rapid adaptation to edaphic arid habitats by reduction of size. This ability is very distinct in the Mitrophyllinae (Ihlenfeldt 1971b) that contribute a large number of genera to the obligate quartz-field flora. The explosive diversification within certain lineages has resulted in the fine-scale discrimination of habitats and in the existence of many closely related taxa occurring in similar habitats separated by a few kilometres. Consequently, the quartz-field flora seems to provide a manageable and hence ideal model system for studies which aim to test the hypothesised recent origin of the Succulent Karoo Flora. To investigate the adaptive radiation and ecological speciation, respective studies should be based on molecular phylogeny and phylogeography on population as well as species level. Habitat ecological and physiological data will examine the adaptations to microclimatic and edaphic particularities which seem to vary on population level (A. Ellis, pers. comm.). In order to understand the mechanisms of the near-sympatric speciation, future studies should also focus on phenology and pollination biology, dispersal biology, and establishment. Such studies, which give insight into the processes and time frame of the most recent evolutionary changes in the Succulent Karoo might also allow to state hypotheses on the adaptational abilities of the flora for future climate change.

V ACKNOWLEDGEMENTS

I would like to thank Norbert Jürgens for introducing me to the quartz fields, the supervision of this study and for the general support during the long time of our co-operation. I am greatly indebted to my colleagues at the Universities of Cologne and Hamburg, Thorsten Becker, Uwe Becker, Barbara Engelschall, Inge Gotzmann, Berit Hachfeld, Stefanie Nussbaum, Pia Parolin, Rosemarie Scheferhoff, Anja Schulte, and Joachim Thiede for their friendship and support, for the joint field trips and the numerous fruitful discussions. Anja Schulte kindly provided data for the zonal vegetation of the Knervlakte.

The Western Cape Nature Conservation Board and the Northern Cape Nature Conservation Services (South Africa) as well as the Ministry of Environment and Tourism (Namibia) kindly provided permits for the extensive field campaigns. I would like to express my thanks to the National Botanical Research Institute (NBRI) in Windhoek for the kind support and co-operation. I would also like to thank the South African Weather Bureau for the data and satellite images which they provided for the analysis of the microclimatic measurements.

The field work would not have been possible without the generous travel grants of the Cactus and Succulent Society of America (CSSA), Deutscher Akademischer Austausch-Dienst (DAAD), Deutsche Kakteen Gesellschaft e.V. (DKG), the International Organisation for Succulent Plant Study (IOS), Käthe Hacks Stiftung, Merensky Stipendien Stiftung, and the Stifterverband für die Deutsche Wissenschaft. I am grateful for their support.

I would like to express my deep gratitude to the Bolus Herbarium and the Compton Herbarium in Cape Town as well as to the National Herbarium of Namibia in Windhoek who strongly supported the research activities with technical provisions and identification. Particularly I would like to thank Jo Beyers, Pascale Chesselet, Graham Duncan, Cornelia Klak, Gillian Maggs-Kölling, John Manning, Terry Trinder-Smith, and De Sniyman. For the identifications of several specimens I also would like to thank Peter Bruyns, Maïke Gerbaulet, Steven Hammer, Heidrun Hartmann, Hans-Dieter Ihlenfeldt, Ulrich Meve, Bertil Nordenstam, Mike Struck, Dagmar Stüber, and Jan Vlok.

I am greatly indebted to Günter Miehllich, Alex Gröngröft, and Monika Voss of the Institute of Soil Science at the University of Hamburg. They generously supplied the laboratory facilities and experience for the soil analyses which were conducted within this study.

Without the ever friendly and supportive staff of the National Parks Board, the Western and the Northern Cape Nature Conservation Board, the fieldtrips would have been far less successful and enjoyable. Their logistic, technical, and scientific support as well as unfailing hospitality and encouragement were extremely helpful if not indispensable. Therefore I would like to express my sincere gratitude to Lisl and Tom Barry, Hugo Bezuidenhout, Elbe Cloete, Paddy Gordon, Deon Hignett, Kobus Kritzinger, Annelise Le Roux, Eben Le Roux, Alan Martin, Wessel Pretorius, Martin Scott, Heidi Streitberger, Johan Taljaard, Colette van Deventer, and Sunette van Romburgh.

A hearty thanks goes to Debra and Bernhard Agenbacht (Vanrhynsdorp), J. P. Adriaanse (Vredendal), Sariana and Peter de Bod (Ladismith), Hendrik Booysen (Montagu), J. and R. Kennedy (Springok), Neu Marleen and Hokkie Kotze (Nuwerus), M. and M. Kotze (Nuwerus), Tinus Kotze (Vanrhynsdorp), Boutie Louw (Lutzville), Douglas and Alastair Moodie (Grabouw), Christo Paulsen (Vanrhynsdorp), Louis Pienaar (Vanrhynsdorp), Japi du Plessis (Ladismith), W.F.H. Pool (Bitterfontein), Cheryl and Nico Pretorius (Warmbad), M. and M. Smith

(Vanrhynsdorp), Bruni and Johan de Villiers (Riversdale), Chris de Villiers (Vanrhynsdorp), Uwe Vogel (Hamburg), Annelie and Gerd van der Westhuizen (Nuwerus), Buys and Margaretha Wiese (Vanrhynsdorp), as well as numerous unnamed farmers. Their hospitality, technical support, and permission to work on their farms is highly esteemed. I. Roth-Hornung (Cologne) as well as Alfred and Waltraud Krause (Hamburg) generously provided facilities for the office work.

Over several years Nick Koch provided storage, housing, “car sitting”, and technical support in the Knersvlakte. Cornelia Klak and Peter Bruyns offered their hospitality when ever I stayed in Cape Town. I owe a great debt of gratitude to the South African and German colleagues for joint field trips, inspirational discussions and technical support: Richard Cowling, Philip Desmet, Allan Ellis, Cornelia Klak, Michael Kuhlmann, Detlev Metzger, Manuela Ott, Annelise Le Roux, as well as Hans and Helga Zimmer. Hans-Dieter Ihlenfeldt communicated to me his stimulating ideas on the flora of the quartz fields and Laco Mucina gave valuable advice for the vegetation classification.

The most important and inevitable moral support came from my dear friends and family Barbara Engelschall, Berit Hachfeld, Steven Hammer, Wiebke and Jan Hinsch, Till Krause, Pia Parolin, as well as Gunda and Volkart Schmiedel.

The endless text editing and proof reading by Mariam Akhtar-Schuster, Berit Hachfeld, Steven Hammer, Jan and Wiebke Hinsch, Michael Kuhlmann, Till Krause, and Pia Parolin as well as the delineation of several figures by Katrin Behrens and Julika Doerffer deserve recognition.

Lastly I thank Till Krause for his inspirations, most critical readings, invaluable advises, and constant support.

VI REFERENCES

- Acocks, J.P.H. 1988. *Veld types of South Africa*. Memoirs of the Botanical Survey of South Africa. No. 57. Leistner, O.A. Pretoria: Botanical Research Institute, pp.1-146.
- Adams, P. 1981. Australian saltmarshes. *Wetlands (Australia)* 1(1):8-10.
- Adams, P., Wilson, N.C., & Huntley, B. The phytosociology of coastal saltmarsh vegetation in New South Wales. *Wetlands (Australia)* 7(2):35-86.
- Adler, G.H. 1992. Endemism in birds of tropical Pacific islands. *Evolutionary Ecology* 6:296-306.
- Amit, R. & Gerson, R. 1986. The evolution of Holocene reg (gravelly) soils in deserts. - An example from the Dead Sea region. *Catena* 13:59-79.
- Anderberg, A.A. & Bremer, K. 1991. Parsimony analysis and cladistic reclassification of the *Relbania* generic group (Asteraceae-Gnaphalieae). *Annals of the Missouri Botanical Garden* 78:1061-1072.
- Anonymous 1998. *Gibbaeum* threatened. *Sabonet News*: 24-25.
- AG Boden. 1994. *Bodenkundliche Kartieranleitung*. 4 ed. Hannover: 1-392 p.
- Axelrod, D.I. & Raven, P.H. 1978. Late Cretaceous and Tertiary vegetation history. In: *Biogeography and Ecology of Southern Africa*. edited by Werger, M.J.A. The Hague: W. Junk, p. 77-130.
- Bagnold, R.A. 1953. *The physics of blown sand and desert dunes*. London, pp. 1-88.
- Bamford, M.K. & De Wit, M.J. 1993. Taxonomic description of fossil wood from Cainozoic Sak Rivier terraces, near Brandvlei, Bushmanland, South Africa. *Palaeontologia Africana* 30:71-80.
- Baskin, J.M. & Baskin, C.C. 1988. Endemism in rock outcrop plant communities on unglaciated eastern United States: an evaluation on the roles of edaphic, genetic, and light factors. *Journal of Biogeography* 15:829-840.
- Barkman, J.J. 1988. New systems of plant growth forms and phenological plant types. In: *Plant form and vegetation structure*. edited by Werger, M.J.A. et. al. De Hague: Academic Publishing.
- Bartels, T. 1994. *Untersuchungen zu Ursachen der Biodiversität ausgewählter Gebiete in der Knersvlakte (Südafrika) anhand von Landschaftstransekten*. University of Hamburg. :1-101.
- Becker, T. & Getzin, S. 2000. The fairy circles of Kaokoland (North-West Namibia) - origin, distribution, and characteristics. *Basic and Applied Ecology* 1(2):149-159.
- Bittrich, V. & Hartmann, H.E.K. 1988. The Aizoaceae - a new approach. *Botanical Journey of the Linnean Society* 97:239-254.
- Box, T.W. 1961. Relationships between plants and soils of four range plant communities in south Texas. *Ecology* 43:794-810.
- Brown, N.E. 1927. *Muiria hortenseae* N.E.Br. *The Gardeners' Chronicle* 83:116-117.
- Brown, N.E. 1928. *Mesembryanthemum* and some new genera separated from it. *Gardeners' Chronicle* 84:472-492.

- Brown, R.W. 1971. Distribution of plant communities in southeastern Montana badlands. *American Midland Naturalist* 85:458-477.
- Brown, J.H. & Kodric-Brown, A. 1977. Turnover rates in insular biogeography: an effect of migration on extinction. *Ecology* 58:445-449.
- Bruyns, P.V. 1989. Three new species of *Tylecodon* (Crassulaceae) from the western Cape. *South African Journal of Botany* 55(3):332-336.
- Bruyns, P. 1992. New taxa from the arid regions of southern Africa. *South African Journal of Botany* 58(1):50-55.
- Büdel, B. & Wessels, D.C.J. 1991. Rock inhabiting blue-green algae/cyanobacteria from hot arid regions. *Algological Studies* 94: 385-398.
- Burgess, T.L. & Shmida, A. 1988. Succulent growth-forms in arid environments. In: *Arid lands today and tomorrow*, edited by Whitehead, E.E., Hutchinson, C.F., Timmermann, B.N., & Varady, R.G. Boulder, Colorado: Westview Press, p. 383-395.
- Campbell, B.D., Stafford Smith, D.M., & Ash, A.J. 1999. A rule-based model for the functional analysis of vegetation change in Australasian grasslands. *Journal of Vegetation Science* 10:723-730.
- Cantero, J.J., Leon, R., Cisneros, J.M., & Cantero, A. Habitat structure and vegetation relationships in central Argentina salt marsh landscapes. *Plant Ecology* 137:79-100, 1998.
- Chapin, F.S., Schulze, E.-D., & Mooney, H.A. 1992. Biodiversity and ecosystem processes. *Trends in Ecology and Evolution* 7a:107-108.
- Chapman, V.J. 1975. The salinity problem in general, its importance, and distribution with special reference to natural halophytes. *Ecological Studies* 15:7-24.
- Carrasco, A.E., McGinnis, W., Gehring, W.J., & DeRobertis, E.M. 1984. Cloning of a X.laevis gene expressed during early embryogenesis coding for a peptide region homologous to Drosophila homoeotic genes. *Cell* 37:409-414.
- Cody, M.L. 1973. Character convergence. *Annual Reviews of Ecology and Systematics* 4:189-211.
- Cody, M.L. 1989. Growth-form diversity and community structures in desert plants. *Journal of Arid Environments* 17:199-209.
- Cody, M.L. 1991. Niche theory and plant growth form. *Vegetatio* 97:39-55.
- Cody, M.L. & Mooney, H.A. 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. *Annual Reviews of Ecology and Systematics* 9:265-321.
- Coetzee, J.A. 1978. Climatic and biological changes in south western Africa during the late Cainozoic. *Palaeoecology of Africa* 10-11:13-29.
- Cole, D.T. 1988. *Lithops. Flowering stones*. Acorn Books, Randburg.
- Cooke, R.U. & Warren, A. 1973. *Geomorphology in Deserts*, London: B.T. Batsford Ltd, pp. 1-374.
- Cooke, R.U., Warren, A., & Goudie, A.S. 1993. *Desert geomorphology*, London: B.T. Batsford Ltd., pp. 1-394.
- Corte, A.E. 1963. Particle sorting by repeated freezing and thawing. *Science* 142:499-501.

- Cowling, R.M. & Hilton-Taylor, C. 1999. Plant biogeography, endemism and diversity. pp. 42-56. In: Dean, W.R.J. & Milton, S.J. (eds.), *The Karoo: ecological patterns and processes*. Cambridge University Press, Cambridge.
- Cowling, R.M., Gibbs Russell, G.E., Hoffman, M.T., & Hilton-Taylor, C. 1989. Patterns of plant species diversity in southern Africa. In: *Biotic Diversity in southern Africa. Concepts and Conservation*. edited by Huntley, B.J. Cape Town: Oxford University Press, p. 19-50.
- Cowling, R.M., Esler, K.J., Midgley, F.G. & Honig, M.A. 1994. Plant functional diversity, species diversity and climate in arid semi-arid southern Africa. *Journal of Arid Environments* 27:141-158.
- Cowling, R.M., Cartwright, C.R., Parkington, J.E., & Allsopp, J.C. 1999a. Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: implications for late quaternary vegetation and climates in winter rainfall fynbos biome. *Journal of Biogeography* 26:367-378,
- Cowling, R.M., Esler, K.J. & Rundel, P.W. 1999b. Namaqualand, South Africa - an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology* 142:3-21.
- Cox, C.B. & Moore, P.D. 1993. *Biogeography - An ecological and evolutionary approach*, Oxford, London, Edinburgh etc. Blackwell Scientific Publications, pp. 1-326.
- Daiyuan, P., Bouchard, A., Legendre, P., & Gerald, D. 1998. Influence of edaphic factors on the spatial structure of inland halophytic communities: a case study in China. *Journal of Vegetation Science* 9:797-804.
- Danin, A. & Orshan, G. 1990. The distribution of Raunkiaer life forms in Israel in relation to the environment. *Journal of Vegetation Science* 1:41-48.
- Danserau, P. 1951. Description and recording of vegetation upon a structural basis. *Ecology* 32:172-229.
- Dean, W.R.J. & Yeaton, R.I. 1993. The effects of harvester and *Messor capensis* nest-mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. *Journal of Arid Environments* 25:249-260.
- Dean, W.R.J., Milton, S.J., & Jeltsch, F. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* 41(1):61-79.
- de Beer, C.H., Gresse, P.G., & Theron, J.N. 1999. Cenozoic deposits. In: *The geology of sheet 3118 Calvinia*, Council for Geoscience of South Africa (pre-print).
- Desmet, P.G. 1996. Vegetation and restoration potential of the arid coastal belt between Port Nolloth and Alexander Bay, Namaqualand, South Africa. University of Cape Town. M.Sc. thesis.
- Desmet, P.G. & Cowling, R.M. 1999a. Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa. *Plant Ecology* 142(1-2):23-33.
- Desmet, P.G. & Cowling, R.M. 1999b. The climate of the karoo - a functional approach. pp. 3-16. In: Dean, W.R.J. & Milton, S.J. (eds.), *The Karoo: ecological patterns and processes*. Cambridge University Press, Cambridge.
- Desmet, P.G., Ellis, A.G., & Cowling, R.M. 1998. Speciation in the Mesembryanthemaceae. *Aloe* 35(2):38-43.
- Desmet, P.G., Barret, T., Cowling, R.M., Heijnis, C., Le Roux, A., Lombard, A.T., & Pressey, R.L. 1999. *A systematic plan for a protected area system in the Knersvlakte region of Namaqualand*. Cape Town: Institute for Plant Conservation, University of Cape Town. IPC 9901:1-75.

- De Wit, M.J. & Bamford, M.K. 1993. Fossil wood from the Brandvlei area, Bushmanland as an indication of palaeoenvironmental changes during the Cainozoic. *Palaeontologia Africana* 30:81-89.
- Diamond, J.M. 1972. Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Science* 69:803-806.
- Díaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* 8:463-474.
- Dingle, R.V., Bremner, J.M., Giraudeau, J., & Buhmann, D. 1996. Modern and palaeo-oceanographic environments under Benguela upwelling cells of southern Namibia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123:85-105.
- Duckworth, J.C., Kent, M., & Ramsay, R.M. 2000. Plant functional types: an alternative to taxonomic plant community description in biogeography. *Progress in Physical Geography* 24(4):515-542.
- Duncan, G.D. 1988. *The Lachenalia Handbook*. Pretoria: National Botanic Gardens, pp. 1-71.
- Ellenberg, H. 1981. Reasons for stem succulents being present or absent in the arid regions in the world. *Flora* 171:114-169.
- Ellenberg, H. 1996. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Stuttgart: Verlag Eugen Ulmer, pp. 4-1095.
- Ellenberg, H. & Mueller-Dombois, D. 1966. A key to Raunkiaer plant life forms with revised subdivisions. *Ber.geobot.Inst. ETH* 37:56-73, 1966.
- Eller, B.M. 1982. Strahlungsabsorption von *Argyroderma pearsonii* (N.E.Br.) Schwantes in der Vegetations- und Ruheperiode. *Berichte der Deutschen Botanischen Gesellschaft* 95:333-340.
- Eller, B.M. & Grobbelaar, N. 1986. Diurnal temperature variation in and around a *Lithops lesliei* plant growing in its natural habitat on a clear day. *South African Journal of Botany* 52:403-407.
- Eller, B.M. & Nipkow, A. 1983. Diurnal course of the temperature in a *Lithops* sp. (Mesembryanthemaceae Fenzl) and its surrounding soil. *Plant, Cell and Environment* 6:559-565.
- Eller, B.M. & Ruess, B. 1982. Water relations of *Lithops* plants embedded into the soil and exposed to free air. *Physiologia Plantarum* 55:329-334.
- Ellis, F. 1988. Die gronde van die Karoo. University of Stellenbosch/South Africa. PhD.
- Ellis, A.G. 1999. Population dynamics, gene flow and local adaptation in a heterogeneous environment: implications for niche conservatism and speciation in the genus *Argyroderma* (Mesembryanthema). (unpublished Project Proposal).
- Esler, K.J. & Rundel, P.W. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: the Succulent Karoo and Mojave Desert ecosystems. *Plant Ecology* 142(1-2):97-104.
- Esler, K. J., P. W. Rundel, & R. M. Cowling. 1999. The succulent karoo in a global context: plant structural and functional comparison with North American winter-rainfall deserts. in W. R. J. Dean & S. J. Milton, eds. *The Karoo*. Cape Town: Cambridge University Press, pp 303-313.
- Free, E.E. 1911. Desert pavements and analogous phenomena. *Science* 33:355.
- Gankin, R. & Major, J. 1964. *Arctostaphylos myrtillifolia*, its biology and relationship to the problem of endemism. *Ecology* 45:792-808.

- Gates, D.H., Stoddart, A.L., & Cook, W.C. 1956. Soil as a factor influencing the plant distribution on salt-deserts of Utah. *Ecological Monographs* 26:155-157.
- Gauch Jr., H.G. 1982. *Multivariate analysis in community ecology*. Cambridge: Cambridge University Press, pp. 1-298.
- Geiger, R., Aron, R.H. & Todhunter, P. 1995. *The climate near the ground*. Friedrich Vieweg & Sohn, Braunschweig.
- Gerbaulet, M. 1992a. Die Gattung *Anacampseros* L. (Portulacaceae). I. Untersuchungen zur Systematik. *Botanische Jahrbücher für Systematik* 113(4):477-564.
- Gerbaulet, M. 1992b. Die Gattung *Anacampseros* L. (Portulacaceae) II. Untersuchungen zur Biogeographie. *Botanische Jahrbücher für Systematik* :565-576.
- Gerbaulet, M. 1995. *Phyllobolus* N.E.Br. emend. Bittrich (Aizoaceae): A reassessment of generic boundaries. *Botanische Jahrbücher für Systematik* 117:385-399.
- Gerbaulet, M. 1997. Revision of the genus *Phyllobolus* N.E.Br. (Aizoaceae). *Botanische Jahrbücher für Systematik* 119(2):145-211.
- Gibbs Russell, G.E. 1987. Preliminary floristic analysis of the major biomes in southern Africa. *Bothalia* 17(2):213-227.
- Gibbs Russell, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N.P., Anderson, H.M., & Dallwitz, M.J. 1990. Grasses of southern Africa. *Memoirs of the Botanical Survey of South Africa no 58*.
- Gitay, H. & Noble, I.R. 1997. What are functional types and how should we seek them? In: *Plant functional types. Their relevance to ecosystem properties and global change*. edited by Smith, T.M., Shugart, H.H., & Woodward, F.I. Cambridge: Cambridge University Press, p. 3-19.
- Glen, H.F. 1974. A revision of the Gibbaeinae (Mesembryanthemaceae). MSc, University of Cape Town. :3-180, Master thesis, .University of Cape Town.
- Goldblatt, P. & Manning, J. 1996. Phylogeny and speciation in *Lapeirousia* subgenus *Lapeirousia* (Iridaceae: Ixioideae). *Annals of the Missouri Botanical Garden* 83:346-361.
- Goldblatt, P. & Manning, J. 2000. *Cape Plants. A conspectus of the Cape Flora of South Africa*, Pretoria & St. Louis: National Botanical Institute & Missouri Botanical Garden, pp. 1-743.
- Greig-Smith, P. & Chadwick, M.J. 1965. Data on pattern within plant communities. *J. Ecology* 53:465-474.
- Gresse, P.G. 1992. *The tectono-sedimentary history of the Vanrhynsdorp group*. Pretoria: Department of Mineral and Energy Affairs. pp. 1-163.
- Grime, J.P. 1974. Vegetation classification by reference to strategy. *Nature* 250:26-31.
- Grime, J.P. 1979a. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169-1194.
- Grime, J.P. 1979b. *Plant strategies and vegetation processes*, New York:Wiley, 1979.
- Grime, J.P. 1997. Biodiversity and ecosystem function: The debate deepens. *Science* 277:1260-1261.
- Guerrero-Campo, J., Alberto, F., Hodgson, J., Garcia-Ruiz, J.M., & Montserrat-Marti, G. 1999. Plant community patterns in a gypsum area of NE Spain. I: Interactions with topographic factors and soil erosion. *Journal of Arid Environments* 41:401-410.

- Hachfeld, B. & Jürgens, N. 2000. Climate patterns and their impact on the vegetation in a fog driven desert: The Central Namib Desert in Namibia. *Phytocoenologia* 30(3-4):567-589.
- Hall, H. 1956. *Muiria hortenseae* N.E.Br. and its neighbours. *Cactus and Succulent Journal (GB)* :41-42.
- Hall, L.I. 1984. Three new species of Bulbine (Liliaceae) from the Vanrhynsdorp district, Cape Province. *South African Journal of Botany* 3:356-358.
- Hammer, S.A. 1993a. Macro-observations on *Cheiridopsis* N.E.Br. and *Odontophorus* N.E.Br. (Aizoaceae). *Bradleya* 11:75-87, 1993.
- Hammer, S.A. 1993b. The genus *Conophytum*. A conograph. Succulent Plant Publications, Pretoria.
- Hammer, S.A. 1996. Distracted by *Dactyloopsis*. *Cactus and Succulent Journal (U.S.)* 66:166-168.
- Hammer, S.A. 1999. *Lithops* - Treasures of the veld (Observations on the genus *Lithops* N.E.Br.), British Cactus and Succulent Society.
- Hammer, S.A. & Barnhill, C. 1997. Odes Part Two: Descriptions of New Mesembryanthea. *Bradleya* 15:42-47.
- Hammer, S.A., Opel, M., Schmiedel, U., Smale, T., Jürgens, A., Witt, T. & Rodgeron, C. 2001. *Dumpling and His Wife. New Views of Conophytum N.E.Br.* East Anglia Engraving. London. In press.
- Hanski, I. 1995. Effects of landscape pattern on competitive interactions. In: *Mosaic landscapes and Ecological Processes*. edited by Hansson, L., Fahring, L., & Merriam, G. London: Chapman & Hall, p. 203-224.
- Hartmann, H.E.K. 1973. *Untersuchungen zur Morphologie und Systematik der Gattung Argyroderma N.E.Br. (Mesembryanthemaceae Fenzl.)*, Univ. Hamburg, pp. 1-135.
- Hartmann, H.E.K. 1976. Monographie der Gattung *Odontophorus* N.E.Br. (Mesembryanthemaceae Fenzl). Monographien der Subtribus Leipoldtiinae Sch. I. *Botanische Jahrbücher* 97:161-225.
- Hartmann, H.E.K. 1977. Monographie der Gattung *Argyroderma* N.E.Br. (Mesembryanthemaceae FENZL). *Mitteilung des Instituts der Allg. Botanik Hamburg* 15:121-235.
- Hartmann, H.E.K. 1981. Ecology, distribution and taxonomy in Mesembryanthemaceae as a basis for conservation decisions. pp. 297-303. In: Syngé, H (ed.), *The Biological Aspects of Rare Plant Conservation*. John Wiley & Sons Ltd.
- Hartmann, H.E.K. 1988. Monographien der Subtribus Leipoldtiinae - VII Monographie der Gattung *Cephalophyllum* (Mesembryanthemaceae). *Mitteilung des Instituts der Allg. Botanik Hamburg* 22:93-187.
- Hartmann, H.E.K. 1991. Mesembryanthea. *Bolus Herbarium* 13:75-157.
- Hartmann, H.E.K. 1992. *Ihlenfeldtia*, a new genus in Mesembryanthea (Aizoaceae). *Botanische Jahrbücher für Systematik* 141(1):29-50.
- Hartmann, H.E.K. 1994. On the phytogeography and evolution of Mesembryanthea (Aizoaceae). Seyani, J.H. and Chikuni, A.C. (Eds.), *AETFAT Proceedings, Malawi*:2:1165-1180.
- Hartmann, H.E.K. 1996. Miscellaneous taxonomic notes on Aizoaceae. *Bradleya* 14:29-56.

- Hartmann, H.E.K. 1998. New combinations in Ruschioideae, based on studies in *Ruschia* (Aizoaceae). *Bradleya* 16:44-91.
- Hartmann, H.E.K. & Gölling, H. 1993. A monograph of the genus *Glottiphyllum* (Mesembryanthema, Aizoaceae). *Bradleya* 11:1-49.
- Hartmann, H.E.K. & Bruckmann, C. 2000. The capsules of *Drosanthemum* Schwantes (Ruschioideae, Aizoaceae). *Bradleya* 18:75-112.
- Hartmann, H.E.K. & Liede, S. 1986. Remarks upon distribution and ecology of *Pleiospilos* SCHWANTES s.str. and *Tanquana* H.E.K. HARTMANN & LIEDE (Mesembryanthemaceae). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 21:117-125.
- Hartmann, H.E.K. & Stüber, D. 1993. Studies on the Mesembryanthema (Aizoaceae): On the spiny Mesembryanthema and the genus *Eberlanzia* (Aizoaceae). *Contrib. Bolus Herbarium* 15:1-75.
- Hennekens, S.M. 1996. *Turbo(Veg). Software package for input, processing, and presentation of phytosociological data*. Wageningen: IBN-DLO, pp. 1-52.
- Herman, P. 1993. In: *Plants of southern Africa: names and distribution*, edited by Arnold, T.H. & De Wett, B.C., p. 774-776.
- Hilliard, O.M. 1983. *Inuleae, Asteraceae*, Pretoria: Botanical Research Institute.
- Hilton-Taylor, C. 1994. Western Cape Domain (Succulent Karoo). Republic of South Africa and Namibia. In: *Centres of Plant Diversity. A guide and strategy for their conservation*. edited by Davis, S.D., Heywood, V.H., & Hamilton, A.C.WWF for Nature & IUCN, p. 204-224.
- Hilton-Taylor, C. 1996a. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. In: *The Biodiversity of African Plants*. edited by van der Maesen, L.J.G. et. al. The Hague: Kluwer Academic Publishers, 1996, p. 58-72.
- Hilton-Taylor, C. 1996b. Red data list of southern African plants. *Strelitzia* 4:1-117.
- Hilton-Taylor, C. & Le Roux, A. 1989. Conservation status of the fynbos and karoo biomes. In: *Biotic Diversity in Southern Africa. Concepts and Conservation*. edited by Huntley, B.J. Cape Town: Oxford University Press, p. 202-223.
- Hilton-Taylor, C. 1996a. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. In: *The Biodiversity of African Plants*. edited by van der Maesen, L.J.G. et. al. The Hague: Kluwer Academic Publishers, p. 58-72.
- Hilton-Taylor, C. 1996b. Red data list of southern African plants. *Strelitzia* 4:1-117.
- Hoare, D.B., Victor, J.E., Lubke, R.A., & Mucina, L. 2000. Vegetation of the coastal fynbos and rocky headlands south of George, South Africa. *Bothalia* 30(1):87-96.
- Hoffman, M. T. & R. M. Cowling. 1987. Plant physiognomy, phenology and demography. Pages 1-34 in R. M. Cowling & P. W. Roux, eds. *The Karoo Biome: a preliminary synthesis*. Part 2: Vegetation and history. Pretoria: CSIR.
- Hoffman, M.T. 1996a. Lowland Succulent Karoo. In: *Vegetation of South Africa, Lesotho and Swaziland*, edited by Low, A.B. & Rebelo, A.G. Pretoria: Department of Environmental Affairs and Tourism, p. 60-61.
- Hoffman, M.T. 1996b. Upland Succulent Karoo. In: *Vegetation of South Africa, Lesotho and Swaziland*. edited by Low, A.B. & Rebelo, A.G. Pretoria: Department of Environmental Affairs & Tourism, p. 59-60.

- Hoffman, M.T. 1996c. Strandveld succulent Karoo. In: *Vegetation of South Africa, Lesotho and Swaziland*. edited by Low, A.B. & Rebelo, A.G. Pretoria: Department of Environmental Affairs & Tourism, p. 59.
- Ihlenfeldt, H.-D. 1971a. Über ontogenetische Abbreviationen und Zeitkorrelationsänderungen und ihre Bedeutung für Morphologie und Systematik. *Ber.Deutsch.Bot.Ges.* 84:91-107.
- Ihlenfeldt, H.-D. 1971b. Zur Morphologie und Taxonomie der Mitrophyllinae Schwantes (Mesembryanthemaceae). *Ber.Deutsch.Bot.Ges.* 84(11):655-660.
- Ihlenfeldt, H.-D. 1975. Some trends in the evolution of the Mesembryanthemaceae. *Boissiera* 24:249-254.
- Ihlenfeldt, H.-D. 1978. Morphologie und Taxonomie der Gattung Oophytum N.E.Br. (Mesembryanthemaceae). *Botanische Jahrbücher für Systematik* 99(2/3):303-328.
- Ihlenfeldt, H.-D. 1983. Dispersal of Mesembryanthemaceae in Arid Habitats. *Sonderbd.naturwiss.Ver.Hamburg* 7:381-390.
- Ihlenfeldt, H.-D. 1988. Morphologie und Taxonomie der Gattungen Diplosoma Schwantes und Maughaniella L.Bolus (Mesembryanthemaceae). *Beitr.Biol.Pflanzen* 63:375-401.
- Ihlenfeldt, H.-D. 1994. Diversification in an arid world: The Mesembryanthemaceae. *Annual Reviews of Ecology and Systematics* 25:521-546.
- Ihlenfeldt, H.-D. 1997. The systematic position of the genus *Drosanthemopsis* Rauschert and a revision of the genus *Jacobsenia* L.Bolus & Schwantes (Mesembryanthemaceae). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 27:109-126.
- Ihlenfeldt, H.-D. & Jörgensen, S. 1973. Morphologie und Taxonomie der Gattung Monilaria (Schwantes) Schwantes s.str. (Mesembryanthemaceae) (Monographie der Mitrophyllinae Schwantes I). *Mitt. Staatsinst. Allg. Bot. Hamburg* 14:49-94.
- Inglis, D.R. 1965. Particle sorting and stone migration by freezing and thawing. *Science* 148:1616-1617.
- Jähmig, U. 1994. Charakterisierung der Böden der Namib unter besonderer Berücksichtigung der Vegetation (Nationalpark Richtersveld - Südafrika - und andere Standorte). Institut für Bodenkunde, Universität Hamburg. :1-162, 1993. Diplom.
- Jenny, M., Smettan, U., & Facklam-Moniak, M. 1990. Soil-vegetation relationship at several arid microsites in the Wadi Araba (Jordan). *Vegetatio* 89:149-164.
- Jessup, R.W. 1960. Stony tableland soils of the southwestern portion of the Australian arid zone and their evolutionary history. *Journal of Soil Science* 11:188-196.
- Jongman, R.H.G., ter Braak, C.J.F., & van Tongeren, O.F.R. 1995. *Data analysis in community and landscape ecology*. Cambridge: Cambridge University Press, pp. 1-292.
- Jürgens, N. 1986. Untersuchungen zur Ökologie sukkulenter Pflanzen des südlichen Afrika. *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 21:139-365.
- Jürgens, N. 1991. A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegetatio* 97: 21-38.
- Jürgens, N. 1992. Vegetation der Namib. Ein Beitrag zur ökologischen Gliederung, Phytogeographie und Florengeschichte einer afrikanischen Trockengebietsflora. 1-452. Habilitationsschrift. University of Hamburg.

- Jürgens, N. 1995. Contributions to the phytogeography of *Crassula*. In: *Evolution and Systematics of the Crassulaceae*, edited by t'Hart, H. & Egli, U. Leiden: Backhuys Publishers, p. 136-150.
- Jürgens, N. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* 6:495-514.
- King, L. 1978. The geomorphology of central and southern Africa. In: *Biogeography and Ecology of Southern Africa*, edited by Werger, M.J.A. The Hague: W. Junk, p. 1-18.
- Klak, C. & Linder, H.P. 1998. Systematics of *Psilocaulon* N.E.Br. and *Caulipsolon* Klak *gen. nov.* (Mesembryanthemoideae, Aizoaceae). *Botanische Jahrbücher für Systematik* 120(3):301-375.
- Kruckeberg, A.R. & Rabinowitz, D. 1985. Biological aspects of endemism in higher plants. *Annual Reviews of Ecology and Systematics* 16:447-479.
- Kubitzki, K., von Sengbusch, P., & Poppendieck, H.-H. 1991. Parallism, its evolutionary origin and systematic significance. *Aliso* 13:191-206.
- Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T.D.A. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* 12:474-478.
- Leach, L.C. 1980. A review on *Tridentea* Haw. (Asclepiadaceae). *Excelsa* :1-69.
- Leemans, R. 1997. The use of plant functional type classifications to model global land cover and simulate the interactions between the terrestrial biosphere and the atmosphere. In: *Plant functional types: their relevance to ecosystem properties and global change*, edited by Smith, T.M., Shugart, H.H., & Woodward, F.I. Cambridge: Cambridge University Press, p. 289-318.
- Leistner, O.A. (Ed.). *Flora of South Africa*. Various years and volumes: Botanical Research Institute & Department of Agriculture and Water Supply, South Africa.
- Leistner, O.A. 2000. Seed plants of southern Africa: families and genera. *Strelitzia (Pretoria)* 10.
- Le Roux, A. 1984. 'N fitososiologiese studie van die Hester Malan-Natuurreservaat. University of Pretoria. :1-230.
- Le Roux, A. & Boucher, C. 1993. Flora of Namaqualand. Unpublished work.
- Le Roux, A., Perry, P., & Kyriacou, X.L. 1989. South Africa. In: *Plant phenomorphological studies in mediterranean type ecosystems*, edited by Orshan, G. Dordrecht: Kluwer, p. 159-346.
- Le Roux, A., Hilton-Taylor, C., Struck, M., Gerbaulet, M., & Jürgens, N. 1995. Bewaringsbelang van die Knersvlakte. Cape Town: Western Cape Nature Conservation, p. 1-17.
- Lewis, G.J. 1959. The genus *Babiana*. With 23 plates by the author and 10 photos. *Jl South.Afr.Bot. Supplementary Volume*(3):139-146.
- Linder, H.P., Meadows, M.E., & Cowling, R.M. 1992. The history of the Cape flora. In: *The ecology of fynbos*. edited by Cowling, R.M. Cape Town: Oxford University Press, p. 113-134.
- Lovegrove, B.G. & Siegfried, W.R. 1986. Distribution and formation of Mima-like earth mounds in the western Cape Province of South Africa. *South African Journal of Science*. 82:432-436.
- Low, A.B. & Rebelo, A.G. 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: Dept. of Environmental Affairs & Tourism, pp. 1-85.
- Lowdermilk, W.C. & Sundling, H.L. 1950. Erosion pavement, its formation and significance. *Trans.Am.Geoph.Union* 31:96-100.

- Lustig, L.K. 1965. Clastic sedimentation in Deep Springs Valley, California. *U.S.Geol.Surv.Prof.Pap.* 352-F:131-192.
- MacArthur, R.H. & Wilson, E.O. 1963. An equilibrium theory of island biogeography. *Evolution* 17:373-387
- MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press, 1-203p.
- Maneveldt, G. 1995. Succulent wonders of the Knersvlakte. *Veld & Flora* :81-82.
- McCune, A.R. 1997a. How fast is speciation? Molecular, geological, and phylogenetic evidence from adaptive radiation of fishes. In: *Molecular evolution and adaptive radiation*. edited by Givnish, T.J. & Sytsma, K.J. Cambridge: Cambridge University Press, p. 585-610.
- McCune, B. 1997b. Influence of noisy environmental data on canonical correspondence analysis. *Ecology* 78:2617-2623.
- McGinnis, W., Garber, R.L., Wirz, J., Kuroiwa, A., & Gehring, W.J. 1984. A homologous protein-coding sequence in *Drosophila* homoeotic genes and its conservation in other metazoans. *Cell* 37:403-408.
- McIntyre, S., Díaz, S., Lavorel, S., Landsberg, J., & Forbes, T.D.A. 1999. Disturbance response in vegetation - towards a global perspective on functional traits. *Journal of Vegetation Science* 10:604-608
- Meadows, M.E. & Watkeys, M.K. 1999. Palaeoenvironments. In: *The Karoo. Ecological patterns and processes*. edited by Dean, W.R.J. & Milton, S.J. Cambridge: Cambridge University Press, p. 25-41.
- Meve, U., Schmiedel, U., & Marais, E.M. 2000. *Pelargonium quarcticola* (Geraniaceae), a new species from the Knersvlakte. *South African Journal of Botany* 66 (2): 96-98.
- Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African Cichlid fishes. *Trends in Ecology and Evolution* 8(8):279-284.
- Meyer, S.E., Garcia-Moya, E., & Lagunes Espinoza, A.L.C. 1992. Topographic and soil effects on gypsophile plant community patterns in Central Mexico. *Journal of Vegetation Science* 3:429.
- Midgley, G.F. & Musil, C.F. 1990. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Province. *South African Journal of Botany* 56(2):158-166.
- Midgley, F.G. & van der Heyden, F. 1999. Form and function in perennial plants. pp. 91-106, In: Dean, W.R.J. & Milton, S.J. (eds.), *The Karoo: ecological patterns and processes*. Cambridge University Press, Cambridge.
- Midgley, F.G., Hannah, L., Roberts, R., MacDonald, D.J., & Allsopp, J.C. 2001. Have Pleistocene climatic cycles influenced species richness patterns in the Greater Cape Mediterranean Region? *J Mediterranean Ecology*, in press.
- Milton, S.J. 1990. Life styles of plants in four habitats in an arid Karoo shrubland. *South African Journal of Ecology* 1:63-72.
- Milton, S.J. & Wiegand, T. 2000. How grazing turns rare seedling recruitment events to non-events in arid environments. In: *Sustainable land-use in deserts*, edited by Breckle, S.-W., Veste, M., & Wucherer, W. Heidelberg: Springer, p. 197-207.

- Milton, S.J. & Yeaton, R.I. 1993. The influence of harvester ant *Messor capensis* nest-mounds on the productivity and distribution of some plant species on the southern Karoo, South Africa. *Vegetatio* 106:21-35.
- Milton, S.J., Dean, W.R.J., & Kerley, G.I.H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and vertebrate fauna. *Trans.Roy.Soc.S.Afr.* 48(1):15-46.
- Milton, S.J., Yeaton, R.I., Dean, W.R.J. & Vlok, J.H.J. 1997. Succulent karoo. pp. 131-166. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds.), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Montana, C. 1990. A floristic-structural gradient related to land forms in the southern Chihuahua Desert. *Journal of Vegetation Science* 1:669-674.
- Moore, J.M. & Picker, M.D. 1991. Heuweltjies (earth mounds) in the Clanwilliam District, Cape Province, South Africa: 4000 year old termite nests. *Oecologia* 86:424-432.
- Moulden, J.C. 1905. Origin of pebble-covered plains in desert regions. *Trans.Am.Inst.Min.Eng.* 35:963-964.
- Müller, M.A.N. 1985. *Gräser Südwestafrika/Namibias*, Windhoek: Direktorat für Holzwirtschaft und Forstwirtschaft, Department für Landwirtschaft und Naturwuschutz Südwestafrika/Namibia, pp. 3-286.
- Müller-Doblies, U. & Müller-Doblies, D. 1984. Zur Kenntnis der Gattung *Androcymbium* (Colchicaceae) im südlichen Afrika: Zwei Synonyma und fünf neue Arten. *Willdenowia* 14:279-189.
- Musick, H.B. 1975. Barrenness of desert pavement in Yuma County, Arizona. *Journal of the Arizona University of Science* 10:24-28.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Nel, C.G. 1953. *The Gibbaeum Handbook*. A genus of highly succulent plants, native to South Africa, London: Blandford Press.
- Nobel, P.S. 1980. Morphological, surface temperatures and northern limits of columnar cacti in the Sonoran Desert. *Ecology* 61:1-7.
- Nobel, P.S. 1981. Influence of photosynthetically active radiation on cladode orientation, stem tilting and height of cacti. *Ecology* 62:982-990.
- Nobel, P.S. 1984. Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia* 62:310-317.
- Nobel, P.S. 1988. Principles underlying the prediction of temperature in plants, with special reference to desert succulents. In: *Plant and Temperatures*. Edited by Long, S.P. and Woodward, F.I. Society of Experimental Biology, p. 1-23.
- Nobel, P.S. 1989. Shoot temperatures and thermal tolerances for succulent species of *Haworthia* and *Lithops*. *Plant, Cell and Environment* 12:643-651.
- Nobel, P.S., Geller, G.N., Kee, S.C. & Zimmerman, A.D. 1986. Temperatures and thermal tolerances for cacti exposed to high temperatures near soil surface. *Plant, Cell and Environment* 9:279-287.
- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43:5-21.

- Nordenstam, B. 1964a. New combinations in the Calenduleae. *Comp. Newsl.* 25:46-49.
- Nordenstam, B. 1964b. Studies in South African Liliaceae. II. Two small species of *Bulbine*. *Botaniska Notiser* 117(2):183-187.
- Nordenstam, B. 1969. Phytogeography of the genus *Euryops* (Compositae). A contribution to the phytogeography of southern Africa. *Opera Botanica* 23:1-77.
- Nordenstam, B. 1970. Notes on South African Iridaceae: *Lapeirousia* and *Babiana*. *Botaniska Notiser* 123.
- Nordenstam, B. 1976. Re-classification of *Chrysanthemum* L. in South Africa. *Botaniska Notiser*. 129:137-165.
- Nordenstam, B. 1986. The genus *Relbania* (Compositae). *Opera Botanica* 40:56-59.
- Nordenstam, B. 1987a. A new species of *Pentzia* (Compositae-Anthemideae) from the western Cape Province. *Botanische Jahrbücher für Systematik* 108(2/3):195-199.
- Nordenstam, B. 1987b. *Pelargonium caroli-benrici* (Geraniaceae), a new species from the Western Cape Province. *Plant Systematics Evolution* 155:333-337.
- Okland, R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological analysis. *Journal of Vegetation Science* 7:289-292.
- Orians, G.H. & Solbrig, O.T. (Eds.). 1977. Convergent evolution in warm deserts. Stroudsburg Pennsylvania: Dowden, Hutchinson & Ross, Inc.
- Orloci, L. & Stofella, S. 1986. A taxon-free numerical approach to the study of plant communities. *Ann. Arid Zone* 25:171-190.
- Orshan, G. 1989. *Plant pheno-morphological studies in Mediterranean type ecosystems*, Dordrecht: Kluwer Academic Press. pp. 1-404.
- Orshan, G., Le Roux, A., & Montenegro, G. 1984. Distribution of monocharacter growth form types in mediterranean plant communities of Chile, South Africa and Israel. *Bull. Soc. bot. Fr.* 131(2/3/4):427-439.
- Palmer, A.R., Crook, B.J.S., & Lubke, R.A. 1988. Aspects of the vegetation and soil relationships in the Andries Vosloo Kudu Reserve, Cape Province. *South African Journal of Botany* 54:309-314.
- Palmer, A.R. & Hoffman, M.T. 1997. Nama Karoo. pp. 167-188. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds.), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Parolin, P. 2001. Seed expulsion in fruits of *Mesembryanthema* (Aizoaceae). *Flora* 196: 313-322.
- Parkington, J.E., Cartwright, C.R., Cowling, R.M., Baxter, A.J., & Meadows, M.E. 2000. Paleovegetation at the last glacial maximum in the western Cape, South Africa: wood charcoal and pollen evidence from Elands Bay Cave. *South African Journal of Science* 95:543-546.
- Partridge, T.C. 1993. Warming phases in southern Africa during the last 150,000 years: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101:237-244.
- Partridge, T. C. 1997. Evolution of landscape. Pages 5-20 in R. M. Cowling, D. M. Richardson, & S. M. Pierce, eds. *Vegetation of Southern Africa*. Cambridge: Cambridge University Press.
- Partridge, T. C. & R. R. Maud. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology* 90: 179-208.

- Partridge, T.C., Avery, D.M., Botha, G.A., Brink, J.S., Deacon, J., Herbert, R.S., Maud, R.R., Scholtz, A., Scott, L., Talma, A.S., & Vogel, J.C. 1990. Late Pleistocene and Holocene climatic change in southern Africa. *South African Journal of Science* 86:302-306.
- Perry, P. 1984. Ten new species of *Eriospermum* Jacquin (Liliaceae) from the western Cape. *Jl South.Afr.Bot.* 50(4):503-534.
- Pierce, S.M. & Gerbault, M. 1997. *Brownanthus* Schwantes (Mesembryanthemoideae, Aizoaceae): two new species and a new combination from the Richtersveld and southwestern Namibia. *Aloe* 34(1&2):42-44.
- Pilbeam, J., Rodgerson, C., & Tribble, D. 1999. *Adromischus*. Holbury (UK):Cirio Publishing, pp. 1-104.
- Pillar, V. 1999. On the identification of optimal plant functional types. *Journal of Vegetation Science* 10:631-640.
- Poppendieck, H.-H. 1976. Untersuchungen zur Morphologie und Taxonomie der Gattung *Mitrophyllum* Schwantes s. lat. *Botanische Jahrbücher für Systematik* 97:339-413.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. Parts I, II. *Ecology* 43:185-215-410-432.
- Proctor, J. & Woodell, S.R.J. 1975. The ecology of serpentine soils. *Adv. Ecol. Res.* 9:255-284.
- Raunkiaer, C. *Plant life forms*, Oxford:1937.
- Rebello, A.G. 1996. South & South-west Coast Renosterveld. In: *Vegetation of South Africa, Lesotho and Swaziland*, edited by Low, A.B. & Rebello, A.G. Pretoria: Department of Environmental Affairs and Tourism, p. 67.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*, Cambridge: Cambridge University Press.
- Rowley, G.D. 1970. Succulent Compositae. *Cactus and Succulent Journal (GB)* 25(3):79.
- Rubio, A. & Escudero, A. 2000. Small-scale spatial soil-plant relationship in semi-arid gypsum environments. *Plant and Soil* 220:139-150
- Rumrich, U., Rumrich, M. & Lange-Bertalot, H. 1989. Diatomeen als "Fensteralgen" in der Namib-Wüste und anderen ariden Gebieten von SWA/Namibia. *Dinteria* 20:23-30.
- Rumrich, U., Rumrich, M. & Lange-Bertalot, H. 1992. Diatomeen unter Steinen in der Namib-Wüste und angrenzenden Savannen. *Acta Biologica Benrodis* 4:53-66.
- Rundel, P.W. & Nobel, P.S. 1991. Structure and function in desert root systems. In: *Plant root growth. An ecological perspective*. edited by Atkinson, D. Oxford: Blackwell Scientific Publications, p. 349-378.
- Rutherford, M.C. & Westfall, R.H. 1986. Biomes of Southern Africa - an objective categorization. *Mem.Bot.Surv.S.Afr.* 54:1-98.
- Rutherford, M.C., Westfall, R.H., O'Callaghan, M., Powrie, L.W., Hurford, J.L., & Schulze, R.E. 1996. Predicting survival in new environments through analytical GIS applications. *Environmental Software* 11:113-121.
- Sauer, N. 1979. *Dinteranthus* - Additional notes. *Aloe* 17(3+4):95-102.
- Sauer, N. 1980. *Dinteranthus* - Additional notes (Continued from Vol. 17(3&4), 1979). *Aloe* 18(1&2):17-20.

- Schachtschabel, P., Blume, H.-P., Brümmer, G., Hartge, K.-H. & Schwertmann, U. 1992. *Lehrbuch der Bodenkunde*, Stuttgart:Ferdinand Enke Verlag, pp. 1-491.
- Schaefer, M. 1992. *Ökologie*, Jena: Gustav Fischer, pp. 5-433.
- Schieferstein, B. & Loris, K. 1992. Ecological investigations on lichen fields on the Central Namib. I. Distribution patterns and habitat conditions. *Vegetatio* 98:113-128.
- Schulze, E.-D. 1982. Plant life forms and their carbon, water and nutrient relations. In: *Physiological plant ecology. 2. Water relations and carbon assimilation*. edited by Lange, O.L., Nobel, P.S., Osmond, C.B., and Ziegler, H. Berlin: Springer Verlag, p. 616-676.
- Shmida, A. 1981. Mediterranean vegetation in California and Israel: similarities and differences. *Israel Journal of Botany*30:105-123.
- Schmiedel, U. 1994. *Standortökologische und strukturelle Untersuchungen zur Vegetation der Quarzflächen in der Knersvlakte (Südafrika)*, Univ. Hamburg, pp. 1- 143.
- Schmiedel, U. 1997. Sukkulente Spezialisten auf Quarz. Ein weltweit einzigartiger Standort und seine Bedeutung für die Artenvielfalt in den Trockengebieten des südliche Afrikas. *Kakteen und andere Sukkulente* 48(10):217-225.
- Schmiedel, U. 2001a. *Conophytum* and the southern African quartz fields. edited by Hammer, S.A et al. *Dumpling and His Wife. New Views of Conophytum* N.E.Br. East Anglia Engraving. London, in press.
- Schmiedel, U. 2001b. Succulent specialists from southern African quartz fields. Tracing the ecology of a fascinating flora. *The Cactus and Succulent Journal (US)* 73(4): 170-175.
- Schmiedel, U. & Jürgens, N. 1999. Community structure on unusual habitat island: quartz-fields in the Succulent Karoo, South Africa. *Plant Ecology* 142:57-69.
- Smith, T.M., Shugart, H.H., & Woodward, F.I. 1997. *Plant functional types: Their relevance to ecosystem functioning*. Cambridge: Cambridge University press, pp. 1-369.
- Schulte, A. 1994. *Untersuchungen zur Vegetation der Sukkulenten Karoo (Südafrika) entlang einem grossräumigen Klimagradienten*. Diploma thesis, University of Hamburg. :1-149,
- Schulze, R.E. 1997. Climate. pp. 21-42. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds.), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Schulze, R.E. & McGee, O.S. 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. pp. 19-52. In: Werger, M.J.A. (ed.), *Biogeography and Ecology of southern Africa*. W. Junk, The Hague.
- Scott, J.D. & van Breda, N.G. 1937a. Preliminary studies on the root systems of renosterbos on the Worcester Veld Reserve. *South African Journal of Science* 33:560-569.
- Scott, J.D. & van Breda, N.G. 1937b. Preliminary studies on the root systems of *Galenia africana* on the Worcester Veld Reserve. *South African Journal of Science* 34:268-274.
- Scott, J.D. & van Breda, N.G. 1938. Preliminary studies on the root systems of *Pentzia incana*-forma on the Worcester Veld Reserve. *South African Journal of Science* 35:280-187.
- Scott, J.D. & van Breda, N.G. 1939. Preliminary studies on the root systems of *Euphorbia mauretanica*, *Euphorbia burmannii*, and *Ruschia multiflora* on the Worcester Veld Reserve. *South African Journal of Science* 36:227-235.

- Scott, L. 1994. Palynology of late Pleistocene hyrax middens, south-western Cape Province, South Africa: a preliminary report. *Historical Biology* 9:71-81.
- Scott, L. & Bousman, C.B. 1990. Palynological analysis of hyrax middens from southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 79:367-379.
- Scott, L. & Coorenmans, B. 1992. Pollen in recent *Procavia* (hyrax) and *Petromus* (dassie rat) and bird dung in South Africa. *Journal of Biogeography* 19:205-215.
- Scott, L. & Vogel, J.C. 1992. Short-term changes of climate and vegetation revealed by pollen analysis of hyrax dung in South Africa. *Review of Palaeobotany and Palynology* 74:283-291.
- Scott, L., Steenkamp, M., & Beaumont, P.B. 1995. Palaeoenvironmental conditions in South Africa at the Pleistocene-Holocene transition. *Quaternary Science Reviews* 14:937-947.
- Scott, L., Anderson, H.M., & Anderson, J.M. 1997. Vegetation history. In: *Vegetation of Southern Africa*. edited by Cowling, R.M., Richardson, D.M., & Pierce, S.M. Cambridge: Cambridge University Press, p. 62-84.
- Sharon, D. 1962. On the nature of hamadas in Israel. *Zeit. für Geom.* 6:129-147.
- Shmida, A. 1981. Mediterranean vegetation in California and Israel: similarities and differences. *Israel Journal of Botany* 30:105-123.
- Siesser, W.G. 1980. Late Miocene origin of the Benguela upwelling system of northern Namibia. *Science* 208:283-285.
- Smith, F.R. & Yeaton, R.I. 1998. Disturbance by the mound-building termite, *Trinervitermes trinervoides*, and vegetation patch dynamics in semi-arid, southern African grassland. *Plant Ecology* 137:41-53.
- Smith, G.F., Chesselet, P., van Jaarsveld, E.J., Hartmann, H.E.K., Hammer, S.A., van Wyk, B.-E., Burgoyne, P., Klak, C., & Kurzweil, H. 1998. *Mesembs of the world*, Pretoria: Briza Publications, pp. 1-405.
- Snijman, D. 1992. Notes on the Strumariinae (Amaryllidaceae-Amaryllideae). Six new taxa in *Strumaria* and *Hessea* from the central and northwestern Cape, South Africa, and southern Namibia. *Bothalia* 22(1):1-11.
- Spellerberg, I.F. & Sawyer, J.W.D. 1999. *In introduction to applied biogeography*. Cambridge: Cambridge University Press, pp. 1-243.
- Sørensen, T. 1948. A method for establishing groups of equal magnitudes in plant sociology based on similarity of species content. *Kongelige Danske Videnskabernes Selskab* 23:1-34.
- Springer, M.E. 1958. Desert Pavement and Vesicular Layer of Some Soils of the Desert of the Lahontan Basin, Nevada. *Soil Sci.Soc.Proc.* 22:63-66.
- Steinschen, A.K., Görne, A., & Milton, S.J. 1996. Threats to the Namaqualand flowers: outcompeted by grass or exterminated by grazing. *South African Journal of Science* 92:237-242.
- Steponkus, P.L. 1981. Responses to extreme temperatures. Cellular and sub-cellular bases. In: *Physiological plant ecology*. edited by Lang, O.L., Nobel, P.S., Osmond, C.B., & Ziegler, H. New York: Springer-Verlag, p. 372-437.
- Stock, W.D., Allsopp, N., van der Heyden, F. & Witkowski, E.T.F. 1997. Plant form and function. pp. 376-396. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (eds.), *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.

- Stock, W.D., Dlamini, T.S., & Cowling, R.M. 1999. Plant induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecology* 142(1-2):161-167.
- Struck, M. 1995. Land of blooming pebbles: flowers and their pollinators in the Knersvlakte. *Aloe* 32(3&4):56-64.
- Sturmbauer, C. 1998. Explosive speciation in cichlid fishes of the African Great Lakes: a dynamic model of adaptive radiation. *Journal of Fish Biology* 53(A):18-36.
- Taylor, C.H. 1996. Cederberg vegetation and flora. *Strelitzia* 3. Pretoria: National Botanical Institute pp. 1-75.
- ter Braak, C.J.F. & Smilauer, P. 1998. *Canoco Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Wageningen: Centre for Biometry Wageningen, pp. 1-351.
- t' Hart, H. 1995. Intrafamilial and generic classification of the Crassulaceae. In: *Evolution and Systematics of the Crassulaceae*, edited by t' Hart, H. & Eggli, U. Leiden: Backhuys, p. 159-172.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. 1997. The Influence of functional diversity and composition on ecosystem processes. *Science* 277:1300-1302.
- Tölken, H.R. 1977a. *A revision of the genus Crassula in southern Africa*, Cape Town: Bolus Herbarium, pp. 1-595.
- Tölken, H.R. 1977b. New taxa and new combination in the genus *Cotyledon*. *Bothalia* 12(2):191-194.
- Tölken, H.R. 1985. *Crassulaceae*, Botanical Research Institute & Department of Agriculture and Water Supply, South Africa, pp. 1-244.
- Turner, J.S. & Picker, M.D. 1993. Thermal ecology of an embedded dwarf succulent from southern Africa (*Lithops* ssp: Mesembryanthemaceae). *Journal of Arid Environments* 24:361-385.
- van Coller, A. & Stock, W.D. 1994. Cold tolerance of the southern African succulent *Cotyledon orbiculata* L. across its geographical range. *Flora* 189:89-94.
- van Jaarsveld, E.J. 1987. The succulent riches of South Africa and Namibia. *Aloe* 24:45-92.
- van Jaarsveld, E.J. 1998. *Tylecodon peculiaris* (Crassulaceae), a new species from the Northern Knersvlakte region (Western Cape). *Aloe* 35(1):10-11.
- van Oudtshoorn, F.P. 1991. *Guide to the grasses of South Africa*. Pretoria: Briza Publications.
- van Rooyen, M.W., Theron, G.K., & Grobbelaar, N. 1979a. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld: 1 General observations. *Jl South.Afr.Bot.* 45:279-293.
- van Rooyen, M.W., Theron, G.K., & Grobbelaar, N. 1979b. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld: 2 The therophyte populations. *Jl South.Afr.Bot.* 45:433-452.
- van Rooyen, M.W., Theron, G.K., & Grobbelaar, N. 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. *Journal of Arid Environments* 19:133-145.
- Veste, M., Herppich, W., & von Willert, D.J. 2001. Variability of CAM in leaf-deciduous succulents from the Succulent Karoo (South Africa). *Basic and Applied Ecology* 2(3):283-288.

- Vogel, S. 1955. Niedere "Fensterpflanzen" in der südafrikanischen Wüste. Eine ökologische Sondierung. *Beiträge zur Biologie der Pflanzen* 31:45-135.
- von Willert, D.J., Eller, B.M., Werger, M.J.A., & Brinckmann, E. 1990. Desert succulents and their life strategies. *Vegetatio* 90:133-143.
- von Willert, D. J., B. M. Eller, M. J. A. Werger, E. Brinckmann, & H.-D. Ihlenfeldt. 1992. *Life strategies of succulents in deserts with special reference to the Namib desert*. 1 ed. Cambridge, New York, Melbourne, Sidney, Port Chester: Cambridge Univ Press. 1-331 p.
- von Willert, D.J., Matyssek, R & Herppich, W. 1995. *Experimentelle Pflanzenökologie*. Georg Thieme, Stuttgart.
- Waisel, Y. 1972. *Biology of halophytes*, New York: Academic Press.
- Walker, B.H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:19-23.
- Walther, J. 1924. *Das Gesetz der Wüstenbildung in Gegenwart und Vorzeit*. Leipzig:Quelle und Meyer, pp. 1-421.
- Ware, S. 1990. Adaptations to substrate - and lack of it - in rock outcrop plants - *Sedum* and *Arenaria*. *American Journal Botany* 77:1095-110.
- Watkeys, M.K. 1999. Soils of the arid south-western zone of Africa. In: *The Karoo. Ecological patterns and processes*. edited by Dean, W.R.J. and Milton, S.J. Cambridge: Cambridge University Press, p. 17-25.
- Weather Bureau.1988. *Climate of South Africa. Climate statistics up to 1984*. Department of Environment Affairs. Pretoria.
- Weier, E., van der Werft, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10:609-620.
- Werger, M.J.A. 1978. Biogeographical division of southern Africa. In: *Biogeography and Ecology of Southern Africa*. edited by Werger, M.J.A. The Hague: W. Junk, p. 147-170.
- Werger, M.J.A. 1986. The Karoo and Southern Kalahari. pp. 283-360. In: Evenari, M., Noy-Meir, I. & Goodall, D.W. (eds.), *Hot Deserts and Arid Shrublands*, B. Elsevier, Amsterdam.
- Werger, M.J.A. & Ellis, R.P. 1981. Photosynthetic pathways in the arid regions of South Africa. *Flora* 171:64-75.
- Whitehead, D.R. & Jones, C.E. 1969. Small islands and the equilibrium theory of insular biogeography. *Evolution* 23:171-179.
- Whittaker, R.J. 1998. *Island Biogeography. Ecology, Evolution, and Conservation*. Oxford:Oxford University Press. pp. 1-285.
- Whittaker, R.H. & Niering, W.A. 1965. Vegetation of the Santa Catalina Mountains, Arizona (II). A gradient analysis of the south slope. *Ecology* 46:429-452.
- Williamson, G. 1996. New *Bulbine* species (Asphodelaceae) from the northwestern Cape. *Haseltonia* 4:13-23.
- Williamson, G. & Kennedy, H.C. 1997. A new *Conophytum* from the north-east Richtersveld. *Cactus and Succulent Journal(U.S.)* 69(4):205-208.

Yeaton, R.I. & Esler, K.J. 1990. The dynamics of a succulent karoo vegetation. A study of species association and recruitment. *Vegetatio* 88:103-113.

Zimmerman, N.F. 1996. The genus *Schwantesia* Dinter. *Cactus and Succulent Journal (U.S.)* 68:257-266.

Zimmerman, N.F. & Hartmann, H.E.K. 1995. Studies in *Schwantesia*. The rediscovery of *S. borchersii*. *Cactus and Succulent Journal (U.S.)* 67:162-165.

Zohary, M. 1942. The vegetational aspects of Palestine soils. *Palestine Journal of Botany* 2:200-246.

VII SUMMARY

The subject of this thesis is the flora, vegetation, and habitat ecology of quartz-covered stone pavements, i.e., quartz fields. These present unusual habitat islands which are found in five areas distant from each other in the arid regions of southern Africa (western South Africa and southeastern Namibia). The areas are situated in two biomes, which are also subjected to different rainfall regimes, the Succulent Karoo in the winter rainfall zone and the Nama Karoo in the summer rainfall zone. Despite the contrasting ecological conditions in the two biomes, the vegetation of the quartz fields in all areas is characterised by the dominance of compact, leaf-succulent dwarf-shrubs. The vegetation thus contrasts significantly with the surrounding, mainly shrubby, vegetation. These dwarf-shrubs which derived from distantly related lineages or even different plant families, indicate convergent evolution in adaptation to special habitat conditions. Moreover, 155 plant taxa (species and subspecies) are entirely restricted to these quartz fields, the majority being local or regional endemics. 67 % of the quartz field taxa are Mesembryanthema (Aizoaceae).

In order to get insight into the composition and history of the obligate quartz-field flora, its floristic and structural composition, phytogeographical pattern and ecological and phylogenetic background were analysed. It revealed that the obligate quartz-field flora has a strong correspondence to the Succulent Karoo Flora but overemphasises the characteristic floristic and structural features of the latter. Based on the phytogeographical patterns of the quartz-field taxa six quartz-field phytochoria were defined, i.e., the Little Karoo, Knersvlakte, Riethuis-Wallekraal, Southern Richtersveld, Northern Richtersveld, and the Bushmanland-Warmbad Phytochorion. The regional floras of these phytochoria showed general correspondence with respect to floristic and structural composition, thus supporting the hypothesis of the convergent evolution. But also regional differences emerged.

Based on preliminary phylogenetic data and palaeo-environmental reconstruction, an interpretation of the floral history of the quartz-field flora is given. The six phytochoria seem to originate from four centres of origin, i.e., the Little Karoo, the Knersvlakte, the Richtersveld, and the Bushmanland-Warmbad area. The Riethuis-Wallekraal Phytochorion consists mainly of taxa which originate from the Knersvlakte or the Richtersveld area. The palaeo-environmental reconstruction indicates that the quartz-field flora of southern Africa evolved only during the post-glacial warming and drying (15000 years PB).

For the vegetation-ecological investigations, vegetation relevés and soil samples from quartz fields and adjacent zonal habitats from all phytochoria were analysed. 72 plant communities of the vegetation were described and their distribution along edaphic and topographical gradients analysed by employing Correspondence and Canonical Correspondence Analysis (CA, CCA). In general, the soils of quartz fields were shallower compared to those of adjacent zonal habitats. In all areas, except the Bushmanland-Warmbad area, two different groups of quartz-field habitats, representing extremes of a continuum, were identified. One group was characterised by high salt content, neutral to slightly acid soil pH, and low stone content. The other group was characterised by low salt content, low soil pH, and high stone content. The two groups house a completely different flora and vegetation and were thus separated in all analyses. Analyses of vegetational and edaphic data of quartz fields and adjacent, zonal habitats were carried out using multivariate direct gradient analysis (CCA) in order to identify those factors that control the peculiar composition of growth forms on quartz fields. The results revealed highly similar patterns of growth-form composition in relation to similar edaphic gradients in all areas.

Microclimatic measurements inside and outside quartz fields were conducted. Quartz fields showed lower daily maximum temperature for the air near the ground than surrounding zonal soils. This has a measurable impact on the dwarf plants growing on quartz fields. This microclimatic regime which enhances the general characteristics of the winter rainfall conditions is assumed to be responsible for the overemphasising of the characteristic features of the Succulent Karoo Flora in the obligate flora of the quartz fields even outside the winter rainfall zone.

VIII ZUSAMMENFASSUNG

Gegenstand der Untersuchung sind die Flora, Phytogeographie, Vegetation und Standortökologie der Quarzflächen des südlichen Afrika. Quarzflächen sind inselhaft verbreitete Sonderstandorte, deren Bodenoberfläche dicht mit weißem Quarzgrus bedeckt ist, und die durch eine eigenständige Flora und Vegetation gekennzeichnet sind. Quarzflächen sind in zwei Biomen des südlichen Afrika zu finden, dem Sukkulenten Karoo Biom und dem Nama Karoo Biom. Beide Biome werden zwei unterschiedlichen Florenreichen zugeordnet, der Kapflora (Sukkulenten Karoo) und der Paläotropis (Nama Karoo), die durch unterschiedliche Niederschlagssysteme charakterisiert sind: die Kapflora durch Winterregen und die Paläotropis durch Sommerregen. Trotz der kontrastierenden ökologischen Bedingungen in den beiden Biomen, die auf den zonalen Standorten zur Ausprägung strukturell und floristisch ganz unterschiedlicher Vegetation führt, zeigt die Vegetation der Quarzflächen beider Biome große Übereinstimmung und hebt sich aufgrund struktureller Merkmale deutlich von der umgebenden, zonalen Vegetation ab. Diese besteht überwiegend aus aufrechten, strauchigen Wuchsformen, in der Sukkulenten Karoo zu einem großen Anteil aus blatt- aber auch achsensukkulenten Pflanzen, in der Nama Karoo aus Gräsern und nicht-sukkulente Sträuchern. Dagegen werden die Quarzflächen durch kompakte, bodennahe Blattsukkulenten dominiert. Die verzweigten Wuchsformen stammen von taxonomisch gut abgegrenzten Gruppen sogar verschiedenen Pflanzenfamilien ab, was auf eine konvergente Evolution in Adaption an besondere Standorteigenschaften hinweist.

Ziel der vorliegenden Arbeit ist es, die floristische Zusammensetzung, phylogenetische Herkunft und rezente Phytogeographie der Quarzflächen-Flora zu untersuchen sowie die steuernden Standortfaktoren der Sonderstandorte Quarzflächen zu ermitteln und deren Einfluß auf die floristische und strukturelle Vegetationszusammensetzung darzustellen.

Die Untersuchungen zur Quarzflächen-Flora zeigte, daß 155 Pflanzentaxa (Arten und Unterarten) ausschließlich auf Quarzflächen beschränkt sind. Es handelt sich ganz überwiegend um Vertreter der Mesembryanthema, Aizoaceae (ehem. Mesembryanthemaceae, 67 %) und Crassulaceae (10 %). Die Mehrzahl von ihnen sind Lokalendemiten. Aufgrund einer phytogeographischen Analyse wurden sechs Phytochorien der Quarzflächen-Flora definiert: im Sukkulenten Karoo Biom die Kleine Karoo, die Knersvlakte, das Riethuis-Wallekraal Gebiet, das südliche und nördliche Richtersveld; im Nama Karoo Biom das Pofadder-Warmbad Gebiet. Die Auswertung phylogenetischer und phytogeographischer Daten zeigte auf, daß die obligate Quarzflächen-Flora des südlichen Afrika vier Entstehungszentren hat, die Kleine Karoo, die Knersvlakte, des Richtersveld und das Buschmannland-Warmbad Gebiet. Die Quarzflächen-Flora des Riethuis-Wallekraal Phytochorions wird überwiegend von Taxa gestellt, die ihren phylogenetischen Ursprung in der Knersvlakte oder den Richtersveld-Phytochoria zu haben scheinen. Das Phytochorion im südlichen Richtersveld ist mit sieben, sehr isoliert vorkommenden Endemiten nur schwach begründet und scheint einen gemeinsamen Ursprung mit dem Phytochorion im nördlichen Richtersveld zu haben.

Andere Untersuchungen, wie molekularphylogenetische Studien (J. Thiede und C. Klak, persönliche Mitteilung) sowie eine Rekonstruktion der Paläo-Umweltbedingungen von Midgley und Mitarbeitern (Midgley *et al.* 2001) deuten darauf hin, daß die Sukkulenten Karoo und damit auch die obligate Quarzflächen-Flora des südlichen Afrika

möglicherweise erst in jüngster Zeit, während der nacheiszeitlichen Erwärmung und Aridisierung des südwestlichen Afrika (vor etwa 15 000 Jahren) entstanden sein könnten.

Vergleichende Analysen zur strukturellen und floristischen Zusammensetzung der obligaten Quarzflächen-Flora zeigten eine Übereinstimmung mit der gesamten Flora der Sukkulenten Karoo, wobei deren typischen Merkmale (z.B. Dominanz von Blattsukkulenz sowie von Mesembryanthema, Aizoaceae, und Crassulaceae) in der Quarzflächen-Flora besonders stark ausgeprägt waren.

Für die vegetationsökologischen Untersuchungen wurden 1200 Vegetationsaufnahmen (modifizierte Braun-Blanquet-Methode) auf Quarzflächen und angrenzenden zonalen Standorten in allen Gebieten im südlichen Afrika durchgeführt (in der Kleinen Karoo, Knervslakte, Riethuis-Wallekraal Gebiet, Richtesveld, und im Buschmannland-Warmbad Gebiet). Dabei wurde auch die zonale Vegetation der Knervslakte, einem Vielfältigkeitszentrum der Quarzflächen-Flora im südlichen Namaqualand, flächig erfaßt und analysiert. Für dieses Gebiet wurde auch eine Vegetationskarte erstellt, die in die Vegetationskarte vom Namaqualand, herausgegeben von A. Le Roux, und der *New Vegetationmap of South Africa*, herausgegeben vom National Botanical Institute / South Africa, eingehen wird.

Für etwa 1040 Vegetationsaufnahmen wurden auch topographische Standorteigenschaften notiert und Bodenproben entnommen, die auf ihre bodenchemischen und -physikalischen Eigenschaften untersucht wurden (Bodenmächtigkeit, Bodenart, Gesteinsgehalt, pH, elektrische Leitfähigkeit, Carbonatgehalt, sowie für ausgewählte Proben der Gehalt pflanzenrelevanter Ionen). 72 Pflanzengemeinschaften wurden in Vegetationstabellen ausgewiesen und beschrieben. Mit Einsatz multivariater Statistik, direkter und indirekter Gradientenanalyse (Correspondence, Analysis und Canonical Correspondence Analysis), wurde deren Verteilung entlang edaphischer und topographischer Gradienten dargestellt und untersucht. Die Böden der Quarzflächen waren in der Regel flachgründiger als die der angrenzenden zonalen Standorte. In allen untersuchten Gebieten, außer im Buschmannland-Warmbad Gebiet, konnten auf den Quarzflächen zwei Standorttypen, die zwei Extreme eines Kontinuums darstellen, unterschieden werden. Ein Standorttyp war durch hohen Salzgehalt (> 2 mS/cm), leicht sauren bis neutralen Boden-pH (pH 5-7) und geringen Gesteinsgehalt im Boden (< 50 %) gekennzeichnet. Der zweite Standorttyp war charakterisiert durch geringen Salzgehalt (< 1 mS/cm), geringen Boden-pH (pH 3-5) und hohen Gesteinsgehalt im Boden (> 60 %). Beide Standorttypen wiesen deutlich getrennte Floreninventare und Vegetationseinheiten auf, was zu einer klaren Trennung der Typen in allen Analysen führte. Die Verbreitung der Wuchsformen auf den Quarzflächen in ihrer Abhängigkeit von edaphischen Standortfaktoren wurde mit direkten Gradienten-Analysen (Canonical Correspondence Analyses) untersucht. Die Untersuchungen haben für die verschiedenen Gebiete eine große Übereinstimmung hinsichtlich der Verbreitungsmuster der Wuchsformtypen entlang von topographischen und edaphischen Gradienten aufgezeigt. Mit zunehmender Aridisierung des Standortes (Zunahme an Flachgründigkeit, Skelettgehalt, Salzgehalt) nahm auch die Reduktion der Wuchsformen zu (Abnahme an Wuchshöhe, Verzweigung, Anzahl an Blättern etc.). Größere, weniger abgeleitete Wuchsformen wiesen einen geringeren Grad an Standortspezialisierung auf, z.B. hinsichtlich Neigung der Fläche, Dichte und Größe des Gesteinsbelags, Skelett- oder Salzgehalt im Boden, auf als die stark reduzierten Wuchsformtypen.

Als weiterer standortökologisch relevanter Faktor wurden mit Pt100-Sensoren über mehrere Jahre kontinuierlich die Temperaturen der Bodenoberfläche und der bodennahen Luft von Böden mit bzw. ohne Quarzbelag untersucht. Für die bodennahe Luft von

Quarzgrus bedeckten Böden wurden geringere Tagesmaxima-Temperaturen ermittelt als für benachbarte Böden ohne Quarzbelag (Differenz bis zu 5 °C). Die Bodenoberflächen der Quarzflächen dagegen wiesen nur an heißen Sommertagen (November bis April) geringere Temperaturen auf (bis 4 °C), während sie im Winter bis zu 6 °C höhere Temperaturen aufwiesen als die Vergleichsflächen ohne Quarzbelag. Vergleichsmessungen von Blattoberflächentemperaturen von einer typischen Quarzflächen besiedelnden Blattsukkulente auf und neben den Quarzflächen in der Knersvlakte (*Argyroderma* spp., Aizoaceae) sowie in der Kleinen Karoo (*Gibbaeum cryptopodium*, Aizoaceae) ergaben höhere Tagesmaximal-Temperaturen für Pflanzen, die außerhalb der Quarzflächen wuchsen. Temperaturdifferenzen von 3-5 °C wurden ermittelt. Als eine Ursache für die meßbar milderen oberflächennahen Temperaturen auf den Quarzflächen wurde die bis zu 15 % höhere Reflexion der Globalstrahlung auf den Quarzflächen angenommen.

In situ Vergleichsmessungen zu Oberflächentemperaturen von Quarz- und Tonschiefersteinen in der Kleinen Karoo zeigten keine signifikanten Unterschiede zwischen den beiden Gesteinen, weder hinsichtlich der Maxima- noch der Minima-Temperaturen. Ein Vergleich mit der Oberflächentemperaturen mit den Taupunkttemperatur umgebenden Luft wies darauf hin, daß die Quarzflächen keine wirksameren Taufallen zu sein scheinen als andere gesteinsbedeckte Böden. Es wird jedoch vermutet, daß sich der Gesteinsbelag durch Herabsetzung der Evaporation sowie die Vergrößerung der Kondensationsfläche grundsätzlich begünstigend auf den Wasserhaushalt des Oberbodens auswirkt. Eine resultierende geringfügige zusätzliche Wasserversorgung könnte für die diese Böden besiedelnde Zwergpflanzen mit oberflächennahen Wurzeln bedeutsam sein.

Die vorliegenden Daten wiesen darauf hin, daß das Temperaturregime auf den Quarzflächen die typischen Eigenschaften der Winterregengebiete, gemäßigte und vorhersagbare Temperaturen und Feuchtigkeitsversorgung, noch verstärkt. Es wird daher vermutet, daß dieser Umstand auch verantwortlich sein könnte für die besondere Ausprägung der strukturellen Merkmale der Flora der Sukkulente Karoo in der spezialisierten Flora der Quarzflächen. Diese Ausprägungen konnten selbst für die außerhalb der Sukkulente Karoo vorkommende Quarzflora des Buschmannland-Warmbad Gebiets aufgezeigt werden.

IX APPENDICES

Appendix 1. Check list of the taxa of the obligate quartz-field flora

Taxa	Family	Reference	Distribution
<i>Strumaria villosa</i> Snijman	Amaryllidaceae	Snijman 1992	Richtersveld North
<i>Tridentea herrei</i> (Nel) Leach	Asclepiadaceae	Leach 1980	Richtersveld North
<i>Tridentea umdausensis</i> (Nel) Leach	Asclepiadaceae	Leach 1980	Richtersveld North to Bushmanland-Wb
<i>Bulbine diphylla</i> Schltr. ex V. Poellnitz	Asphodelaceae	Nordenstam 1964b	Knervlakte
<i>Bulbine haworthioides</i> B. Nordenstam	Asphodelaceae	Nordenstam 1964b	Knervlakte
<i>Bulbine louwii</i> L. I. Hall	Asphodelaceae	Hall 1984	Knervlakte
<i>Bulbine margarethae</i> L. I. Hall	Asphodelaceae	Hall 1984	Knervlakte
<i>Bulbine quartzicola</i> G. Williamson	Asphodelaceae	Williamson 1996	Richtersveld North
<i>Bulbine truncata</i> G. Williamson	Asphodelaceae	Williamson 1996	Richtersveld North & South
<i>Bulbine wiesei</i> L. I. Hall	Asphodelaceae	Hall 1984	Knervlakte
<i>Lasiopogon minutus</i> (B. Nordenstam) Hilliard & Burt	Asteraceae	Hilliard 1983	Knervlakte
<i>Leucoptera oppositifolia</i> B. Nordenstam	Asteraceae	Nordenstam 1976	Knervlakte
<i>Leucoptera subcarnosa</i> B. Nordenstam	Asteraceae	Nordenstam 1976	Knervlakte
<i>Oedera silicicola</i> (Bremer) Anderb. & Bremer	Asteraceae	Nordenstam 1968, Anderberg & Bremer 1991	Knervlakte
<i>Othonna hallii</i> B. Nordenstam	Asteraceae	Nordenstam 1964a	Knervlakte
<i>Othonna intermedia</i> Compton	Asteraceae	U. Schmiedel, unpubl. data	Knervlakte
<i>Othonna lepidocaulis</i> Schlechter	Asteraceae	Rowley 1970	Knervlakte to Riethuis-Wallekraal
<i>Pentzia peduncularis</i> B. Nordenstam	Asteraceae	Nordenstam 1987a	Knervlakte
<i>Senecio aloides</i> DC.	Asteraceae	P. V. Bruyns, pers. comm.	Knervlakte to southern Namibia
<i>Androcymbium cruciatum</i> U. & D. Müller-Doblies	Colchicaceae	Müller-Doblies & Müller-Doblies 1984	Richtersveld North
<i>Adromischus nanus</i> (N.E.Br.) V. Pöllnitz	Crassulaceae	Pilbeam 1999	Richtersveld North to Bushmanland-Wb
<i>Crassula alstonii</i> Marloth	Crassulaceae	Tölken 1977a	Richtersveld North & South
<i>Crassula barklyi</i> N.E Brown	Crassulaceae	Tölken 1977a	Knervlakte to Riethuis-Wallekraal
<i>Crassula columnaris</i> Thunb. ssp. <i>columnaris</i>	Crassulaceae	Tölken 1977a	Southwestern Cape
<i>Crassula columnaris</i> Thunb. ssp. <i>prolifera</i> Friedr.	Crassulaceae	Tölken 1977a	Bushmanland-Wb, N Richtersveld to Knervlakte
<i>Crassula congesta</i> N. E. Brown ssp. <i>laticephala</i> (Schonl.) Tölken	Crassulaceae	Tölken 1977a	Little Karoo
<i>Crassula grisea</i> Schoenland	Crassulaceae	Tölken 1977a	Richtersveld South to Riethuis-Wallekraal
<i>Crassula mesembrianthemopsis</i> Dinter	Crassulaceae	Tölken 1977a	Bushmanland-Namib
<i>Crassula multiceps</i> Harv.	Crassulaceae	Tölken 1977a	Knervlakte

<i>Crassula plegmatoides</i> Friedr.	Crassulaceae	Tölken 1977a	Richtersveld North
<i>Crassula susannae</i> Rauh & Friedr.	Crassulaceae	Tölken 1977a	Riethuis- Wallekraal
<i>Tylecodon occultans</i> (Tölken) Tölken	Crassulaceae	Tölken 1977b	Knersvlakte
<i>Tylecodon peculiaris</i> van Jaarsveld	Crassulaceae	van Jaarsveld 1998	Knersvlakte
<i>Tylecodon pusillus</i> Bruyns	Crassulaceae	Bruyns 1989	Richtersveld North
<i>Tylecodon pygmaeus</i> (W. f. Barker) Tölken	Crassulaceae	Tölken 1977b	Knersvlakte
<i>Tylecodon sulphureus</i> (Tölken) Tölken	Crassulaceae	Tölken 1977b	Bushmanland- Warmbad
<i>Tylecodon tenuis</i> (Tölken) Bruyns	Crassulaceae	Bruyns 1992	Knersvlakte
<i>Eriospermum titanopsoides</i> P.L. Perry	Eriospermeaceae	Perry 1984	Knersvlakte
<i>Pelargonium caroli-henrici</i> B.Nordenstam	Geraniaceae	Nordenstam 1987b	Knersvlakte
<i>Pelargonium quarcicola</i> Meve & E.M. Marais	Geraniaceae	Meve <i>et al.</i> 2000	Knersvlakte
<i>Lachenalia patula</i> Jacq.	Hyacinthaceae	Duncan 1988	Knersvlakte
<i>Babiana lewisiana</i> B.Nordenstam	Iridaceae	Nordenstam 1970,	Knersvlakte
<i>Babiana pilosa</i> G.J.Lewis	Iridaceae	Lewis 1959	Knersvlakte
<i>Lapeirousia lewisiana</i> B.Nordenstam	Iridaceae	Nordenstam 1970	Knersvlakte
<i>Acrodon quarcicola</i> H.E.K.Hartmann	Mesembryanthema	Hartmann 1996	Swellendam
<i>Argyroderma congregatum</i> L.Bolus	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma crateriforme</i> N.E.Brown	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma delectii</i> C.A.Maass	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma framesii</i> L.Bolus ssp. <i>framesii</i>	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma framesii</i> L.Bolus ssp. <i>hallii</i> (L.Bolus) H.E.K.Hartmann	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma patens</i> L.Bolus	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma pearsonii</i> (N.E.Brown) Schwantes	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma ringens</i> L.Bolus	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma subalbum</i> (N.E.Brown) N.E.Brown	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Argyroderma testiculare</i> (Aiton) N.E.Brown	Mesembryanthema	Hartmann 1977	Knersvlakte
<i>Aspazoma amplexens</i> (L.Bolus) N.E.Brown	Mesembryanthema	U. Schmiedel, unpubl. data	Richtersveld South to Riethuis- Wallekraal
<i>Cephalophyllum caespitosum</i> H.E.K.Hartmann	Mesembryanthema	Hartmann 1988	Knersvlakte
<i>Cephalophyllum pulchellum</i> H.E.K.Hartmann	Mesembryanthema	Hartmann 1988	Knersvlakte
<i>Cephalophyllum regale</i> L.Bolus	Mesembryanthema	Hartmann 1988	Richtersveld North
<i>Cephalophyllum spissum</i> H.E.K.Hartmann	Mesembryanthema	Hartmann 1988	Knersvlakte
<i>Cheiridopsis velox</i> S.A. Hammer	Mesembryanthema	Hammer 1993a	Richtersveld North
<i>Conophytum armianum</i> S.A.Hammer	Mesembryanthema	Hammer 1993b	Richtersveld North
<i>Conophytum auriflorum</i> Tischer	Mesembryanthema	Hammer 1993b	Richtersveld North
<i>Conophytum blandum</i> L.Bolus	Mesembryanthema	Hammer 1993b	Richtersveld North
<i>Conophytum burgeri</i> L.Bolus	Mesembryanthema	Hammer 1993b	Bushmanland- Warmbad
<i>Conophytum calculus</i> (A.Berger) N.E.Brown ssp. <i>calculus</i>	Mesembryanthema	Hammer 1993b	Knersvlakte
<i>Conophytum calculus</i> (A.Berger) N.E.Brown ssp. <i>vanzylii</i> (Lavis) S.A.Hammer	Mesembryanthema	Hammer 1993b	Bushmanland- Warmbad
<i>Conophytum concavum</i> L.Bolus	Mesembryanthema	Hammer 1993b	Riethuis- Wallekraal
<i>Conophytum friedrichiae</i> (Dinter) Schwantes	Mesembryanthema	Hammer 1993b	Bushmanland- Warmbad
<i>Conophytum hammeri</i> G.Williamson & Kennedy	Mesembryanthema	Williamson & Kennedy 1997	Richtersveld North & South
<i>Conophytum irmae</i> S.H. Hammer & C. Barnhill	Mesembryanthema	Hammer & Barnhill 1997	Richtersveld North
<i>Conophytum lithopsoides</i> L.Bolus ssp. <i>koubergense</i> (L.Bolus) S.A.Hammer	Mesembryanthema	Hammer 1993b	Bushmanland- Warmbad
<i>Conophytum lithopsoides</i> L.Bolus ssp. <i>lithopsoides</i>	Mesembryanthema	Hammer 1993b	Richtersveld North to Bushmanland- Wb
<i>Conophytum marginatum</i> Lavis	Mesembryanthema	Hammer 1993b	Bushmanland- Warmbad

<i>Conophytum maughanii</i> N.E.Brown ssp. armeniacum S.A.Hammer	Mesembryanthema	Hammer 1993b	Richtersveld North & South
<i>Conophytum maughanii</i> N.E.Brown ssp. latum (Tischer) S.A.Hammer	Mesembryanthema	Hammer 1993b	Richtersveld North
<i>Conophytum maughanii</i> N.E.Brown ssp. maughanii	Mesembryanthema	Hammer 1993b	Richtersveld North to Bushmanland-Wb
<i>Conophytum obscurum</i> N.E.Brown ssp. vitreopapillum (Rawe) S.A.Hammer	Mesembryanthema	Hammer 1993b	Riethuis-Wallekraal
<i>Conophytum phoenicium</i> S.A.Hammer	Mesembryanthema	Hammer 1993b	Richtersveld North
<i>Conophytum ratum</i> S.A.Hammer	Mesembryanthema	Hammer 1993b	Bushmanland-Warmbad
<i>Conophytum smorenskaduense</i> de Boer	Mesembryanthema	Hammer 1993b	Bushmanland-Warmbad
<i>Conophytum subfenestratum</i> Schwantes	Mesembryanthema	Hammer 1993b	Knersvlakte
<i>Conophytum violaciflorum</i> Schick & Tischer	Mesembryanthema	Hammer 1993b	Richtersveld North & South
<i>Dicrocaulon brevifolium</i> N.E.Brown	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon grandiflorum</i> Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon humile</i> N.E.Brown	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon longifolium</i> spec. nov. Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon microstigma</i> (L.Bolus) Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon nanum</i> spec. nov.	Mesembryanthema	U. Schmiedel, unpubl. data	Knersvlakte
<i>Dicrocaulon neglectum</i> spec. nov. Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon nodosum</i> (A.Berger) N.E.Brown	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon prostratum</i> spec. nov. Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon pseudonodosum</i> spec. nov. Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Knersvlakte
<i>Dicrocaulon ramulosum</i> (L.Bolus) Ihlenfeldt	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Riethuis-Wallekraal
<i>Dicrocaulon spissum</i> N.E.Brown	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Riethuis-Wallekraal
<i>Dinteranthus microspermus</i> (Dinter & Derenb.) Schwantes ssp. <i>microspermus</i>	Mesembryanthema	Sauer 1979	Bushmanland-Warmbad
<i>Dinteranthus microspermus</i> (Dinter & Derenb.) Schwantes ssp. <i>puberulus</i> (N.E.Brown) N.Sauer	Mesembryanthema	Sauer 1979	Bushmanland-Warmbad
<i>Dinteranthus pole-evansii</i> (N.E.Brown) Schwantes	Mesembryanthema	Sauer 1979	Bushmanland-Warmbad
<i>Dinteranthus vanzylii</i> (L.Bolus) Schwantes	Mesembryanthema	Sauer 1979	Bushmanland-Warmbad
<i>Dinteranthus wilmotianus</i> L.Bolus ssp. <i>impunctatus</i> N.Sauer	Mesembryanthema	Sauer 1979	Bushmanland-Warmbad
<i>Dinteranthus wilmotianus</i> L.Bolus ssp. <i>wilmotianus</i>	Mesembryanthema	Sauer 1979	Bushmanland-Warmbad
<i>Diplosoma luckhoffii</i> (L.Bolus) Schwantes ex Ihlenfeldt	Mesembryanthema	Ihlenfeldt 1988	Knersvlakte
<i>Diplosoma retroversum</i> (Kensit) Schwantes	Mesembryanthema	Ihlenfeldt 1988	Verlorenvley, West Coast
<i>Gibbaeum album</i> N.E.Brown	Mesembryanthema	Nel 1953, Glen 1974	Little Karoo
<i>Gibbaeum cryptopodium</i> (Kensit) L.Bolus	Mesembryanthema	Nel 1953, Glen 1974	Little Karoo
<i>Gibbaeum dispar</i> N.E.Brown	Mesembryanthema	Nel 1953, Glen 1974	Little Karoo
<i>Gibbaeum esterhuyseniae</i> L.Bolus	Mesembryanthema	Nel 1953, Glen 1974	Swellendam

<i>Gibbaeum haagei</i> Schwantes	Mesembryanthema	Nel 1953, Glen 1974	Swellendam
<i>Gibbaeum heathii</i> (N.E.Brown) L.Bolus	Mesembryanthema	Nel 1953, Glen 1974	Little Karoo
<i>Gibbaeum petrense</i> (N.E.Brown) Tischer	Mesembryanthema	Nel 1953, Glen 1974	Little Karoo
<i>Gibbaeum pubescens</i> (Haw.) N.E.Brown	Mesembryanthema	Nel 1953, Glen 1974	Little Karoo
<i>Glottiphyllum oligocarpum</i> L.Bolus	Mesembryanthema	Hartmann & Gölling 1993	Eastern Cape
<i>Glottiphyllum peersii</i> L.Bolus	Mesembryanthema	Hartmann & Gölling 1993	Eastern Cape
<i>Ihlenfeldtia excavata</i> (L.Bolus) H.E.K.Hartmann	Mesembryanthema	Hartmann 1992	Richtersveld North to Bushmanland-Wb
<i>Ihlenfeldtia vanzylii</i> (L.Bolus) H.E.K.Hartmann	Mesembryanthema	Hartmann 1992	Bushmanland-Warmbad
<i>Jacobsenia hallii</i> L.Bolus	Mesembryanthema	Ihlenfeldt 1997	Knersvlakte
<i>Jacobsenia vaginata</i> (L.Bolus) Ihlenfeldt	Mesembryanthema	Ihlenfeldt 1997	Riethuis-Wallekraal to Richtersveld South
<i>Lapidaria margaretae</i> (Schwantes) Dinter & Schwantes	Mesembryanthema	Brown 1928	Bushmanland-Warmbad
<i>Lithops divergens</i> L.Bolus var. <i>divergens</i>	Mesembryanthema	Cole 1988, Hammer 1999	Knersvlakte
<i>Lithops helmutii</i> L.Bolus	Mesembryanthema	Cole 1988, Hammer 1999	Richtersveld North & South
<i>Lithops herrei</i> L.Bolus	Mesembryanthema	Cole 1988, Hammer 1999	Richtersveld North
<i>Lithops meyeri</i> L.Bolus	Mesembryanthema	Cole 1988, Hammer 1999	Richtersveld North
<i>Lithops olivacea</i> L.Bolus	Mesembryanthema	Cole 1988, Hammer 1999	Bushmanland-Warmbad
<i>Meyerophytum globosum</i> comb. nov.	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Riethuis-Wallekraal
<i>Meyerophytum meyeri</i> (Schwantes) Schwantes	Mesembryanthema	H.-D. Ihlenfeldt, pers. comm.	Richtersveld South to Riethuis-Wallekraal
<i>Mitrophyllum grande</i> N.E.Brown	Mesembryanthema	Poppendieck 1976	Richtersveld North
<i>Mitrophyllum mitratum</i> (Marloth) Schwantes	Mesembryanthema	Poppendieck 1976	Richtersveld North & South
<i>Monilaria chrysoleuca</i> (Schlechter) Schwantes	Mesembryanthema	Ihlenfeldt & Jörgensen 1973	Knersvlakte
<i>Monilaria moniliformis</i> (Thunb.) Ihlenfeldt & Jörg.	Mesembryanthema	Ihlenfeldt & Jörgensen 1973	Knersvlakte
<i>Monilaria obconica</i> Ihlenfeldt & Jörg.	Mesembryanthema	Ihlenfeldt & Jörgensen 1973	Richtersveld North & South
<i>Monilaria pisiformis</i> (Haw.) Schwantes	Mesembryanthema	Ihlenfeldt & Jörgensen 1973	Knersvlakte
<i>Monilaria scutata</i> (L.Bolus) Schwantes ssp. <i>obovata</i> Ihlenfeldt & Jörg.	Mesembryanthema	Ihlenfeldt & Jörgensen 1973	Richtersveld South to Riethuis-Wallekraal
<i>Monilaria scutata</i> (L.Bolus) Schwantes ssp. <i>scutata</i>	Mesembryanthema	Ihlenfeldt & Jörgensen 1973	Riethuis-Wallekraal
<i>Muiria hortenseae</i> N.E.Brown / <i>Gibbaeum hortenseae</i> (N.E.Br.) Thiede & Klak	Mesembryanthema	Hall 1956, Thiede & Klak in Goldblatt & Manning 2000	Little Karoo
<i>Nelia meyeri</i> Schwantes	Mesembryanthema	S. A. Hammer, pers. comm.	Richtersveld North & South
<i>Octopoma connatum</i> (L.Bolus) L.Bolus	Mesembryanthema	Hartmann 1998	Richtersveld North
<i>Odontophorus angustifolius</i> L.Bolus	Mesembryanthema	Hartmann 1976	Richtersveld North
<i>Odontophorus nanus</i> L.Bolus	Mesembryanthema	Hartmann 1976	Richtersveld North
<i>Oophytum nanum</i> (Schlechter) L.Bolus	Mesembryanthema	Ihlenfeldt 1978	Knersvlakte
<i>Oophytum oviforme</i> (N.E.Brown) N.E.Brown	Mesembryanthema	Ihlenfeldt 1978	Knersvlakte

<i>Phyllobolus abbreviatus</i> (L.Bolus) Gerbaulet	Mesembryanthea	Gerbaulet 1997	Knervlakte
<i>Phyllobolus digitatus</i> (Aiton) Gerbaulet ssp. <i>digitatus</i>	Mesembryanthea	Gerbaulet 1997	Knervlakte
<i>Phyllobolus digitatus</i> (Aiton) Gerbaulet ssp. <i>littlewoodii</i> (L.Bolus) Gerbaulet	Mesembryanthea	Gerbaulet 1997	Knervlakte
<i>Phyllobolus herbertii</i> (N.E.Brown) Gerbaulet	Mesembryanthea	Gerbaulet 1997	Knervlakte Richtersveld North, South to Riethuis-Wallekraal
<i>Phyllobolus prasinus</i> (L.Bolus) Gerbaulet	Mesembryanthea	Gerbaulet 1997	Knervlakte
<i>Phyllobolus tenuiflorus</i> (Jacq.) Gerbaulet	Mesembryanthea	Gerbaulet 1997	Knervlakte
<i>Pleiospilos nelii</i> Schwantes	Mesembryanthea	Hartmann & Liede 1986	Eastern Cape
<i>Polymita steenbokensis</i> H.E.K.Hartmann	Mesembryanthea	Hartmann 1996	Richtersveld North & South
<i>Schlechteranthus hallii</i> L.Bolus	Mesembryanthea	C. Klak, pers. comm.	Richtersveld North
<i>Schlechteranthus maximiliani</i> Schwantes	Mesembryanthea	C. Klak, pers. comm.	Richtersveld North & South
<i>Schwantesia borchersdii</i> L.Bolus	Mesembryanthea	Zimmermann 1995	Bushmanland-Warmbad
<i>Anacampseros herreana</i> V.Poellnitz	Portulacaceae	Gerbaulet 1992a	Richtersveld North
<i>Anacampseros papyracea</i> E.Fenzel ssp. <i>papyracea</i>	Portulacaceae	Gerbaulet 1992a	Little Karoo to Great Karoo
<i>Anacampseros papyracea</i> E.Meyer ex Fenzel ssp. <i>namaensis</i> Gerbaulet	Portulacaceae	Gerbaulet 1992a	Richtersveld North to Bushmanland-Wb
<i>Anacampseros recurvata</i> Schoenland	Portulacaceae	Gerbaulet 1992a	Richtersveld North & South
<i>Zygophyllum teretifolium</i> Schlechter	Zygophyllaceae	U. Schmiedel, unpubl. data	Knervlakte

Taxa	Growth form	drought deciduous	leaf-succulent	stem-succulent	stem succulent, stem assim	roots fleshy / tuber	non-succulent
<i>Strumaria villosa</i> Snijman	G	+				+	
<i>Tridentea herrei</i> (Nel) Leach	miC	+		+	+		
<i>Tridentea umdausensis</i> (Nel) Leach	miC	+		+	+		
<i>Bulbine diphylla</i> Schltr. ex V. Poellnitz	G	+	+			+	
<i>Bulbine haworthioides</i> B. Nordenstam	G	+	+			+	
<i>Bulbine louwii</i> L. I. Hall	G	+	+			+	
<i>Bulbine margarethae</i> L. I. Hall	G	+	+			+	
<i>Bulbine quartzicola</i> G. Williamson	G	+				+	
<i>Bulbine truncata</i> G.Williamson	G	+	+			+	
<i>Bulbine wieseii</i> L. I. Hall	G	+	+			+	
<i>Lasiopogon minutus</i> (B. Nordenstam) Hilliard & Burt	T nsucc	+					+
<i>Leucoptera oppositifolia</i> B. Nordenstam	meC nsucc						
<i>Leucoptera subcarnosa</i> B. Nordenstam	meC nsucc						
<i>Oedera silicicola</i> (Bremer) Anderb. & Bremer	meC nsucc						+
<i>Othonna hallii</i> B.Nordenstam	H	+	+			+	
<i>Othonna intermedia</i> Compton	H	+	+			+	
<i>Othonna lepidocaulis</i> Schlechter	H	+	+			+	
<i>Pentzia peduncularis</i> B.Nordenstam	miC						

	nsucc						
<i>Senecio aloides</i> DC.	H	+	+				+
<i>Androcymbium cruciatum</i> U. & D. Müller-Doblies	G	+					+
<i>Adromischus nanus</i> (N.E.Br.) V. Pöllnitz	nC co			+			
<i>Crassula alstonii</i> Marloth	nC sg			+			
<i>Crassula barklyi</i> N.E Brown	nC co			+			
<i>Crassula columnaris</i> Thunb. ssp. <i>columnaris</i>	nC sg			+			
<i>Crassula columnaris</i> Thunb. ssp. <i>prolifera</i> Friedr.	nC sg			+			
<i>Crassula congesta</i> N. E. Brown ssp. <i>laticephala</i> (Schonl.) Tölken	miC			+			
<i>Crassula grisea</i> Schoenland	miC			+			
<i>Crassula mesembrianthemopsis</i> Dinter	nC st			+			+
<i>Crassula multiceps</i> Harv.	nC co	+	+				+
<i>Crassula plegmatoides</i> Friedr.	miC			+			
<i>Crassula susannae</i> Rauh & Friedr.	nC st			+			+
<i>Tylecodon occultans</i> (Tölken) Tölken	nC st	+	+				+
<i>Tylecodon peculiaris</i> van Jaarsveld	H	+	+				+
<i>Tylecodon pusillus</i> Bruyns	H	+	+				+
<i>Tylecodon pygmaeus</i> (W. f. Barker) Tölken	nC others	+	+		+		+
<i>Tylecodon sulphureus</i> (Tölken) Tölken	nC others	+	+		+		+
<i>Tylecodon tenuis</i> (Tölken) Bruyns	nC others	+	+				+
<i>Eriospermum titanopsoides</i> P.L. Perry	G	+					+
<i>Pelargonium caroli-henrici</i> B.Nordenstam	H nsucc	+					+
<i>Pelargonium quarcicola</i> Meve & E.M. Marais	G	+					+
<i>Lachenalia patula</i> Jacq.	G	+	+				+
<i>Babiana lewisiana</i> B.Nordenstam	G	+					+
<i>Babiana pilosa</i> G.J.Lewis	G	+	+				+
<i>Lapeirousia lewisiana</i> B.Nordenstam	G	+					+
<i>Acrodon quarcicola</i> H.E.K.Hartmann	nC co			+			
<i>Argyroderma congregatum</i> L.Bolus	nC sg			+			
<i>Argyroderma crateriforme</i> N.E.Brown	nC st			+			
<i>Argyroderma deletatii</i> C.A.Maass	nC st			+			
<i>Argyroderma framesii</i> L.Bolus ssp. <i>framesii</i>	nC sg			+			
<i>Argyroderma framesii</i> L.Bolus ssp. <i>hallii</i> (L.Bolus) H.E.K.Hartmann	nC sg			+			
<i>Argyroderma patens</i> L.Bolus	nC sg			+			
<i>Argyroderma pearsonii</i> (N.E.Brown) Schwantes	nC sg			+			
<i>Argyroderma ringens</i> L.Bolus	nC st			+			
<i>Argyroderma subalbum</i> (N.E.Brown) N.E.Brown	nC sg			+			
<i>Argyroderma testiculare</i> (Aiton) N.E.Brown	nC sg			+			
<i>Aspazoma amplexens</i> (L.Bolus) N.E.Brown	miC	+	+		+	+	
<i>Cephalophyllum caespitosum</i> H.E.K.Hartmann	nC co			+			
<i>Cephalophyllum pulchellum</i> H.E.K.Hartmann	nC co			+			
<i>Cephalophyllum regale</i> L.Bolus	nC co			+			
<i>Cephalophyllum spissum</i> H.E.K.Hartmann	nC co			+			
<i>Cheiridopsis velox</i> S.A. Hammer	nC co			+			
<i>Conophytum armianum</i> S.A.Hammer	nC st	+	+				
<i>Conophytum auriflorum</i> Tischer	nC sg	+	+				

<i>Conophytum blandum</i> L.Bolus	nC sg	+	+
<i>Conophytum burgeri</i> L.Bolus	nC sg	+	+
<i>Conophytum calculus</i> (A.Berger) N.E.Brown ssp. <i>calculus</i>	nC sg	+	+
<i>Conophytum calculus</i> (A.Berger) N.E.Brown ssp. <i>vanzylii</i> (Lavis) S.A.Hammer	nC sg	+	+
<i>Conophytum concavum</i> L.Bolus	nC st	+	+
<i>Conophytum friedrichiae</i> (Dinter) Schwantes	nC st	+	+
<i>Conophytum hammeri</i> G.Williamson & Kennedy	nC sg	+	+
<i>Conophytum irmae</i> S.H. Hammer & C. Barnhill	nC sg	+	+
<i>Conophytum lithopsoides</i> L.Bolus ssp. <i>koubergense</i> (L.Bolus) S.A.Hammer	nC sg	+	+
<i>Conophytum lithopsoides</i> L.Bolus ssp. <i>lithopsoides</i>	nC sg	+	+
<i>Conophytum marginatum</i> Lavis	nC sg	+	+
<i>Conophytum maughanii</i> N.E.Brown ssp. <i>armeniacum</i> S.A.Hammer	nC st	+	+
<i>Conophytum maughanii</i> N.E.Brown ssp. <i>latum</i> (Tischer) S.A.Hammer	nC st	+	+
<i>Conophytum maughanii</i> N.E.Brown ssp. <i>maughanii</i>	nC st	+	+
<i>Conophytum obscurum</i> N.E.Brown ssp. <i>vitreopapillum</i> (Rawe) S.A.Hammer	nC co	+	+
<i>Conophytum phoenicium</i> S.A.Hammer	nC st	+	+
<i>Conophytum ratum</i> S.A.Hammer	nC st	+	+
<i>Conophytum smorenskaduense</i> de Boer	nC sg	+	+
<i>Conophytum subfenestratum</i> Schwantes	nC st	+	+
<i>Conophytum violaciflorum</i> Schick & Tischer	nC sg	+	+
<i>Dicrocaulon brevifolium</i> N.E.Brown	miC	+	+
<i>Dicrocaulon grandiflorum</i> Ihlenfeldt	meC	+	+
<i>Dicrocaulon humile</i> N.E.Brown	miC	+	+
<i>Dicrocaulon longifolium</i> spec. nov. Ihlenfeldt	meC	+	+
<i>Dicrocaulon microstigma</i> (L.Bolus) Ihlenfeldt	miC	+	+
<i>Dicrocaulon nanum</i> spec. nov.	nC sg	+	+
<i>Dicrocaulon neglectum</i> spec. nov. Ihlenfeldt	miC	+	+
<i>Dicrocaulon nodosum</i> (A.Berger) N.E.Brown	meC	+	+
<i>Dicrocaulon prostratum</i> spec. nov. Ihlenfeldt	miC	+	+
<i>Dicrocaulon pseudonodosum</i> spec. nov. Ihlenfeldt	miC	+	+
<i>Dicrocaulon ramulosum</i> (L.Bolus) Ihlenfeldt	meC	+	+
<i>Dicrocaulon spissum</i> N.E.Brown	meC	+	+
<i>Dinteranthus microspermus</i> (Dinter & Derenb.) Schwantes ssp. <i>microspermus</i>	nC sg		+
<i>Dinteranthus microspermus</i> (Dinter & Derenb.) Schwantes ssp. <i>puberulus</i> (N.E.Brown) N.Sauer	nC sg		+
<i>Dinteranthus pole-evansii</i> (N.E.Brown) Schwantes	nC sg		+
<i>Dinteranthus vanzylii</i> (L.Bolus) Schwantes	nC st		+
<i>Dinteranthus wilmotianus</i> L.Bolus ssp. <i>impunctatus</i> N.Sauer	nC sg		+
<i>Dinteranthus wilmotianus</i> L.Bolus ssp. <i>wilmotianus</i>	nC sg		+
<i>Diplosoma luckhoffii</i> (L.Bolus) Schwantes ex Ihlenfeldt	nC sg	+	+

<i>Diplosoma retroversum</i> (Kensit) Schwantes	nC others	+	+	
<i>Gibbaeum album</i> N.E.Brown	nC sg		+	
<i>Gibbaeum cryptopodium</i> (Kensit) L.Bolus	nC st	+	+	
<i>Gibbaeum dispar</i> N.E.Brown	nC sg		+	
<i>Gibbaeum esterhuyseniae</i> L.Bolus	nC co		+	
<i>Gibbaeum haagei</i> Schwantes	nC co		+	
<i>Gibbaeum heathii</i> (N.E.Brown) L.Bolus	nC sg		+	
<i>Gibbaeum petrense</i> (N.E.Brown) Tischer	nC sg		+	
<i>Gibbaeum pubescens</i> (Haw.) N.E.Brown	nC co		+	
<i>Glottiphyllum oligocarpum</i> L.Bolus	nC co		+	
<i>Glottiphyllum peersii</i> L.Bolus	nC co		+	
<i>Ihlenfeldtia excavata</i> (L.Bolus) H.E.K.Hartmann	nC co		+	
<i>Ihlenfeldtia vanzylii</i> (L.Bolus) H.E.K.Hartmann	nC co		+	
<i>Jacobsenia hallii</i> L.Bolus	nC co		+	
<i>Jacobsenia vaginata</i> (L.Bolus) Ihlenfeldt	nC co		+	
<i>Lapidaria margaretae</i> (Schwantes) Dintes & Schwantes	nC sg		+	
<i>Lithops divergens</i> L.Bolus var. <i>divergens</i>	nC st		+	
<i>Lithops helmutii</i> L.Bolus	nC st		+	
<i>Lithops herrei</i> L.Bolus	nC st		+	
<i>Lithops meyeri</i> L.Bolus	nC st		+	
<i>Lithops olivacea</i> L.Bolus	nC st		+	
<i>Meyerophytum globosum</i> comb. nov.	nC co	+	+	
<i>Meyerophytum meyeri</i> (Schwantes) Schwantes	miC	+	+	
<i>Mitrophyllum grande</i> N.E.Brown	meC	+	+	
<i>Mitrophyllum mitratum</i> (Marloth) Schwantes	meC	+	+	
<i>Monilaria chrysoleuca</i> (Schlechter) Schwantes	miC	+	+	+
<i>Monilaria moniliformis</i> (Thunb.) Ihlenfeldt & Jörg.	meC	+	+	+
<i>Monilaria obconica</i> Ihlenfeldt & Jörg.	miC	+	+	+
<i>Monilaria pisiformis</i> (Haw.) Schwantes	miC	+	+	+
<i>Monilaria scutata</i> (L.Bolus) Schwantes ssp. <i>obovata</i> Ihlenfeldt & Jörg.	miC	+	+	+
<i>Monilaria scutata</i> (L.Bolus) Schwantes ssp. <i>scutata</i>	miC	+	+	+
<i>Muiria hortenseae</i> N.E.Brown (<i>Gibbaeum hortenseae</i>)	nC sg	+	+	
<i>Nelia meyeri</i> Schwantes	miC		+	
<i>Octopoma connatum</i> (L.Bolus) L.Bolus	miC		+	
<i>Odontophorus angustifolius</i> L.Bolus	miC		+	
<i>Odontophorus nanus</i> L.Bolus	miC		+	
<i>Oophytum nanum</i> (Schlechter) L.Bolus	nC sg	+	+	

<i>Oophytum oviforme</i> (N.E.Brown) N.E.Brown	nC sg	+	+		
<i>Phyllobolus abbreviatus</i> (L.Bolus) Gerbaulet	H	+	+		+
<i>Phyllobolus digitatus</i> (Aiton) Gerbaulet ssp. <i>digitatus</i>	nC co	+	+	+	+
<i>Phyllobolus digitatus</i> (Aiton) Gerbaulet ssp. <i>littlewoodii</i> (L.Bolus) Gerbaulet	nC co	+	+	+	+
<i>Phyllobolus herbertii</i> (N.E.Brown) Gerbaulet	H	+	+		+
<i>Phyllobolus prasinus</i> (L.Bolus) Gerbaulet	H	+	+		+
<i>Phyllobolus tenuiflorus</i> (Jacq.) Gerbaulet	H	+	+		+
<i>Pleiospilos nelii</i> Schwantes	nC sg		+		
<i>Polymita steenbokensis</i> H.E.K.Hartmann	meC		+		
<i>Schlechteranthus hallii</i> L.Bolus	meC		+		
<i>Schlechteranthus maximilianii</i> Schwantes	meC		+		
<i>Schwantesia borchersii</i> L.Bolus	nC co		+		
<i>Anacampseros herreana</i> V.Poellnitz	nC others			+	+
<i>Anacampseros papyracea</i> E.Fenzel ssp. <i>papyracea</i>	nC others			+	+
<i>Anacampseros papyracea</i> E.Meyer ex Fenzel ssp. <i>namaensis</i> Gerbaulet	nC others			+	+
<i>Anacampseros recurvata</i> Schoenland	nC others			+	+
<i>Zygophyllum teretifolium</i> Schlechter	miC	+	+		

Appendix 2. Non-endemic taxa of the obligate QFF listed according to the number of QDS they were recorded for.

Family	Name	No of QDS
Crassulaceae	<i>Crassula columnaris</i> ssp. <i>prolifera</i>	32
Crassulaceae	<i>Crassula columnaris</i> ssp. <i>columnaris</i>	28
Aizoaceae	<i>Ihlenfeldtia excavata</i>	17
Portulacaceae	<i>Anacampseros papyracea</i> ssp. <i>namaensis</i>	16
Portulacaceae	<i>Anacampseros papyracea</i> ssp. <i>papyracea</i>	14
Crassulaceae	<i>Crassula grisea</i>	14
Aizoaceae	<i>Meyerophytum meyeri</i>	13
Asteraceae	<i>Senecio aloides</i>	11
Aizoaceae	<i>Aspazoma amplectens</i>	10
Crassulaceae	<i>Crassula mesembryanthemopsis</i>	10
Aizoaceae	<i>Phyllobolus prasinus</i>	10
Portulacaceae	<i>Anacampseros recurvata</i>	9
Crassulaceae	<i>Crassula alstonii</i>	9
Crassulaceae	<i>Crassula barklyi</i>	9
Aizoaceae	<i>Conophytum maughanii</i> ssp. <i>maughanii</i>	8
Aizoaceae	<i>Monilaria scutata</i> ssp. <i>obovata</i>	7
Asteraceae	<i>Tridentea umdausensis</i>	6
Aizoaceae	<i>Schlechteranthus maximilianii</i>	5
Aizoaceae	<i>Conophytum maughanii</i> ssp. <i>armeniicum</i>	4
Aizoaceae	<i>Jacobsenia vaginata</i>	4
Aizoaceae	<i>Nelia meyeri</i>	4
Crassulaceae	<i>Adromischus nanus</i>	3
Aizoaceae	<i>Conophytum lithopsoides</i> ssp. <i>lithopsoides</i>	3
Asteraceae	<i>Othonna lepidocaulis</i>	2

IX.1 Description of the plant communities

IX.1.1 Communities of the Little Karoo and adjacent areas

A) Major Association: The quartz field vegetation south of the Langeberge (Community # 1)

1 *Gibbaeum haagei*-*Delosperma asperulum* Succulent Dwarf Shrub Community

Floristic composition: The community is characterised by the occurrence of *Delosperma asperulum*, *Gibbaeum haagei*, and *Pentaschistis eriostoma*. *G. haagei* (syn.: *G. austricola*) represents the diagnostic species of the community. The species inventory of the community shows little overlap with the obligate quartz-field flora north of the Langeberge in the Little Karoo. Only two taxa of the community were recorded on quartz fields north of the Langeberge. *Delosperma asperulum* occurs within the *Gibbaeum album* Community (# 3). *Pentaschistis eriostoma* was recorded for the *Gibbaeum velutinum* Community (# 2) and for fynbos communities of the Cederberg (Taylor 1996) and the coastal fynbos near George (Hoare *et al.* 2000).

Total cover and species richness: The total cover (19%) of the vegetation is very high compared to other communities of the quartz-field vegetation. The species richness is low (3-5 spp.).

Structural composition: The community is clearly dominated by subglobose nano-chamaephytes, micro- and mega-chamaephytes are of minor importance.

Distribution and habitat: The community is restricted to the quartz fields of the Swellendam area south of the Langeberge. It typically inhabits moderate to steep slopes which are covered with medium-sized quartz debris (6-20 cm Ø). The silty, soft soils are shallow (< 20 cm) and have low stone content (22% weight). The electrical conductivity is moderately high (in the average 2 mS/cm) and the soil pH is very low (median = 4.1 pH).

Conservation status: The community is endemic to a small area in the Swellendam area where they are restricted to quartz fields. The area south of the Langeberge is intensively used for agricultural purposes and ploughed to a large extent. Only very shallow and rocky soils as well as hills are left out. The present distribution of the community is limited to the island-like, unploughed hillocks. It is likely that the occurrence of the community is denser than presently known but due to the severe decrease of suitable habitats, the community has to be regarded as extremely threatened.

Notes: *Gibbaeum haagei* is restricted to the community whereas *Delosperma asperulum* and *Pentaschistis eriostoma* have a broad distribution: *D. asperulum* is recorded from Namaqualand to Riversdale and *P. eriostoma* has a broad distribution from the Namaqualand to the Eastern Cape (Goldblatt & Manning 2000).

The vegetation communities of the Barrydale-Vanwyksdorp area

Community Group B (# 2-4)

2 *Gibbaeum velutinum* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species is *G. velutinum*. Common species with constancy > I are *Berkheya cuneata*, *Pteronia flexicaulis* and *Elytropappus rhinocerotis*. The latter typically dominates the surrounding vegetation (Renosterveld).

Total cover and species richness: The total cover of the vegetation (< 10 %) as well as the species richness per relevés (5 spp.) are low.

Structural composition: The community is clearly structured into two layers: a low layer of compact, leaf-succulent nano-chamaephytes and a high layer of non-succulent mega-chamaephytes and phanerophytes.

Distribution and habitat: The community is restricted to the southern fringe of the Little Karoo between Barrydale and Muiskraal. It inhabits soft, poorly weathered shale bands on gentle to steep slopes of small hills or mountains with or without quartz cover. These shale bands are often situated between dense stands of *Elytropappus rhinocerotis* (renosterbos) which represents the typical vegetation of this geology in the Karoo. The soils are shallow (5 cm) and the stone content in soil is typically high (median = 50 % by weight). The *Gibbaeum velutinum* Succulent Dwarf Shrub Community occurs on acid soils (< 5 pH) which has a comparatively low salt content (< 2 mS/cm).

Conservation status: The entire distribution and the density of occurrence of the community is not sufficiently known yet. However, according to the present stage of knowledge the community seems to be vulnerable due to the geographical restriction and its ecological specialisation.

3 *Gibbaeum angulipes* Succulent Dwarf Shrub Community

Floristic composition: The only diagnostic species are *G. angulipes* and *Haworthia aspera*, of which the latter is also found elsewhere in communities not recorded within this study. Both species are leaf-succulent dwarf shrubs. *G. angulipes* is also the dominating species. Other species are poorly represented. As in Community # 2, *Elytropappus rhinocerotis* (renosterbos) dominates the surrounding vegetation at most localities and therefore is also found in this community but with low constancy and cover values only. Common species are *Mesembryanthemum longistylum*, which is also common to Communities # 4 -7, as well as *Chrysocoma ciliata*.

Total cover and species richness: The total cover of the vegetation is comparatively high and surpasses most of the other communities of the quartz fields. This is mainly due to the growth form of *G. angulipes* which is a mat-forming dwarf shrub that may cover up to 12 % of the soil surface. The number of species per relevé in return is low: up to 6 species per relevé. The accessory species, such as *T. robusta*, are either widespread or without diagnostic value (e.g., *Glottiphyllum nelii*).

Structural composition: The vegetation is typically dominated by repent nano-chamaephytes, namely *G. angulipes*. Other nano-chamaephyteous as well as micro- and mega-chamaephyteous growth forms occur with very low cover values only.

Distribution and habitat: The community is restricted to a small area around Muiskraal (3321C) between Groot Phisantefontein and Karreekloof where it occurs on quartz fields but also on pavements with a high percentage of dark-coloured sandstone or shale. The soils are usually shallow and the fine-material has a soft texture due to the high percentage of silt. The salinity is low to moderate (median = 0.5 mS/cm). The soil pH is very acid (median = 4.1 pH).

Conservation status: The community is locally common and is also found along road sides. However, due to its local endemism the community has to be regarded as vulnerable.

4 *Gibbaeum album* Succulent Dwarf Shrub Community

Floristic composition: The only diagnostic species of the community is *G. album* which is also the dominating species. Accessory species are the locally restricted species *Gibbaeum angulipes* and *G. petrense*, as well as widespread taxa, e.g., *Atriplex lindleyi* ssp. *inflata*, *Chrysocoma ciliata*, *Psilocaulon articulatum*, and *Pteronia succulenta*.

Total cover and species richness: The total cover of the vegetation varies but is typically low (< 5 %). Also the number of species per relevé is very low (4 spp.) and below most of the other communities of the quartz-field vegetation of the Little Karoo and adjacent areas.

Structural composition: The community is mainly dominated by nano-chamaephytes whereas micro- and mega-chamaephytes are of subordinate importance. Other growth forms occur with low constancy and low cover values only.

Distribution and habitat: The community is found on top or on gentle slopes of low quartz hills in the Springfontein-Muiskraal area in the southern fringe of the Little Karoo (3321CC). The shallow soils are densely covered by medium-sized quartz debris. The stone content in soil is typically low (< 35 % by weight). The fine-material consists mainly of fine-grained components (silt and clay). Of high significance for the habitat of the community is the extremely high salt content (average = 4.5 mS/cm). Due to the high NaCl content the soil pH comparatively high (slightly acid to neutral).

Conservation status: The diagnostic species *Gibbaeum album* and hence the community has a small range-size of distribution.. The area of distribution is used for range land farming with sheep and it is not covered by any conservation area. Due to its geographical and ecological restriction and lack of conservation the community has to be regarded as extremely vulnerable.

Community Group C (# 5 - 7)

5 *Gibbaeum dispar* Succulent Dwarf Shrub Community

Floristic composition: The community is defined by the occurrence of *G. dispar* which is also the dominating species. The accessory species *Mesembryanthemum longistylum*, which is common to the Communities 4 to 7 is also found with high constancy. *Hereroa tenuifolia*, *Malephora lutea* and species of the SG E and F as well as non-diagnostic species occur with very low constancy and low cover values only.

Total cover and species richness: The density of the plant cover of the community is thin. The total cover lays typically below 6 %. Also the number of species recorded per relevé was low (4-9 ssp). This corresponds well with most of the other *Gibbaeum*-dominated communities of the area.

Structural composition: The community is characterised by a dense occurrence of nano-chamaephytes. Among them micro- and mega-chamaephytes occur but with very low constancy and cover values only.

Distribution and habitat: The *Gibbaeum dispar* Community is restricted to a small area between Kromkloof (Springfontein area, 3321CC) and Vanwyksdorp (3321CD). It is typically found on exposed, poorly weathered shale bands with or without quartz cover. These shale bands are often covered with foliose lichens. The fine-material is restricted to crevices or forms a thin layer on top of the bedrock and contains a high stone content (median = 56 % by weight). The soil is well drained and the salt content is usually very low (< 1 mS/cm). The soil pH varied between moderately acid and slightly alkaline (5.2-7.4 pH).

Conservation status: The community is only known from a few, small and highly isolated localities. The occurrence of the community is probably not sufficiently known yet but due to its regional and ecological restriction the community has to be regarded as highly vulnerable and threatened.

6 *Zeuktophyllum suppositum* Succulent Dwarf Shrub Community

Floristic composition: The community is defined by the diagnostic species *Zeuktophyllum suppositum* (Hartmann 1998) as well as *Crassula tetragona* ssp. *acutifolia*, *Gazania lichtensteinii*, *Othonna carnososa*, and *Prenia tetragona*, of which *Z. suppositum* is an endemic of the Little Karoo. The dominating species are *Z. suppositum* or *Hereroa tenuifolia* (SG E). In contrast to most of the other communities of the quartz-field vegetation the dominance of the two species in this community is not as significant but the community shows a very heterogeneous composition. Common species with high constancy are *Anacampseros papyracea* ssp. *papyracea*, *Psilocaulon articulatum*, and *Chrysocoma ciliata* (SG T). *Mesembryanthemum longistylum* (SG F), one of the diagnostic species for the Association Group C, occurs with high constancy.

Total cover and species richness: The median total cover recorded for the relevés was 6.5 % (range = 1.7 - 8.8 %). In contrast to most of the other communities of the quartz-field vegetation of the Little Karoo, the number of species per relevé is typically high (> 6 spp.) and typically associated with a high constancy of more widespread species of the SG T to U.

Structural composition: The community is mainly dominated by shrubby, micro- and mega-chamaephytes which are mainly leaf-succulent. Nano-chamaephytes are rare and represented by low cover values only.

Distribution and habitat: Due to the small range-size of distribution of *Z. suppositum*, the community is restricted to a very small area between Kromkloof and Miertjieskraal (3321CC) in the southern part of the Little Karoo. The community is found on a similar type of habitats as the *Gibbaeum dispar* Community: rocky, poorly weathered, shale bedrock with shallow, skeletal soils. Also the slightly acid soil pH (4.8-7.1) and the very low electrical conductivity determined for the soils (median = 0.6 mS/cm) corresponds well with those of the localities of the *G. dispar* Community. However, the *Z. suppositum* Succulent Dwarf Shrub Community is usually found on steeper slopes and on bedrock which is weathered more thoroughly and results in deeper substrate but has a high stone content though.

Conservation status: The entire distribution and frequency of occurrence of the community is not sufficiently known but according to the present state of knowledge the community is locally restricted and very rare. Hence, it has to be considered as highly vulnerable and threatened.

7 *Gibbaeum petrense* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species are *G. petrense*, *Salsola* spec. (Schmiedel 104753) and *Gibbaeum hortenseae*. The latter is largely endemic to the Springfontein farm and forms very localised, monotypic stands which may represent communities of their own (Brown 1927, Hall 1956). Common species with high constancy are *Pteronia succulenta* and *Psilocaulon articulatum* (SG T).

Total cover and species richness: The total cover of the vegetation depends mainly on the cover values of *G. petrense* which is the dominating species. The species richness is comparatively low (mean value = 6 spp.).

Structural composition: Nano-chamaephytes dominate the vegetation. At some localities they reach very high cover values. However, several micro- and mega-chamaephyteous species occur within the community but typically they have very low cover values only.

Distribution and habitat: The community is restricted to a small area in the southern fringe of the Little Karoo where it is typically found on gentle slopes or foothills with shallow soils (5 cm), moderate stone content (median: 36 % by weight) and very high salinity (median = 4.6 mS/cm). The soil pH is about neutral to slightly alkaline.

Conservation status: In correspondence with the previous communities this community is also restricted to a small area which is not been protected yet. Due to the very local occurrence and the ecological specialisation of the community (extremely saline quartz fields), the community has to be regarded as highly vulnerable.

Communities of the quartz fields that mainly occur between Kruisrivier and Calitzdorp in the central and northern part of the Little Karoo: Association Group D (# 8-15)

8 *Gibbaeum cryptopodium* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species of the community is *G. cryptopodium* (incl. *G. pilosulum*) which also dominates the vegetation in the majorities of the stands. Common species that occur with high constancy are *Pteronia pallens* and *Pt. succulenta*.

Total cover and species richness: The total cover is low (< 10 %) to very low (< 5 %) at most of the localities. For some relevés high numbers of species (15 - 22 spp.) were recorded whereas other were particularly species poor (<< 5 spp.).

Structural composition: The community has a multi-storeyed structure comprising low-growing, leaf-succulent nano-chamaephytes as well as fruticose, mega-chamaephytes of which the majority are non- to sub-succulent. At some localities also micro-chamaephytes reach high cover values. The nano-chamaephytes typically dominate the vegetation.

Locality and habitat: The community is widespread in the northern Little Karoo: it was recorded for the broad valleys of the Anysberg area (Eyerpoort, Touwsfontein, Vrede), the area north of the Warmwaterberg, the Ockertskraal area as well as for the vicinity of Calitzdorp in the eastern part of the Little Karoo. It mainly occurs on flats or gentle slopes of low hills. The soil surface is typically moderately to densely covered with fine to medium-sized quartz debris which, however, can partly be mixed with shale or sandstone gravel. At some few localities the community was also recorded for desert pavements with no quartz but a very high percentage of sandstone gravel. The salinity in soil is often very high (> 3 mS/cm) but for several localities very low values were recorded (< 1 mS/cm). The soil pH is typically slightly alkaline (pH 6.5 - 8) and the occurrence of carbonate was recorded for several sites which is unusual for quartz-field habitats.

Conservation status: The community is widespread and locally abundant and was also recorded for the Anysberg Nature Reserve (CNC). But, due to the fact that the major part of its distribution area is used for commercial sheep farming as well as game farms, the community is threatened.

9 *Gibbaeum pubescens* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species of the community is *Gibbaeum pubescens*, which also dominates the vegetation at most of the stands. Common species with high constancy are *Pteronia pallens*, *Pt. succulenta* and *Berkheya spinosa*. Other species of SG E, J, T and U occur with low constancy only (< III).

Two sub-communities are recognised:

9.1 *Gibbaeum pubescens*-*G. cryptopodium* Sub-Community

9.2 *Gibbaeum pubescens*-*Berkheya cuneata* Sub-Community

The sub-communities differ from each other with respect to their habitat ecology (Chapter III.6.1) and are defined by the occurrence of *Gibbaeum cryptopodium* which occurs in Sub-Community # 9.1 as differential species. Also, *Berkheya cuneata*, which occurs with high constancy

in the *G. pubescens-Berkheya cuneata* Sub-Community but is largely absent from the *G. pubescens-G. cryptopodium* Sub-Community.

Locality and habitat: The community is found on quartz fields with moderate to dense quartz cover which is often mixed with high percentage of shale debris. This is a significant difference to the other quartz-field communities of the northern Little Karoo which are typically found on soils with a dense and pure cover of quartz debris or - at a few localities - on soils with sandstone rubble. The habitats of the *Gibbaeum pubescens* Succulent Dwarf Shrub Community are further characterised by shallow soils with a high stone content. The fine-material consists of silty sand to clayey loam. Regarding the soil chemistry, the community shows a high tolerance. The soil acidity varies between pH 4 and pH 8.5 and between very low (< 0.01 mS/cm) and very high (> 5 mS/cm) salt content. However, the *Gibbaeum pubescens-G. cryptopodium* Sub-Community usually occurs on neutral to alkaline soils (pH > 7, median = 7.5 pH) and very high salt content (> 2 mS/cm, median = 4.8 mS/cm). In contrast, the *G. pubescens-B. cuneata* Sub-Community showed higher variation with respect to soil pH and salinity and the average values are considerably lower (median = 6.0 pH and 1.4 mS/cm).

9.1 *Gibbaeum pubescens-G. cryptopodium* Sub-Community

Floristic composition: The differential species of the sub-community is *G. cryptopodium*. Besides, *G. cryptopodium* is the diagnostic species of the *G. cryptopodium*-dominated Community (8). *G. pubescens* and *G. cryptopodium* are dominating the vegetation. The abundance of the two species vary considerably mainly depending on the composition of the stone pavement: High cover values of *G. cryptopodium* were only recorded for sites with dense quartz cover on soil surface whereas *G. pubescens* may dominate on both, pavements with high or low percentage of quartz debris. The sub-community houses the same array of common species than the sister syntaxon Sub-Community 9.2.

Total cover and species richness: Total cover and species richness of this sub-community is similarly low as of the Sub-Community 9.2.

Structural composition: The sub-community is mainly dominated by subterranean nano-chamaephytes and dense, cushion-like micro-chamaephytes. Fruticose mega-chamaephytes represent the second storey of the sub-community but are represented with low cover values only.

Locality and habitat: Up to now the Community has only been recorded for the quartz-field area north of the Warmwaterberg (from Eyerpoort to Jakkalsfontein). It is there found on level plains. The quartz cover is moderate to dense, often mixed with shale. The average soil pH is slightly alkaline (pH 7.5) and the salinity of the soil is very high for most of the stands (average 4.7 mS/cm). The high percentage of clayey loam in the fine-material corresponds well with the closely related *G. cryptopodium* Community.

Conservation status: Due to its geographically limitation and ecological specialisation on quartz fields, the community has to be regarded as vulnerable. However, the distribution of the community is also covered by the Anysberg Nature Reserve (CNC) which is a valuable contribution to its conservation.

9.2 *Gibbaeum pubescens-Berkheya cuneata* Sub-Community

Floristic composition: The sub-community is characterised by the occurrence of *Gibbaeum pubescens* and *Berkheya cuneata* which, however, occurs with an mediate constancy only (class III). In contrast to the *G. pubescens-G. cryptopodium* Sub-Community (9.1), *Gibbaeum cryptopodium* is absent.

Total cover and species richness: The total cover of the vegetation is low, typically below 10 %. The average number of species per relevé is 10 spp. which is in line with most of the quartz field communities.

Structural composition: The sub-community is clearly dominated by compact, leaf-succulent micro-chamaephytes. Among them, there are fruticose, non-succulent micro- and mega-chamaephytes, which seldom reach high cover values.

Locality and habitat: The sub-community was recorded for the area north and east of the Warmwaterberg, between Touwsfontein farm in the west and Lemoenshoek in the east. It occurs on very gentle slopes of small hills or shale bands or on slightly inclined valley bottoms. The soil surface is moderately or densely covered with quartz debris which is often mixed with dark shale. At some localities the shale component even dominates. The fine-material is sandy silt or clayey loamy. The soils are shallow (median 12.5 cm) and rich in stone content (30-70 %). Regarding soil chemical properties, the sub-community covers a comparative wide range of properties. The pH varies between acid and slightly alkaline but pH below 7 predominate and the electrical conductivity can be high (> 3 mS/cm) but usually ranges below that.

Conservation status: Due to its geographical limitation to an area which is mainly used for agricultural purposes and its restriction to quartz fields, the sub-community has to be regarded as vulnerable. However, the new extension of the Anysberg Nature Reserve (Touwsfontein farm) covers parts of the distribution area of the sub-community and is therefore a valuable contribution to its conservation.

10 *Pteronia pallens*-*Aridaria noctiflora* ssp. *defoliata* Shrubland Community

Floristic composition: The community represents the characteristic *Pteronia pallens*-dominated stands outside the quartz fields of the Little Karoo. Besides *Aridaria noctiflora* ssp. *defoliata*, which occurs with low constancy only, the community does not comprise any diagnostic species but houses numerous common species that are also found in communities on quartz fields and in other special habitats (SG T and U) of which only *Malephora lutea*, *Lycium cinereum*, and *Salsola* spec. (Schmiedel 102066 HBG) occur with high constancy.

Total cover and species richness: With respect to total cover of the vegetation (median = 9.6 %) and the number of species per relevés, the community does not differ significantly from the other communities of special habitats such as quartz fields or other rocky habitats.

Structural composition: The community is dominated by fruticose, mega-chamaephytes which are mainly non- or sub-succulent. Micro-chamaephytes occur with low constancy and low cover values only. Nano-chamaephytes are largely absent but at some localities repent chamaephytes reach high cover values.

Locality and habitat: The most characteristic feature of the habitats are the high carbonate content determined for most of the localities. Non of the quartz-field communities showed any association with carbonate. Merely for the *G. shandii* Succulent Dwarf Shrub Community (13) such substrate was recorded, less frequently though. Due to the high carbonate content, the soil pH is typically neutral to alkaline (7-8 pH). The electrical conductivity values determined for the corresponding soils were very low (often < 0.1 mS/cm). Regarding the soil depth the community does not differ significantly from most of the quartz-field habitats.

Conservation status: Not threatened.

Notes: *Pteronia pallens* is a common species of the intermountain plains of the Little Karoo. It has been recorded with high constancy but low cover values for most of the quartz-field

communities (5-15) as well. *P. pallens* is supposed to be unpalatable and has often been interpreted as indicator for overgrazing (Yeaton & Esler 1990, Milton & Wiegand 2000).

11 *Gibbaeum gibbosum* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species of the community is *G. gibbosum* which also dominates the vegetation. Common species with higher constancy are *Pteronia pallens*, *Pt. succulenta* (SG T and U), and *Psilocaulon junceum* (SG S).

Total cover and species richness: The total cover of the vegetation varies strongly but is typically below 15 % (median = 9.8 %). The average number of species per relevé recorded was about 10 spp.

Structural composition: The community is characterised by two storeys: a low storey of compact nano-chamaephytes and a high storey of shrubby mega-chamaephytes that at some localities even dominate the vegetation. Micro-chamaephytes are of subordinate importance.

Distribution and habitat: The community is widespread in the central and western part of the Little Karoo and is even found north of the Swartberge in the southern fringe of the Ceres Karoo. It is typically found on nearly level plains or pediments with a moderate to dense pavement of dark-brown shale and less frequently on quartz fields. The substrate can be shallow to moderately thick (up to 30 cm). The stone content in soil differed considerably (1 - 75 % by weight). The community typically colonises soils of low salinity (median = 0.8 mS/cm) and slightly acid soil to alkaline soil pH (5-8 pH).

Conservation status: Widespread but locally rare in the western and central Little Karoo. Probably not threatened.

12 *Gibbaeum geminum* Succulent Dwarf Shrub Community

Floristic composition: *Gibbaeum geminum* is the diagnostic and dominating species of the community. Among the common species only *Zygophyllum retrofractum* (Species group J) and *Psilocaulon articulatum* (Species group U) occur with high constancy.

Total cover and species richness: The total cover of the vegetation varies strongly between very low (< 5 %) and very high (> 30 %) which mainly depends on abundance of the dominant species *G. geminum*. In the average the total cover of the sites recorded was low (median = 9.8 %). The community is typically poor in species number and comprises less than 10 spp. per relevé.

Structural composition: The community is dominated by the low-growing, mat-forming nano-chamaephyte *G. geminum*, accompanied by a low cover of micro-chamaephytes and fruticose mega-chamaephytes.

Distribution and habitat: The community occurs on level plains in the central part of the Little Karoo between Middelpaas (north of the Warmwaterberg) and Ockertskraal in the east (3320D-3321C). The soil surface is moderately covered with a stone pavement of quartz, shale or sandstone. The soils are shallow and the stone content in soil is comparatively low (< 50 % by weight). The fine-material of the substrate consists mainly of fine-grained fractions (sandy loam or loamy sand). The soil has an unusually high pH (neutral to alkaline) and very high values for electrical conductivity were determined (6.6 mS/cm) although at some localities the electrical conductivity was low (0.06 mS/cm).

Conservation status: The community is geographically restricted to the central part of the Little Karoo where it seems to be locally rare. However, the distribution and frequency of the community is not sufficiently known yet.

13 *Gibbaeum shandii* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species of the community are *G. shandii* and *Rhinephyllum muirii*, compact dwarf shrubs with succulent leaves. *G. shandii* is the dominating species which also occurs with high constancy. The taxon has been recognised as a subspecies of *G. pubescens* by Glen (1974). However, the differences in habit and the anatomy of the epidermal hairs may argue for the species rank of the taxon (Thiede, personal communication).

Total cover and species richness: The total cover is high (> 15 %) and surpasses the average cover of the quartz-field vegetation where shrubby species occur with high cover values, i.e., *Pteronia pallens*, *Hereroa tenuiflora*, and *Tripteris sinuata* var. *linearis*. But at most stands the total cover was low << 10 % thus resulting in a low average total cover (8.4 %). Also the average number of species per relevé was comparatively low (10 spp).

Structural composition: The community is dominated by both, leaf-succulent as well as non-succulent, fruticose mega-chamaephytes. However, compact micro-chamaephytes dominate at localities where the mega-chamaephytes have low cover values.

Locality and habitat: The community is restricted to broad valleys of the area north of the Warmwaterberg in the central Little Karoo. It occurs there either on moderately or sparsely covered quartz fields or on stone pavements with high coverage of dark shale debris. The soils have low salt content (0.45 mS/cm) and are slightly alkaline (pH = 7.3). At some localities carbonate was detected.

Conservation status: Due to the regional limitation and low frequency of occurrence the community has to be regarded as vulnerable.

14 *Gibbaeum heathii* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species are *G. heathii* and *Salsola* spec (Schmiedel 90151 HBG). *G. heathii* also dominates the vegetation at most stands but also *Salsola* spec. as well as *Pteronia pallens* (SG T) often occur with high cover values. Common species with high constancy are: *Hereroa tenuifolia* (SG E), *Zygophyllum retrofractum*, *Pteronia viscosa* (SG J), *Pteronia pallens*, and *Tetragonia robusta* (SG T)

Total cover and species richness: Although at one stand a high total cover was recorded (21.4 %, Relevé no. 9195), the average value for the total cover of the vegetation is low (4.9 %). The species richness varied considerably between 2 and 16 species but the median of the figures for all recorded relevés (7 spp.) was in line with the majority of the communities of the quartz-field vegetation of the Little Karoo.

Structural composition: The growth-form composition of the community is heterogeneous, comprising nano-, micro-, and mega-chamaephytes. However, the subglobose nano-chamaephytes (*G. heathii*) dominate. At some localities the mega-chamaephytes reach higher cover values which result in a two-storeyed vegetation.

Locality and habitat: The community is widespread in the northern part of the Little Karoo from Kruisrivier (3320CA) to Calitzdorp (3321DA). It is mainly found on level plains or plateaux of low hills which are typically covered by medium-sized quartz debris which is often mixed with sandstone or shale. The shallow to moderately deep soils (5-25 cm) consist of loamy sand or

clayey-sandy loam with medium stone content (40 % by weight). The soil pH is generally neutral to slightly alkaline and the salinity is high to very high (0.29 - 9.8 mS/cm).

Conservation status: According to the present state of knowledge not threatened.

15 *Gibbaeum pachypodium* Succulent Dwarf Shrub Community

Floristic composition: The dominating species are *G. pachypodium*, *C. congesta*, Asteraceae Gen. spec. 109859), of which *G. pachypodium* occurs with the highest constancy and represents the dominating species. Common species with high constancy are *Hereroa tenuifolia* (SG E), *Tripteris sinuata* var. *linearis* (SG T), *Berkbeya cuneata*, and *Pteronia flexicaulis* (SG U).

Total cover and species richness: Depending on the cover values of the dominant species *G. pachypodium*, the total cover of the vegetation varied significantly between < 5 % and > 25 %. The average number of species per relevé (8 spp.) is in line with most of the *Gibbaeum* communities recorded here.

Structural composition: The community is dominated by compact, cushion-like micro- and nano-chamaephyteous growth forms of *G. pachypodium* and *Gibbaeum heathii*. However, the constant occurrence of fruticose, non-succulent mega-chamaephytes (e.g., *Pteronia flexicaulis*, *Tripteris sinuata* var. *linearis*, *Berkbeya cuneata*, and Asteraceae Gen. spec. (Schmiedel 109859) as well as fruticose, leaf-succulent micro- and nano-chamaephytes (e.g., *Hereroa tenuifolia*, *Crassula congesta*) results in a heterogeneous structure comprising compact and upright, shrubby growth forms.

Locality and habitat: The community is restricted to a very small area around Ockertskraal (3321C) in the central part of the Little Karoo. It occurs there on very gentle slopes, on shallow, stony soils densely covered with medium-sized to coarse quartz debris or sandstone rubble. The soil are slightly acid (pH = 5.0 - 6.5) and moderately saline (< 2.5 mS/cm).

Conservation status: The community has a very restricted range-size of distribution. It seems to be restricted to a few small localities of which one has been dissected by a tarred road. The community has therefore to be considered as extremely threatened.

Communities of the vegetation outside the quartz fields of the Little Karoo (# 16)

16 *Psilocaulon junceum* Shrubland Community

Floristic composition: The diagnostic species are *Psilocaulon junceum*, *Drosanthemum duplessiae*, and *Phyllobolus nitidus*. The dominating species are *Psilocaulon junceum* and - at some singular localities - *Malephora lutea* and *Prenia tetragonia*. All dominating species are typical indicators for disturbance and are often found on *beuweltjies* (termitaria) which are characterised by biogenic disturbance and high carbonate content. Other common species of high constancy are *Hereroa tenuifolia* and *Ruschia inclusa*. Species of SG U are completely absent from this community.

Total cover and species richness: The total cover of the community is very high (< 30 %) and surpasses all other communities. The species richness is very low. Only one relevés comprised more than 6 species.

Structural composition: The community is dominated by mega-chamaephytes. Besides, only fruticose, leaf-succulent micro-chamaephytes occur with moderate cover values.

Locality and habitat: The community was recorded for the eastern (Geen Bedrog, 3320CA) and central part (area north of Warmwaterberg) of the Little Karoo. However, it is widespread in the Little Karoo where it typically inhabits *beuweltjies* (Lovegrove & Siegfried 1986, Moore & Picker 1991) with deep, well-drained, alkaline soils with low salt and high carbonate content.

Conservation status: Widespread also outside the Little Karoo. Not threatened.

Notes: The *P. junceum* also occurs in the Namaqualand, south of Buffels Rivier. (Klak & Linder 1998). In the Knersvlakte it has been ubiquitously recorded on outside quartz fields.

Namaqualand *sensu lato*: Knersvlakte, Riethuis-Wallekraal, Richtersveld

For the Phytosociological Table II of the Namaqualand 900 relevés were employed. App. 200 relevés did not fit in any of the vegetation units and were therefore omitted. Since the Knersvlakte turned out to be the centre of diversity of the QFF and vegetation, main focus was set on the vegetation of this region. The vegetation of the entire Knersvlakte, inside and outside the quartz fields was mapped in order to get inside into the differences in vegetation units, species inventories, species richness, growth-form composition in different biotopes within the region.

In total 84 vegetation units for the Namaqualand *sensu lato* were defined. In the Knersvlakte 41 units of the vegetation outside the quartz fields and 24 units of the quartz-field vegetation were distinguished. For the rest of the Namaqualand (mainly the Riethuis-Wallekraal area and the Richtersveld) 19 vegetation units were distinguished.

The communities and Species Groups (SG) were numbered according to their sequence in the Synoptic Table II (Appendix 9) and the Phytosociological Table II (Appendix 10).

IX.1.2 Communities of the Knersvlakte outside quartz fields

The vegetation of the very deep, sandy soils: *Zygophyllum morgsana*-*Othonna cylindrica* Alliance (Community # 1-3)

The alliance is characterised by *Zygophyllum morgsana*, *Othonna cylindrica*, and *Ruschia* sp. (Schmiedel 110277 HBG) as well as other species of SG B. The species are typical inhabitants of deep, sandy soils of the Lowland Succulent Karoo, including the coastal Sandveld (Hoffman 1996a,c). The alliance comprises three communities and two sub-communities:

1 *Eriosephalus recemosus*-*Lebeckia multiflora* Strandveld Community

2 *Cladoraphis spinosa* Spiny Grass Community

2.1 *Cladoraphis spinosa* dominated Sub-Community

2.2 *Cladoraphis spinosa*-*Euphorbia burmannii* Sub-Community

3 *Ruschia ruschiana* aff. (Schmiedel 93302 HBG)-*Antimima excedens* Succulent Shrub Community

In contrast to most of the other communities of the vegetation of the Knersvlakte the communities # 1-3 are characterised by a comparatively high number of diagnostic species (4 - 10 spp.) and are therefore strongly separated from each other and the rest. Community # 1 is restricted to the coast (MHU 1.1) and is typical for the Strandveld Succulent Karoo vegetation (Hoffman 1996c, Acocks 1988). Community # 2 mainly occurs in the sand strip in the southern Knersvlakte (MHU 1.2) but is also found at the alluvial plain in the northeast of the Knersvlakte (near Grootklip se Berg, MHU 1.3). Community # 3 has only been recorded for a Sandveld area east of Lutzville towards Holrivier (southwestern Knersvlakte). All three communities are

restricted to deep (40 - > 100 cm), unstructured and sandy soils with very low stone content, low salinity (< 0.1 mS/cm), slightly acid to slightly alkaline soils (pH 6-8) which rarely contain carbonate. Only community 3 was recorded for shallow soils of about 35 cm depth.

1 *Eriocephalus racemosus*-*Lebeckia multiflora* Strandveld Community

Floristic composition: The vegetation is mainly dominated by *Zygophyllum morgsana* and *Othonna cylindrica* (species group B). The diagnostic species are *E. racemosus*, *L. multiflora*, *Wiborgia obcordata*, *Amellus alternifolius*, *Grielum grandiflorum*, *Salvia lanceolata*, *Trichogyne verticellata*, *Microlooma sagittatum*, *Thesisum spinosum* of the SG C. Most of the species have been described by Acocks (1988) as typical species of the Strandveld Proper (34b).

Total cover and species richness: The total cover of the is moderately high (23-40 %) and the species richness is high (11-28 spp. / relevés). Maximal species richness (28 spp. per relevés) even surpasses that of all other relevés within the Knersvlakte.

Structural composition: The vegetation is dominated by tall, mainly non-succulent shrubs. *Wiborgia obcordata* which is found on small, vegetated palaeo-dunes, reaches a height of more than 2 m and stands out from its surrounding.

Distribution and habitat: Restricted to coastal Sandveld (MHU 1.1), where it occurs on very deep (> 100 cm), weakly structured, finely grained, sandy soils with very low stone content. Due to the strong drainage of the soil, the soil is slightly acid (pH 5.5-6.6) and the salinity very low (<< 0.1 mS/cm).

2 *Cladoraphis spinosa* spiny grass Community

Floristic composition: The community is characterised by a high constancy of *Cladoraphis spinosa*, a hard, spiny, bushy perennial grass of the Poaceae family, of up to 60 cm height. *C. spinosa* also dominates the community at most sites. Further diagnostic species are *Bromus pectinatus*, *Euphorbia burmannii*, and *Wiborgia sericea* which are grouped into species group D. *Salsola zeyheri*, *Asparagus capensis* var. *capensis* as well as *Tetragonia fruticosa* are well represented, widespread species with no diagnostic value though. *B. pectinatus* is considered to be an invader from Asia (Goldblatt & Manning 2000) and has been recorded for disturbed places of the southern Knersvlakte (Steinschen *et al.* 1996). Its increase has been related to grazing management. Also, the dominance of the spiny, non-palatable *C. spinosa* may very well indicate severe overgrazing on the sandy areas of the Knersvlakte.

Two sub-communities are recognised:

2.1 *Cladoraphis spinosa* dominated Sub-Community

2.2 *Cladoraphis spinosa*-*Euphorbia burmannii* Sub-Community

Sub-community # 2.2 differs from the first by the occurrence of *Euphorbia burmannii*, an upright, much-branched shrub of up to 100 cm height which occurs on sandy and stony flats and slopes from the Namaqualand to the Eastern Cape. The *C. spinosa*-*E. burmannii* Sub-Community is found in broad patches within the *C. spinosa* dominated Sub-Community without obvious habitat preferences but the *C. spinosa* can possibly be interpreted as a degraded form of the *C. spinosa*-*E. burmannii* Sub-Community: *E. burmannii* is highly palatable and therefore heavily grazed by most animals (Bruyns in Le Roux & Boucher in prep.). Also, the lower number in total species due to the absence of several Mesembryanthema species (out of SG B) and the occurrence of *Angea capensis* (SG A), an indicator of disturbance, may indicate a higher rate of overgrazing and disturbance on those sites where the *C. spinosa*-dominated Sub-Community occurs.

Distribution and habitat: The community inhabits deep to very deep weakly structured sandy soils (45-100 cm) of the sand strip in the south of the Knersvlakte (MHU 1.2) but also in other sandy areas along the Sout Rivier (MHU 1.4) and around the Grootklip se Berg in the north of the Knersvlakte (MHU 1.3). Both sub-communities occur on level or gently undulated sites with deep (> 80-150 cm), unstructured, coarse sandy soils, which are free of stones. They have a low salt content (< 0.1 mS/cm) and slightly acid to alkaline soil pH (pH 5.8-8.1). For only very few sites carbonate was determined.

2.1 *Cladoraphis spinosa* dominated Sub-Community

Floristic composition: The sub-community is mainly dominated by *C. spinosa*, in contrast to sub-community # 2.2, can also be associated with *Wiborgia sericea* (SG D), *W. obcordata* (SG C), *Stipagrostis namaquensis* (SG G) - with low constancy though. *Euphorbia burmannii* is absent.

Total cover and species richness: Total cover values vary from very low (7 %) to up to 50 %. The species richness of the sub-community is comparatively low it includes between 3-7 species per relevé only.

Structural composition: The vegetation mainly consists of the spiny, bushy grass and shrubby, non-succulent bushes. Leaf-succulent shrubs are rare.

Distribution and habitat: The sub-community has been recorded for the entire distribution area of the community .

Notes: Due to the dominance of the spiny grass the absence of the very palatable *Euphorbia burmannii* as well as the low number of Mesembryanthema this sub-community can be interpreted as an impoverished variant of the *C. spinosa-Euphorbia burmannii* Sub-Community # 2.2.

2.2 *Cladoraphis spinosa-Euphorbia burmannii* Sub-Community

Floristic composition: Besides *C. spinosa*, *E. burmannii* is the dominating and diagnostic species of this sub-community. In contrast to the Sub-Community # 2.1, some shrubby Mesembryanthema species (*Ruschia* sp. Schmiedel 109653 HBG, *Ruschia* sp. Schmiedel 110277 HBG, *Stoeberia utilis*) as well as *Karoochloa schismoides* may occur within the sub-community. *Wiborgia sericea* and *Wiborgia obcordata* are absent. The widely spread species *Asparagus* c. var. *capensis*, *Salsola zeyheri*, and *Tetragonia fruticosa* occur with the same constancy than in the first sub-community.

Total cover and species richness: Total cover values are generally high (24.5-49.6 %) and surpasses that of the *C. spinosa*-dominated Sub-Community. The same is true for the species richness (6-17 spp. / relevé) if annuals are included.

Structural composition: The sub-community consists of much-branched, fruticose mega-chamaphytes and nano-phanerophytes. Succulent growth forms, both, stem and leaf succulents, are far stronger represented than in the *C. spinosa*-dominated sub-community.

Distribution and habitat: The sub-community is typical for the sand strip of the southern Knersvlakte (MHU 1.2) but has also been recorded for a locality near the coast (east of Lutzville) (MHU 1.1). In contrast to the Sub-Community # 2.1, this sub-community has not been found at the sandy places of the northern part of the Knersvlakte.

3 *Ruschia ruschiana* aff. (Schmiedel 93302 HBG)- *Helichrysum micropoides* Succulent Shrub Community

Floristic composition: The community is characterised by *Ruschia ruschiana* aff. (Schmiedel 93302 HBG), *Helichrysum micropoides*, *Antimima excedens*, *Wahlenbergia annularis*, *Osteospermum pinnatum*,

Vanzyllia annulata, *Schismus barbatus*, and *Senecio arenarius* as diagnostic species (all SG E). The dominating species are *R. ruschiana* aff. and *H. mircopoides*. Besides the diagnostic species several more wide spread species occur with high constancy, several of which indicate disturbance: *Oncosiphon piluliferum*, *Mesembryanthemum guericbianum* (SG A). Other associated species such as *Leipoldtia schultzei*, *Ruschia* sp. (Schmiedel 110277 HBG) (SG B), *Ruschia versicolor* (SG I) are typical inhabitants of immobile, sandy places.

Total cover and species richness: Total cover values are very high (36-48 %) even compared to the other vegetation units of sandy habitats of the area. Also the average number of species per relevé for this community is high (18-21 spp. / relevé). It surpasses those of most other communities.

Structural composition: The community is dominated by fruticose, leaf-succulent dwarf shrubs (mega-chamaephytes) and numerous non-succulent annuals.

Distribution and habitat: The community has only be recorded for the moderately undulated coastal area east of Lutzville (western Knersvlakte. MHU 1.1). It occurs on moderately deep, sandy soils (app. 35 cm) which are free of stones. The salinity is very low (< 0.1 mS/cm), and the soil pH about neutral (6.8 - 7.2 pH) and showed a high constancy of low carbonate content.

Deep to moderately shallow, sandy soils of the central and northern Knersvlakte: *Ruschia* sp. (Schmiedel 104621 HBG)- *Drosanthemum curtophyllum* Alliance (Communities # 4-8)

Floristic composition: The *Ruschia* sp. (Schmiedel 104621 HBG)-*D. curtophyllum* Alliance represents the vegetation of the moderately deep to shallow sandy soils of the central and northern parts of the Knersvlakte. It is characterised by the low growing shrub *R. sp.* (Schmiedel 104621 HBG), the small dense dwarf-shrub forming *D. curtophyllum* and the small densely tufted, perennial grass *Stipagrostis obtusa*.

Distribution and habitat: The communities within this alliance are characteristic for shallow to moderately deep sandy soils whereas each community has particular habitat preferences which vary between moderately deep soils of alluvial plains in the northern Knersvlakte (Communities # 4-6, 7.2) and very shallow, sandy soils between round spots in the northwestern plains of the Knersvlakte (MHU 2.2) which were apparently impoverished by long lasting denudation of organic material by ants and termites (# 7.1, 7.3, 8).

4 *Stipagrostis namaquensis* Grass Veld Community

Floristic composition: The diagnostic and dominating species is *S. namaquensis*. The diagnostic species of the Alliance, i.e., *Ruschia* (Schmiedel 104621 HBG), and *Stipagrostis obtusa*, occur with low cover values. Further species, which are more wide spread on sandy places in the Knersvlakte, such as *Angea capensis*, *Conicosia pugioniformis* ssp. *pugioniformis*, *Leipoldtia schultzei* (SG A), and *Asparagus capensis* var. *capensis* (SG BI) occur with low constancy and low cover values only.

Total cover and species richness: Total cover values (10-30 %) and the species richness (4-9 spp. / relevé) are moderately low for this community.

Structural composition: The community is strongly dominated by perennial grass. Fruticose, leaf succulent chamaephytes of the SGs A and F occur but with low constancy.

Distribution and habitat: The community occur in the sandy alluvial plains in the central Knersvlakte (MHU 1.4) and around Grootklip se Berg in the northeastern Knersvlakte (MHU

1.3). The soils are moderately deep (30-100 cm), sandy and have low stone content (0-20 %). The salinity in soil is very low (> 0.1 mS/cm), the soil pH is slightly acid to neutral (6-7.5 pH), typically free of carbonate.

5 *Ruschia robusta* Succulent Shrub Community

Floristic composition: *Ruschia robusta* (Mesembryanthema, Aizoaceae) is the diagnostic species and mainly dominates the community. Besides *R. robusta*, only *Augea capensis* (Zygophyllaceae) and *Salsola zeyheri* (Cheonopodiaceae) also occur with high constancy and at some localities with high cover values. The dominance of *A. capensis* seems to increase on overgrazed places in particular.

Total cover and species richness: Total cover values (11-26 %) are moderately low. The community is poor in species (4 -7 spp. per relevé).

Structural composition: The vegetation is dominated by leaf succulent shrubs of up to 50 cm height. Low growing leaf succulent and semi-succulent shrubs (*Salsola* sp.) are of subordinate importance.

Distribution and habitat: The community occurs alluvial plains of the northeastern part of the Knersvlakte (MHU 1.3). The soils are intermediately deep (25-80 cm), sandy, weakly structured and have a very low stone content. The soil pH is slightly alkaline (7-8 pH) and carbonate content has been determined for some of the localities. The salinity in soil is very low (< 0.1 mS/cm).

Notes: *Ruschia robusta* typically occurs in the mountainous areas of the central Namaqualand and in the Bushmanland and therefore inhabits the ecotone between winter and summer rainfall area. The occurrence of *R. robusta* in the Northern Knersvlakte, where it dominates vast parts of the alluvial plains, can be interpreted as a result of increased summer rainfall influence in those parts of the Knersvlakte. See also the *Brownanthus ciliatus* Dwarf Shrub Community (# 9).

6 *Ruschia versicolor* Succulent Shrub Community

Floristic composition: The diagnostic and dominating species is *R. versicolor*, a low growing shrub with ascending to spreading branches. Besides, species that are typical for shallow, sandy to stony soils, such as *Zygophyllum retrofractum*, *Galenia papulosa* (SG A), *Drosanthemum curtrophyllum*, *Ruschia* sp. (Schmiedel 104621 HBG) (SG F), *Galenia fruticosa*, and *Leipoldtia schultzei* occur. The latter with high cover values but moderate constancy. *Salsola zeyheri* occurs with very high constancy but low cover values only.

Total cover and species richness: Total cover values for the community (5-25 %) are moderately low. The number of species per relevé varied from very low (3spp.), where the community is clearly dominated by *R. robusta* only, to high (15spp.).

Structural composition: The community is dominated by low growing leaf succulent shrubs. Non-succulent shrubs and grasses are of secondary importance.

Distribution and habitat: The community has been found on shallow soils of the alluvial plains in the north (MHU 1.3) but also in other sandy parts of the Knersvlakte (MHU 1.4). It typically occurs on very shallow (10 cm) and stony soils to moderately deep (45 cm) sandy soils with low stone content. The soil pH is typically very low (4.6 - 6 pH) and free of carbonate but where low carbonate content has been determined, the soil pH was even above 7 pH. The salinity in soil was low but slightly higher than at the habitats of the other communities of the alliance ($< 1 - > 0.1$ mS/cm).

7 *Leipoldtia calandra*-*Ruschia lisabeliae* Succulent Shrub Community

Floristic composition: The diagnostic species of the community are *L. calandra* and *R. lisabeliae*. Further species with high constancy are *Drosanthemum curtophyllum* (SG F) and *Salsola zeyheri* (SG BI).

Three sub-communities are recognised:

7.1 *Leipoldtia calandra*-dominated Succulent Dwarf Shrub Sub-Community

7.2 *Drosanthemum curtophyllum* Succulent Dwarf Shrub Sub-Community

7.3 *Ruschia* sp. (Schmiedel 104621 HBG)-Succulent Shrub Sub-Community

Total cover and species richness: Total cover values are generally low in the Community. The lowest average values was recorded for the *Leipoldtia calandra*-dominated Sub-Community (median = 14 %). The average values were slightly higher for the other two sub-communities (median 22 and 23.2 %). The species richness varies strongly among the sub-communities. The Sub-Community # 7.1 and # 7.3 are comparatively poor in species numbers per relevé (2-7 spp. per relevé) whereas 7.2 is comprises rich in species (8-13 spp./ relevé).

Structural composition: The community is dominated by leaf succulent dwarf shrubs or shrubs. The latter are mainly represented by low growing, with ascending to creeping branches. Non- or semi-succulent shrubs are of low importance.

Distribution and habitat: The sub-communities are typical for the broad and plain heuweltjie veld of the northern part of the Knersvlakte, where it occurs on shallow, impoverished soils of the interspace between the heuweltjies (MHU 2.1.2). But is had also been recorded for sandy sites in the Rooiberg area, southwestern Knersvlakte. It is generally found on level plains or very gentle slopes. Regarding the soil depth the sub-communities vary strongly: Sub-communities 7.1 and 7.2 are restricted on shallow sandy soil (10-30 cm), whereas sub-community 7.3 was only found on very deep sandy soils (60- > 100 cm). The stone content is usually low, only in sub-community 7.2 stone contents of up to 20-50 % were recorded. The soil pH for all sub-communities is moderately acid to neutral (6-7 pH). Most of the sites were free of carbonate content. The salinity for the Sub-Communities # 7.1 and # 7.3 is very low (< 0.1 mS/cm) but slightly higher in # 7.2 (0.1 - 1 mS/cm).

7.1 *Leipoldtia calandra*-dominated Succulent Dwarf Shrub Sub-Community

Floristic composition: The diagnostic and only dominant species of the community is *L. calandra*, an erect, fruticose, strongly branched dwarf shrub with short, succulent leaves. *Augea capensis*, *Drosanthemum schoenlandianum* (SG A), and *Galenia fruticosa* (SG BI) are the only species that occur with higher constancy, but with low cover values.

Total cover and species richness: Total cover values are low (11.2-26 %) and the sub-community is also very poor in species number. It typically comprises only 6 or less species per relevé.

Structural composition: The dominating growth forms erect dwarf shrubs with short, sub-spheroid, succulent leaves. However, non-succulent shrubs (e.g., *Galenia fruticosa*) and leaf succulent facultative perennials (*Augea capensis*) also occur but with low cover values.

Distribution and habitat: The sub-community has only be recorded for the broad and plain heuweltjie veld in the northern part of the Knersvlakte (MHU 2.1.2). It is found there on the impoverished, sandy soils between the heuweltjies, whereas the heuweltjies are dominated by strong mega-chamaephyteous shrubs, such as *Stoeberia fruticosa*, *Psilocaulon leptarthron*, *Drosanthemum otzenianum*, *Lycium* spp. surrounded by *Ruschia subsphaerica*. The sub-community is ecologically very closely related to sub-community 7.2 *Drosanthemum curtophyllum* Succulent Dwarf Shrub Sub-Community and *Cephalophyllum parvibracteatum* Succulent Dwarf Shrub Community (8). The soil is

shallow, forming a thin layer of sandy fine material with low stone content on duripan crust. The soil pH is slightly alkaline to neutral (6.6 -7 pH) and free of carbonate. The salinity is very low (< 0.1 mS/cm).

7.2 *Drosanthemum curtophyllum* Succulent Dwarf Shrub Sub-Community

Floristic composition: The only diagnostic species of the sub-community is *D. curtophyllum* (SG F) which is also the dominating species of the sub-community. Other accompanying species of the sub-community with high constancy are *Leipoldtia calandra*, *Ruschia lisabeliae* (SG J), *Cephalophyllum framesii* (SG P), *Gazania lichtensteinii*, and *Salsola zeyheri* (SG BI).

Total cover and species richness: Total cover values range between 16.3 and 35.4 %. Compared to the other sub-communities of the *L. calandra*-*R. lisabeliae* Succulent Shrub Community, the species numbers per relevés are high (8-13 spp. / relevé) in sub-community 7.2

Structural composition: The sub-community is dominated by leaf-succulent dwarf shrubs which are erect, scrawling or creeping. Semi-succulent shrubs (*Salsola zeyheri*) or annuals (*Gazania lichtensteinii*) are of low importance with respect to cover values.

Distribution and habitat: The sub-community occurs in the flat heuweltjie veld of the northern part of the Knersvlakte (MHU 2.1.2) but also in shallow sandy soils in the Rooiberg area (southwestern part of the Knersvlakte, MHU 1.2). At some sites the stone content is quite high (50 %) and surpasses that of the habitats of sub-communities # 7.1 and # 7.3. In the north it is typically found on the same type of very shallow, impoverished, sandy soils between the heuweltjies as have been described for sub-community # 7.1. The soil pH is similar to that of the habitats of sub-community # 7.1 (6-7.3 pH). In contrast to sub-communities # 7.1 and # 7.3, the salinity in soil is generally higher (0.1 - 2 mS/cm).

7.3 *Ruschia* sp. (Schmiedel 104621 HBG) Succulent Shrub Sub-Community

Floristic composition: *Ruschia* sp. (Schmiedel 104621 HBG) is the diagnostic species of the sub-community. It also dominates the vegetation. This *Ruschia* is an ascending to creeping, low growing *Ruschia* of the subgenus *Sarmentosa*. *Leipoldtia calandra* (SG J) and *Salsola zeyheri* (SG BI) are the only other accompanying species with high constancy.

Total cover and species richness: The total cover values are between 5.2 and 25 % (median = 20 %). Regarding species richness, the sub-community is comparatively poor in species, only 5-7 species were recorded per relevé.

Structural composition: Low growing, ascending to creeping, leaf-succulent shrubs dominate the vegetation. Erect dwarf-succulents (*L. calandra*) and semi-succulent shrubs (*S. zeyheri*) typically occur with low cover values.

Distribution and habitat: The sub-community occurs in the alluvial plains of the northern Knersvlakte (MHU 1.3) on deep (60-100 cm) sandy soils with low stone content. The soils are slightly acid (6.3 - 6.8 pH) and carbonate has been determined for one locality only. The salinity is very low (< 0.1 mS/cm).

8 *Cephalophyllum parvibracteatum* Dwarf Shrub Community

Floristic composition: *C. parvibracteatum* and *Hallianthus planus* represent the diagnostic species of the community. However, only *C. parvibracteatum* occur with high constancy and high cover values. Besides them, only species of SG A, SG F, and SG BI occur within the community but only *Tetragonia fruticosa* (SG BI) reaches a constancy class of III.

Total cover and species richness: The community shows typically low total cover values. The median is 11.5 % whereas at the maximum total cover values of 25.8 % was recorded. The species numbers per relevé are low, they range between 3 - 11 spp. / relevés.

Structural composition: The sparse vegetation of the community is dominated by compact leaf-succulent dwarf shrubs. Other growth forms are represented by low cover values and constancy only.

Distribution and habitat: The community is restricted to the northern part of the Knersvlakte, where it is found on the impoverished, shallow, sandy sites between heuweltjies (MHU 2.1.2, see also 7.1 and 7.2) as well as on shallow sandy patches in the alluvial plains around Grootklip se Berg (MHU 1.3). The soil consists of a shallow (5-20 cm) layer of fine material with a low to moderate stone content above bedrock or (more often) duripan crusts. The soil pH is slightly acid (5.3 pH) to slightly alkaline (7.2 pH). No carbonate has been determined. The salinity varies between very low (< 0.1 mS/cm) to slightly saline (2 mS/cm).

Vegetation of the shale bands: *Brownanthus ciliatus*-*Ruschia spinosa* Dwarf Shrub Community

9 *Brownanthus ciliatus* - *Ruschia spinosa* Dwarf Shrub Community

Floristic composition: The diagnostic species of the community with the highest constancy are *Brownanthus ciliatus*, *Ruschia spinosa*, *Rhinephyllum macradenium*, and *Arenifera stylosa* (SG L) which occur from the proper winter rainfall zone into the March and March / November rainy season (Hartmann & Stüber 1993, Smith *et al.* 1998).

Four sub-communities are recognised:

- 9.1 *Brownanthus ciliatus* -dominated Dwarf Shrub Sub-Community
- 9.2 *Ruschia spinosa*-dominated Dwarf Shrub Sub-Community
- 9.3 *Rhinephyllum macradenium* Dwarf Shrub Sub-Community
- 9.4 *Arenifera stylosa* Dwarf Shrub Sub-Community

Total cover and species richness: The total cover values are low for the sub-communities 9.1 to 9.2 (median < 14 %). Only the *Arenifera stylosa* Dwarf-Shrubs Sub-Community shows higher cover values of up to 46 % (median = 23.6 %). The number of species per relevés is moderate and ranges between 3 and 11. Among the sub-communities the species richness varies. Sub-community 9.3 is considerably poor in species (3-6 spp. / relevés) whereas for the other sub-communities the species richness ranges between 5 and 11 species / relevé.

Structural composition: The vegetation is generally sparse and low, dominated by leaf-succulent dwarf shrubs with cushion forming or erect growth forms.

Distribution and habitat: The community is typically found on the shale bands in the southern and eastern parts of the Knersvlakte (MHU 4) but has also been recorded for eroded, shallow, sandy soils in the alluvial plains of the northern Knersvlakte (MHU 1.3). On the shale bands it occurs on level plains or hilltops and moderate to steep slopes. The soils are shallow (maximum of 30 cm soil depth) and have a high stone content. The stones generate from the in situ weathering bedrock of dark grey mudstone. The soil pH ranges between moderately acid to slightly alkaline (5.3 - 8 pH). At some sites carbonate has been recorded. The salinity is below 1 mS/cm at most sites. Higher values of electrical conductivity (2 mS/cm) are rare and have been recorded for the *Ruschia spinosa* dominated sub-community (9.2) only.

Notes: The high dominance of spiny (*Arenifera stylosa*, *Ruschia spinosa*) and non-palatable, poisonous species (*Tylecodon wallichii*), indicates a strong grazing pressure on the vegetation of the shale bands (MHU 4), which most probably have a lower carrying capacity than the major habitat units 1 (deep sandy soils) and 2 (loamy soils).

9.1 *Brownanthus ciliatus* -dominated Dwarf Shrub Sub-Community

Floristic composition: The sub-community is dominated by *B. ciliatus* only. Accompanying species with higher constancy, such as *Augea capensis*, *Malephora purpureo-crocea*, *Phyllobolus nitidus* (SG A), are typical indicators for disturbance or generally wide spread in the non-quartz vegetation of the Knersvlakte (*Salsola zeyheri*, SG BI).

Total cover and species richness: The total cover value of the sub-community is low. Total cover values between 5.5 and 25.5 % (median = 10.8 %!) were recorded. The species richness of the sub-community is intermediate to moderate (3-10 spp. / relevé).

Structural composition: The vegetation is typically sparse and is dominated by low growing, mat or cushion forming leaf-succulent shrubs.

Distribution and habitat: As described for the community.

9.2 *Ruschia spinosa*-dominated Dwarf Shrub Sub-Community

Floristic composition: The sub-community is dominated by *R. spinosa*, an erect, fruticose, leaf-succulent, and thorny dwarf shrub of up to 20 cm height. Only *Brownanthus ciliatus* (SG L) and *Tripteris sinuata* var. *sinuata* (SG BI) occur with higher constancy.

Total cover and species richness: The total cover value is low (7-17.8 %, median 12 %). The species richness is moderately high (6 - 11 spp / relevé).

Structural composition: The sub-community is dominated by a sparse vegetation of erect fruticose, thorny dwarf shrubs. Other growth forms occur with low constancy and low cover values only.

Distribution and habitat: As described for the community.

9.3 *Rhinephyllum macradenium* Dwarf Shrub Sub-Community

Floristic composition: The diagnostic and dominating species is *R. macradenium*, a compact, leaf-succulent dwarf shrub. *B. ciliatus* and *R. spinosa* (SG L) occur with low cover values only. Other species that are typical for rocky, shallow habitats, such as *Tripteris sinuata* var. *sinuata* or *Pteronia ciliata* (SG BI) occur with higher cover values yet with low constancy only.

Total cover and species richness: Total cover values for the sub-community range between 9 and 22 % (median = 13.25 %). The community is very poor in species. The species numbers per relevés were between 3 and 6.

Structural composition: The sub-community is dominated by compact, leaf-succulent dwarf-shrubs. Other growth forms occur with low cover values only.

Distribution and habitat: As described for the community.

9.4 *Arenifera stylosa* Dwarf Shrub Sub-Community

Floristic composition: *Arenifera stylosa* (syn.: *Eberlanzia stylosa*), *Tylecodon wallichii*, *Eriocephalus ericoides*, and *Cheiridopsis cigarettifera* are the diagnostic species of the sub-community. *Ruschia spinosa*, a diagnostic species of the community, as well as *Asparagus capensis* var. *capensis*, *Pteronia ciliata*, *Tripteris sinuata* var. *sinuata* also occur with high constancy but seldom reach high cover values. Due to the high ratio of spiny (*A. stylosa*, *R. spinosa*, *A. c.* var. *capensis*) and non-palatable species

(*T. wallichii*) within the sub-community, the occurrence of the sub-community might be interpreted as an indicator for overgrazing.

Total cover and species richness: The total cover values of the sub-community is high (12.6-45.8 %) compared to the other sub-communities of the community. The species richness within the sub-community is moderate (6-10 spp. / relevé).

Structural composition: The sub-community is dominated by erect, leaf-succulent dwarf shrubs; but also taller, non-succulent erect shrubs occur among them, with low cover values though.

Distribution and habitat: As described for the community.

Vegetation of loamy-sandy, moderately deep soils of the Knersvlakte:

***Psilocaulon leptarthron-Euphorbia muricata* Alliance (Community # 10-20)**

Floristic composition: The diagnostic species of the alliance are grouped in SG M. They are all widespread and not restricted to the Knersvlakte. However, in the Knersvlakte, they are characteristic for the alliance and hardly found within other major vegetation units. In addition, species of SG A occur with high constancy and some species may even dominate the vegetation.

Locality and habitat: The alliance is restricted to the sandy loam soils which are mainly found in the southern Knersvlakte, south of the east-west running sand strip but also as isolated islands between the shale bands (MHU 2.2), in the small scale mosaics of quartz fields in the central Knersvlakte (MHU 3.2, 3.3) and sporadically in the northern part of the Knersvlakte (MHU 2.1). The *Drosanthemum roseatum* Succulent Shrub Community even occurs up to the Namaqualand lowland near Soebatsfontein (3917AB).

The alliance comprises 11 communities:

- 10 *Ruschia patulifolia* Succulent Shrub Community
- 11 *Drosanthemum roseatum* Succulent Shrub Community
- 12 *Cephalophyllum framesii* Succulent Dwarf Shrub Community
- 13 *Ruschia stricta* var. *turgida* Succulent Shrub Community
- 14 *Drosanthemum deciduum* Succulent Shrub Community
- 15 *Drosanthemum hispidum* Succulent Shrub Community
- 16 *Atriplex lindleyi* ssp. *inflata* Annual Weed Community
- 17 *Salsola zeyheri*-*Galenia fruticosa* Semi-Succulent Shrub Community
- 18 *Melolobium candicans*-*Hermannia cuneifolia* Thorny Shrub Community
- 19 *Ruschia subsphaerica* Succulent Shrub Community
- 20 *Aridaria serotina*-*Ruschia* sp. (Bartels 93268 HBG) Succulent Shrub Community

10 *Ruschia patulifolia* Succulent Shrub Community

Floristic composition: The diagnostic species of the community is *R. patulifolia*, an erect, fruticose shrublet up to 30 cm high with short succulent leaves. *Phyllobolus nitidus* and *Drosanthemum schoenlandianum* (SG A) and *Salsola zeyheri* (SG BI) occur with high constancy and at some sites with high cover values, indicating frequent disturbance. Other species are recorded with low constancy only.

Total cover and species richness: Total cover values of the community is low to moderately high (13.3-50.2 %, median = 27 %). The species numbers per relevés vary strongly between very low and - at some sites - extremely high (3-22 spp. / relevé). However, the median species number is low (5 spp. / relevé). Where the species numbers are high it is mainly due to the occurrence of indicators of disturbance, such as *Malephora purpureo-crocea*, *Drosanthemum* cf. *muirii*, *Drosanthemum diversifolium*, and *Psilocaulon dinteri*.

Structural composition: The community is very homogeneous and mainly dominated by erect, fruticose leaf-succulent shrubs only.

Distribution and habitat: The community has been recorded for the central Knersvlakte in between the small scale mosaic of quartz fields (MHU 3.2, 3.3, 3.4) and for the northwestern border of the Knersvlakte. It typically occurs in the direct surrounding heuweltjies on moderately deep (26-40 cm), soft loamy-sandy soils with low to very high stone content (1-50 %). The soil pH is alkaline (6.6 - 7.9 pH) which is mainly due to the frequent occurrence of carbonate in the soil around the heuweltjies. The salinity in soil is low to moderate (< 0.1 - 2.2 mS/cm).

11 *Drosanthemum roseatum* Succulent Shrub Community

Floristic composition: *D. roseatum* is the diagnostic species of the community which also dominates the vegetation. *D. roseatum* is an erect, fruticose, leaf-succulent shrub of up to 30 cm in height. The taxonomic membership of the taxon is unclear. Due to the lack of closing bodies of the fruit, *D. roseatum* has been described as *Drosanthemum*. However, more recent studies showed that it rather seems to be a member of the *Lampranthus* group (Klak, personal communication). *Salsola zeyheri* (SG BI) is the only other species that occurs with high constancy and may also reach high cover values.

Total cover and species richness: The community has moderately low total cover values (9.2 - 33 %, median = 16.2 %). The species richness is usually low. For most relevés less than 10 (3-8) species per relevés were recorded.

Structural composition: The vegetation is a very homogeneously structured, dominated by erect, fruticose shrubs with spheroid, succulent leaves

Distribution and habitat: The community occurs around cemented heuweltjies among quartz fields in the central Knersvlakte (MHU 3.2, 3.3), around heuweltjies in more sandy places (MHU 1.4) as well as on dolomite on Aties and neighbouring farms (MHU 5, Figure 40). Outside the Knersvlakte it has been recorded for the Riethuis area near Soebatsfontein (3017AB). Like the *R. patulifolia* Succulent Shrub Community (# 10) this community is largely restricted to the soft and moderate to deep soils (15-50 cm) with low to high stone content (1-50 %). The soils are typically slightly alkaline (> 7-8.2 pH) and most have a high carbonate content. Due to the soft and well drained soil, the salinity is very low at most sites (< 1 mS/cm).

12 *Cephalophyllum framesii* Succulent Dwarf Shrub Community

Floristic composition: The diagnostic species is *Cephalophyllum framesii* which also dominates the vegetation. *C. framesii* is a reptant dwarf shrub with terete, succulent leaves. *Drosanthemum scheonlandianum*, *Phyllobolus nitidus* (SG A), *Ruschia subsphaerica*, (SG U), *Salsola zeyheri*, *Drosanthemum diversifolium*, *Psilocaulon dinteri*, and *Galenia fruticosa* (SG BI) occur with high constancy but low cover values.

Total cover and species richness: Total cover values of the community are moderately low (6.2-30.7 %, median = 17.2 %). The species richness is comparatively high with 8-11 species at most of the relevés.

Structural composition: The community is dominated by reptant leaf-succulent dwarf shrubs but with erect, fruticose shrubs in between.

Distribution and habitat: The community is widespread in the Knersvlakte on shallow loamy-sandy soils between the quartz fields in the central Knersvlakte (MHU 3.2, 3.3, 3.4) and on loamy flats in the alluvial plains in the northern Knersvlakte (MHU 1.3). The soils are typically moderately shallow (15-45 cm) with low stone content (1-20 %). The soil pH is alkaline (7.2-8.5 pH) but seldom combined with carbonate content. The salinity is low (< 1 mS/cm) to moderately high (2.7 mS/cm) but occasionally can be very high (8.2 mS/cm).

13 *Ruschia stricta* var. *turgida* Succulent Shrub Community

Floristic composition: The community is characterised by the occurrence of *Ruschia stricta* var. *turgida* (SG Q) which also dominates the vegetation. Other common and widespread species (SG A, SG BI) that are frequently found in other communities of the alliance are largely absent. *Salsola zeyheri* is the only accompanying species that occurs with high constancy.

Total cover and species richness: Total cover values are moderately low (10.4-40 %, median = 17.9 %). Despite the low number of diagnostic and constant species, the richness in species is comparatively high at most relevés (4-10 spp. / relevé). This is mainly due to the high number of species that occur sporadically with low constancy.

Structural composition: The vegetation structure is very homogeneous, mainly consisting of erect, sparsely branched shrubs with a few, spheroid, succulent leaves. Non- or semi-succulent shrubs are rare.

Distribution and habitat: The community typically occurs in the southwestern part of the Knersvlakte, south of the Rooiberg towards Moedverlor and Holrivier (MHU 3.4) where it covers vast parts of the sandy, gypsiferous soils of plains and gentle sloping foot hills between the quartz mountains. The soil is deep (20 - 70 cm), soft, sandy and poor in stone content (1-20 %). The soil pH varies between slightly alkaline (6.1 pH) and alkaline (8.1 pH). Carbonate has been only recorded for singular sites. Due to the soft and well drained soil structure, salinity is usually low at these sites.

14 *Drosanthemum deciduum* Succulent Shrub Community

Floristic composition: *D. deciduum*, an erect, sparsely branched shrub with deciduous, succulent leaves, is the diagnostic species of the community. However, a number of species occur with high constancy and often high cover values, i.e., *Drosanthemum globosum*, *D. schoenlandianum* (SG A), *Atriplex lindleyi* ssp. *inflata*, *Salsola zeyheri*, *Psilocaulon dinteri*, and *Galenia fruticosa* (SG BI). Several of them are recognised as indicators for disturbance.

Total cover and species richness: The total cover values of the community range between 10.4 and 74.4 %. Despite the high maximum value, the majority of the sites have comparatively low total cover values (median 19.3 %). The species richness is moderately high for some sites (up to 17 spp. / relevé) due to the high number of widespread species of the SG A and SG BI that occur with low constancy only. For the majority of the relevés, however, species numbers below 10 were recorded (7-17 spp. / relevé, median = 8 spp. / relevé).

Structural composition: The vegetation consists of various erect, fruticose shrubs of about 30 cm height, of which the majority are leaf-succulent.

Distribution and habitat: The community is mainly found in the southern Knersvlakte on sandy-loamy, moderately deep soils, south of the sand strip, which are also found as isolated islands in between the shale bands of the eastern Knersvlakte (MHU 2.2). Occasionally, it has been

recorded for some parts of the northeastern edge of the Knersvlakte near the Kamdanie and the Krom Rivier (MHU1.3).

Notes: *Drosanthemum deciduum* H.E.K. Hartmann & Bruckmann is a newly described species (Hartmann & Bruckmann 2000) which seems to be endemic to the Knersvlakte which is closely related to *D. inornatum* (L.Bolus) L. Bolus from the Richtersveld (Hartmann & Bruckmann 2000). Both species are leaf-deciduous, a feature which is otherwise absent in *Drosanthemum*.

15 *Drosanthemum hispidum* Succulent Shrub Community

Floristic composition: *D. hispidum*, a scrawling, leaf-succulent shrub an opportunistic pioneer, is the diagnostic species (SG S) of the community. *Drosanthemum globosum* (SG A) and *Asparagus capensis* var. *capensis*, and *Galenia fruticosa* (SG BI) typically occur with high constancy but low cover values as accompanying species, whereas *Salsola zeyheri* (SG BI) occur with high cover values. At some sites also *Atriplex lindleyi* ssp. *inflata* may reach high cover values.

Total cover and species richness: The total cover of the *D. hispidum* Succulent Shrub-Community is very high, compared to other communities in the area. The species richness of the community is moderately low (5-11 spp. / relevé). Most of the species which have been recorded for the community occur with very low constancy only.

Structural composition: The sparse vegetation is dominated by scrawling, leaf-succulent shrubs which are accompanied by a few erect, non- or semi-succulent shrubs.

Distribution and habitat: The community is characteristic for the loamy soils north and west of Vanrhynsdorp along the N7 and the R27 to Vredendal, respectively (MHU 2.2). The area has experienced mechanically disturbance by the gypsum mines. But also elsewhere, the community is found on disturbed and overgrazed areas, such as the sandy-loamy soils between Vanrhynsdorp and the Vanrhyns Pass to Nieuwoudtville at the escarpment (MHU 2.2). The loamy soils here are moderately deep (15-45 cm) and often high in stone content (1-50 %). The soils are slightly acid to slightly alkaline (5.9-8.2 pH) but poor in carbonate. The salinity is always low (< 1 mS/cm).

Notes: The dominance of pioneers and its distribution points out the community as indicator for disturbance and overgrazing.

16 *Atriplex lindleyi* ssp. *inflata* Annual Weed Community

Floristic composition: The annual Australian invader, *Atriplex lindleyi* ssp. *inflata* (SG BI), is the diagnostic species of the community. *Salsola zeyheri* (SG BI), *Augea capensis* and *Malephora purpureo-crocea* (SG A) are accompanying species. *Salsola zeyheri* reaches low cover values only. *A. capensis* and *M. purpureo-crocea* also represent the diagnostic species of the two of the 3 sub-communities:

16.1 *Atriplex lindleyi* ssp. *inflata*-*Stipa capensis* Sub-Community

16.2 *Atriplex lindleyi* ssp. *inflata*-*Malephora purpureo-crocea* Sub-Community

16.3 *Atriplex lindleyi* ssp. *inflata*-*Augea capensis* Sub-Community

Several of the widespread, eurytopic species of the SG A and SG BI were recorded for the community although with relatively low constancy. Most of the species are pioneers (e.g., *Drosanthemum* spp, *Phyllobolus nitidus*, *Caulipsolon rapaceum*).

Total cover and species richness: Total cover value varies between the sub-community. Very high cover values (median = 70 %) have been recorded for the *A. lindleyi* ssp. *inflata*-*Stipa capensis* Sub-Community (16.1) whereas the total cover values of the other two sub-communities are lower (medians < 30 %). The community is comparatively low in species numbers (3-11 spp. / relevé). The majority of the relevés comprise seven or less species only.

Structural composition: The community is dominated by non-succulent annuals and erect to scrawling leaf-succulent shrubs.

Distribution and habitat: The community occurs on severely disturbed and overgrazed areas of the loamy-sandy to sandy parts of the Knersvlakte (MHU 1.3, 2.1, 2.2, 4) whereby the three sub-communities prefer different soil conditions: The *A. lindleyi* ssp. *inflata*-*Stipa capensis* Sub-Community occurs on disturbed areas of the southern Knersvlakte between Vanrhynsdorp and the Gifberg (MHU 2.2). The *A. lindleyi* ssp. *inflata*-*M. purpureo-crocea* Sub-Community is mainly found in alluvial, loamy soils of run-on areas along drainage lines of the shale bands (MHU 4). The *A. lindleyi* ssp. *inflata*-*Augea capensis* Sub-Community inhabits sandy places of the alluvial plains (MHU 1.3) and heuweltjie veld (MHU 2.1) of the northern Knersvlakte.

16.1 *Atriplex lindleyi* ssp. *inflata*-*Stipa capensis* Annual Weed Sub-Community

Floristic composition: The sub-community consists of *A. lindleyi* ssp. *inflata* as diagnostic species of the community as well as *Galenia africana*, *Asparagus capensis* ssp. *capensis*, *Galenia fruticosa* (SG BI), *Oxalis* spec. and *Stipa capensis* (SG M). The latter is also the diagnostic species of the sub-community. In contrast to the other two sub-communities of the Community *M. purpureo-crocea* and *Augea capensis* are absent.

Total cover and species richness: Due to the very high density of *Stipa capensis*, the total cover value of the sub-community extremely high (39.5 - 82.5 %, median = 70 %). The species richness is moderately low. It ranges between 5 and 7 species per relevés.

Structural composition: The sub-community is clearly dominated by annual, non-succulent weeds and unpalatable, erect, non-succulent shrubs, with a high percentage of thorny species.

Distribution and habitat: The sub-community occurs on level plains or steep slopes of overgrazed areas south of Vanrhynsdorp (MHU 2.2, 5). The soils are shallow to moderately deep (15-45 cm) and the stone content varies between very low and high (1-50 %).

Notes: Between Vanrhynsdorp and the Gifberg as well as the Matzikamma, the mean annual rainfall is higher than in the central and northern part of the Knersvlakte, due to orographic rains. Higher annual rainfall may allow higher yearly increment of plant biomass. Together with the vicinity to the town (Vanrhynsdorp) this might be the reason for a higher stocking rate in that area which results in severe overgrazing. To date, the grazing seems to rely mainly on annual weeds of which the majority are invaders from overseas (*Bromus pectinatus*, *Atriplex lindleyi* ssp. *inflata*) (Steinschen *et al.* 1996).

16.2 *Atriplex lindleyi* ssp. *inflata*-*Malephora purpureo-crocea* Sub-Community

Floristic composition: The opportunistic species *Malephora purpureo-crocea* (SG A) is the diagnostic species of the sub-community which dominates the vegetation together with *A. lindleyi* ssp. *inflata*, the indicator species of the community. *Phyllobolus nitidus* (SG A) and *Salsola zeyheri* (SG BI) also occur with high constancy.

Total cover and species richness: The total cover of the community is moderately high (18 - 42 %, median = 28.5 %). Low species richness (< 8spp. / relevé) had been recorded for most relevés, however, at some sites the sub-community houses up to 12 species per relevés.

Structural composition: Crawling leaf-succulent shrubs and non-succulent annuals dominate the vegetation. Erect, semi-succulent shrubs only occur with low cover values.

Distribution and habitat: The sub-community typically occurs on alluvial, loamy soils of run-on areas along drainage lines of the shale bands in the eastern Knersvlakte (MHU 4), parallel to the escarpment. The soils are shallow to moderately deep (10-50 cm), the stone content varies from

low (1 %) to high (50 %). The soil pH is nearly neutral to slightly alkaline (6.7 - 8.4 pH). At some localities high carbonate content has been determined. The salinity of the soil is low (< 1 mS/cm).

16.3 *Atriplex lindleyi* ssp. *inflata*-*Augea capensis* Sub-Community

Floristic composition: The sub-community is characterised by the occurrence of *Augea capensis* (SG A) in addition to *A. lindleyi* ssp. *inflata* the diagnostic species of the community. *Salsola zeyheri* and *Psilocaulon dinteri* (SG BI) are the only other species that occur with high constancy.

Total cover and species richness: Total cover value of the sub-community is generally low (12.8 - 18.5 %, median = 17.9 %). Its species richness is also mostly low (3-4 spp. / relevés). However, higher species numbers of up to 12 species per relevé have been recorded (PNR 6941).

Structural composition: The sub-community comprises leaf-succulent and non-succulent annual to perennial, erect herbs. Perennial shrubs occur with low cover values only.

Distribution and habitat: The sub-community is found on moderately deep (40-50 cm), sandy soils with low stone content (< 15 %) of the alluvial plains (MHU 1.3) and the heuweltjie veld (MHU 2.1.1) in the northern Knersvlakte. The soil pH is slightly alkaline (7.7-8.3 pH) but carbonate has only be recorded for a single relevé. The soil salinity is very low (< 1 mS/cm).

Notes: The distribution area of *Augea capensis* (Zygophyllaceae) covers mainly the broad transition zone between summer and winter rainfall area. In the Knersvlakte, it dominates in the northeastern part towards the escarpment where the influence of summer rainfall increases.

17 *Salsola zeyheri*-*Galenia fruticosa* Shrub Community

Floristic composition: The *Salsola zeyheri* Community is closely related to the *Drosanthemum deciduum* Community (14) and the *Atriplex lindleyi* ssp. *inflata* Community (27). In contrast to the latter *Salsola zeyheri* occurs with high constancy and high cover values, whereas *A. lindleyi* ssp. *inflata* and *Malephora purpureo-crocea* occur with low constancy and. *D. deciduum* is absent. *Galenia fruticosa* is the only other species that occurs with high constancy and high cover values.

Total cover and species richness: The median value for the total cover values is relatively low (median = 18.9 %) although several relevés comprised very high total cover values (up to 60 %). The species richness is low to moderately high for most sites (3-13 spp. / relevé) but can be very high (24 spp. / relevé, PNR 2910.1) after good rains (as in winter 1993). The high species richness was than due to high numbers of geophyteous and annual species.

Structural composition: The community is dominated by semi- and non-succulent, erect shrubs. Annuals and geophytes can be abundant after good rains.

Distribution and habitat: The community is widespread on plain, overgrazed areas with loamy soils of the Knersvlakte (MHU 2.1.1, 2.2) and in the Namaqualand lowland. It inhabits sandy-loamy soils of various depths (10-70 cm) and low to high stone content in soil (1 - 50 %). The soil pH varies between slightly acid to alkaline (5.9-8.5 pH). High soil pH is often associated with high carbonate content (C 1-4). The salinity in soil is low for most sites (< 1 mS/cm) but at the sites in the Namaqualand lowland, very high salinity values have been found (> 4 mS/cm).

18 *Melolobium candicans*-*Hermannia cuneifolia* Thorny Shrub Community

Floristic composition: *M. candicans*, *H. cuneifolia* and *Tribolium ebinatum* are the diagnostic species of the community. They are accompanied by *A. capensis* var. *capensis* (SG BI) with high constancy and moderate cover values.

Total cover and species richness: In correspondence with the *Salsola zeyheri-Galenia fruticosa*-Community (17), the total cover values vary between low (11 %) and very high (65.2 %). At most sites, however, the total cover is comparatively low (<< 20 %, median = 14 %). The species richness of the community is low (5-7 spp. / relevé).

Structural composition: The community is dominated by erect, non-succulent shrubs, most of which are thorny.

Distribution and habitat: The community has been recorded for the hilltops of the Troe-Troe River on the Aties farm only (MHU 5). It occurs there on the moderately deep (30 cm) soils overlaying dolomite bedrock. Due to the high carbonate content of the bedrock, the soil pH is high (8.3 pH) whereas the soil salinity is below 1 mS/cm.

Notes: Due to the clear dominance of thorny species a severe grazing impact on the area can be hypothesised. This hypothesis can be supported by the extensive occurrence of the *Atriplex lindleyi ssp. inflata*-Community (16).

19 *Ruschia subsphaerica* Succulent Shrub Community

Floristic composition: The *Ruschia subsphaerica* Succulent Shrub-Community is characterised by the occurrence of *R. subsphaerica* as diagnostic species. *R. subsphaerica* is an erect, fruticose, basitonic shrub with spheroid, succulent leaves. The general appearance of the shrub resembles *R. robusta* which replaces *R. subsphaerica* on the alluvial plains in the northern Knersvlakte (Community 5), but is shorter. *Drosanthemum globosum*, *D. schoenlandianum* (SG A) and *Salsola zeyheri* (SG BI) accompany the community with high constancy. Other species of SG A, SG M, and SG BI occur with low constancy only. Three sub-communities are recognised:

19.1 *Ruschia subsphaerica* dominated sub-community

19.2 *Ruschia subsphaerica* - *Ruschia patulifolia* sub-community

19.3 *Ruschia subsphaerica*-*Drosanthemum roseatum* sub-community

In contrast to the *Ruschia subsphaerica* dominated sub-community the other sub-communities are characterised by the occurrence of diagnostic species of the *R. patulifolia* and *D. roseatum* Communities which are related to the *Ruschia subsphaerica* Community regarding species composition and habitat ecology.

Total cover and species richness: Total cover value of the community is moderately high. Sub-communities 19.1 and 19.2 may even reach very high values of > 60 % at some sites. However, at the majority of the sites the total values are moderate (median = 16 - 26 %). The number of perennial species of the community is low, it ranges between 3 and 8 species per relevé. However, after good rains numerous geophyteous and annual (grasses and dicotyledoneous) species have been recorded, increasing the species richness considerably (> 20 spp. / relevé).

Structural composition: The community is strongly dominated by basitonic, stout shrubs of 30-40 cm height with spheroid, perennial succulent leaves. Other chamaephyteous growth forms are of low importance. Annual herbs and grasses may occur after sufficient rains with high cover values.

Distribution and habitat: The community is widespread in the Knersvlakte where it occurs on level plains in close vicinity to heuweltjies (MHU 2.1.1, 3). Only the *Ruschia subsphaerica*-dominated Sub-Community (19.1) has been frequently recorded on slopes. Due to the high density of heuweltjies in the southern part of the heuweltjie veld of the northern Knersvlakte, the community may continuously cover a vast area. In the mosaics of quartz fields the community has an island-like distribution, being always connected to the more sparse heuweltjies. The soils are moderately deep (12-50 cm), depending on the distance to the heuweltjies. The stone content varies from very low to high (1-60 %). Due to the vicinity to the heuweltjies, the carbonate

content is usually high and the soil pH is alkaline (> 7 - 8.7 pH). Due to the well drained, soft soils, the salinity is usually very low (< 0.1 - 1 mS/cm).

19.1 *Ruschia subsphaerica* dominated Sub-Community

Floristic composition: In contrast to the other sub-communities, this sub-community has no additional diagnostic species. *R. subsphaerica* and at some sites *S. zeyheri* are dominating. *Angea capensis*, *Drosanthemum globosum*, and *D. schoenlandianum* occur with high constancy.

Total cover and species richness: As described for the Community

Structural composition: As described for the Community

Distribution and habitat: As described for the community, but more often found on slopes than the other two sub-communities.

19.2 *Ruschia subsphaerica* -*Ruschia patulifolia* Sub-Community

Floristic composition: The sub-community is characterised by the occurrence of *Ruschia patulifolia*, which accompanies *R. subsphaerica*, *Salsola zeyheri*, *Drosanthemum globosum* and *D. schoenlandianum* which are typical for the Community in general.

Total cover and species richness: As described for the community.

Structural composition: As described for the community.

Distribution and habitat: As described for the community.

19.3 *Ruschia subsphaerica*-*Drosanthemum roseatum* Sub-Community

Floristic composition: In addition to *R. subsphaerica* as the diagnostic species of the community, as well as the *D. globosum*, *D. schoenlandianum*, and *Salsola zeyheri*, *D. roseatum* and *Phyllobolus nitidus* occur with high constancy but low cover values within this sub-community.

Total cover and species richness: As described for the community.

Structural composition: As described for the community.

Distribution and habitat: As described for the community.

20 *Aridaria serotina* Succulent Shrub Community

Floristic composition: The community is characterised by the occurrence of the erect, fruticose, leaf-succulent shrubs *Aridaria serotina* and *Ruschia* sp. (Bartels 93268 HBG) as diagnostic species and dominating species which are accompanied by *Drosanthemum globosum*, *D. schoenlandianum*, (SG A), *Salsola zeyheri*, *Tetragonia fruticosa*, *Galenia fruticosa*, and *Didelta carnosus* (SG BI) with high constancy. Among the accompanying species only *D. globosum* reaches high cover values. The community comprises two sub-communities:

20.1 *Aridaria serotina*-dominated Sub-Community

20.2 *Aridaria serotina*-*Ruschia* sp. (Bartels 93268 HBG) Sub-Community

Total cover and species richness: Total cover value is moderate at most sites (< 44 %). The species richness differs between the two sub-communities. In the *Aridaria serotina* dominated Sub-Community the species richness varies between moderately low to high (5-21 spp. / relevé) whereas it is continuously high (10-22 spp. / relevé) in the *Aridaria serotina*-*Ruschia* sp. (Bartels 93268 HBG) Sub-Community.

Structural composition: The structural composition of the community is very heterogeneous. Leaf-succulent shrubs of up to 50 cm height dominate in both sub-communities but shorter as low growing as well as non- to semi-succulent shrubs also occur with high constancy.

Distribution and habitat: The community is found on shallow to moderately deep loamy-sandy soils of the quartz-field mosaics in the central Knersvlakte (MHU 3) where it is found on soils without quartz cover as well as of the shale bands in the east (MHU 4). The soils have a high loam and silt content (silty sand or sandy loam) and at some sites a very high stone content. The high silt content is characteristic for the soils of the quartz-field mosaics of the Knersvlakte (see Communities C). The soils are acid to slightly alkaline (5.5 to 8.2 pH). Very acid soils (pH 4.0-4.6) have been recorded at a few localities of the *A. serotina*-dominated Sub-Community. The soil salinity was low (< 1 mS/cm) at all sampled sites.

20.1 *Aridaria serotina*-dominated Sub-Community

Floristic composition: In addition to the diagnostic species of the community, i.e., *Aridaria serotina*, as well as the accompanying species *Drosanthemum globosum*, *D. schoenlandianum*, *Salsola zeyheri*, *Tetragonia fruticosa*, *Galenia fruticosa*, and *Didelta carnosia*, the sub-community differs from the second Sub-Community by the frequent occurrence of *Zygophyllum divaricatum* and *Augea capensis*.

Total cover and species richness: The total cover values and the species richness of the sub-community are low to moderately high (total cover values: 11.5 - 43.5 %, median = 16 %; species richness: 5-21 spp. / relevé).

Structural composition: As described for the community.

Distribution and habitat: The Sub-Community occurs on shallow to moderately deep, sandy-loamy soils of the shale bands in the east (MHU 4) and the quartz-field mosaic in the western and central Knersvlakte (MHU 3.2, 3.3, 3.4). Depending on the microhabitat, the soils may have very high stone content (60 %). The soil pH is acid to slightly alkaline (4 - 7.8 pH), whereas carbonate is rare. The salinity in soil is generally moderately low (0.1-1 mS/cm).

20.2 *Aridaria serotina*-*Ruschia* sp. (Bartels 93268 HBG) Sub-Community

Floristic composition: The second sub-community has *Ruschia* sp. (Bartels 93268 HBG), *Tripterys hyoseroides*, and *Antimima intervallaris* as diagnostic species. *R. lasti* which dominates the sub-community and occurs with the highest constancy is an undescribed species of the subgenus *Tumidula* which seems to be endemic to the Knersvlakte and has only been recorded for the mosaics of quartz fields and surrounding soils without quartz cover where it is typical for the vegetation outside the quartz fields. Besides the accompanying species of the Community, *Ruschia subsphaerica* as well as the annuals *Oncosiphon piluliferum*, *Mesembryanthemum guerichianum* as well as the geophytic species *Oxalis pes-caprae* occur with high constancy whereas they are rare or absent on the other sub-community. In contrast, *Zygophyllum divaricatum* and *Augea capensis* which frequently occur in the *A. serotina*-dominated Sub-Community are absent here.

Total cover and species richness: Total cover values are moderate (15.7 - 37.2 %), at most sites, the community had cover values of > 20 % (median = 23 %). The community is generally rich in species. All relevés comprised 10 or more species.

Structural composition: As described for the community.

Distribution and habitat: The sub-community is restricted to the mosaic of quartz fields where it is found on soils without quartz cover (MHU 3.2, 3.3, 3.4). It is found here on the non-quartz soils only which are typically moderately deep (10-46 cm) and partly rich in stone content (1-70

%). The soil acidity is slightly acid to slightly alkaline (5.5-8.2 pH). Soil pH above 7.8 is often associated with carbonate content. The soils typically have low salinity (< 1 mS/cm).

IX.1.3 Communities of the Knersvlakte inside the quartz fields

***Salsola* sp. (Schmiedel 93110 HBG)-*Argyroderma pearsonii* Alliance (Community # 21-30)**

Floristic composition: The alliance is characterised by five highly salt tolerant species (*Salsola* sp. (Schmiedel 93110 HBG), *Argyroderma pearsonii*, *Mesembryanthemum fastigiatum*, *M. stenandrum*, *Tylecodon pygmaeus*). The ten communities that form part of the Alliance (# 21-30) are all characterised by the superior dominance of one particular species. However, only four communities (# 27-30) are defined by proper diagnostic species (SG AA-AD) whereas the other communities are characterised by the dominance of species that also occur with high constancy but low cover values in all other communities of the Alliance (SG X, Y, and Z).

21 *Drosanthemum diversifolium*-dominated Community

22 *Argyroderma fissum*-dominated Community

23 *Argyroderma delaetii*-dominated Community

24 *Cephalophyllum spissum*-dominated Community

25 *Argyroderma pearsonii*-dominated Community

26 *Mesembryanthemum fastigiatum*-dominated Community

27 *Oophytum nanum* Community

28 *Phyllobolus digitatus* ssp. *digitatus* Community

29 *Oophytum oviforme* Community

30 *Monilaria pisiformis* Community

Locality and habitat: The *Salsola* sp. (Schmiedel 93110 HBG)-*A. pearsonii* Alliance is endemic to the Knersvlakte where it is common on moderately to extremely saline quartz fields. The habitats are situated on level plains or slopes of small hills. The communities vary considerably from each other regarding topography, as well as chemical and physical soil conditions.

21 *Drosanthemum diversifolium*-dominated Community

Floristic composition: The *Drosanthemum diversifolium*-dominated Community is defined by the significant dominance of *Drosanthemum diversifolium*, whereas other species occur with very low cover values only. *D. diversifolium* is not restricted to quartz fields, in contrast, it is also a characteristic element of the communities of the loamy sandy soils outside the quartz fields in the quartz-field mosaic (MHU 3) of the Knersvlakte, such as the *C. framesii* Community (# 12) and the *Ruschia* sp. (Bartels 93268 HBG) Community (# 20). However, this community with its characteristic dominance of *D. diversifolium* accompanied with the typical species of the saline quartz fields (SG Y and Z) is restricted to quartz fields.

Total cover and species richness: The total cover varies strongly with the cover values of *Drosanthemum diversifolium*. At most of the localities the total cover value was comparatively low (< 10 %). The community is considerably poor in species. The average number of species per relevé is 6 spp.

Structural composition: The vegetation structure of the community is clearly characterised by *D. diversifolium* which is a fruticose micro-chamaephyte with succulent leaves. Mega-chamaephytes, i.e., *Salsola zeyheri* and *Psilocaulon dinteri*, occur with low constancy and low cover values. *P. dinteri* is an erect, decumbent or prostrate shrublet with an assimilating, succulent axis. It occurs in this community as an erect mega-chamaephyte. The remaining species of the community, subterranean nano-chamaephytes or low growing, succulent therophytes, respectively, occur with very low cover values and have therefore only little effect on the vegetation structure.

Locality and habitat: The community inhabits level plains or moderate slopes of densely covered quartz fields of the central and northern quartz-field area of the Knersvlakte. The soil is shallow to moderately deep (median = 21 cm) and the soil texture is sandy loam with typically low stone content (median = 27 % weight). Due to frequent occurrence of carbonate in soil and high salinity (median = 2.7 mS/cm), the soil pH is typically slightly alkaline (median = 7.15 pH).

Conservation status: *Drosanthemum diversifolium* is an endemic species of the Knersvlakte but is not restricted to the quartz fields. However, the community is only known from the quartz fields.

22 *Argyroderma fissum*-dominated Community

Floristic composition: The community is dominated by *Argyroderma fissum* (SG X). *Cephalophyllum spissum* the very similar growth form and ecologically related to *A. fissum*, *Argyroderma delaetii*, and *Drosanthemum diversifolium* occur with high constancy. Other species of SG X-Z occur with lower constancy (Class II).

Total cover and species richness: The total cover value varies strongly between very low (> 5 %) and comparatively high (> 20 %), depending on the cover values of the dominating species, i.e., *Argyroderma fissum*. The community is comparatively rich in species (median = 9.5 species / relevé).

Structural composition: The growth-form composition of the vegetation is dominated by compact nano-chamaephytes (*Argyroderma fissum*, *Cephalophyllum spissum*) and micro-chamaephytes (*Drosanthemum diversifolium*, *Monilaria pisiformis*). Mega-chamaephytes (*Salsola zeyheri*, *Salsola* sp. (Schmiedel 93110 HBG) are represented with a very low percentage only. Consequently, the average height of the vegetation of the Variant is low.

Locality and habitat: The community is wide spread and very common in the central quartz fields of the Knersvlakte. It is typically found on gentle slopes with moderately deep soils (median = 20 cm) and dense quartz cover. The fine material is dominated by silty or clayey loam and has a low to high stone content (median 30 %). The soils are extremely saline (median = 5.3 mS/cm) and are densely covered with small to medium quartz gravel. The soil pH is about neutral (median = 6.9 pH). Carbonate is absent at most sites.

Conservation status: The community is very common in the Knersvlakte where it may cover large quartz fields. However, it is geographically restricted to the Knersvlakte and due to its restricted range of distribution, it has to be considered endangered.

23 *Argyroderma delaetii*-dominated Community

Floristic composition: The *Argyroderma delaetii*-dominated Community is characterised by a high to very high density of *Argyroderma delaetii* (SG Y). The abundance of this subterranean nano-chamaephyte can be extremely high (up to 50 %), resulting in a dense pavement of plants.

Total cover and species richness: The total cover of the vegetation varies with the abundance of the dominating species, i.e., *Argyroderma delaetii*, which may be quite high (up to 50 %). The species richness is uniformly low (< 10 spp.).

Structural composition: The growth-form composition of the *Argyroderma delaetii*-dominated Community is defined by dwarf growth forms (nano-chamaephytes). Micro- (*Drosanthemum diversifolium*) and mega-chamaephytes (*Salsola* sp. Schmiedel 93110 HBG, *Sarcocornia xerophila*) as well as annuals are of low importance. They occur with low frequency and low cover values only. Due to the subterranean habit of *A. delaetii*, the sites of the *A. delaetii* Community often appear to be completely unvegetated.

Locality and habitat: The community is frequently found on level or gently sloping, saline quartz fields of the central and northern Knersvlakte. In contrast to the *Argyroderma pearsonii*-dominated Community (23), which is typically found on extremely saline quartz fields (electrical conductivity > 6 mS/cm) with relatively high soil pH (pH 6 - 7.6), this community is mainly found on soils with a salt content below 6 mS/cm (median = 4.5 mS) and a low soil pH (5.4 - 6.7 pH).

Conservation status: *Argyroderma delaetii* is endemic to the Knersvlakte and an obligate quartz-field species. Due to the seemingly emptiness of the quartz fields inhabited by the *A. delaetii*-dominated Community, it is highly vulnerable: such places are often destroyed by off-road driving vehicles.

24 *Cephalophyllum spissum*-dominated Community

Floristic composition: The community is characterised by the dominance of *C. spissum* (SG Y). Also *D. diversifolium* (SG X), *J.* sp. (Schmiedel 93110 HBG), *Tylecodon pygmaeus* (SG Z) and *A. delaetii* (SG Y) occur with high constancy (Class III) but only *Argyroderma delaetii* reaches frequently cover values above 1 % (= 1 in Table II).

Total cover and species richness: The total cover is typically low (< 10 %). The species richness is high at some localities (> 20 spp.), however, the average species number per relevé was comparatively low (7 spp.).

Structural composition: The community is clearly dominated by compact and subterranean nano-chamaephytes. Micro- and mega-chamaephytes as well as therophytes are represented by rather low cover values only.

Locality and habitat: The community occurs on gentle to moderate slopes of low hills in the central part of the Knersvlakte. It is found there on quartz fields with a moderate quartz cover of small to medium-sized quartz debris and moderate stone content (median = 38 % weight). The soils are saline (median = 3 mS/cm) and slightly acid to alkaline (median = 6.8 pH).

Conservation status: The community is restricted to the quartz fields of the Knersvlakte. It mainly comprises species endemic to the Knersvlakte and obligate quartz-field dwellers. Due to its geographical and ecological restriction, it is highly vulnerable.

25 *Argyroderma pearsonii*-dominated Community

Floristic composition: The community is characterised by the dominance of *A. pearsonii* (SG Z). Other species of SG X, Y, and Z (e.g., *Salsola* sp. Schmiedel 93110 HBG, *M. fastigiatum*, *T. pygmaeus*, and *C. spissum*) occur with high constancy but very low cover values only (≤ 1 %).

Total cover and species richness: The total cover of the community depends on the cover value of the dominating species, i.e., *A. delaetii*. The cover values of *A. pearsonii* are up to 15 % (= 6 in Phytosociological Table II, Appendix 10), however, it hardly reaches the density of *A. delaetii* (50 %) in the *A. delaetii*-dominated Community (# 23). All other species are represented by ≤ 1 % cover values (= 1 in Phytosociological Table II, Appendix 10). The community is particularly poor in number of species per relevé. The species spectrum recorded is restricted to very halo-tolerant taxa.

Structural composition: The community is dominated by nano-chamaephytes whereas micro- (*Drosanthemum diversifolium*) and mega-chamaephytes (*Salsola* sp. (Schmiedel 93110 HBG)) are of minor importance. Consequently, and due to the mimetic appearance of *A. pearsonii* the habitats of the community often appear to be empty.

Locality and habitat: The community is typically found in the central part of the Knersvlakte on the extremely saline quartz fields (> 6 mS/cm) along the drainage lines of the Sout Rivier. The quartz fields are densely covered with small to medium (2 - 20 mm \emptyset) quartz stones. The soil is moderately deep (median = 35 cm) and rich in loam and loamy sand. The soil pH is about neutral (median = 6.9 pH).

Conservation status: The dominating species of the community, i.e., *A. pearsonii* is restricted to the central quartz fields of the Knersvlakte (Arizona and Quaggas Kop area only) and an obligate quartz-field species. Due to the empty appearance of the habitats such sites are often misused for off-road driving and parking. Consequently, the community is highly vulnerable.

24 Mesembryanthemum fastigiatum-dominated Community

Floristic composition: The community is dominated by *Mesembryanthemum fastigiatum* (SG Z), a succulent annual. Among the species that frequently occur in the *Salsola* sp. (Schmiedel 93110 HBG)-*A. pearsonii* Alliance (i.e., SG X-Z), only *A. pearsonii* and *Tylecodon pygmaeus* occur with high constancy. Both species and *M. fastigiatum* seemed to have highest tolerance to salinity.

Structural composition: The characteristic species are succulent annuals (*M. fastigiatum*) or nano-chamaephytes with highly succulent leaves. The vegetation is therefore of very low height.

Total cover and species richness: The cover values are generally very low (median 2.6). However, the cover values of the annual *M. fastigiatum* vary extremely with the seasonal precipitation. The community is rather poor in number of species per relevé: Only three species occur with high constancy within the community.

Locality and habitat: The community is the characteristic vegetation of quartz-covered salt pans of the Knersvlakte. It occurs on level quartz fields which are densely covered with small (2-20 mm \emptyset), angular quartz stones. The soils of silty or sandy loam are usually quite saline (median 5.6 mS/cm) and have a quite neutral soil pH (median = 7.25 pH).

Conservation status: *T. pygmaeus* and *A. pearsonii* are obligate quartz-field species. *M. fastigiatum* is a common species of the Knersvlakte which occurs at various open sites where the water supply is sufficient (road reserve, disturbed areas). Although often found on quartz fields, *M. fastigiatum* is not restricted to that habitat. However, all members of this community are strictly (*T. pygmaeus*, *A. pearsonii*) or largely (*M. fastigiatum*) endemic to the Knersvlakte.

27 *Oophytum nanum* Community

Floristic composition: The diagnostic species of the *Oophytum nanum* Community is *Oophytum nanum* (SG AA) which also dominates the vegetation (monodominant community). Species of SG X-Z also occur with high constancy but usually low cover values.

Total cover and species richness: The total cover is relatively low (approx. 8 %) and the species numbers per relevé are intermediate compared to other quartz fields communities of the Knersvlakte (median = 7.5).

Structural composition: Due to the occurrence of some micro- (*Drosanthemum diversifolium*) and mega-chamaephytes (*Salsola zeyberi*, *Salsola* sp. Schmiedel 93110 HBG), the community is more heterogeneously structured than the previous. However, the majority of the species and the dominating species are nano-chamaephytes.

Locality and habitat: The *Oophytum nanum* Community is found on level quartz fields (plains or plateaux) or on gentle slopes of the central and northern part of the Knersvlakte. The slopes are often but not exclusively exposed to south-west or south. The soils have high (> 1 mS/cm) to extremely high (> 10 mS/cm) electrical conductivity values (median = 3.8) and have a comparatively low soil pH (4.7-6.8 pH, median = 6.1). The low soil pH distinguishes the habitat of *Oophytum nanum* Community (# 27) from those of the closely related *Argyroderma pearsonii* (# 25) and the *A. delaetii* Community (# 23). The lower soil pH may also be the reason for the occurrence of some species from the non-saline quartz fields of the Knersvlakte (*Gazania krebsiana*, *Monilaria pisiformis*, *Tetragonia verrucosa*) which were also recorded for this community, with very low constancy and cover values though.

Conservation status: *Oophytum nanum* is widespread in the quartz fields of the Knersvlakte. However, it is endemic to the quartz fields of the Knersvlakte where it inhabits a particular habitat. The soft bodies of the plant are very fragile and due to the high density of the *Oophytum nanum* community can be easily destroyed by trespassing or off-road driving.

28 *Phyllobolus digitatus* ssp. *digitatus* Community

Floristic composition: The diagnostic taxa of the *Phyllobolus digitatus* ssp. *digitatus* Community are *P. digitatus* ssp. *digitatus* (syn: *Dactyloopsis digitata* ssp. *digitata*), and *Othonna intermedia* of the SG AB. Other species that are characteristic for the *Salsola* sp. (Schmiedel 93110 HBG)-*Argyroderma pearsonii* Alliance, SG X-Z) occur with high constancy (such as *Argyroderma pearsonii*, *Cephalophyllum spissum*, *Drosanthemum diversifolium*, *Salsola* sp. (Schmiedel 93110 HBG), *Tylecodon pygmaeus*, and *Oophytum oviforme*).

Total cover and species richness: The total cover values of the community depend on the annual rainfall. Hence the occurrence of the *Othonna intermedia*, *Phyllobolus abbreviatus*, *Senecio aloides* (H Dic) as well as the size of the *P. digitatus* ssp. *digitatus* plants vary strongly with the precipitation. For the same reason also the number of species per relevé varies. One relevé (3075.0) comprises 19 species whereas on other relevés only 4 or 5 species (relevé no. 4677.4, 5638.0) were recorded. But the average number of species per relevé for this community is relatively high (9 spp.) compared to most of the other quartz-field communities.

Structural composition: The growth-form composition of the community is mainly dominated by compact nano-chamaephytes. However, mega- and micro-chamaephytes also occur with higher cover values (above 3 %). Therefore, the community shows a heterogeneous structure of low and high growth forms. Also geophytes (*Othonna intermedia*) play an important role.

Locality and habitat: The community is restricted to the central part of the Knersvlakte. It regularly occurs there on gentle to very steep slopes or edges along rivers (rivier) on very soft, silty fine-material from in situ weathered, yellow-brown phyllite. The fine-material typically has low stone content which often derived from the underlying bedrock. The very steep slopes in particular are mostly exposed to east. The soil surface is densely covered with fine to medium quartz stones. The soil has high to extremely high salinity (up to 9 mS/cm, median = 3.3 mS/cm). The soil pH is slightly acid (pH about 6.5) and carbonate is absent from these sites.

Conservation status: The *Phyllobolus digitatus* ssp. *digitatus* Community is endemic to the quartz fields of the Knersvlakte and largely restricted to a particular type of habitat at the phyllite hills along the Sout Rivier in the Quaggas Kop area of the central Knersvlakte. Parts of this area which were also the habitats of the community were destroyed for the construction of the railway of the Sishen-Saldanha line in the early 1970ies. Yet, the main habitat of the community (mainly steep slopes) is of little use for any agricultural or other purpose and not seldom even hard to reach.

29 *Oophytum oviforme* Community

Floristic composition: The *Oophytum oviforme* Community is characterised by the occurrence of *Oophytum oviforme* (SG AC) which dominates the community with very high cover values (up to 33 %). Other species that occur with high frequency but low cover values are *Argyroderma pearsonii*, *Salsola* sp. (Schmiedel 93110 HBG), and *Tylecodon pygmaeus* (SG Z). Species groups W, X and Z are largely absent or only represented with low constancy. The typical occurrence in the vicinity of the *Phyllobolus digitatus* ssp. *digitatus* Community (# 28) the reason for the frequent occurrence of *Oophytum oviforme* in the latter community and, vice versa.

Although the two species of *Oophytum* (*O. nanum* and *O. oviforme*) differ only little in terms of growth form as well as size, form and texture of leaves, they differ significantly with respect to their syntaxonomic membership: the two species hardly occur sympatrically. This is due to the different geographical distribution of the species which only overlap at a small area in the Quaggas Kop area of the central Knersvlakte (Ihlenfeldt 1978). However, even where their distribution overlap, they are found to be vicariant.

Total cover and species richness: The species numbers per relevé are usually low (4 species per relevé), however, the total cover values (median = 30.6 %) are very high compared to other quartz-field Communities.

Structural composition: The sub-community is clearly dominated by nano-chamaephytes. Micro-chamaephytes occur with very low cover values only. Mega-chamaephytes are absent.

Locality and habitat: The community is restricted to the Moedverlor and Quaggas Kop area of the central quartz-fields of the Knersvlakte. With respect to habitat ecology the *O. oviforme* Community differs only gradually from the *O. nanum* Community (# 27). The latter is more common on gentle slopes or level plains whereas the first is often found on upper slopes and edges of plateaux above steep slopes, in close neighbourhood and at the upper section of a topographic gradient of *P. digitatus* ssp. *digitatus*. The soils of the habitat of the *O. oviforme* Community had typically higher electrical conductivity values (> 3 mS/cm) and lower soil pH (pH < 6) than the habitats of the *O. nanum* Community.

Conservation status: Due to the geographical restriction of the Community to the Moedverlor and the Quaggas Kop area of the Central Knersvlakte, the Community has to be regarded as extremely vulnerable.

30 *Monilaria pisiformis* Community

Floristic composition: The *Monilaria pisiformis* Community is defined by the occurrence of *Monilaria pisiformis* (SG AD) and *Conophytum minutum* var. *minutum* (SG AE), the diagnostic species of the *Salsola* sp. (Schmiedel 93110 HBG)-*A. pearsonii* Alliance (SG Z) as well as the more eurytopic quartz-field species (SG X and Z). The frequent occurrence of *Conophytum minutum* var. *minutum* within the community shows the strong affinity of the community to more acid quartz fields of the Knersvlakte which are characteristic for *C. m.* var. *minutum*.

Total cover and species richness: The total cover values of the sub-community is low as it is typical for the quartz-field vegetation in general (median = 6.8 %). The number of species per relevé varied strongly, but the median of the numbers of species was relatively high (8.5 species per relevé) compared to the other vegetation communities of the quartz fields.

Structural composition: The growth-form composition of the vegetation is characterised by micro-chamaephytes but is diversified by the occurrence of mega- and nano-chamaephytes.

Locality and habitat: The community occurs on level or slightly exposed sites of the central part of the Knersvlakte. The shallow soils with a silty soil texture are rich in stone content (median = 61.5 % weight) and are densely covered with medium to coarse quartz debris. The quartz stones at the soil surface is typically covered with crustose lichens. The soil pH of the habitats are far below the soils of other communities of the *Salsola* sp. (Schmiedel 93110 HBG)-*A. pearsonii* Alliance (median = 5.3 pH). The salinity is comparatively low (median = 2.1 mS/cm). The soil conditions show strong affinities to those of the acid quartz fields of the Knersvlakte. Often, the sites inhabited by the community cover less than 20 m² and occur island-like among other, more saline quartz fields.

Conservation status: The community is restricted to the distribution area of *Monilaria pisiformis* which roughly covers the central part of the Knersvlakte. Here, it occurs on a very special and locally restricted quartz-field habitats. Consequently, the community has to be designated as highly vulnerable.

31 *Conophytum minutum* var. *minutum* Community

Floristic composition: The *Conophytum minutum* var. *minutum* Community is characterised by the same diagnostic species (Species group AI) as the *Cephalophyllum spissum*-*Monilaria pisiformis* Community (# 30) of the *Salsola* sp. (Schmiedel 93110 HBG)-*A. pearsonii* Alliance but it misses its diagnostic species (SG Z). Also, species group X and Z that are well represented in the *Monilaria pisiformis* Community are largely absent. *Conophytum minutum* var. *minutum* dominates the *C. m.* var. *minutum* Community whereas *M. pisiformis* and the other species occur with very low cover values only. Also, in contrast to the communities of the *S. seidig*-*A. pearsonii* Alliance, some species of the communities of the acid quartz-fields, *Ruschia burtoniae* (SG AK) as well as *Antimima watermeyeri* (SG BI) were recorded for the *C. minutum* var. *minutum* Community. Very few ubiquitous species (SG BI) were recorded for the community.

The co-occurrence of species of both main soil types, i.e., saline and acid quartz fields, in this community reveals its intermediate position between the two main quartz-field habitats.

Total cover and species richness: *C. m.* var. *minutum* may occur with very high density and cover values (up to 40 %, PNR 3066). Therefore and irrespective of the typically low cover values of the other taxa within the community, the total cover of the vegetation is relatively high (median

11.4 %). The number of species per relevé is comparatively low (5 spp.) and below most of the other communities.

Structural composition: The growth-form composition in the community is characterised by the high cover values of nano-chamaephytes. Micro- and mega-chamaephytes are of minor importance.

Locality and habitat: The community is typically found on small patches of shallow soils with silty fine-material and high stone content in soil. The habitats resemble very much those of the *Monilaria pisiformis* Community (# 30). In fact they often occur next to each other. Like the habitats of the latter, the sites preferred by the *C. m. var. minutum* Community seem to be strongly weathered quartz veins or outcrops. Also, the quartz cover comprises a high percentage of coarse fractions. However, the *C. m. var. minutum* Community prefers lower salinity (< 1 mS/cm) and lower soil pH (< pH 5) than the *M. pisiformis* Community.

Conservation status: *Conophytum minutum* var. *minutum* is a widespread between Vanrhynsdorp (Knersvlakte) and Riethuis-Wallekraal (Hammer 1993b) where it is not restricted to quartz fields but occurs on outcrops of different lithology and on other soils. However, the *C. minutum* var. *minutum* Community is restricted to a particular quartz-field habitat and is geographically restricted to the Central Knersvlakte. Due to its geographical and ecologically restriction the community should be regarded as vulnerable.

32 *Brownanthus corallinus* Community

Floristic composition: The diagnostic species of the community are *Brownanthus corallinus*, and *Dicrocaulon nanum* indet. (SG AJ). *Salsola* sp. (Schmiedel 102410 HBG), *Spergularia media*, and *Ficinia lateralis* (SG AG) are characteristic accompanying species of the community. At most sites *Brownanthus corallinus* dominates the vegetation but also *Salsola Salsola* sp. (Schmiedel 102410 HBG) and *Dicrocaulon nanum* spec. nov. (H.-D. Ihlenfeldt, pers. comm.) may occur with high cover values (up to 10 %). The community shows low floristic relationship to any of the other quartz-field communities but shares the species of SG AF-AH) with the communities of the *Conophytum calculus* ssp. *calculus* Group which is typical for the acid quartz fields of the Knersvlakte.

Total cover and species richness: The total cover values of the vegetation can be very low (app. 2-3 %). Most of the relevés have higher cover values. With a median value of 6.4 % it was in the same range with most of the other communities of the quartz-field vegetation. The numbers of species per relevés is comparatively low (median = 4 spp.) and close to the species-poor communities of the very saline soils (*Argyroderma pearsonii* Community or the *O. oviforme* Community).

Structural composition: The community is dominated by mega-chamaephytes (*Brownanthus corallinus*) and micro-chamaephytes (*Salsola* sp. Schmiedel 102410 HBG, *Spergularia media*). The latter, however, are represented by low cover values only. Consequently, regarding the growth-form composition, the community differs clearly from the other vegetation communities of saline quartz fields which are clearly dominated by nano-chamaephytes.

Locality and habitat: The *Brownanthus corallinus* Community is widespread in the Knersvlakte and occurs even in the Riethuis-Wallekraal Phytocorion. It typically inhabits gentle to steep slopes of hillocks which are densely covered with medium to coarse quartz debris. The soils are moderate to highly saline (< 1 - > 5 mS/cm) and have low soil pH (mainly < pH 5).

Conservation status: The community is widespread in the Knersvlakte and occurs even in the Riethuis-Wallekraal Phytochorion. At the present stage of knowledge, it does not seem to be particularly vulnerable.

The *Conophytum calculus* ssp. *calculus* Group (Community # 33 - # 39)

The *Conophytum calculus* ssp. *calculus* Group is characterised by the constant occurrence of *C. calculus* ssp. *calculus* (SG AK) which typically occurs with low cover values. *C. calculus* ssp. *calculus* is an obligate quartz-field taxon and endemic of the Knersvlakte. The communities within the group typically inhabit acid, non-saline quartz fields. They are largely restricted to the Knersvlakte but also spread to the north into the Riethuis-Wallekraal Phytochorion. Outside the Knersvlakte, however, the communities occur without their diagnostic species. Further species with high constancy within the group but not restricted to it are *Crassula columnaris* ssp. *prolifera*, *Crassula deceptor*, *Pteronia ciliata*, (SG W), *Euphorbia hamata* *Gazania krebsiana*, *Hirpicium alienatum*, *Senecio aloides*, *Spergularia media* (SG AG), *Tripteris sinuata* var. *sinuata*, and *Tetragonia verrucosa* (SG BI).

The following Communities belong in this group:

- 33 *Ruschia burtoniae* Community
- 34 *Monilaria chrysoleuca* var. *chrysoleuca* Community
- 35 *Monilaria moniliformis* Community
- 36 *Dicrocaulon brevifolium* Community
- 37 *Dicrocaulon pseudonodosum* Community
- 38 *Dicrocaulon longifolium* Community
- 39 *Dicrocaulon nodosum* Community

33 *Ruschia burtoniae* Community

Floristic composition: *Ruschia burtoniae* is the only diagnostic and dominating species of the community (SG AK) which represents a monodominant vegetation unit. Further species that occur with high constancy are *Conophytum minutum* var. *minutum* (SG AE) as well as those which are characteristic for the acid quartz fields in general (SG AF-AH). *Antimima watermeyeri*, *Lampranthus watermeyeri*, *Tripteris sinuata* var. *sinuata* (SG AI) and *C. calculus* ssp. *calculus* are of particular high constancy.

Total cover and species richness: The total cover of the community which varied between < 5 % and > 15 % largely depends on the cover values of *Ruschia burtoniae*. The number of species per relevé varied extremely between only one species (monotypic *Ruschia burtoniae* stands) and up to 18 species per relevé. The average number of species (median = 7 spp.) does not differ significantly from those of most of the other communities of the quartz field vegetation. The long list of species that occur with low constancy and in the community is due to the high number of relevés recorded (36 relevés).

Structural composition: The dominating growth forms within the community are fruticose megachamaephytes (*Lampranthus watermeyeri*, *R. burtoniae*, *Tetragonia verrucosa*) and micro-chamaephytes (*Antimima watermeyeri*). Nano-chamaephytes play a subordinate role.

Locality and habitat: The *Ruschia burtoniae* Community is largely restricted to the Knersvlakte, but was also recorded for the area between Knersvlakte and Riethuis-Wallekraal. It typically occurs on plateaux or gentle slopes of poorly weathered shale which is often but not always covered with medium to coarse quartz debris. If the sites are exposed to the western direction (facing the

coast) the coarse quartz debris may be covered by crustose and foliose lichens. Due to the often poor state of weathering the stone content in soil is high (median = 50 %) and the soils are shallow (median = 16 cm). The fine-material which derives in situ from the weathering bed rock contains high fractions of silt. The characteristic feature of these sites is the extremely low soil pH (median = 4.4 pH) and the low soil electrical conductivity (median = 0.5 mS/cm).

Notes: The taxonomic position of *Ruschia burtoniae* is still unclear. Although designated as a *Ruschia* species, shape of the fruits and their lack of closing bodies as well as the bluish colour of the relatively soft leaves indicate the close relation of the taxon to the *Lampranthus* group. *R. burtoniae* is widespread in the Knersvlakte, the southern parts of the Namaqualand and even in the western fringe of the Nama Karoo in the Nieuwoudtville region.

Conservation status: The community is very widespread in the Knersvlakte and in the central Namaqualand where it often covers extensive sites. Therefore, it is not threatened.

34 *Monilaria chrysoleuca* var. *chrysoleuca* Community

Floristic composition: The *Monilaria chrysoleuca* var. *chrysoleuca* Community is defined by a high constancy and cover values of *Monilaria chrysoleuca* var. *chrysoleuca* (SG AL) and the characteristic species of the acid quartz fields (SG AF-AH), e.g., *Conophytum calculus* ssp. *calculus*, *Crassula columnaris* ssp. *prolifera*, *Gazania krebsiana*, and *Tripteris sinuata* var. *sinuata*.

Total cover and species richness: The total cover of the vegetation lie between 3.7 and 11.8 %. However, the majority of the recorded sites had cover values of about 6 to 7 %. The number of species per relevé varied significantly between 4 and 19 spp. In average the species number per relevé is about 11 spp. which is high compared to most of the other communities of the quartz fields.

Locality and habitats: It inhabits gentle to steep slopes of hills of the Central and Northern quartz fields of the Knersvlakte covered with medium to coarse quartz debris. Regarding the central quartz fields of the Knersvlakte it occurs in all three areas (Arizona, Moedverlor, and Quaggas Kop area) but is restricted to the distribution of the diagnostic taxon, which is absent from the western part of the Moedverlor area (Holrivier and Koekenaap).

As a member of the *C. c.* ssp. *calculus* Group the community typically inhabits acid (median = 5.8 pH), non-saline quartz fields (median = 1.1 mS/cm) with high percentage of coarse quartz debris in the quartz cover at soil surface. The community is found on plateaux, or on the upper section of gentle or (less often) steeper slopes which are often exposed to south, south-west or west. In agreement with the habitats of the *Ruschia burtoniae* Community, it occurs on soil with high stone content (median = 56 % weight) and the fine-material contains high silt content. The soil pH is usually higher than that of the habitat of the *Ruschia burtoniae* Community (# 33).

Structural composition: The community is dominated by micro- and mega-chamaephytes. Nano-chamaephytes are represented by low cover values.

Notes: *Monilaria chrysoleuca* var. *polita* (Ihlenfeldt & Jörgensen 1973) occurs in a very restricted area at the northern quartz fields of the Knersvlakte where it inhabits the same habitat as the typical variety. The syntaxonomic relation of the variety is not sufficiently known yet.

Conservation status: *M. c.* var. *chrysoleuca* and *C. calculus* ssp. *calculus* are endemic to the Knersvlakte and obligate quartz-field taxa. The community is restricted to particular quartz fields of the Knersvlakte. It has to be regarded as not common and therefore vulnerable.

35 *Monilaria moniliformis* Community

Floristic composition: The diagnostic species of the community is *Monilaria moniliformis* and *Argyroderma congregatum* (SG AM) of which the first occurs with high constancy and high cover values. Other species of lower constancy and typically low cover values are *C. c.* ssp. *calculus*, *Crassula columnaris* ssp. *prolifera*, *Tetragonia verrucosa*, *Tripteris sinuata* var. *sinuata*, and *Ruschia burtoniae* which are generally characteristic for the *Conophytum c.* ssp. *calculus* Group (Communities # 33-39).

Total cover and species richness: The total cover values of the vegetation was between 5 and 12.6 % and the average number of species per relevé was 8 spp.

Structural composition: In accordance with the other communities of the *C. c.* ssp. *calculus* Group, the community is characterised by the dominance of mega- and micro-chamaephytes whereas nano-chamaephytes and other growth forms are of minor importance.

Locality and habitat: The community inhabits plateaux and slopes of quartz hills with medium quartz debris but also higher percentage of coarse fractions do occur. The soils are of intermediate depth (median = 24 cm), the stone content varies between low (< 10 %) and high (70 % by weight) and the fine material is rich in silt. The soil chemistry varied considerably between low soil pH with low electrical conductivity and neutral soil pH with high salinity. However, the majority of the sites showed moderately acid pH (median = 4.5) and low salinity (median = 1.1 mS/cm).

Conservation status: Widespread on the central quartz fields of the Knersvlakte and not very particular regarding soil chemistry (pH, salinity). Obviously not threatened.

36 *Dicrocaulon brevifolium* Community

Floristic composition: The diagnostic species of the *Dicrocaulon brevifolium* Community is *Dicrocaulon brevifolium* (SG AL) which also dominates the vegetation by reaching cover values of up to 30 %. Other taxa hardly have cover values above 1 % (= 1 in Phytosociological Table II, Appendix 10). In correspondence with other communities of the *C. c.* ssp. *calculus* Group, *C. calculus* ssp. *calculus*, *Tylecodon reticulatus*, *Crassula deceptor*, *Gazania krebsiana*, *T. verrucosa*, and *Senecio aloides* do occur with high constancy.

Total cover and species richness: Depending on the cover values of the dominating species, *D. brevifolium*, the total cover of the vegetation varies strongly. However, the majority of the recorded sites have an intermediate total cover of about 7 to 12 %. The average number of species per relevé was 10.5 (median). This is similar to the *Ruschia burtoniae* Community of the same group (11 spp.) but higher than most of the other communities of the (saline) quartz fields.

Structural composition: Micro-chamaephytes and to a lower extent, micro-chamaephytes dominate the vegetation of the community. Nano-chamaephytes are only represented with low cover values.

Locality and habitat: The *Dicrocaulon brevifolium* Community typically occurs along drainage lines on south-west to south-east facing slopes of the central quartz hills in the Knersvlakte. The quartz cover may comprise a high percentage (up to 50 %) of coarse fractions (20-60 mm Ø). The soils are loamy to silty and contain high stone content (median = 60 % weight). The soils have a low pH (median = 4.8 pH) and low to moderate salinity (median = 1.5 mS/cm).

Conservation status: The community is restricted to a particular habitat of the central quartz fields of the Knersvlakte where it is locally common. However, its regional restriction makes the community vulnerable.

37 *Dicrocaulon pseudonodosum* Community

Floristic composition: *D. pseudonodosum*, *Pelargonium quarciticola*, *P. incrassatum* and *Phyllobolus herbertii* (SG AO) are the diagnostic species of the *Dicrocaulon pseudonodosum* Community. *D. pseudonodosum*, a shrubby leaf-succulent dwarf shrub dominates with high cover values. Besides the characteristic species of the acid quartz fields (SG AF-AH) also those that occur more frequently on saline quartz fields (SG W and Z) are found in the community, with low constancy though.

Total cover and species richness: The total cover of the vegetation was comparatively high (median = 13 %), the number of species per relevé (11.5 spp.) corresponds with those of most of the other communities of the group, with the only exception of *M. moniliformis* which is lower (8 spp.).

Structural composition: The community is significantly dominated by mega-chamaephytes. Micro- and nano-chamaephytes and other growth forms are of minor importance.

Locality and habitat: The community is restricted to the northern part of the Knersvlakte. Its habitat corresponds well with those of other communities of the group: The community is found on slopes which are covered with quartz debris which comprises high percentage of coarse fragments. But the community was also found on poorly weathered granite (relevé no. 9772.0). The soil pH is low (median = 5.4 pH) but not as low as has been recorded for most sites of the *D. brevifolium*, the *D. longifolium*, the *Monilaria moniliformis*, and the *Ruschia burtoniae* Community but similar to those of the *M. chrysoleuca* var. *chrysoleuca* Community (# 34). The electrical conductivity is higher as for most of the other communities of the group (median = 1.5 mS/cm) which is comparable with values determined for habitats of the *D. brevifolium* and the *D. nodosum* Community.

Conservation status: The community is restricted to the northern quartz fields of the Knersvlakte and the northern part of the central quartz fields (Arizona area: Flaminkvlakte). The entire area is comparatively little known and rarely investigated by botanists. Yet, the community has to be regarded as vulnerably due to its geographically restricted occurrence.

38 *Dicrocaulon longifolium* Community

Floristic composition: The diagnostic species are *D. longifolium* which also occurs with high cover values, *Argyroderma crateriforme* and *Tylecodon occultans* (SG AP). Further species that were recorded for the community are SG AG among the characteristic species of the acid quartz fields of the Knersvlakte.

Total cover and species richness: The total cover of the vegetation is usually comparatively high (10.5 %) and corresponds with those of the *Dicrocaulon brevifolium* Community. But the number of species per relevés (9 spp.) is largely in line with most of the communities of the group.

Structural composition: The community is dominated by mega-chamaephytes. The nano-chamaephytes on soil surface represent another layer which usually has low cover values.

Locality and habitat: The community inhabits gentle upper slopes with dense pavement of quartz debris or sandstone in the western quartz fields of the Knersvlakte. The soils have high stone

content (65 % by weight), high percentage of silt, low soil pH (median = 4.6 pH) and low electrical conductivity (median 0.3 mS/cm), as it is typical for the group. The soil depth, however, is comparatively high (median = 40 cm).

Conservation status: The community is restricted to acid, non-saline soils of the western quartz fields of the Knersvlakte. Due to its ecologically and geographically restriction the community has to be regarded as vulnerable.

39 *Dicrocaulon nodosum* Community

Floristic composition: The *Dicrocaulon nodosum* Community is defined by the occurrence of *D. nodosum* (SG AQ) as well as the characteristic species of the *Conophytum calculus* ssp. *calculus* Group: *Hirpicium alienatum*, *Monilaria chrysoleuca* var. *chrysoleuca*, *Ruschia burtoniae*, *Tetragonia verrucosa*, and *Tripteris sinuatum* var. *sinuatum*. *C. calculus* ssp. *calculus* occurs with low constancy.

Total cover and species richness: The total cover of the vegetation was comparatively high (median = 16.6 %) and even surpasses some communities outside the quartz fields of the Knersvlakte (communities 1-20). In contrast, the numbers of species per relevés is comparatively low and is largely in line with several of the communities of the saline quartz fields.

Structural composition: The community is dominated by mega- and micro-chamaephytes. No nano-chamaephyte occur with higher constancy or cover value.

Locality and habitat: In correspondence with the *D. pseudonodosum* Community the community is restricted to the northern quartz fields of the Knersvlakte and to the adjacent Hardeveld (west of Bitterfontein). It prefers acid quartz fields which have a higher salinity than the rest of the group (median = 2.5 mS/cm). The soils are shallow (median = 14 cm), skeletal (median = 55 % weight) and rich in silt. The soil pH is as low as it is typical for most of the communities of the group (median = 4.7 pH).

Conservation status: Due to its geographical and ecological restriction the community has to be regarded as vulnerable.

IX.1.4 Communities of the Riethuis-Wallekraal area

40 *Monilaria scutata* var. *obovata* Community

Floristic composition: The diagnostic taxa of the community *Monilaria scutata* var. *obovata*, *Euphorbia celata* and *Pharnaceum dichotomum* (SG AS) which are both absent from any other community recorded. *P. ciliata*, *Gazania krebsiana* (SG AF) and *Tetragonia verrucosa* (SG BI), the characteristic species of the acid quartz fields of the entire Namaqualand, as well as *Hirpicium alienatum* (SG AG), a typical species of the acid quartz fields of the Knersvlakte and the central Namaqualand, also occur with high constancy.

Total cover and species richness: The total vegetation cover within the community differed considerably (4.6-18.6 %) as did the number of species per relevé (4-15 spp.). However, the very species poor variant seems to be less common.

Locality and habitat: The *M. s.* var. *obovata* Community is largely restricted to the Riethuis-Wallekraal area but was also recorded for quartz-field near Harras (north of Wolfberg, 2917CB) in the northern part of the central Namaqualand. It typically occurs on moderate slopes with a

medium density of quartz cover consisting of medium-sized and coarse quartz debris. The shallow soils (median = 10 cm) are loamy sand have a high stone content (median = 52 % weight). The soil pH is acid (median = 5.1 pH) but the electrical conductivity is comparatively high (median = 3.2 mS/cm).

Structural composition: The community is dominated by micro- and mega-chamaephytes, nano-chamaephytes occur with low cover values only.

Conservation status: The *M. scutata* var. *obovata* community occurs in the central Namaqualand between Riethuis-Wallekraal and Harras (north of Wolfberg). However, the community is not very common and is mainly restricted to smaller patches only.

41 *Jacobsenia vaginata* Community

The *Jacobsenia vaginata* Community inhabits the very saline quartz fields of the Riethuis-Wallekraal Phytochorion of the central Namaqualand. The diagnostic species are *J. vaginata* (formerly known as *Drosanthemopsis vaginata* Rauschert) and *Conophytum concavum* (SG AT), whereas only *J. vaginata* reaches high cover values. However, despite the increased salt content, the number of accompanying species is not restricted to particularly halo-tolerant taxa and comprises several species groups: *Salsola* sp. (Schmiedel 93117 HBG) (MG M), *Crassula deceptor* (SG W) *Salsola* (Schmiedel 102410 HBG), (SG AG), *Meyerophytum globosum*, *Cephalophyllum inaequale* (SG AR) and *Ruschia leucosperma* SG AY). Among them, only *S.* sp. (Schmiedel 102410 HBG) and *R. leucosperma* occur with high constancy (class III).

Two sub-communities can be distinguished:

41.1 *Jacobsenia vaginata*-*Meyerophytum globosum* Sub-Community

41.2 *Jacobsenia vaginata*-dominated Sub-Community

41.1 *Jacobsenia vaginata*-*Meyerophytum globosum* Sub-Community

Floristic composition: The *Jacobsenia vaginata*-*Meyerophytum globosum* Sub-Community is characterised by the occurrence of *M. globosum* (L. Bolus) Ihlenfeldt comb. nov. (unpublished) which was formerly known as *Monilaria globosa* (L. Bolus) L. Bolus and *Cephalophyllum inaequale* (SG AR). Both species are not entirely restricted to the community but define the sub-community as differential species. Also, *Gazania krebsiana* (SG AF) and *Hirpicium alienatum* (SG AG) occur with high constancy, whereas they are absent in the *J. vaginata*-dominated Sub-Community. *J. vaginata* occurs with low cover values only.

Total cover and species richness: The total cover of the vegetation is as low as in *J. vaginata*-dominated Sub-Community (median = 4.3 %) but the number of species per relevé is considerably higher (10-14 spp.) than in the Sub-Community (3-9 spp).

Structural composition: Micro-chamaephytes dominate the growth-form composition of the vegetation. Nano- and mega-chamaephytes are only represented with low cover values.

Locality and habitat: The sub-community inhabits level and moderately to extremely saline (median = 3.24 mS/cm) quartz fields in the Riethuis-Wallekraal area. The soil pH is only slightly acid (median = 6.35 pH). The stone content (median = 40 % weight) of the shallow soils (median = 17 cm) is higher than of those of the *J. vaginata*-dominated Sub-Community.

Conservation status: The sub-community is restricted to the saline quartz fields of the Riethuis-Wallekraal Phytochorion which is now well protected by the newly established conservation area at the Oubees farm (National Parks Board).

41.2 *Jacobsenia vaginata*-dominated Sub-Community

Floristic composition: The sub-community is characterised by no diagnostic species of its own but *J. vaginata* typically occurs with high cover values. Furthermore, *Atriplex lindleyi* ssp. *inflata*, *Psilocaulon dinteri*, and *Salsola* sp. (Schmiedel 102410 HBG) which are absent from the *J. vaginata*-*M. globosum* Sub-Community occur, although with low constancy.

Total cover and species richness: The sub-community has low total cover values (2.5-6.6 %) and low numbers of species per relevé (3-8 spp.) which lies below the numbers of the *J. vaginata*-*M. globosum* Sub-Community.

Structural composition: The vegetation of the sub-community is typically dominated by micro-chamaephytes, nano- and mega-chamaephytes are mainly represented by lower cover values.

Locality and habitat: The topography and soil conditions are largely identical with those of the *J. vaginata*-*M. globosum* Sub-Community, however, along a topo-sequence it often occurs above the *J. vaginata*-dominated Sub-Community. But the stone content tends to be lower (median = 22 % weight) and the soil pH of most of the sites is higher (median = 7.5 pH) than for the other sub-community.

Conservation status: The sub-community is restricted to the saline quartz fields of the Riethuis-Wallekraal Phytochorion which is now well protected by the newly established conservation area at the Oubees farm (National Parks Board).

42 *Dicrocaulon spissum* Community

Floristic composition: The only diagnostic and clearly dominating species of the community is *Dicrocaulon spissum* (SG AU). Beside *D. spissum*, only species of SG AG (*Pteronia ciliata*, *G. krebsiana*), SG AG (*Spergularia media*, *Hirpicium alienatum*) and SG BI (*Tetragonia verrucosa*) occur with high constancy which are typical associated with acid quartz fields of the Namaqualand.

Total cover and species richness: The community typically has a low total cover (< 10 %) and low number of species per relevé (< 10 spp.).

Structural composition: The community is dominated by fruticose micro-chamaephytes. Mega-chamaephytes occur with high frequency but low cover values whereas nano-chamaephytes are represented with low constancy and very cover values only.

Locality and habitat: The community is restricted to the Riethuis-Wallekraal Phytochorion where it inhabits plateaux, plains or gentle slopes of hillocks which are covered with coarse quartz debris. The shallow soils (6-23 cm) of loamy-silty sand are moderately saline (median = 0.62 mS/cm) and typically very acid (median = pH 4.8).

Conservation status: The community is restricted to acid quartz fields of the Riethuis-Wallekraal Phytochorion of the central Namaqualand. Due to its geographical and ecological restriction the community has to be regarded as vulnerable. However, a good part of the distribution area of the community is covered by the new conservation area at Oubees (east of Riethuis farm).

43 *Dicrocaulon ramulosum* Community

Floristic composition: *Dicrocaulon ramulosum* and *Limonium dregeanum* (SG AV) present the diagnostic species of the Community which is closely related to the *D. spissum* Community (42) but differs from the latter by the absence of *D. spissum* (SG AU), *Gazania krebsiana* (SG AF) and *Hirpicium alienatum* (SG AG) as well as by the presence of *Psilocaulon dinteri* and *Salsola zeyheri* (SG BI). However, the community is not yet sufficiently documented.

Structural composition: The community is dominated by micro- and mega-chamaephytes. Nano-chamaephytes are completely absent.

Locality and habitat: The community is restricted to the Riethuis-Wallekraal Phytochorion and occurs there on quartz covered slopes with neutral soils and moderate salinity. The habitat ecology of the community is not sufficiently known. However, the *D. ramulosum* Community seems to cope better with high salinity and high soil pH than the *D. spissum* Community.

Conservation status: The community is restricted to the Riethuis-Wallekraal area. Its ecology and composition is too little known to judge its vulnerability.

44 *Ruschia viridifolia* Community

Floristic composition: The diagnostic species (SG AW) are hardly found on the quartz fields of the Knersvlakte or central Namaqualand but are characteristic for the mountainous Namaqualand: *Ruschia viridifolia* and *Ehrharta barbinodis*. Also, these accompanying species that occur with highest constancy, e.g., *Gazania krebsiana* (SG AF) and *Tetragonia verrucosa* (SG BI) are also typically found on acid, rocky quartz fields of the Knersvlakte and the central Namaqualand.

Total cover and species richness: The total cover of the vegetation is moderate (median = 14 %) but the number of species per relevés is comparatively high (median = 14 ssp./ relevé).

Structural composition: The growth-form composition of the vegetation is dominated by mega-chamaephytes and with lower cover values, micro-chamaephytes.

Locality and habitat: The *Ruschia viridifolia* Community typically occurs on rocky habitats of quartz or granite outcrops of the central part of the Knersvlakte and in the Riethuis-Wallekraal area. The habitat is characterised by slopes with rocks and (partly) boulders of different lithology (quartz, granite, gneiss). The texture of the deep soils (median = 28.5 cm) varies between silty and loamy sand or sandy loam. Due to the rocky habitats the stone content of the soil is high (median = 60 % weight). The soil pH is (median = 5.8 pH) and salinity are low (median 1.44 mS/cm).

Conservation status: The community is widespread in the Knersvlakte and the Riethuis-Wallekraal area. However, its vulnerability is not sufficiently known.

45 *Monilaria scutata* var. *scutata* Community

Floristic composition: The *Monilaria scutata* var. *scutata* Community is characterised by the exclusive occurrence of *M. s.* var. *scutata* as well as *Clorophytum crassinerve*, *Phyllobolus sinuatus*, *Brunsvigia radula* and *Othonna rechingeri* which also occur with high constancy (SG AX). Additional species which have no diagnostic values but are typical for the acid, non-saline quartz fields of the Knersvlakte and the central Namaqualand are *Senecio aloides* (SG W), *Gazania krebsiana*, *Pteronia ciliata* (SG AF) and *Antimima watermeyeri*, *Tetragonia verrucosa* (SG BI).

Total cover and species richness: The total cover values (median = 8.3 %) as well as the numbers of species per relevé (9.5 ssp. / relevé) are intermediate and differ very little among the recorded sites.

Structural composition: The community is dominated by mega- and micro-chamaephytes. Nano-chamaephytes hardly occur.

Locality and habitat: The typical habitat of the community are level plateaux or gentle slopes of the Riethuis-Wallekraal Phytochorion of the central Namaqualand. The density of the quartz cover is comparatively low (median = 85 %), comprising a high percentage of coarse debris (median = 6 %). The soils are shallow (13.5 cm) and have a low to very high stone content in soil (median = 31 % weight). The soil texture is silty sand. The soil pH is low (median = 4.36 pH) and the electrical conductivity compared to other acid quartz fields relatively high (median = 1.44 mS/cm).

Conservation status: The community is limited to the southern part of the Riethuis-Wallekraal Phytochorion which is in line with the distribution area of *M. scutata* var. *scutata*. It occurs there on particular habitats only. The distribution area of the Community is not covered by the new conservation area at the Oubees farm (east of the Riethuis farm), the community should be regarded as highly vulnerable.

IX.1.5 Communities of the Richtersveld

46 *Ruschia leucosperma* Community

Floristic composition: The *Ruschia leucosperma* Community is characterised by the presence and dominance of *R. leucosperma*. *C. regale*, which also occurs with high constancy is represented with low cover values only. *Hypertelis salsoloides* and *Gazania lichtensteinii* (SG BI) are recorded with high constancy whereas species that frequently occur on the quartz-field and related habitats of the Richtersveld (SG BH) as well as the diagnostic species of the *Antimima* sp. (Schmiedel 104874 HBG) Group (SG AY) are presented with low constancy only.

Total cover and species richness: The total cover of the community is moderately high (median = 12.4 %) and the species richness is in line with most of the other quartz-field Communities of the Richtersveld (10 ssp/ relevé).

Structural composition: The community is dominated by small, erect and densely branched, leaf-succulent, fruticose micro-chamaephytes. Compact, leaf-succulent nano-chamaephytes and non-succulent or sub-succulent chamaephytes and are occur with low cover values only.

Locality and habitats: The community is found in the central Namaqualand into the Richtersveld where it inhabits broad plains and gentle slopes. At some localities the soils are sparsely or densely covered with small to medium sized (< 60 mm) quartz gravel. The soils are shallow to moderately deep (median = 18 cm) and consists of silty to loamy sand with a moderately low stone content (median = 33 %). The soils are about neutral (median = 7 pH) and typically free of carbonate content. Salinity is generally low (median = 0.322 mS/cm).

Conservation status: The community is widespread and often covers broad areas.

47 *Cephalophyllum regale*-dominated Community

Floristic composition: The community is clearly dominated by *C. regale* which is where as *Ruschia leucosperma* occurs with high constancy (Class III) but low cover values only. The diagnostic species of the *Antimima* sp. (Schmiedel 104874 HBG) Group (SG AY) are frequently presented of which *A.* sp. (Schmiedel 104874 HBG), *A.* sp. (Schmiedel 102039 LP), and *Ruschia paucipetala* may reach high cover values.

Total cover values and species richness: The vegetation cover of the community is typically spares (median = 7.9 %). The species numbers are in line with most of the other quartz fields communities of the area (10 spp./ relevé).

Locality and habitat: The community is restricted to the southern and mountainous Richtersveld where it inhabits gentle slopes with spares to dense quartz cover medium sized quartz debris. The soils are silty sandy and have a moderate stone content (median = 40 % weight), slightly acid soil pH (median = 6.6 pH) and low electrical conductivity (median = 0.3 mS/cm) without carbonate content.

Structural composition: The community is very heterogeneously structured comprising fruticose, erect mega- and micro-chamaephytes as well as compact nano-chamaephytes.

Conservation status: Not sufficiently known.

48 *Aspazoma amplexans* Community

Floristic composition: The community is very rich in species and heterogeneous in its composition, however, *Aspazoma amplexans* dominates the vegetation but *Cephalophyllum regale* (SG AZ) is presented with very high constancy.

Total cover and species richness: The total cover of the vegetation (median = 9 %) is in line with the average of quartz-field vegetation and despite the high number of species that are recorded for the entire community, the average number of species per relevés (median = 10) corresponds with most of the non-saline quartz fields of the Namaqualand *sensu lato*

Structural composition: The vegetation is dominated by low-growing growth forms, fruticose, erect micro-chamaephytes and compact nano-chamaephytes. Mega-chamaephytes are of minor importance.

Locality and habitat: Compared to other quartz-field communities of the Richtersveld, the community is wide spread. It covers the area from the mountainous Richtersveld in the north to the central Namaqualand in the south. The community is found on gentle do deep slopes which are typically moderately covered with medium-sized to coarse quartz debris. The soils are very shallow (median = 14.5 cm) and have a moderate to high stone content (median = 46 %). The soil texture comprises silty to loamy sand. The soil pH is slightly acid to slightly alkaline (median = 6.8 pH) and the salinity is typically low (0.7 mS/cm).

Conservation status: Widespread in the Namaqualand. Not threatened.

49 *Eberlanzia cyathiformis* Community

Floristic composition: *Ruschia cyathiformis* is the dominating species of the community whereas *Leipoldtia laxa*, *Ceraria fruticulosa*, and *Ruschia atrata* are represented with low constancy and low cover values only (SG BC). *Cheiridopsis robusta* and *Euphorbia ephedroides* (SG BCG) as well as

Drosanthemum muiirii Nord (SG BI) also occur with high constancy. The latter frequently inhabits heuweltjies of the northern Knersvlakte (U. Schmiedel, unpubl. data). However, due to the low number of relevés, this community is poorly documented and this description is in a preliminary state still.

Total cover and species richness: The total cover values determined for the sampling relevés are considerably low (6.6 %), however, on well developed heuweltjies the community can reach far higher cover values. Also the species richness varies strongly although the mean values are comparably high (11 spp./relevés).

Structural composition: The community is dominated by leaf-succulent, scrawling mega-chamaephytes whereas erect micro- and mega-chamaephytes are of nominal importance.

Locality and habitats: The *Ruschia cyathiformis*-dominated community is widespread in the northwestern part of Namaqualand, between the central Namaqualand to the mountainous Richtersveld. It is mainly found gentle where it typically covers the heuweltjies but can also occur on more rocky habitats such as upper slopes and as outcrops as well as quartz fields. The soils where it has been recorded for are moderately deep (median = 17 cm), and partly very rich in stone content (40 %). As it is characteristic for heuweltjies, the soil pH is slightly alkaline (7.8 pH) and carbonate has been determined, although with a small percentage. The salinity was generally moderately low.

Conservation status: The community is widespread and very frequent in some areas. Although insufficiently known, it does not seem to be threatened.

Notes: The typical spectrum of habitats inhabited by this community is insufficiently represented in this table.

50 *Schlechteranthus hallii* Community

Floristic composition: The *Schlechteranthus hallii* Community is characterised by the SG BD (*S. hallii*, *Euphorbia gummifera*, *Conophytum gratum*, *Galenia dregeana*) among which *Schlechteranthus hallii* occurs with the highest constancy and highest cover values. Beyond that merely SG BH is well represented but with rather low constancy.

Total cover and species richness: The total cover of the vegetation is extremely low (median = 5.2 %) whereas the specie richness is in line with the other communities (9 spp. / relevé).

Locality and habitat: The community is typically found in the Richtersveld and the northern part of the central Namaqualand. It exclusively colonises quartz outcrops rocky quartz fields on upper slopes or hill tops which are characterised by high stone content (53 %), acid (median = 5.2 pH), non-saline (median = 0.57 mS/cm).

Structural composition: The community is dominated by mega-chamaephytes. Nano-chamaephytes occur with low constancy and low cover values and only.

Conservation status: Restricted to the Richtersveld and the northern part of the central Namaqualand where it occurs on rocky, non-saline quartz fields. Due to its particular ecology and limited distribution vulnerable.

51 *Brownanthus pubescens* Community

Floristic composition: It is characterised by *B. pubescens* and *Euphorbia decussata*. Whereas *E. decussata* is a widespread and more eurytopic species (which might also be due to the very broad species concept), *B. pubescens* presents the diagnostic species. *Ruschia inconspicua* merely occurs in one sub-community. Other accompanying species occur with low constancy.

Based on the occurrence of *R. inconspicua* and *Hypertelis salsoloides*, two sub-communities are recognised:

51.1 *B. pubescens*-dominated Community

51.2 *B. pubescens*-*Ruschia inconspicua* Community

Total cover values and species richness: Cover values (7.5 % and 5.1 %) as well as species richness (5.5 and 4 spp. / relevés) are similarly low for both sub-communities.

Structural composition: The community is dominated by erect leaf-succulent micro-chamaephytes of which the percentage of stem-succulents varies between the sub-communities. Nano-chamaephytes and other growth forms are of minor importance.

Locality and habitat: The *Brownanthus pubescens* Community is typically found in the southwestern Richtersveld on gentle slopes with or without quartz cover. The soils are moderately shallow (median = 20 cm) and rich in silt content. The alkaline soils (> 7 pH) have a moderate to very high salt content but typically lack carbonate.

Conservation status: Not sufficiently known.

51.1 *Brownanthus pubescens*-dominated Sub-Community

Floristic composition: The sub-community is characterised by the significant dominance of *Brownanthus pubescens* and the absence of *Ruschia inconspicua*. and *Hypertelis salsoloides* whereas other species are rare and occur with very low cover values only.

Total cover and species richness: The total cover (7.5 %) and species richness (5.5 spp./relevé) of the vegetation is typically very low.

Structural composition: In contrast to the second sub-community, stem-succulent micro-chamaephytes with deciduous succulent leaves dominate.

Locality and habitat: With respect of habitat conditions this sub-community differ very little from the second, however, the electrical conductivity is generally lower (median = 0.24 mS/cm).

Conservation status: Not sufficiently known.

51.1 *Brownanthus pubescens*-*Ruschia inconspicua*-Sub-Community

Floristic composition: The sub-community differs from the first by the occurrence of the *Ruschia inconspicua* (SP BE) and *Hypertelis salsoloides* (SG BI).

Total cover values and species richness: The total cover varies between moderately high (max 18.7 %) and very low (median = 5.1 %) and the numbers of species per relevé are generally very low (median = 4 spp.).

Structural composition: The sub-community is dominated either by stem-succulent micro-chamaephytes or micro-chamaephytes without succulent stems but perennial, succulent leaves.

Locality and habitat: In contrast to the first sub-community, the electrical conductivity is typically higher (median = 2 mS/cm).

Conservation status: Not sufficiently known.

52 *Brownanthus pseudoschlichtianus* Community

Floristic composition: *Brownanthus pseudoschlichtianus* and *Prenia tetragona* present the diagnostic species of the community among which the first strongly dominates the vegetation. The generally species poor community comprises very few accompanying species which all occur with very low constancy only. Merely *Eberlanzia cyathiformis* and *Cheiridopsis robusta* reach constancy class II.

Total cover and species richness: The community reaches moderately high cover values at some places ($> 18\%$). However, the median value is comparatively low (median = 10.8 %). The species richness is typically very low (median = 3.5 spp./ relevé).

Structural composition: The community is dominated by stem-succulent mega-chamaephytes with deciduous, succulent leaves.

Locality and habitat: The community covers the broad, level plains in the southern and mountainous Richtersveld almost completely and not found on quartz fields. The soils are moderately deep (median = 20 cm) and characterised by silty or loamy sand and a moderate stone content. The soil pH is high (median = 7.88 pH) which is also due to the frequent occurrence of carbonate.

Conservation status: The community is very widespread and covers broad areas lowlands of the southern Richtersveld. However, due to the strong grazing pressure on the plains and subsequent overgrazing and soil erosion, the community is potentially threatened, depending on future land-use practices.

IX.1.6 Communities of the Bushmanland-Warmbad area

1 *Zygophyllum decumbens* Community

Floristic composition: The community is defined by the exclusive occurrence of *Zygophyllum decumbens*. It is also the dominating species of the monodominant community. Other species occur with very low constancy and very low cover values.

Total cover and species richness: The total cover values of the community are low (median = 7 %) and the number of species per relevé was always far below 10 (median = 4 spp. / relevé).

Structural composition: The community was characterised by the occurrence of fruticose, leaf-succulent micro-chamaephytes. Nano-chamaephytes occur with very low cover values and low constancy only.

Locality and habitat: The community was recorded for the Warmbad area where it occurs on quartz slopes or hill tops. The typically shallow soils (median = 8.5 cm) of loamy or silty sand are rich in stone content (median = 70 %). The soils have a slightly alkaline pH (7.8 pH) and may have carbonate content. The salt content is always very low (< 0.1 mS/cm).

2 *Lithops julii* Community

Floristic composition: The *Lithops julii* Community only comprises *L. julii* as diagnostic species, which occurs with very low cover values, though. Its status as a vegetation community seems to be questionable. However, *Lithops julii* never reach high cover values (neither do hardly any other *Lithops* species) and exclusively inhabits certain habitats where it forms nearly-monotypic stands.

Total cover and species richness: The total cover values of the community is typically very low (median < 1 %). Also the species numbers per relevé are low (median = 2).

Structural composition: The community is dominated by nano-chamaephytes, micro- and mega-chamaephytes occur with low constancy only.

Locality and habitat: The community occurs on level plains in the vicinity of Warmbad. The soils are shallow, rich in stone content and consist of silty or loamy sand which are often covered with small to medium sized quartz debris. The soil pH is about neutral (pH 7) and the salinity in soil very low (< 1 mS/cm).

3 *Oropetium capensis* Community

Floristic composition: The community is defined by the short-leaved Poaceae species *Oropetium capense* and other species of Species Group D (*Tripteris sinuata* var. *sinuata*, *Tetragonia reduplicata*, *Anacampseros papyracea* ssp. *namaensis*, *Dinteranthus wilmotianus* ssp. *impunctatus*) which occur with very low cover values and constancy only.

The community comprises 4 sub-communities

- 3.1 *Oropetium capense*-*Ruschia odontocalyx* Sub-Community
- 3.2 *Oropetium capense*-*Lithops julii* Sub-Community
- 3.3 *Oropetium capense*-*Galenia fruticosa* Sub-Community
- 3.4 *Oropetium capense* species poor Sub-Community

The sub-communities differ regarding presence or absence of species group E and H which comprise some obligate quartz-field taxa but several widespread shrubs of the Nama Karoo biome.

3.1 *Oropetium capense*-*Ruschia odontocalyx* Sub-Community

Floristic composition: The sub-community is largely dominated by *Ruschia odontocalyx* which is accompanied by numerous species of Species Group D, E, and F. Merely *Oropetium capense* and *R. odontocalyx*, however, occur with high constancy and reach high cover values.

Total cover and species richness: The total cover values are moderately high (median = 9.3 %). The species richness ranges between 3 and 12 species per relevé (median = 8) and is thus high compared to most of the other quartz-field communities and sub-communities of the area.

Structural composition: The sub-community is dominated by the mega-chamaephyteous *R. odontocalyx* which is leaf- and stem-succulent and by small, tufted grass. The species richness of the community results in a comparatively heterogeneous structural composition which comprises also non- or semi-succulent mega-chamaephytes but also several nano-chamaephytes.

Locality and habitat: On low and strongly weathered quartz outcrops or gently sloped quartz patches of the Warmbad area. The soils are slightly deeper than for most of the other quartz-field

communities of the area (15 cm) and moderately rich in stone content (40 % in weight). The loamy sand is slightly alkaline (pH 7.6) and has very low salt content (0.03 mS/cm).

3.2 *Oropetium capense*-*Lithops julii* Sub-Community

Floristic composition: The sub-community is characterised and largely dominated by *Oropetium capense* and *Lithops julii* as a differential species. The latter occurs with low constancy only. The species of the species groups E and F occur with higher constancy than they do in the other sub-communities of the *Oropetium capense* Community.

Total cover and species richness: The total cover values are high for most sites which is mainly due to the high cover values of *O. capense*. The number of species per relevés is high (8 spp. / relevé) compared to other quartz-field communities or sub-communities of the area.

Structural composition: The community is dominated by short tufts of grass but also comprises several chamaephyteous growth forms (nano- to mega-chamaephytes) which all occur with low cover values only.

Locality and habitat: The level quartz fields of the Warmbad area with low to moderate soil depth (12.5 cm) present the typical habitat. The stone content of the loamy sandy soil is typically high (60 % in weight). The soil pH is neutral to slightly alkaline (median = 7.1 pH) and the salinity very low (0.03 mS/cm).

3.3 *Oropetium capense*-*Galenia fruticosa* Sub-Community

Floristic composition: The *Oropetium capense*-*Galenia fruticosa* Sub-Community is poorer in species than the previous sub-communities of the *Oropetium capense* Community. *O. capense* is the dominating species and is accompanied with high constancy only by *Galenia fruticosa* (SG J). The latter species, however, has a very broad distribution and is found at several communities within the area. Other accompanying species are rare.

Total cover and species richness: The total cover of the sub-community is relatively high (11.7 %) but the number of species per relevé (5.5) comparatively low.

Structural composition: The dominating growth forms are small tufted grass and semi-succulent, fruticose mega-chamaephytes. Other growth-form types occur with very low cover values.

Locality and habitat: On quartz outcrops or quartz hillocks of the Warmbad and the Pofadder area. It inhabits shallow soils (10 cm) with moderate stone content. The soil texture is loamy sand. The soil pH is slightly alkaline and the soils are poor in salt content (0.1 mS/cm) and no carbonate was determined.

3.4 *Oropetium capense* species poor Sub-Community

Floristic composition: The species poor sub-community is dominated by *Oropetium capense* (SG D). Other species of species group D only occur with very low constancy and low cover values. *Conophytum preasectum* and *Trachyandra* spec. (7382) (Species group H) which were recorded for this sub-community occur with very low constancy though. Species of the species group E and F which are characteristic for the other sub-communities are absent here.

Total cover and species richness: The sub-community has moderately low cover values (7.5 %) and is poor in number of species (median = 3.5 species per relevé).

Structural composition: The sub-community consist of short, tufted grass and very few nano-chamaephytes and mega-chamaephytes. Succulents are scarce.

Locality and habitat: The sub-communities is found on gentle hillocks or level plains with dense cover of small to medium sized quartz debris. The soil consists of loamy sand and is moderately skeletal (45 % in weight). The soil pH is slightly alkaline (7.36 pH) and low in salt content (0.03 mS/cm).

4 *Drosanthemum* spec. (Schmiedel 102344 HBG) Community

Floristic composition: The community is clearly defined by the occurrence of *Drosanthemum* sp. (Schmiedel 102344 HBG), *Ruschia muricata*, and *Ruschia* sp. (Schmiedel 102350 HBG) which form species group J. *Drosanthemum diversifolium* and *Ruschia muricata* are clearly dominating whereas *R. sp.* occurs with low cover values only. *Anacampseros albissima* (SG J) which is largely ubiquitously found in all quartz-field communities of the Bushmanland-Warmbad area was recorded for this community with very high constancy.

Total cover and species richness: The total cover values are moderately high (median = 11.5 %). The species richness is low (5 spp. / relevés) for the community.

Structural composition: The community is dominated by fruticose, leaf-succulent micro-chamaephytes.

Locality and habitat: The community has only be recorded for the western Bushmanland (east of Springbok) where it occurs on level quartz fields with high stone content in soil (60 % in weight). The soil texture is silty sand. The soil pH is slightly acid (median 6.8 pH) and the salinity in soil is below that of other quartz-field of this area (0.28 mS/cm).

Notes: The diagnostic species of the community, *D. sp.* (Schmiedel 102344 HBG), seems to be closely related to *Drosanthemum hispidum* L. (Schwantes) which is widespread in the Succulent Karoo (compare Community # 21 in the Knersvlakte)

IX.2 Tables and figures

Appendix 3. Species names, family and Raunkiaer's growth form of the species in the phytosociological table (Phytosociological Table I) of the relevés from the Little Karoo and adjacent area.

Species names	Family	Growth form (Raunkiaer)
Adromischus filicaulis (Eckl. & Zeyh.) C.A.Sm. ssp. marlothii (Schoenl.) Toelken	Crassulaceae	NaCh
Adromischus triflorus (L.f.) A.Berger	Crassulaceae	NaCh
Anacampseros papyracea (E.Mey. ex Fenzl) G.D.Rowley ssp. papyracea	Portulacaceae	NaCh
Antegibbaeum fissoides (Haw.) Schwantes ex C.Weber	Aizoaceae (Mesembryanthema)	NaCh
Aridaria noctiflora (L.) Schwantes ssp. defoliata (Haw.) Gerbaulet	Aizoaceae (Mesembryanthema)	MeCh
Asparagus recurvispinus (Oberm.) Fellingham & N.L.Mey.	Asparagaceae	MeCh
Asteraceae Gen. spec. 109859	Asteraceae	MeCh
Atriplex lindleyi Moq. ssp. inflata (F.Muell.) Paul G.Wilson	Chenopodiaceae	T
Augea capensis Thunb.	Zygophyllaceae	T
Berkheya cuneata (Thunb.) Willd.	Asteraceae	MeCh
Berkheya spinosa (L.f.) Druce	Asteraceae	MeCh
Blepharis inermis (Nees) C.B.Clarke	Acanthaceae	MiCh
Chrysocoma ciliata L.	Asteraceae	MeCh
Conophytum joubertii Lavis	Aizoaceae (Mesembryanthema)	NaCh
Crassula capitella Thunb. ssp. thyrsoflora (Thunb.) Toelken	Crassulaceae	NaCh
Crassula columnaris Thunb. ssp. columnaris	Crassulaceae	NaCh
Crassula congesta N.E.Br.	Crassulaceae	NaCh
Crassula deltoidea Thunb.	Crassulaceae	NaCh
Crassula pyramidalis Thunb.	Crassulaceae	MiCh
Crassula subaphylla (Eckl. & Zeyh.) Harv. var. subaphylla	Crassulaceae	MiCh
Crassula tecta Thunb.	Crassulaceae	NaCh
Crassula tetragona L. ssp. acutifolia (Lam.) Toelken	Crassulaceae	NaCh
Delosperma asperulum (Salm-Dyck) L.Bolus	Aizoaceae (Mesembryanthema)	MiCh
Dicoma rehmanioides Less.	Asteraceae	MiCh
Drosanthemum crassum L.Bolus	Aizoaceae (Mesembryanthema)	MeCh
Drosanthemum delicatulum (L.Bolus) Schwantes	Aizoaceae (Mesembryanthema)	MiCh
Drosanthemum duplessiae L.Bolus	Aizoaceae (Mesembryanthema)	MiCh
Drosanthemum giffenii (L.Bolus) Schwantes	Aizoaceae (Mesembryanthema)	MiCh
Drosanthemum montaguense L.Bolus	Aizoaceae (Mesembryanthema)	MeCh
Drosanthemum roridum L.Bolus (cf.)	Aizoaceae (Mesembryanthema)	MeCh
Elytropappus rhinocerotis (L.f.) Less.	Asteraceae	NP
Eriocephalus ericoides (L.f.) Druce	Asteraceae	MeCh
Euphorbia decussata E.Mey. ex Boiss.	Euphorbiaceae	MeCh
Felicia fascicularis DC.	Asteraceae	MiCh
Felicia filifolia (Vent.) Burt Davy	Asteraceae	MeCh
Gazania krebsiana Less.	Asteraceae	NaCh
Gazania lichtensteinii Less.	Asteraceae	T
Gibbaeum album N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum angulipes (L.Bolus) N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum cryptopodium (Kensit) L.Bolus	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum dispar N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum geminum N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum gibbosum (Haw.) N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum haagei Schwantes	Aizoaceae (Mesembryanthema)	NaCh

Gibbaeum heathii (N.E.Br.) L. Bolus	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum hortenseae (N.E.Br.) Thiede & Klak	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum pachypodium (Kensit) L.Bolus	Aizoaceae (Mesembryanthema)	MiCh
Gibbaeum petrense (N.E.Br.) Tischer	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum pubescens (Haw.) N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum shandii N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Gibbaeum velutinum (L.Bolus) Schwantes	Aizoaceae (Mesembryanthema)	NaCh
Glottiphyllum neilii N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Glottiphyllum salmii (Haw.) N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Haworthia aspera Haw.	Asphodelaceae	NaCh
Haworthia viscosa (L.) Haw.	Asphodelaceae	NaCh
Hereroa sp. 110134	Aizoaceae (Mesembryanthema)	NaCh
Hereroa tenuifolia L.Bolus	Aizoaceae (Mesembryanthema)	MiCh
Lycium cinereum Thunb. <i>sensu lato</i>	Solanaceae	NP
Malephora lutea (Haw.) Schwantes	Aizoaceae (Mesembryanthema)	MiCh
Mesembryanthemum longistylum DC.	Aizoaceae (Mesembryanthema)	MeCh
Mesembryanthemum subtruncatum L. Bolus	Aizoaceae (Mesembryanthema)	T
Octopoma octojuge (L.Bolus) N.E.Br.	Aizoaceae (Mesembryanthema)	MiCh
Octopoma quadrisepalum (L.Bolus) H.E.K.Hartmann	Aizoaceae (Mesembryanthema)	MiCh
Osteospermum microphyllum DC.	Asteraceae	MeCh
Othonna carnosus Less.	Asteraceae	NaCh
Pentaschistis eriostoma (Nees) Stapf	Poaceae	MeCh
Pentzia incana (Thunb.) Kuntze	Asteraceae	MeCh
Phyllobolus nitidus (Haw.) Gerbaulet	Aizoaceae (Mesembryanthema)	MeCh
Phyllobolus splendens (L.) Gerbaulet ssp. splendens	Aizoaceae (Mesembryanthema)	MeCh
Plumbago tristis Aiton	Plumbaginaceae	MiCh
Polygala empetrifolia Hoult.	Polygalaceae	MeCh
Prekia tetragona (Thunb.) Gerbaulet	Aizoaceae (Mesembryanthema)	MeCh
Psilocaulon articulatum (Thunb.) Schwantes	Aizoaceae (Mesembryanthema)	MiCh
Psilocaulon junceum (Haw.) Schwantes	Aizoaceae (Mesembryanthema)	MeCh
Pteronia empetrifolia DC.	Asteraceae	MeCh
Pteronia flexicaulis L.f.	Asteraceae	MeCh
Pteronia glomerata L.f.	Asteraceae	MeCh
Pteronia pallens L.f.	Asteraceae	MeCh
Pteronia succulenta Thunb.	Asteraceae	MeCh
Pteronia viscosa Thunb.	Asteraceae	MeCh
Rhinephyllum muirii N.E.Br.	Aizoaceae (Mesembryanthema)	NaCh
Rosenia humilis (Less.) K.Bremer	Asteraceae	MeCh
Ruschia cradockensis (Kuntze) H.E.K.Hartmann & Stueber ssp. triticiformis (L.Bolus) H.E.K.Hartmann & Stueber	Aizoaceae (Mesembryanthema)	MeCh
Ruschia cradockensis (Kuntze) H.E.K.Hartmann & Stueber ssp. cradockensis	Aizoaceae (Mesembryanthema)	MeCh
Ruschia inclusa L.Bolus	Aizoaceae (Mesembryanthema)	MiCh
Salsola sp. 102066	Chenopodiaceae	MiCh
Salsola sp. 104699	Chenopodiaceae	MeCh
Salsola sp. 104753	Chenopodiaceae	MeCh
Salsola sp. 110026	Chenopodiaceae	MeCh
Salsola sp. 7302	Chenopodiaceae	MeCh
Salsola tuberculata (Moq.) Fenzl	Chenopodiaceae	MeCh
Sceletium tortuosum (L.) N.E.Br.	Aizoaceae (Mesembryanthema)	MiCh
Senecio radicans (L.f.) Sch.Bip.	Asteraceae	NaCh
Tetragonia robusta (Kunth) C.B. Clarke	Aizoaceae	MeCh
Trichodiadema densum (Haw.) Schwantes	Aizoaceae (Mesembryanthema)	NaCh
Tripteris sinuata DC. var. linearis (Harv.) B.Nord.	Asteraceae	MeCh
Zeuktrophyllum calycinum (L.Bolus) H.E.K. Hartmann	Aizoaceae (Mesembryanthema)	MiCh
Zeuktrophyllum suppositum (L.Bolus) N.E.Br.	Aizoaceae (Mesembryanthema)	MiCh
Zygophyllum retrofractum Thunb.	Zygophyllaceae	MeCh

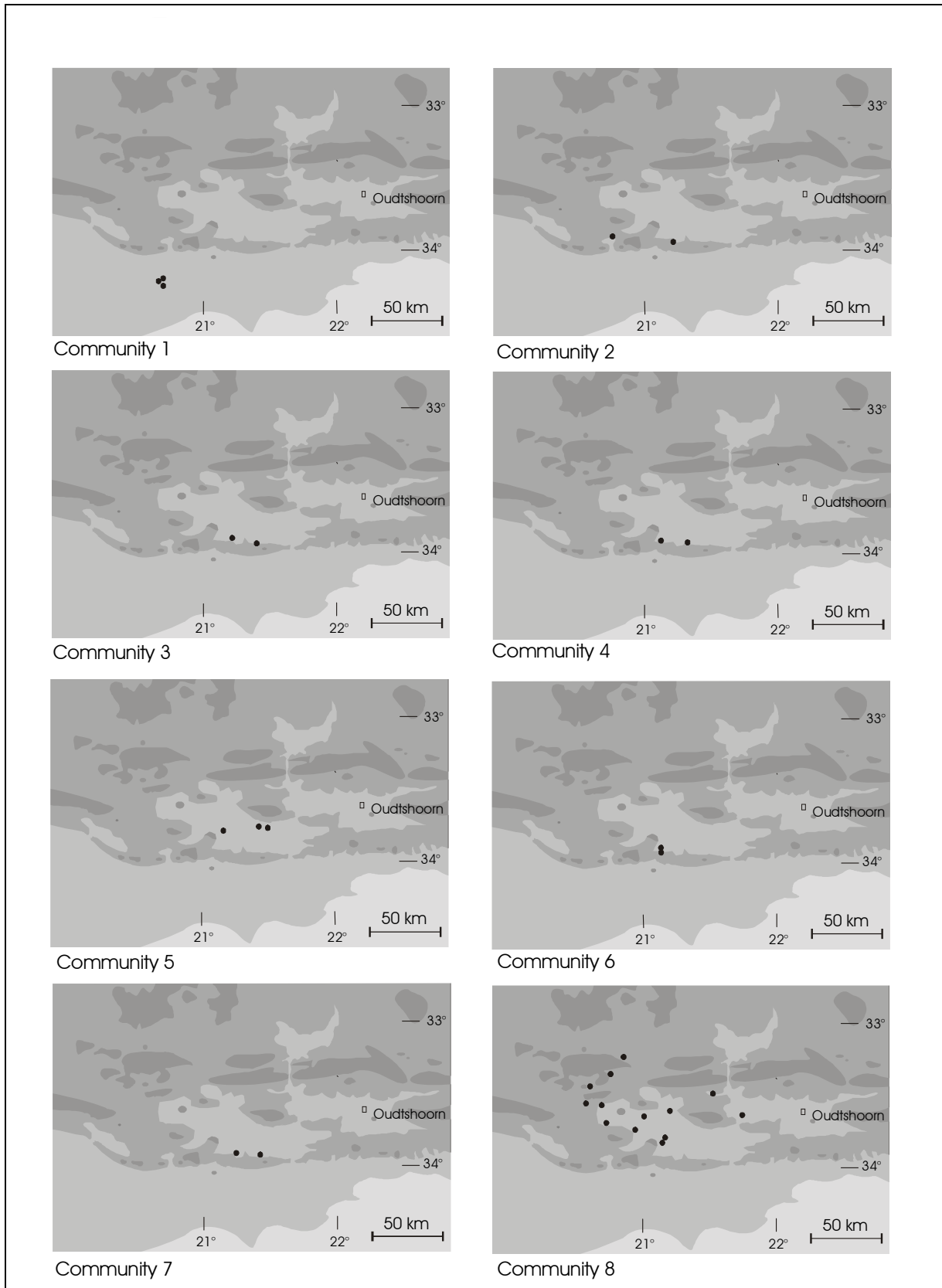
non-diagnostic species

Aizoon sp. 110043	Aizoaceae
Albuca longifolia Baker	Hyacinthaceae
Albuca sp. 9182	Hyacinthaceae
Aloe variegata L.	Asphodelaceae
Antimima fergusoniae (L.Bolus) H.E.K.Hartmann	Aizoaceae (Mesembryanthema)
Antimima sp. 104745	Aizoaceae (Mesembryanthema)
Antimima wittebergensis (L.Bolus) H.E.K.Hartmann	Aizoaceae (Mesembryanthema)
Asparagus capensis L. var. capensis	Asparagaceae
Asparagus species	Asparagaceae
Atriplex semibaccata R. Br.	Chenopodiaceae
Braunsia geminata (Haw.) L.Bolus	Aizoaceae (Mesembryanthema)
Brownanthus ciliatus (Aiton) Schwantes	Aizoaceae (Mesembryanthema)
Bulbine succulenta Compton	Asphodelaceae
Cephalophyllum subulatoides (Haw.) N.E.Br.	Aizoaceae (Mesembryanthema)
Conophytum minimum (Haw.) N.E.Br.	Aizoaceae (Mesembryanthema)
Crassula congesta N.E.Br.	Crassulaceae
Crassula cotyledonis Thunb.	Crassulaceae
Crassula muscosa L. var. muscosa	Crassulaceae
Crassula muscosa L. var. obtusifolia (Harv.) G.D.Rowley	Crassulaceae
Crassula nudicaulis L. var. nudicaulis	Crassulaceae
Crassula nudicaulis L. var. platyphylla (Harv.) Toelken	Crassulaceae
Crassula rupestris Thunb.	Crassulaceae
Crassula subaphylla (Eckl. & Zeyh.) Harv. var. virgata (Harv.) Toelken	Crassulaceae
Crassula tomentosa Thunb.	Crassulaceae
Cylindrophyllum sp.102162	Aizoaceae (Mesembryanthema)
Drosanthemum archeri L.Bolus	Aizoaceae (Mesembryanthema)
Eriocephalus grandiflorus M.A.N. Mueller	Asteraceae
Euphorbia juglans Compton	Euphorbiaceae
Euphorbia pillansii N.E.Br.	Euphorbiaceae
Euphorbia susannae Marloth	Euphorbiaceae
Euryops subcarnosus DC. ssp. subcarnosus	Asteraceae
Fabaceae sp. 110034	Fabaceae
Felicia cana DC.	Asteraceae
Felicia fascicularis DC.	Asteraceae
Galenia africana L	Aizoaceae
Galenia fruticosa (L.f.) Sonder.	Aizoaceae
Galenia papulosa (Eckl. & Zeyh.) Sonder.	Aizoaceae
Geophyte 104793	
Gibbaeum nebrownii Tischer	Aizoaceae (Mesembryanthema)
Glottiphyllum depressum (Haw.) N.E.Br.	Aizoaceae (Mesembryanthema)
Glottiphyllum fergusoniae L.Bolus	Aizoaceae (Mesembryanthema)
Glottiphyllum regium N.E.Br.	Aizoaceae (Mesembryanthema)
Gnidia deserticola Gilg	Thymelaeaceae
Helichrysum asperum (Thunb.) Hilliard & B.L.Burt var. asperum	Asteraceae
Hermannia cuneifolia Jaqc.	Sterculiaceae
Hermannia filifolia L.f.	Sterculiaceae
Hirpicium alienatum (Thunb.) Druce	Asteraceae
Hirpicium integrifolium (Thunb.) Less.	Asteraceae
Hyobanche glabrata Hiern	Scophulariaceae
Lachenalia sp. 5135	Hyacinthaceae
Leipoldtia schultzei (Schltr. & Diels) Friedrich	Aizoaceae (Mesembryanthema)
Limonium dregeanum (C.Presl) Kuntze	Plumbaginaceae
Limonium scabrum (Thunb.) Kuntze	Plumbaginaceae
Malephora flavo-crocea (Haw.) Jacobsen & Schwantes	Aizoaceae (Mesembryanthema)
Malephora sp. 109847	Aizoaceae (Mesembryanthema)

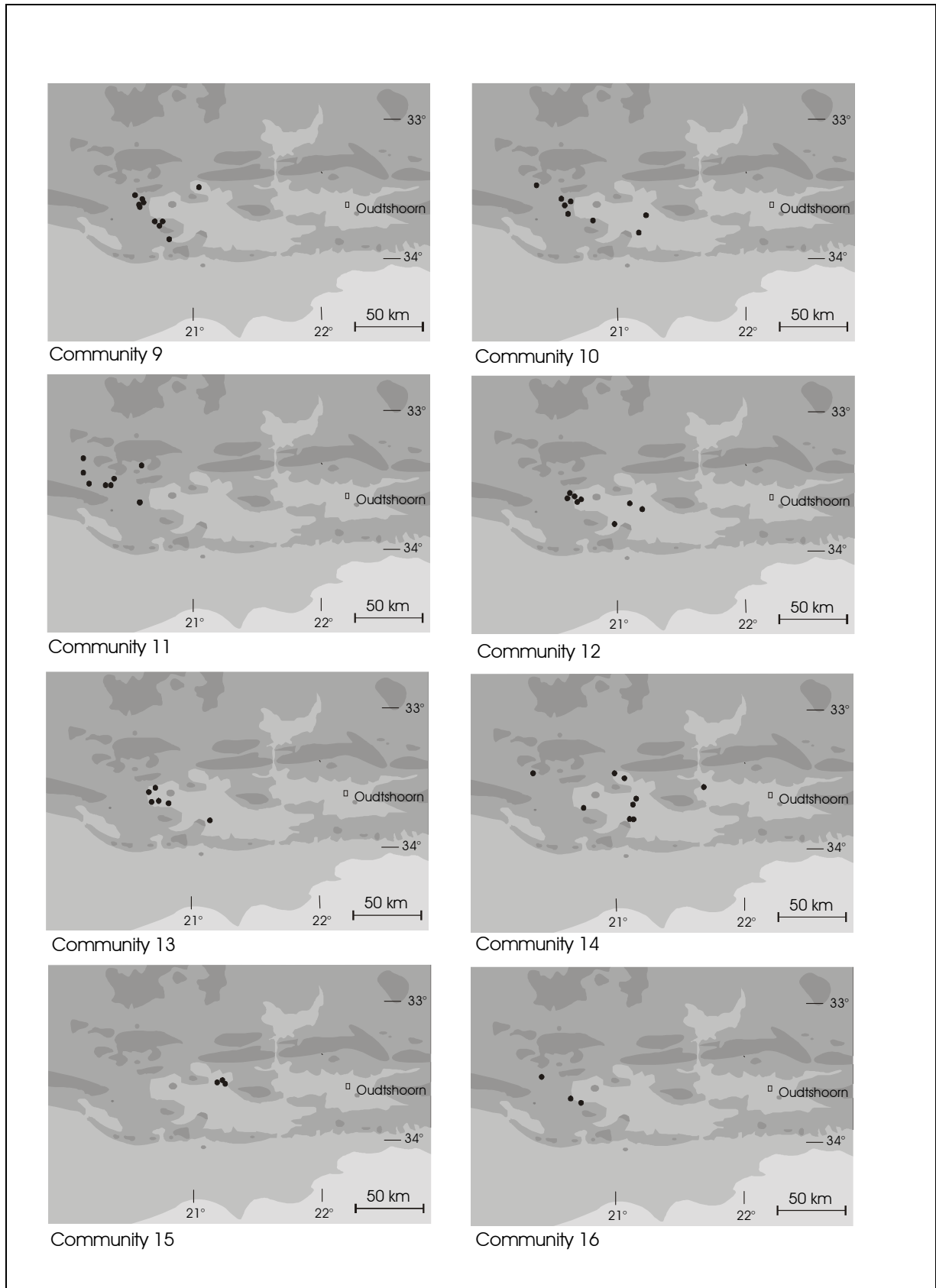
Mesembryanthemum guerichianum Pax	Aizoaceae (Mesembryanthema)
Oedera squarrosa (L.) Anderb. & K.Bremer	Asteraceae
Ornithogalum thyrsoides Jacq.	Hyacinthaceae
Osteospermum polygaloides L.	Asteraceae
Othonna alba Compton	Asteraceae
Othonna protecta Dinter	Asteraceae
Othonna quercifolia DC.	Asteraceae
Oxalis species	Oxalidaceae
Pelargonium sp. 5699	Geraniaceae
Pteronia glauca Thunb.	Asteraceae
Pteronia incana (Burm.) DC.	Asteraceae
Pteronia membranacea L.f.	Asteraceae
Pteronia oblanceolata E.Phillips	Asteraceae
Pteronia staehelinoides DC.	Asteraceae
Pteronia sp. 110033	Asteraceae
Ruschia cymosa (L.Bolus) Schwantes	Aizoaceae (Mesembryanthema)
Ruschia impressa L.Bolus	Aizoaceae (Mesembryanthema)
Ruschia leucosperma L.Bolus	Aizoaceae (Mesembryanthema)
Ruschia spinosa (L.) Dehn	Aizoaceae (Mesembryanthema)
Salsola sp. 7326	Chenopodiaceae
Salsola sp. 9174	Chenopodiaceae
Sarcocaulon salmoniflorum Moffett	Geraniaceae
Selago sp. 104748	Selaginaceae
Senecio sulcicalyx	Asteraceae
Stomatium sp. 104797	Aizoaceae (Mesembryanthema)
Trichodiadema setuliferum (N.E.Br.) Schwantes	Aizoaceae (Mesembryanthema)
Trichodiadema attonsum (L.Bolus) Schwantes	Aizoaceae (Mesembryanthema)
Trichodiadema sp. 5148	Aizoaceae (Mesembryanthema)
Triptaris sinuata DC. var. sinuata	Asteraceae
Triptaris tomentosa (L.f.) Less.	Asteraceae
Tylecodon paniculatus (L.f.) Toelken	Crassulaceae
Tylecodon wallichii (Harv.) Toelken	Crassulaceae
Zygophyllum divaricatum Eckl. & Zeyh.	Zygophyllaceae
Zygophyllum flexuosum Eckl. & Zeyh.	Zygophyllaceae

Crassula congesta	III	.	
S																		
Psilocalon junceum	II	.	.	+	r	II	II	.	I	.	.	V	
Drosanthemum duplessiae	III	
Phyllobolus nitidus	I	III	
T																		
Pteronia pallens	II	III	II	.	III	III	V	III	III	IV	III	II	II	
Malephora lutea	III	IV	II	.	II	II	III	I	II	II	II	.	III	
Tetragonia robusta	.	.	I	.	II	II	II	.	II	III	II	II	II	III	II	II	II	
Tripteris sinuata var. linearis	II	II	.	.	+	I	.	I	III	I	III	.	II	
Lycium cinereum	.	.	I	.	.	II	.	.	+	IV	.	I	II	+	.	.	II	
Ruschia inclusa	r	I	I	II	II	.	.	III	
Prenia tetragona	II	II	.	.	r	.	.	.	+	+	.	II	
Crassula subaphylla var. subaphylla	I	.	.	+	r	II	+	.	.	+	.	II	
Ruschia cradockensis ssp. cradockensis	II	.	.	+	.	.	II	
Drosanthemum crassum	r	II	II	
Augea capensis	II	.	.	.	II	
Drosanthemum roridum	+	II	
Mesembryanthemum subtruncatum	+	.	II
U																		
Anacampseros papyracea ssp. papyracea	II	IV	.	.	I	+	I	.	.	+	I	.	.	
Crassula columnaris ssp. columnaris	.	.	II	I	II	II	.	.	II	I	.	II	I	+	+	.	.	
Salsola sp. 102066	.	.	.	I	.	I	II	.	I	II	III	+	I	II	I	.	.	
Psilocalon articulatum	.	.	.	II	II	IV	III	.	II	II	I	+	IV	II	II	II	.	
Chrysocoma ciliata	.	.	II	II	II	IV	.	.	I	II	II	II	.	II	+	.	.	
Atriplex lindleyi ssp. inflata	.	.	.	II	.	.	II	.	I	r	.	.	II	+	+	II	.	
Pteronia succulenta	.	.	.	II	.	I	IV	.	III	III	I	II	II	+	II	II	.	
Crassula capitella ssp. thyrsoflora	.	.	.	I	I	.	I	+	.	+	.	.	.	
Salsola sp. 104699	.	.	.	II	+	.	+	.	.	.	II	.	.	
Glottiphyllum neilii	.	.	I	r	+	
Trichodiadema densum	.	.	I	.	.	I	.	.	r	r	
Drosanthemum montaguense	.	.	I	.	.	I	.	.	r	I	+	
Antegibbaeum fissoides	.	.	I	I	I	II	.	.	.	I	I	II	I	.	+	II	.	
Pteronia flexicaulis	.	.	III	.	I	.	II	.	+	.	.	+	.	.	.	III	.	
Berkheya cuneata	.	.	II	I	.	.	I	.	r	II	I	+	I	+	.	III	.	
Adromischus triflorus	.	.	I	.	.	II	.	.	r	I	I	.	.	.	+	II	.	
Polygala empetrifolia	.	.	I	.	.	I	II	
Elytropappus rhinocerotis	.	.	II	II	+	

Appendix 5. Phytosociological Table I: Vegetation of the Little Karoo and adjacent areas - see separate folder.



Appendix 6. Distribution of Community # 1-8 of the vegetation of quartz fields and related habitats of the Little Karoo and adjacent areas.



Appendix 7. Distribution of Community # 9-16 of the vegetation of quartz fields and related habitats of the Little Karoo and adjacent areas

Appendix 8. Header data of the Phytosociological Table I: Vegetation of the Little Karoo and adjacent areas

Relieve Nr	Community	Sub-Community	Grid	Latitude [Deg.Min]	Longitude [Deg.Min]	Aspect [degrees]	Slope [percentage]	Soil depth [cm]	Stone cover non-quartz [%]	Stone cover quartz [%]	Stone content in soil [% weight]	Soil texture	Soil pH	Electrical conductivity [mS/cm]	Carbonate [HCl test, class 1-5]	Cover values [%]	Number of species [n]
7284.0	1		3420AD	34.18	20.27	23	6	10	5	90	32 -	4.0	1.95	0	38.1	5	
7285.0	1		3420AD	34.18	20.27	315	6	20	0	86	12 -	5.2	3.11	0	19.0	3	
7286.0	1		3420AD	34.17	20.24	180	17	10	0	93	44 -	3.8	0.43	0	16.0	3	
7287.0	1		3420AD	34.17	20.24	270	3	15	0	90	5 U	4.2	2.12	0	12.0	3	
7073.0	2		3321CC	33.54	21.08	45	22	5	20	80	31 Ut2	4.8	0.49	0	4.2	5	
7290.0	2		3320DC	33.55	20.42	180	10	5	99	0	20 -	4.3	0.51	0	6.1	5	
7291.0	2		3320DC	33.55	20.42	90	5	5	99	0	50 SI	5.7	1.65	0	18.3	6	
7324.0	2		3321CC	33.54	21.08	90	8	10	10	60	54 -	6.0	0.34	0	8.7	11	
7326.0	2		3321CC	33.54	21.08	23	4	5	0	83	69 -	5.0	1.55	0	9.0	4	
7074.0	3		3321CC	33.54	21.08	1	10	5	40	60	42 Ut2	3.8	0.71	0	8.0	5	
7075.0	3		3321CC	33.54	21.08	0	0	5	0	30	62 Su4	4.2	0.50	0	12.2	7	
7078.0	3		3321CD	33.54	21.18	1	12	10	0	100	40 Su4	4.1	2.78	0	10.0	1	
7080.0	3		3321CD	33.54	21.18	90	10	10	0	100	1 Su4	3.7	2.25	0	10.3	4	
7081.0	3		3321CD	33.54	21.18	135	8	20	0	100	10 Su4	5.2	3.30	0	12.0	2	
7086.0	3		3321CD	33.54	21.19	1	6	10	70	30	-	-	-	0	8.5	4	
5694.0	4		3321CC	33.53	21.04	1	2	7	5	75	26 -	-	8.59	0	1.4	7	
5695.0	4		3321CC	33.53	21.04	1	4	16	0	81	34.8 Ut2	6.3	1.21	0	0.0	2	
5696.0	4		3321CC	22.53	21.04	1	22	20	0	100	22 Ut2	6.5	4.62	0	2.2	5	
5698.0	4		3321CC	33.53	21.05	225	4	10	4	92	19 Lt	6.6	4.60	0	2.0	1	
7077.0	4		3321CD	33.54	21.18	180	10	20	0	97	20 SI2	5.1	2.58	0	21.2	4	
7079.0	4		3321CD	33.54	21.18	180	6	10	0	95	62 Ut2	6.3	5.46	0	4.2	4	
7082.0	4		3321CD	33.54	21.18	135	4	5	0	98	30 Lts		3.73	0	1.3	4	
7084.0	4		3321CD	33.54	21.18	135	4	5	0	97	10 Ut2	6.7	4.45	0	16.7	7	
7308.0	5		3321CC	33.49	21.07	0	0	5	99	0	71 -	6.8	1.95	0	5.1	4	
7309.0	5		3321CC	33.49	21.07	1	1	5	90	65	42 -	7.4	0.90	0	5.3	6	
7319.0	5		3321CD	33.45	21.23	45	2	5	15	85	25 -	5.2	0.16	0	5.5	9	
7320.0	5		3321CD	33.46	21.28	90	13	5	0	81	80 -	6.2	0.03	0	3.1	4	
5679.0	6		3321CC	33.52	21.05	1	25	10	45	50	55.5 SI3-Lts	5.1	0.47	0	7.4	14	
5681.0	6		3321CC	33.51	21.05	1	11	24	35	35	34.3 Ls-Su3	7.1	0.79	0	7.6	20	
5683.0	6		3321CC	33.52	21.05	45	25	35	52	45	50 fsu2	5.9	1.40	0	3.2	17	
5684.0	6		3321CC	33.52	21.05	45	25	20	45	50	70 Su3	5.9	0.06	0	6.6	21	
5686.0	6		3321CC	33.51	21.06	45	11	15	8	92	43 Su4	6.6	0.35	0	8.8	19	
5687.0	6		3321CC	33.51	21.06	45	25	15	5	95	10 -	4.9	0.67	0	2.6	16	
5688.0	6		3321CC	33.51	21.06	45	17	9	0	100	58 Ut2	5.8	1.76	0	1.7	8	
7071.0	6		3321CC	33.49	21.06	90	14	5	0	0	60 Su4	4.3	0.55	0	6.4	6	
5680.0	7		3321CC	33.52	21.05	1	16	10	10	85	30 Su3	8.1	2.96	0	2.1	4	
5685.0	7		3321CC	33.52	21.06	250	9	10	0	90	37 Su3	7.0	6.02	0	4.3	11	
5697.0	7		3321CC	33.53	21.05	180	11	7	0	96	36 SI3	7.0	5.67	0	30.5	6	
7322.0	7		3321CD	33.54	21.24	1	2	5	0	90	52 -	7.1	3.56	0	8.2	6	

Appendix 8. cont.

Relieve Nr.	Community	Sub-Community	Grid	Latitude [Deg.Min]	Longitude [Deg.Min]	Aspect [degrees]	Slope [percentage]	Soil depth [cm]	Stone cover non-quartz [%]	Stone cover quartz [%]	Stone content in soil [% weight]	Soil texture	Soil pH	Electrical conductivity [mS/cm]	Carbonate [HCl test, class 1-5]	Cover values [%]	Number of species [n]
5087.0	8		3320CB	33.35	20.30	270	11	2	80	40	70 -	8.1	0.62	0	2.2	6	
5094.0	8		3320CB	33.35	20.30	-	0	9	2	80	34 Lt	7.6	6.83	0	5.6	8	
5107.0	8		3320CB	33.35	20.30	158	2	18	45	45	35 Lt	7.9	1.35	3.2	4.0	12	
5648.0	8		3320DA	33.35	20.39	0	0	22	0	0	20 Lts	7.4	0.66	0	3.3	5	
5649.0	8		3320DA	33.35	20.39	0	0	22	0	90	21.5 Lts	7.4	6.04	0	0.0	1	
5650.0	8		3320DA	33.35	20.39	0	0	22	0	30	43 Ltu	7.3	3.07	0	1.6	3	
5652.0	8		3322DA	33.35	20.39	1	1	25	10	80	14 Lt	7.1	3.00	0	27.6	10	
5653.0	8		3322DA	33.35	20.39	1	1	20	5	76	30 Lt	7.2	5.14	0	0.1	3	
5665.0	8		3320DA	33.35	20.39	1	2	32	5	80	42.3 Lts	6.9	5.91	0	1.2	2	
5666.0	8		3320DA	33.35	20.39	1	2	-	5	81	-	-	-	0	7.5	3	
5667.0	8		3320DA	33.35	20.39	1	2	-	5	70	-	-	-	0	13.0	5	
5668.0	8		3320DA	33.35	20.39	1	2	-	15	60	-	-	-	0	8.1	5	
5669.0	8		3322DA	33.35	20.39	1	2	29	5	36	13 Lts	6.4	0.83	0	10.6	5	
5672.0	8		3321BA	33.40	21.09	135	2	30	25	70	80 Lts	7.1	1.81		7.9	13	
5689.0	8		3321CC	33.49	21.05	180	9	20	5	90	24 Su3	6.3	0.55	0	10.0	14	
5699.0	8		3322BC	33.21	20.44	270	6	30	0	90	50 fS	6.5	0.22	0	6.8	22	
5701.0	8		3322BC	33.21	20.44	90	4	17	0	91	10 -	6.8	3.47	0	11.0	13	
5702.0	8		3322BC	33.21	20.44	90	11	35	0	81	10 Ls	7.1	0.97	2	5.6	15	
5703.0	8		3322BC	33.21	20.44	1	5	20	10	82	10 Su2	7.1	2.16	0	9.3	13	
5704.0	8		3322BC	33.21	20.44	90	11	25	0	90	30 fSu2	6.4	0.19	0	6.1	15	
7068.0	8		3321CC	33.48	21.06	45	10	5	0	80	50 Lts	6.3	4.95	0	4.4	11	
7306.0	8		3320DA	33.42	20.42	0	0	10	20	75	12 -	8.0	1.73	0	3.5	4	
7327.0	8		3320DD	33.47	20.57	180	3	15	88	0	7 Su	8.1	0.25	0	16.5	10	
7329.0	8		3320DD	33.47	20.57	180	1	15	80	15	2 -	8.2	0.39	0	19.4	8	
9154.0	8		3320BD	33.15	20.50	90	1	25	100	0	53 Lts	7.4	1.84	2	6.6	7	
9168.0	8		3321CB	33.38	21.01	180	3	30	80	11	15 Ls	7.7	3.82	0	4.5	5	
9175.0	8		3321DA	33.37	21.43	0	0	10	100	0	18.5 Lst	7.5	4.27	3.3	12.5	9	
9176.0	8		3321DA	33.30	21.30	1	2	5	17	80	27 Lst	7.3	3.11	0	7.4	12	
9185.0	8		2818BD	33.27	20.36	1	1	0	35	30	40 Sl	7.5	1.47	0	3.1	4	
9187.0	8		2818DB	-	-	180	2	25	32	50	10 Su2	8.2	1.57	4	9.8	5	
5064.0	9.1	1	3320CB	33.35	20.30	202	5	14	50	50	75 -	7.6	5.60	0	3.1	4	
5072.0	9.1	1	3320CB	33.35	20.30	315	2	15	0	91	38 Lt	7.4	5.19	0	6.5	11	
5075.0	9.1	1	3320CB	33.35	20.30	180	5	24	0	90	16 Lt	8.0	7.78	0	7.4	8	
5077.0	9.1	1	3320DA	33.40	20.35	0	4	26	0	95	60 Lt	7.4	2.55	1	14.7	13	
5079.0	9.1	1	3320DA	33.40	20.35	0	4	15	0	90	73 Lt	7.1	0.00	0	11.1	18	
5084.0	9.1	1	3320DA	33.40	20.35	-	0	15	0	90	66 Lt	8.5	5.08	0	11.3	7	
5092.0	9.1	1	3320DA	33.40	20.35	-	0	15	0	80	70 Lt	7.2	0.05	0	13.2	8	
5101.0	9.1	1	3320DA	33.40	20.35	180	9	23	0	80	44 Sl	8.0	6.27	2	8.1	11	
5105.0	9.1	1	3320DB	33.43	20.44	0	0	5	10	80	12 -	7.1	3.61	0	10.7	7	
5110.0	9.1	1	3320DA	33.42	20.42	0	0	32	25	40	28 Lt	7.1	4.07	0	4.9	12	
5148.0	9.1	1	3320DA	33.42	20.42	35	5	12	0	96	45 Lt	7.9	2.81	0	9.1	9	
5149.0	9.1	1	3320DA	33.42	20.42	35	5	10	27	71	60 Lt	7.7	6.40	0	6.8	7	
5150.0	9.1	1	3320CB	33.35	20.30	180	8	8	70	80	50 Su	6.8	5.88	0	5.9	10	
5151.0	9.1	1	3320CB	33.35	20.30	270	4	4	20	20	70 Ut	5.4	0.65	0	6.1	7	
5164.0	9.1	1	3320CB	33.35	20.30	0	7	14	65	25	50 Sl	7.7	4.48	1	5.5	9	
7305.0	9.1	1	3320CB	33.35	20.30	-	0	23	0	95	62 Lt	7.5	7.33	0	9.3	8	
7334.0	9.1	1	3320DA	33.42	20.42	0	0	10	20	75	21 -	7.9	1.94	0	7.3	5	
7335.0	9.1	1	3320DB	33.43	20.43	1	2	8	0	92	18 -	7.3	7.60	0	9.3	8	

Appendix 8. cont.

Relieve Nr	Community	Sub-Community	Grid	Latitude [Deg:Min]	Longitude [Deg:Min]	Aspect [degrees]	Slope [percentage]	Soil depth [cm]	Stone cover non-quartz [%]	Stone cover quartz [%]	Stone content in soil [% weight]	Soil texture	Soil pH	Electrical conductivity [mS/cm]	Carbonate [HCl test, class 1-5]	Cover values [%]	Number of species [n]
5065.0	9.2	2	3320DA	33.42	20.42	-	0	26	0	92	32	Lt	7.3	6.23	0	9.0	4
5069.0	9.2	2	3320DA	33.42	20.42	0	4	8	2	98	47	Lt	5.7	2.71	0	9.4	7
5080.0	9.2	2	3320CB	33.35	20.30	330	5	8	5	88	75		7.4	5.08	0	11.0	3
5081.0	9.2	2	3320CB	33.35	20.30	330	0	13	40	50	60	Su	6.7	0.03	0	10.2	20
5082.0	9.2	2	3320CB	33.35	20.30	315	2	3	10	89	60	Sl	7.3	4.91	0	7.0	2
5085.0	9.2	2	3320CB	33.35	20.30	270	7	18	10	60	30	Su	4.7	1.92	0	13.9	7
5088.0	9.2	2	3320CB	33.35	20.30	0	8	14	27	71	75	Lts	7.4	4.95	0	9.2	6
5096.0	9.2	2	3320CB	33.35	20.30	0	2	5	0	85	31	Lt	6.0	1.28	0	2.6	7
5097.0	9.2	2	3320CB	33.35	20.30	0	2	8	0	80	80	Sl	6.2	2.77	0	12.1	16
5102.0	9.2	2	3320CB	33.35	20.30	-	0	14	1	90	19	-	7.2	3.51	0	5.3	6
5108.0	9.2	2	3320CB	33.35	20.30	160	4	12	5	91	50	Lt	7.3	2.93	0	5.3	12
5119.0	9.2	2	3320DA	33.40	20.35	340	1	14	0	90	54	Lt	7.4	7.59	0	4.0	4
5120.0	9.2	2	3320DA	33.40	20.35	340	5	7	0	80	44	Ul	6.1	1.47	0	9.8	12
5123.0	9.2	2	3320DA	33.40	20.35	-	0	14	20	80	42	Su4	4.2	0.09	0	4.7	14
5125.0	9.2	2	3320DA	33.40	20.35	315	2	13	50	40	64	Su4-Ul	4.6	0.14	0	10.7	11
5126.0	9.2	2	3320DA	33.40	20.35	-	0	2	70	10	44	Ul	4.4	1.14	0	3.2	10
5127.0	9.2	2	3320DA	33.4	20.35	260	11	5	20	40	80	Su4	7.2	0.30	0	5.5	12
5128.0	9.2	2	3320DA	33.40	20.35	280	5	13	0	15	27	Ul	7.1	0.42	0	6.8	8
5132.0	9.2	2	3320DA	33.40	20.35	120	13	6	50	4	31	Su	6.9	1.19	0	3.9	11
5134.0	9.2	2	3320DA	33.40	20.35	230	29	14	50	53	65	Su	7.1	0.88	0	8.5	17
5135.0	9.2	2	3320DA	33.40	20.35	220	13	8	80	3	33	Su	5.9	1.20	0	5.7	19
5136.0	9.2	2	3320DA	33.40	20.35	220	13	13	0	85	78	Lu	4.8	2.48	0	7.9	14
5138.0	9.2	2	3320DA	33.40	20.35	180	2	10	0	60	60	Lts	7.6	5.45	0	7.7	11
5140.0	9.2	2	3320DA	33.40	20.35	320	2	10	20	80	85	-	4.0	0.36	0	5.1	10
5142.0	9.2	2	3320DA	33.40	20.35	320	7	22	0	95	68	Lt	4.1	0.82	0	4.6	14
5143.0	9.2	2	3320DA	33.40	20.35	320	7	19	0	80	67	Lt	6.0	0.15	0	11.0	18
5145.0	9.2	2	3320DA	33.40	20.35	270	4	16	70	20	33	Ut	5.6	0.74	0	7.2	6
5146.0	9.2	2	3320DA	33.40	20.35	-	8	12	95	0	66	Ut	5.4	0.26	0	4.1	5
5147.0	9.2	2	3320DA	33.40	20.35	0	2	12	0	95	56	Su	6.6	2.91	0	8.0	3
5152.0	9.2	2	3320DA	33.40	20.35	225	2	12	0	95	68	Lts	6.9	3.59	0	10.1	7
5153.0	9.2	2	3320DA	33.40	20.35	270	4	6	95	5	67	Su	6.6	0.64	0	4.2	10
5161.0	9.2	2	3320DA	33.40	20.35	160	2	9	5	61	85	Su	4.6	0.37	0	7.6	20
5162.0	9.2	2	3320DA	33.40	20.35	0	7	14	5	80	62	Su	5.6	2.36	0	7.6	14
5165.0	9.2	2	3320DA	33.40	20.35	20	2	27	0	90	80	Sl	6.1	1.98	0	10.3	4
5166.0	9.2	2	3320DA	33.4	20.35	20	4	22	1	85	66	Su	4.9	0.36	0	14.1	10
5643.2	9.2	2	3320DA	33.38	20.35	45	9	6	10	70	42	Su	4.7	0.56	0	0.0	16
5645.0	9.2	2	3320DA	33.38	20.35	270	2	17	0	80	52	Lts	4.2	1.15	0	4.3	10
5647.0	9.2	2	3320DA	33.38	20.35	180	4	30	5	90	43.7	Lts	4.2	0.83	0	5.0	17
7292.0	9.2	2	3320DD	33.51	20.52	1	2	25	0	85	20	-	4.1	4.65	0	11.8	9
9160.0	9.2	2	3320DA	33.38	20.36	1	3	30	0	100	50	Su4	4.6	1.75	0	11.4	9
9181.0	9.2	2	3321CA	33.30	21.02	1	2	10	20	75	30	Ls	6.0	4.88	0	7.3	10
9182.0	9.2	2	3320DA	33.39	20.33	112	2	8	172	3	60	Ut	6.5	2.87	0	9.4	10

Relieve Nr	Community	Sub-Community	Grid	Latitude [Deg:Min]	Longitude [Deg:Min]	Aspect [degrees]	Slope [percentage]	Soil depth [cm]	Stone cover non-quartz [%]		Stone cover quartz [%]		Stone content in soil [% weight]	Soil texture	Soil pH	Electrical conductivity [mS/cm]		Carbonate [HCl test, class 1-5]	Cover values [%]		Number of species [n]
									10	6	51	0				78	SI		7.6	0.05	
5076.0	10		3320DA	33.42	20.42	315	10	6	51	0	78	SI	7.6	0.05	0	22.1	11				
5100.0	10		3320CB	33.35	20.30	0	2	18	25	0	60	Su	7.7	0.03	1	10.8	15				
5109.0	10		3320CB	33.35	20.30	160	4	17	80	5	63	Lt	7.9	0.17	3.3	6.7	16				
5115.0	10		3320CB	33.33	20.18	337	4	18	1	3	13	SI	7.6	0.05	4	24.9	15				
5116.0	10		3320DA	33.40	20.35	-	0	32	10	0	17	SI	7.5	0.03	2	14.7	9				
5121.0	10		3320DA	33.40	20.35	340	2	7	50	10	62	SI	7.2	0.17	2	11.3	10				
5124.0	10		3320DA	33.40	20.35	315	2	22	60	0	47	Su4	7.9	0.18	0	6.2	11				
5131.0	10		3320DA	33.40	20.35	280	7	17	0	0	42	Su	8.1	0.10	4	9.3	10				
5137.0	10		3320DA	33.40	20.35	230	13	4	0	20	70	-	7.8	1.22	2	7.2	14				
5141.0	10		3320DA	33.4	20.35	320	15	22	5	75	84	Lt	6.0	0.10	0	8.9	19				
5154.0	10		3320DA	33.40	20.35	180	2	18	21	1	8	Su	7.7	0.06	0	4.4	6				
5157.0	10		3320DA	33.40	20.35	-	0	17	90	0	68	SI	7.8	0.41	4	9.8	8				
5644.0	10		3320DA	33.38	20.35	45	9	18	40	40	53.5	Lts	6.7	2.00	0	5.6	11				
5655.0	10		3322DA	33.35	20.39	1	9	10	50	0	0	Su	-	-	0	10.2	9				
5690.0	10		3321CC	33.49	21.05	180	6	17	69	31	26	-	8.3	1.04	3.3	6.2	9				
7311.0	10		3321CA	33.41	21.10	0	0	20	0	0	5	-	7.7	0.07	0	37.0	7				
5111.0	11		3320CB	33.33	20.18	-	0	11	3	95	60	Su	5.4	1.36	0	37.7	11				
5113.0	11		3320CB	33.33	20.18	0	4	13	40	60	22	Su	5.4	0.00	0	7.1	10				
5114.0	11		3320CB	33.33	20.18	0	4	11	50	45	70	Lt	8.2	0.35	0	7.3	13				
5158.0	11		3320DA	33.40	20.35	180	11	15	100	0	63	SI	6.8	0.49	0	10.0	17				
7337.0	11		3320CA	33.33	20.14	180	4	5	75	0	39	Su	7.2	0.22	0	11.7	6				
7338.0	11		3320CB	33.31	20.19	135	2	30	55	0	18.5	SI	7.9	0.24	0	13.2	6				
9150.0	11		3320AC	33.23	20.02	0	0	30	0	0	1	Ls	6.5	2.86	0	17.5	5				
9186.0	11		2818BD	33.27	20.36	180	1	0	35	25	60	Su2	6.5	0.04	0	9.6	6				
9189.0	11		3320AC	33.28	20.03	0	0	30	1	0	10	Ls	6.8	1.15	0	12.1	6				
9190.0	11		3320CA	33.33	20.04	1	3	20	11	36	30	Su4	6.8	1.53	1	6.6	5				
5074.0	12		3320DA	33.42	20.42	35	2	6	45	50	50	Lt	7.9	4.02	0	7.5	7				
7298.0	12		3320DA	33.41	20.37	0	0	10	0	10	1.5	-	7.8	0.07	0	31.3	9				
7299.0	12		3320DA	33.40	20.40	180	1	17	40	41	38	-	7.9	1.57	0	33.6	7				
7302.0	12		3320DA	33.39	20.44	0	0	17	15	15	20	-	7.9	0.09	0	10.4	7				
7314.0	12		3321CA	33.43	21.10	45	6	5	0	90	44	SI	7.7	1.19	0	5.7	7				
7328.0	12		3320DD	33.47	20.57	180	1	10	60	6	25	-	6.7	0.06	0	11.7	12				
9165.0	12		3320DA	33.41	20.42	270	4	10	87	5	10	Ls	7.8	6.63	0	4.1	4				
9166.0	12		3320DA	33.41	20.42	0	0	18	0	15	15	SI	7.2	3.01	0	8.5	6				
9169.0	12		3321CA	33.39	21.04	180	3	20	90	0	46	Ls	7.9	3.55	2	17.6	8				
5654.0	13		3322DA	33.35	20.39	1	2	28	0	57	39	Lt	7.3	5.73	0	14.2	11				
5656.0	13		3322DA	33.35	20.39	1	2	25	0	80	60	Lt	7.5	4.74	2	3.6	8				
5657.0	13		3322DA	33.35	20.39	1	2	25	10	86	55	Lts	7.6	0.69	0	9.6	17				
5658.0	13		3322DA	33.35	20.39	1	2	20	5	76	25	Lts	6.7	1.25	0	12.2	10				
5659.0	13		3322DA	33.35	20.39	1	2	18	48	52	30	Su	8.1	0.02	3.2	4.0	11				
5660.0	13		3320DB	33.44	20.57	1	1	7	70	7	73	-	6.6	0.93	0	5.7	9				
5662.0	13		3320DA	33.37	20.37	1	1	8	80	0	36	Lst	5.0	0.06	0	8.4	9				
5663.0	13		3322DA	33.35	20.39	1	4	6	90	11	80	Su	6.0	0.45	0	6.7	12				
5664.0	13		3322DA	33.35	20.39	1	7	24	105	1	72	Su	6.9	0.04	0	4.8	10				
7300.0	13		3322DA	33.35	20.39	1	1	17	0	71	15	Su	7.0	0.02	0	6.9	15				
7301.0	13		3322DA	33.35	20.39	270	2	23	0	18	30	Lts	8.0	0.69	4	8.5	17				
7304.0	13		3320DA	33.40	20.40	180	2	10	92	0	28	-	7.3	0.02	0	22.0	5				
7332.0	13		3320DA	33.40	20.45	90	1	10	70	0	33	-	7.5	0.02	0	18.0	5				
9163.0	13		3320DA	33.40	20.43	1	1	7	70	20	24	Su	7.8	2.72	0	7.7	10				
9167.0	13		3320DA	33.40	20.43	0	0	20	60	0	8	Ls	7.3	0.44	0	17.1	6				

Appendix 9. Synoptic Table II: Vegetation of the Knersvlakte and the quartz fields vegetation of the Namaqualand - see separate folder.

Appendix 10. Phytosociological Table II: Vegetation of the Knersvlakte and the quartz fields vegetation of the Namaqualand - see separate folder.

Appendix 11. Names and authors of the diagnostic species recorded for the quartz-field communities in the Bushmanland-Warmbad area

Entire species name	Family
Anacampseros albidiflora Poelln.	Portulacaceae
Anacampseros karasmontana Dinter ex Poelln.	Portulacaceae
Anacampseros papyracea E.Mey. ex Fenzl	Portulacaceae
Arenifera spinescens (L.Bolus) H.E.K.Hartmann	Aizoaceae (Mesembryanthema)
Blepharis furcata (L.f.) Pers.	Acanthaceae
Conophytum friedrichiae (Dinter) Schwantes	Aizoaceae (Mesembryanthema)
Conophytum praesectum N.E.Br.	Aizoaceae (Mesembryanthema)
Crassula mesembryanthemopsis Dinter	Crassulaceae
Dinteranthus wilmotianus ssp. impunctatus L. Bolus	Aizoaceae (Mesembryanthema)
Drosanthemum sp. (Schmiedel 102344 HBG)	Aizoaceae (Mesembryanthema)
Euphorbia decepta N.E.Br.	Euphorbiaceae
Galenia fruticosa (L.f.) Sond.	Aizoaceae
Hermannia spinosa E.Mey. ex Harv.	Sterculiaceae
Hypertelis salsoloides (Burch.) Adamson	Molluginaceae
Lapidaria margaretae (Schwantes) Dinter & Schwantes	Aizoaceae (Mesembryanthema)
Larryleachia tirasmontana (Plowes) Plowes	Apocynaceae
Lithops julii (Dinter & Schwantes) N.E.Br.	Aizoaceae (Mesembryanthema)
Oropetium capense Stapf	Poaceae
Osteospermum sinuatum (DC.) Norl.	Asteraceae
Prenia tetragona (Thunb.) Gerbaulet	Aizoaceae (Mesembryanthema)
Ruschia muricata L.Bolus	Aizoaceae (Mesembryanthema)
Ruschia odontocalyx (Schltr. & Diels) Schwantes	Aizoaceae (Mesembryanthema)
Ruschia spec. (Schmiedel 102350 HBG)	Aizoaceae (Mesembryanthema)
Salsola spec. (Schmiedel 109958 HBG)	Chenopodiaceae
Tetragonia reduplicata Welw. ex. Oliv.	Aizoaceae
Titanopsis hugo-schlechteri (Tischer) (Dinter & Schwantes	Aizoaceae (Mesembryanthema)
Trachyandra spec. (Schmiedel 7382 HBG)	Asphodelaceae
Zygophyllum decumbens Delile	Zygophyllaceae

Appendix 13. Habitat data and median values for the quartz-field communities of the Bushmanland-Warmbad area.

Community No	Releve No	Total cover ann & perenn [%]	Total cover perenn [%]	Species number ann & perenn	Species number perenn only	Quartz cover [%]	Stone cover (non-quartz) [%]	Exposition	Inclination	Soil depth [cm]	Stone content [% weight]	Soil pH	Electr. conductivity	Carbo-nate content	Soil texture
1.00	7353.0	12.11	12.11	4	4	95	0	180.00	8.00	7.00	70.0	7.77	.095	.0	Sl
1.00	7355.0	3.68	3.68	9	9	97	0	.00	.00	5.00	40.0	7.99	.054	.0	Sl
1.00	7356.0	7.11	7.11	5	5	95	0	90.00	5.00	30.00	60.0	7.95	.044	.0	Sl
1.00	9742.0	5.10	5.10	2	1	75	7	155.00	2.00		60.0	7.59	.060	3.2	Su3
1.00	9748.0	9.51	9.51	4	4	80	0	1.00	3.00	10.00	70.0	6.42	.030	2.0	Su4
<i>Median values</i>		7.11	7.11	4.00	4.00	95.00	.00	90.00	3.00	8.50	60.00	7.77	.05	.00	
2.00	7375.0	.02	.02	2	2	80	0	.00	.00	15.00	50.0	7.26	.042	.0	Sl
2.00	7376.0	.01	.01	1	1	91	0	.00	.00	10.00	40.0	6.66	.067	.0	Sl
2.00	9750.0	3.87	3.87	8	6	0	0	.00	.00	5.00	35.0	7.00	.061	.0	Su4
<i>Median values</i>		.02	.02	2.00	2.00	80.00	.00	.00	.00	10.00	40.00	7.00	.06	.00	
3.10	7359.0	9.63	9.63	7	7	93	0	337.00	3.00	5.00	30.0	7.60	.028	.0	Sl
3.10	7367.0	2.41	2.41	9	9	55	0	.00	.00	25.00	70.0	7.60	.027	.0	Sl
3.10	7368.0	9.06	9.06	8	8	90	0	270.00	4.00	10.00	70.0	7.03	.027	.0	Sl
3.10	7377.0	.27	.27	8	8	75	0	.00	.00	15.00	50.0	6.36	.075	.0	Sl
3.10	7378.0	12.26	12.26	13	13	61	0	202.00	1.00	7.00	60.0	7.66	.108	.0	Sl
3.10	7380.0	13.12	13.12	13	13	40	0	180.00	1.00	20.00	60.0	7.20	.141	.0	Sl
3.10	7389.0	13.01	13.01	8	8	97	0	90.00	1.00	15.00	70.0	7.08	.020	.0	Sl
3.10	9747.0	.72	215.30	5	5	75	0	.00	.00	5.00	20.0	5.93	.020	.0	Su3
<i>Median values</i>		9.35	10.95	8.00	8.00	75.00	.00	135.00	1.00	12.50	60.00	7.14	.03	.00	
3.20	7365.0	13.05	13.05	6	6	90	0	22.50	1.00	10.00	20.0	7.36	.032	.0	Sl
3.20	7366.0	7.60	7.60	3	3	40	0	.00	.00	25.00	70.0	8.04	.034	.0	/
3.20	7369.0	17.31	17.41	8	8	87	0	45.00	4.00	15.00	35.0	7.62	.029	.0	Sl
3.20	7370.0	1.51	1.51	6	6	78	0	45.00	1.00	5.00	40.0	7.45	.035	.0	Sl
3.20	7372.0	6.82	6.82	10	10	80	0	270.00	5.00	5.00	26.0	7.55	.024	.0	fS
3.20	7391.0	9.30	9.30	12	12	90	0	.00	.00	15.00	40.0	7.81	.307	.0	Sl
3.20	7393.0	12.86	12.86	9	8	90	0	180.00	7.00	20.00	50.0	6.54	.147	.0	Sl
<i>Median values</i>		9.30	9.30	8.00	8.00	87.00	.00	45.00	1.00	15.00	40.00	7.55	.03	.00	
3.30	7381.0	12.61	12.61	5	5	55	0	180.00	5.00	5.00	70.0	7.50	.135	.0	Sl
3.30	7390.0	12.40	12.40	9	9	90	0	90.00	6.00	17.00	50.0			.0	/
3.30	7398.0	9.87	9.87	10	10	80	5	270.00	2.00	10.00	50.0	7.80	.105	.0	Sl
3.30	7400.0	11.01	11.01	3	3	60	0	90.00	1.00	25.00	20.0	6.11	.016	.0	Sl
3.30	9002.0	2.70	2.70	6	6	32	0	180.00	1.00	4.00	30.0	7.77	.184	.0	Su
3.30	9004.0	12.65	12.65	5	5	70	10	270.00	4.00	10.00	10.0	7.22	.031	.0	Ls
<i>Median values</i>		11.71	11.71	5.50	5.50	65.00	.00	180.00	3.00	10.00	40.00	7.50	.11	.00	
3.40	5426.0	2.05	2.05	8	8	45	50	90.00	2.00	5.00	40.0			.0	Su
3.40	5427.0	14.01	14.01	3	3	80	6	135.00	17.00	20.00	35.0	5.74	.030	.0	fSu2
3.40	5436.0	5.10	5.10	2	2	99	0	20.00	2.00	6.00	40.2	5.24	.272	.0	Su4
3.40	7373.0	.15	.15	2	2	91	0	.00	.00	15.00	50.0	6.71	.059	.0	Sl
3.40	7383.0	10.04	10.04	4	2	75	0	45.00	6.00	20.00	50.0	7.44	.045	.0	Sl
3.40	7385.0	10.56	10.56	8	6	90	0	45.00	8.00	25.00	60.0	7.25	.055	.0	Sl
<i>Median values</i>		7.57	7.57	3.50	2.50	85.00	.00	45.00	4.00	17.50	45.10	6.71	.06	.00	
4.00	5431.0	28.85	28.85	6	6	50	0	90.00	2.00	45.00	37.1	8.36	.595	.0	Su3
4.00	5432.0	15.20	15.20	5	5	81	0	.00	.00	10.00	36.5	6.93	.175	.0	Su4
4.00	5433.0	14.62	14.62	5	5	41	0	.00	.00	10.00	80.0	8.07	.380	2.0	Su
4.00	5434.0	10.92	10.92	5	5	90	0	20.00	2.00	10.00	70.0	6.72	.530	.0	Su
4.00	5435.0	8.12	8.12	5	5	96	0	20.00	2.00	10.00	70.0	6.10	.490	.0	Su
4.00	5437.0	12.12	12.12	4	3	93	0	20.00	2.00	9.00	40.0	4.24	.040	.0	Su
4.00	5438.0	8.60	8.60	3	3	70	0	1.00	2.00	10.00	50.0	7.18	.070	.0	Su
<i>Median values</i>		11.52	11.52	5.00	5.00	85.50	.00	10.50	2.00	10.00	60.00	6.83	.28	.00	

Erklärung

Ich versichere, daß ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Tabellen, Karten und Abbildungen -, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; daß diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; daß sie - abgesehen von unten angegebenen Teilpublikationen - noch nicht veröffentlicht worden ist sowie, daß ich eine solche Veröffentlichung vor Abschluß des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen dieser Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Professor Norbert Jürgens betreut worden.

Veröffentlichte Teilpublikation:

Schmiedel, U. & Jürgens, N. 1999. Community structure on unusual habitat island: quartz-fields in the Succulent Karoo, South Africa. *Plant Ecology* 142:57-69.

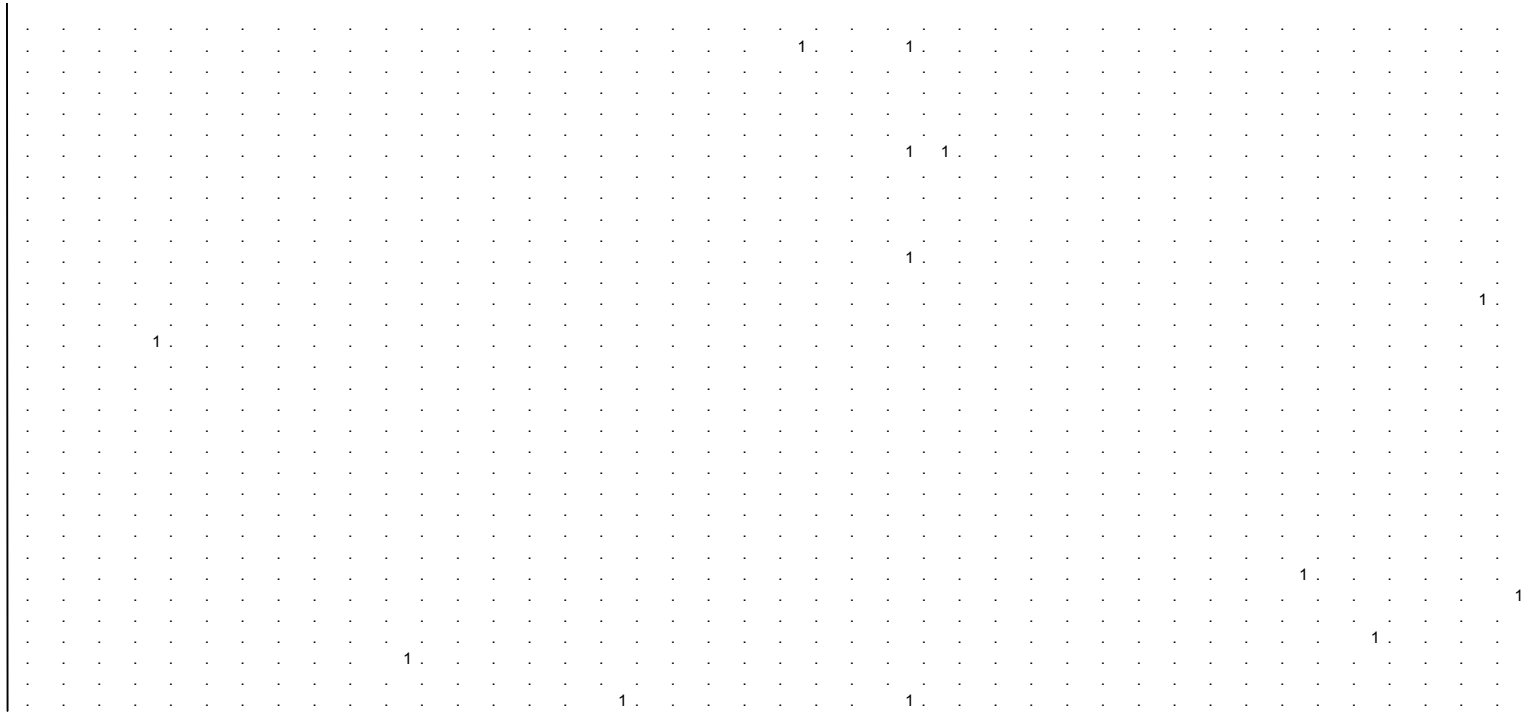
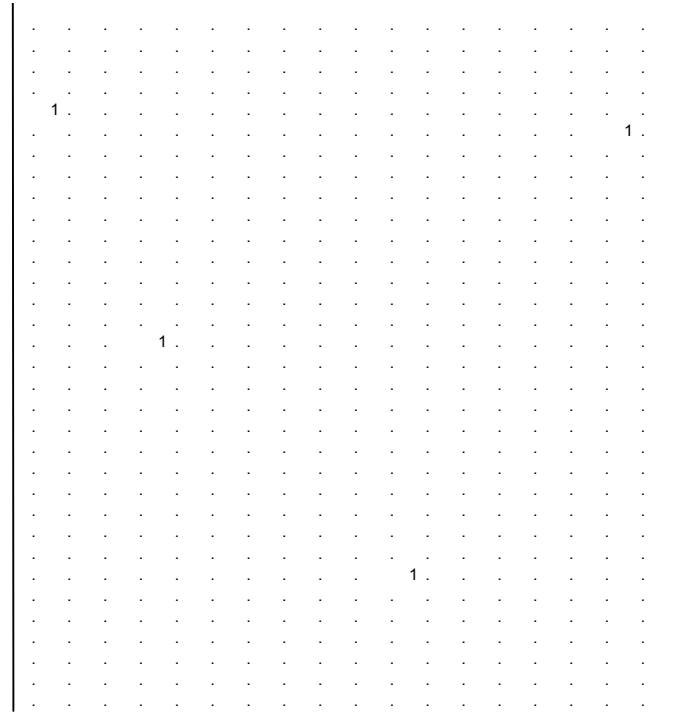
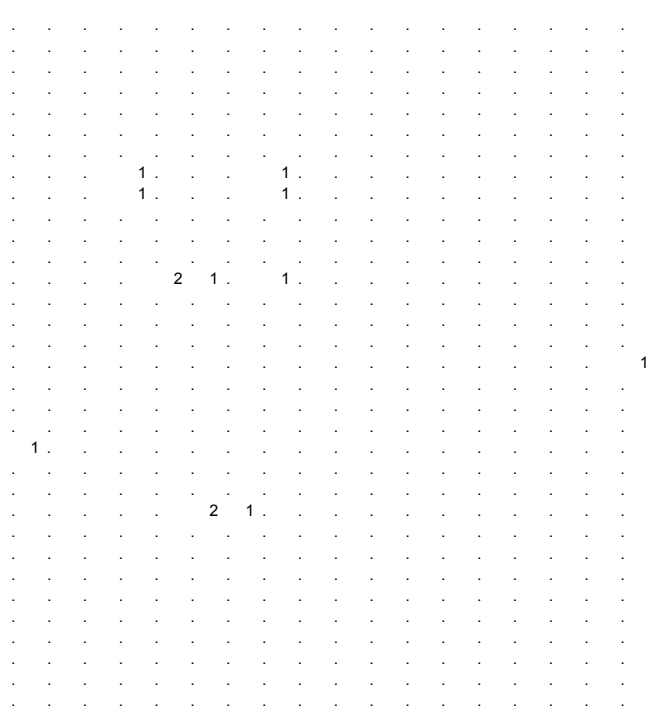
Lebenslauf und wissenschaftlicher Werdegang

Ute Schmiedel

Ute Schmiedel
Lornsenplatz 4
22767 Hamburg
U Schmiedel@botanik.uni-hamburg.de

Geboren am 17.01.1965 in Helsinki/Finnland (deutsche Staatsangehörigkeit)

- | | |
|----------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1971 - 1984 | Besuch der Rudolf-Steiner-Schule in Hamburg-Nienstedten
Abschluß: Allgemeine Hochschulreife |
| Aug. 1985 bis Aug. 1987 | Ausbildung zur Gärtnerin bei Fa. Heinz Clasen (Baumschulen) in Tangstedt bei Pinneberg |
| SoSe 1988 bis WiSe 1993/94 | Studium der Fächer Biologie, Geschichte und Erziehungswissenschaft für das Lehramt an der Oberstufe - Allgemeinbildende Schulen - an der Universität Hamburg |
| August - Oktober 1993 | Forschungsreise nach Südafrika zur Datenerhebung für die Examensarbeit zum Thema „Standortökologische und strukturelle Untersuchungen zur Vegetation der Quarzflächen in der Knersvlakte (Südafrika)“ |
| Dezember 1994 | Abschluß des Studiums: Erste Staatsprüfung für das Lehramt an der Oberstufe |
| Februar - Mai 1995 | Teilnahme an einer Forschungsreise in die Zentrale Namib (Namibia) |
| Seit Juli 1995 | Tätigkeit als Wissenschaftliche Hilfskraft am Botanischen Institut der Universität zu Köln. Forschungsarbeit zu Flora, Vegetation und Ökologie der Quarzflächen im südlichen Afrika. |
| Seit Oktober 2000 | Koordination des botanischen Teilprojekts S06 im BMBF-Projekt <i>BIOTA Southern Africa</i> am Institut für Allgemeine Botanik, Universität Hamburg. |
| Februar 2002 | Beantragung der Zulassung zur Promotion an der Universität zu Köln |



1.

1.

1.

1.

1.

2.

1.

1.

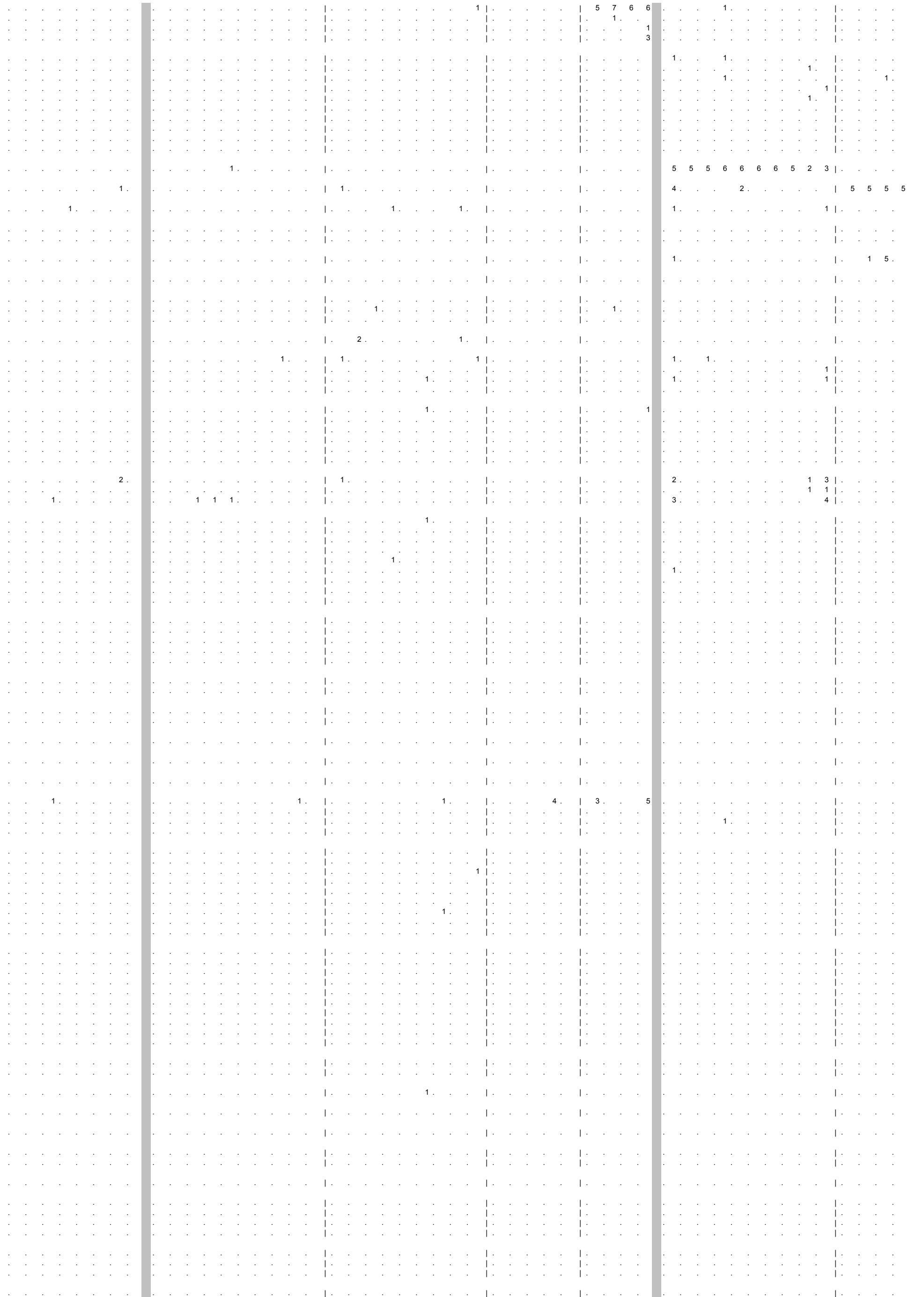
1.

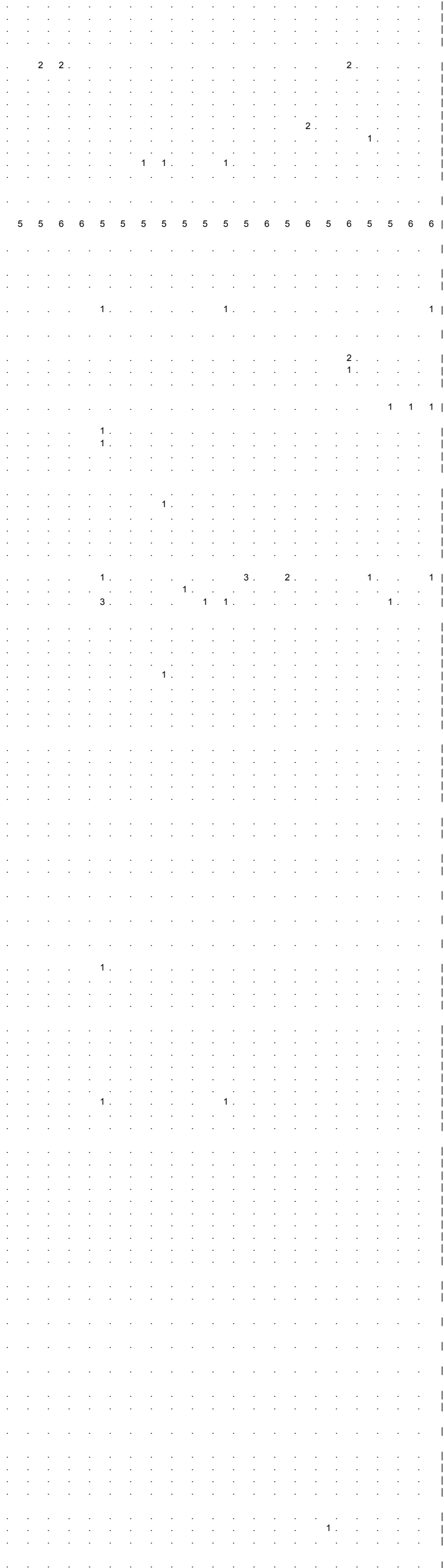
1.

1.

Anacamperos retusa Poelln.
Lachenalia patula Jacq.
Ruschia vanheerdei L.Bolus
Spergularia sp. (Schmiedel 104629 HBG)
Mesembryanthemum longistylum DC.
Trachyandra tortilis (Baker) Oberm.
Pentzia peduncularis B.Nord.
Dicrocaulon humile N.E.Br.
AJ
Brownanthus corallinus (Thunb.) Ihlenf. & Bittrich
Dicrocaulon sp. (Schmiedel 110366 HBG)
AK
Conophytum calculus (A.Berger) N.E.Br. ssp. calculus
Ruschia burtoniae L.Bolus
AL
Monilaria chrysoleuca (Schltr.) Schwantes var. chrysoleuca
AM
Monilaria moniliformis (Thunb.) Ihlenf. & Jörg.
Argyroderma congregatum L.Bolus
AN
Dicrocaulon brevifolium N.E.Br.
AO
Dicrocaulon pseudonodosum sp. nov. (Ihlenfeldt pers. comm.)
Phyllobolus herbertii (N.E.Br.) Gerbault
Pelargonium quarcticola Meve & Marais
Pelargonium incrassatum (Andrews) Sims
AP
Dicrocaulon longifolium spec. nov. (Ihlenfeldt pers. comm.)
Argyroderma crateriforme (L.Bolus) N.E.Br.
Tylecodon occultans (Toelken) Toelken
AQ
Dicrocaulon nodosum spec. nov. (Ihlenfeldt pers. comm.)
AR
Othonna incisa Harv.
Phyllobolus prasinus (L.Bolus) Gerbault
Othonna rechingeri B.Nord.
Meyerophytum meyeri (Schwantes) Schwantes
Senecio sulcicalyx spec. nov. (Bruyns pers. comm.)
Meyerophytum globosum comb. nov. (Ihlenfeldt pers. com.)
Cephalophyllum inaequale L.Bolus
AS
Monilaria scutata (L.Bolus) Schwantes ssp. obovata Ihlenf. & Jörg.
Euphorbia celata R.A.Dyer
Pharnaceum dichotomum L.f.
AT
Jacobsenia vaginata (L.Bolus) Ihlenfeldt comb. nov.
Conophytum concavum L.Bolus
AU
Dicrocaulon spissum N.E.Br.
AV
Dicrocaulon ramulosum (L.Bolus) Ihlenf.
Limonium dregeanum (C.Presl) Kuntze
AW
Ruschia viridifolia L.Bolus
Ehrharta barbinodis Nees ex Trin.
AX
Monilaria scutata (L.Bolus) Schwantes ssp. scutata
Chlorophytum crassinerve (Baker) Oberm.
Phyllobolus sinuosus (L.Bolus) Gerbault
Brunsvigia radula (Jacq.) Aiton
Pharnaceum elongatum (DC.) Adamson
AY
Antimima sp. (Schmiedel 104874 HBG)
Suaeda sp. (Schmiedel 102015 HBG)
Adenoglossa decurrens (Hutch.) B.Nord.
Lithops meyeri L.Bolus
Octopoma connatum (L.Bolus) L.Bolus
Galenia crystallina (Eckl. & Zeyh.) Fenzl
Antimima sp. (Schmiedel 102039 HBG)
Cheiridopsis acuminata L.Bolus
Arenifera pillansii (L.Bolus) Herre
Conophytum maughanii N.E.Br. ssp. latum (Tischer) S.A.Hammer
Nelia pillansii (N.E.Br.) Schwantes
Ruschia paucipetala L.Bolus
Crassula subaphylla (Eckl. & Zeyh.) Harv. var. subaphylla
AZ
Ruschia leucosperma L.Bolus
BA
Cephalophyllum regale L.Bolus
BB
Aspazoma amplexens (L.Bolus) N.E.Br.
Leipoldtia klaverensis L.Bolus
BC
Eberlanzia cyathiformis (L.Bolus) H.E.K.Hartmann
Leipoldtia laxa L.Bolus
Ceraria fruticulosa H.Pearson & Stephens
Ruschia atrata L.Bolus
BD
Schlechteranthus hallii L.Bolus
Euphorbia gummifera Boiss.
Conophytum gratum (N.E.Br.) N.E. Br.
Galenia dregeana Fenzl ex Sond.
BE
Brownanthus pubescens (N.E.Br. ex C.A.Maass) Bullock

+ - I + .
r + . . . II
I
+ r
+
+ r
V
II
II III II II III II
V II II I . . III
+ V I II III
+ V I . .
r
V II II II
+ r +
V III II
+
V
II III II II II
+ III III III IV
. + . . . I
II II I . .
II III II II
V + I . . .
III + . . .
II
V I
+ V
II I II V III
r I . . . II
V IV II
V III II II
+ III III
II III II I
II III +
II II +
II II
I II
I +
I +
+ I +
I +
II III II II V III II II
III V V
II I II V I
+ + II
+ V II II
V III II II
V II II II
V





Conophytum subfenestratum Schwantes

Z

Salsola sp. (Schmiedel 93110 HGB)
Argyrodema pearsonii (N.E.Br.) Schwantes
Mesembryanthemum fastigiatum Thunb.
Tylecodon pygmaeus (W.F.Barker) Toelken
Mesembryanthemum stenandrum (L.Bolus) L.Bolus

2

AA

Oophytum nanum (Schltr.) L.Bolus
Phyllobolus digitatus (Aiton) Gerbaulet ssp. littlewoodii (L.Bolus) Gerbaulet

AB

Phyllobolus digitatus (Aiton) Gerbaulet ssp. digitatus
Pteronia heterocarpa DC.

AC

Oophytum oviforme (N.E.Br.) N.E.Br.

AD

Monilaria pisiformis (Haw.) Schwantes

AE

Conophytum minutum (Haw.) N.E.Br. var. minutum

AF

Pteronia ciliata Thunb.
Gazania krebsiana Less
Pelargonium crithmifolium Sm.
Phyllobolus deciduus (L.Bolus) Gerbaulet

1

1

AG

Spergularia media (L.) C.Presl
Conophytum minutum (Haw.) N.E.Br. var. pearsonii (N.E.Br.) Boom
Cephalophyllum pulchrum L.Bolus
Aspalathus sp. (Schmiedel 110253 HBG)
Crassula capitella Thunb. ssp. thysiflora (Thunb.) Toelken
Ficinia lateralis (Vahl) Kunth
Euphorbia hamata (Haw.) Sweet
Hirpicium alienatum (Thunb.) Druce
Salsola sp. (Schmiedel 102410 HBG)

1

AH

Antimima dualis (N.E.Br.) N.E.Br.
Phyllobolus tenuiflorus (Jacq.) Gerbaulet
Anacamperos retusa Poelln.
Lachenalia patula Jacq.
Ruschia vanheerdei L.Bolus
Spergularia sp. (Schmiedel 104629 HBG)
Mesembryanthemum longistylum DC.
Trachyandra tortilis (Baker) Oberm.
Pentzia peduncularis B.Nord.
Dicrocaulon humile N.E.Br.

AJ

Brownanthus corallinus (Thunb.) Ihlenf. & Bittrich
Dicrocaulon sp. (Schmiedel 110366 HBG)

AK

Conophytum calculus (A.Berger) N.E.Br. ssp. calculus

Ruschia burtoniae L.Bolus

AL

Monilaria chrysoleuca (Schltr.) Schwantes var. chrysoleuca

AM

Monilaria moniiformis (Thunb.) Ihlenf. & Jörg.
Argyrodema congregatum L.Bolus

AN

Dicrocaulon brevifolium N.E.Br.

AO

Dicrocaulon pseudonodosum sp. nov. (Ihlenfeldt pers. comm.)
Phyllobolus herbertii (N.E.Br.) Gerbaulet
Pelargonium quarciticola Meve & Marais
Pelargonium incrassatum (Andrews) Sims

AP

Dicrocaulon longifolium spec. nov. (Ihlenfeldt pers. comm.)
Argyrodema crateriforme (L.Bolus) N.E.Br.
Tylecodon occultans (Toelken) Toelken

AQ

Dicrocaulon nodosum spec. nov. (Ihlenfeldt pers. comm.)

AR

Othonna incisa Harv.
Phyllobolus prasinus (L.Bolus) Gerbaulet
Othonna rechingeri B.Nord.
Meyerophytum meyeri (Schwantes) Schwantes
Senecio sulcicalyx spec. nov. (Bruyns pers. comm.)
Meyerophytum globosum comb. nov. (Ihlenfeldt pers. com.)
Cephalophyllum inaequale L.Bolus

1

AS

Monilaria scutata (L.Bolus) Schwantes ssp. obovata Ihlenf. & Jörg.
Euphorbia celata R.A.Dyer
Pharnaceum dichotomum L.f.

AT

Drosanthemopsis vaginata (L.Bolus) Rauschert
Conophytum concavum L.Bolus

AU

Dicrocaulon spissum N.E.Br.

AV

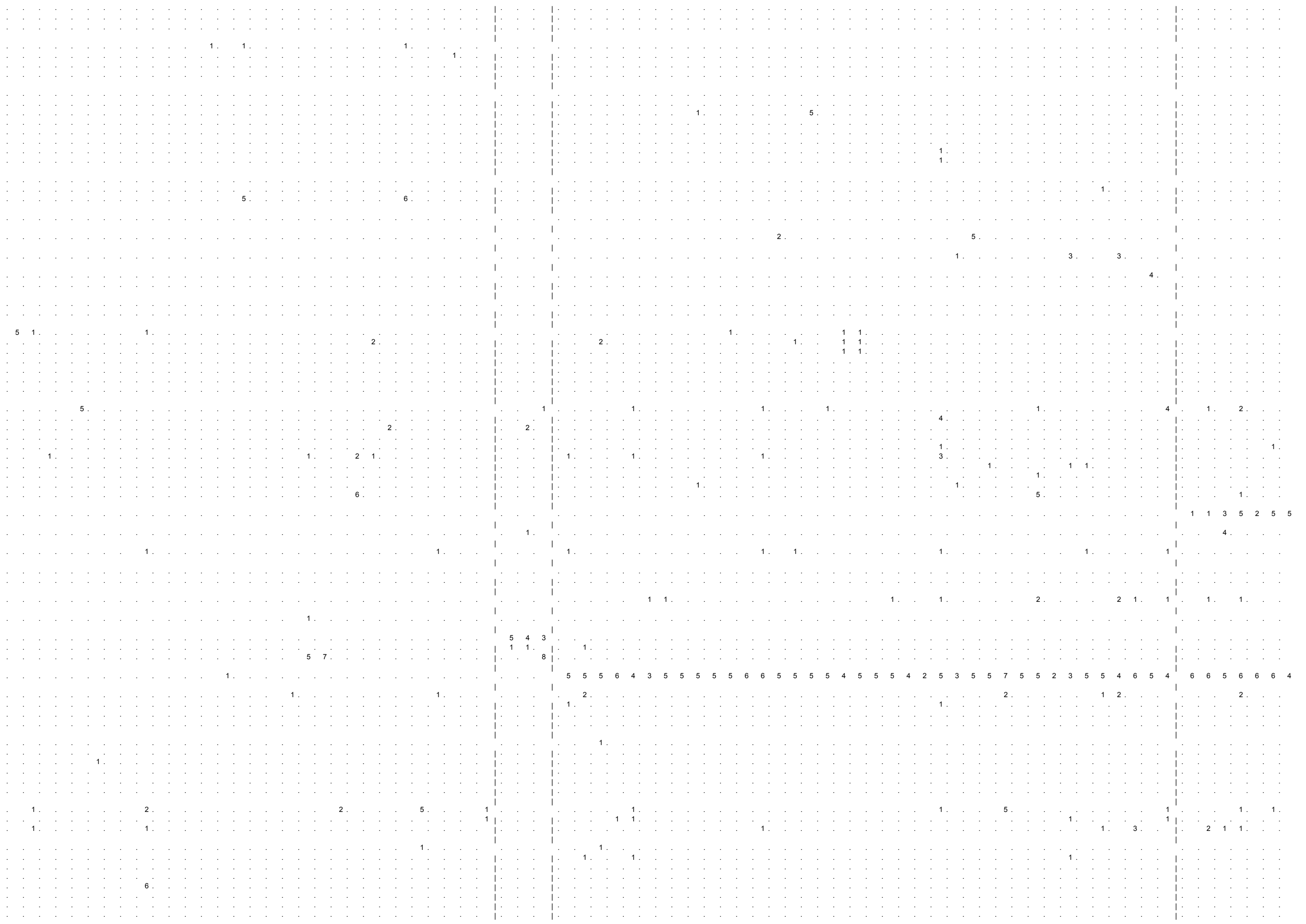
Dicrocaulon ramulosum (L.Bolus) Ihlenf.
Limonium dregeanum (C.Presl) Kuntze

AW

Ruschia viridifolia L.Bolus
Ehrharta barbinodis Nees ex Trin.

AX

Monilaria scutata (L.Bolus) Schwantes ssp. scutata
Chlorophytum crassinerve (Baker) Oberm.



1.

2.

2.

1.

1.

2.

1.

1.

1.

1.

1.

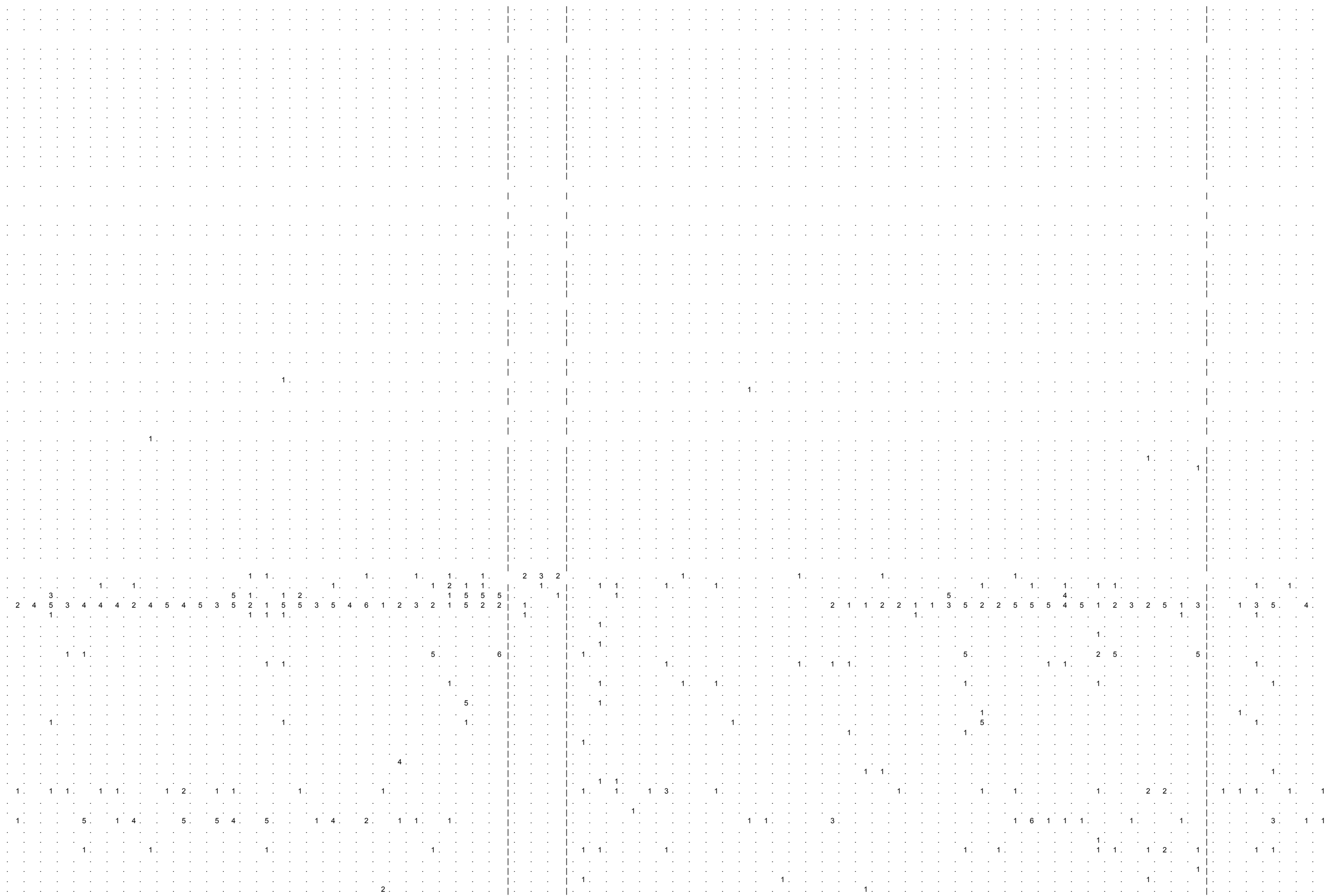
1.

2.

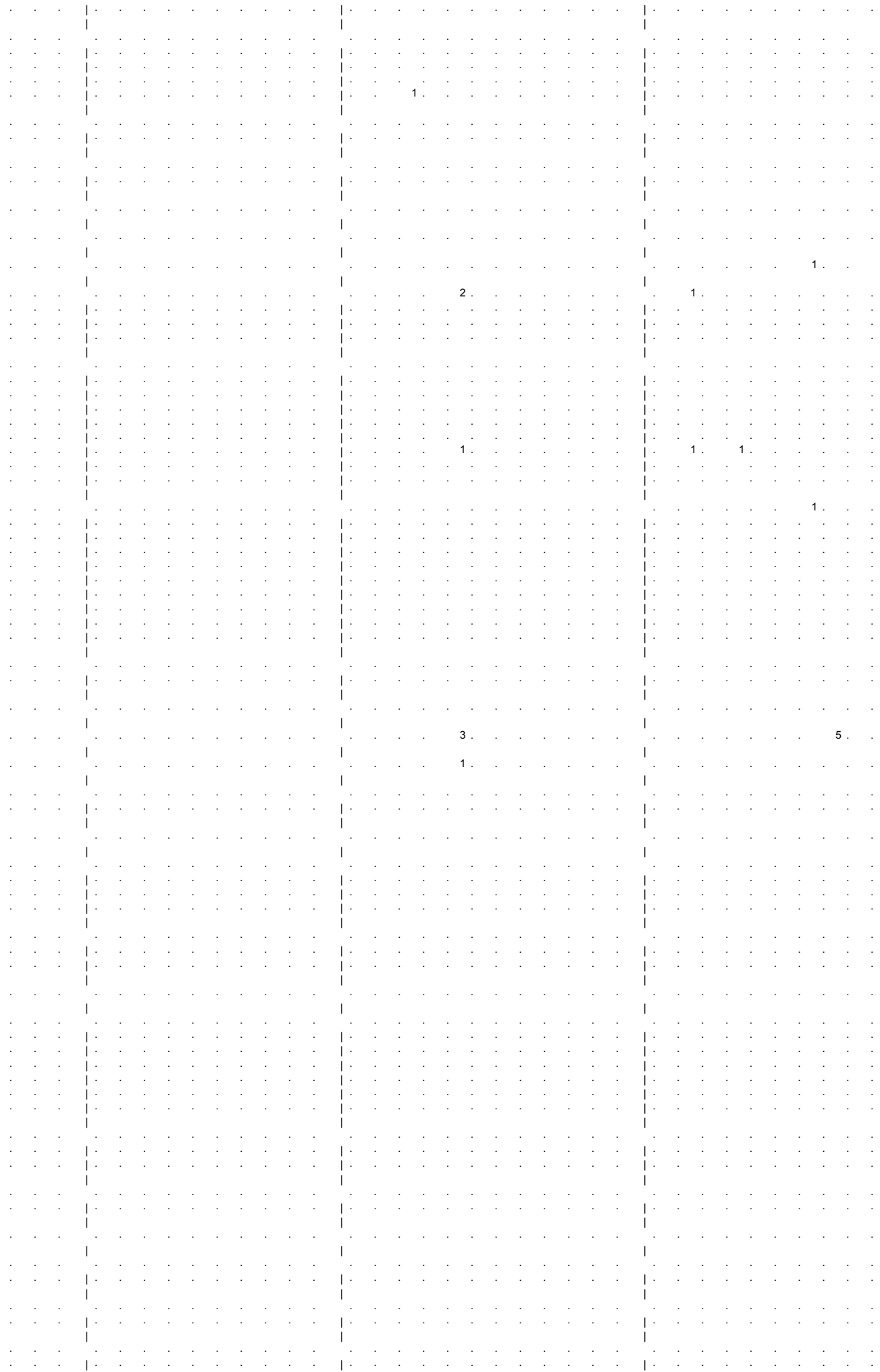
4.

1.

1.



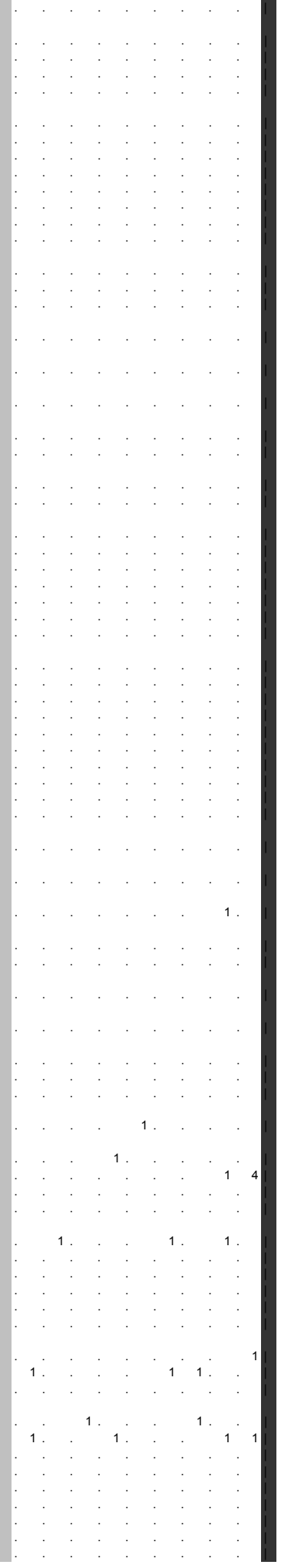
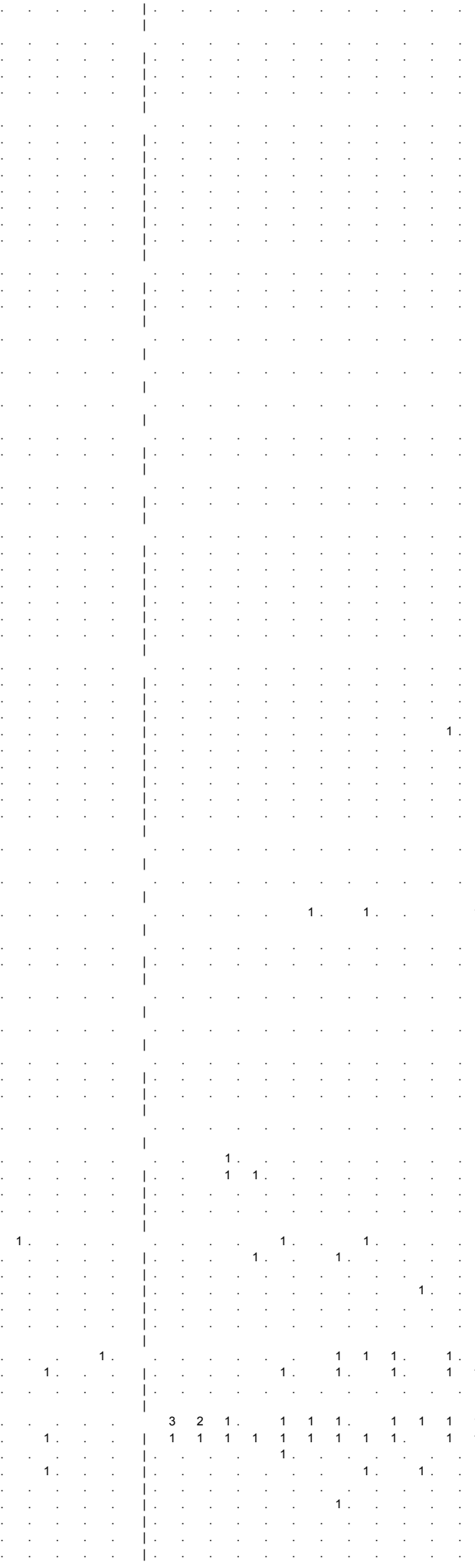
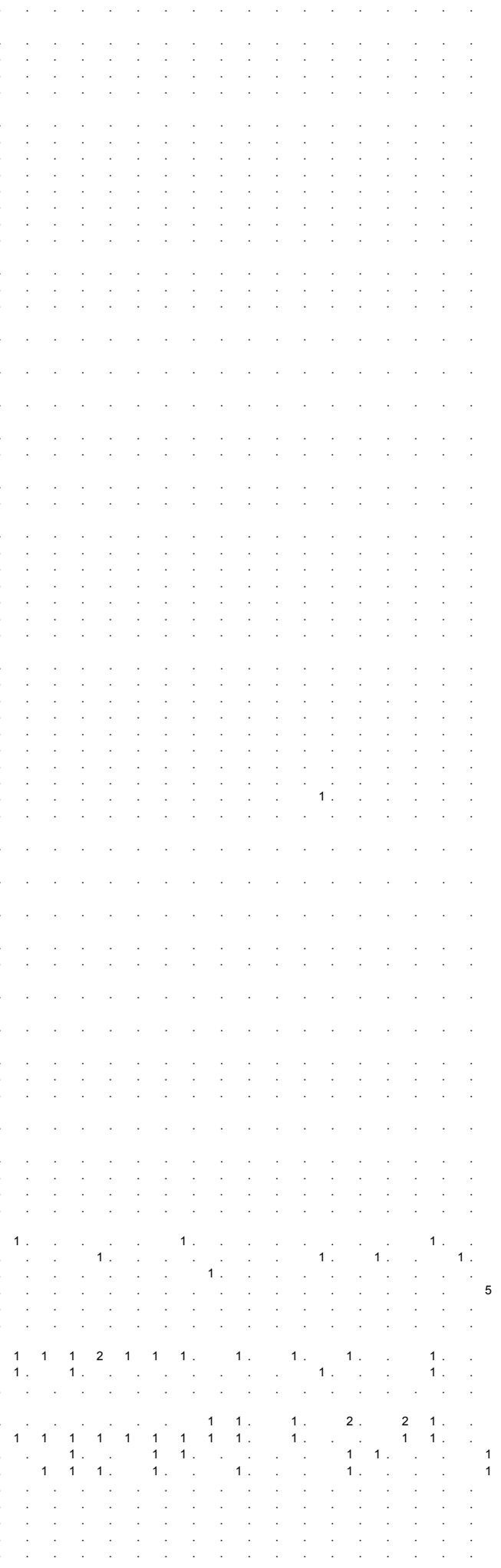
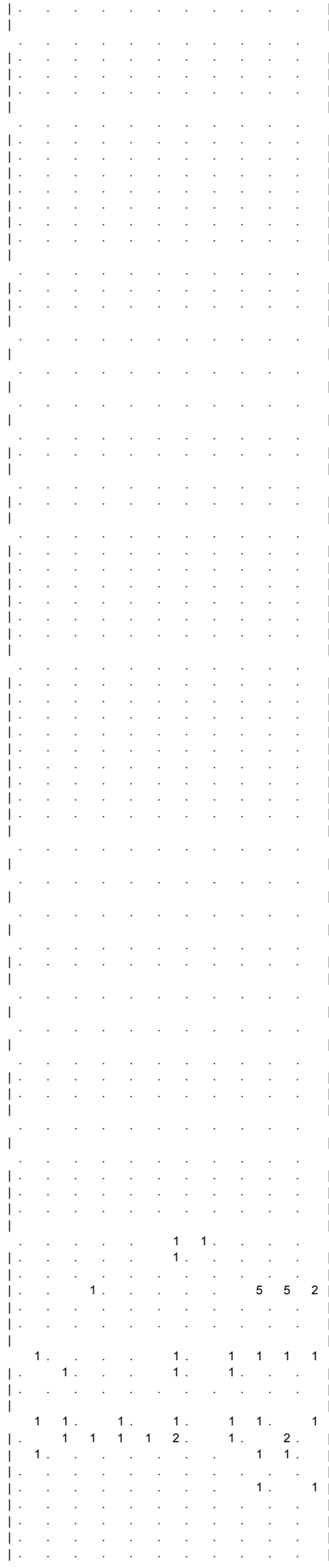
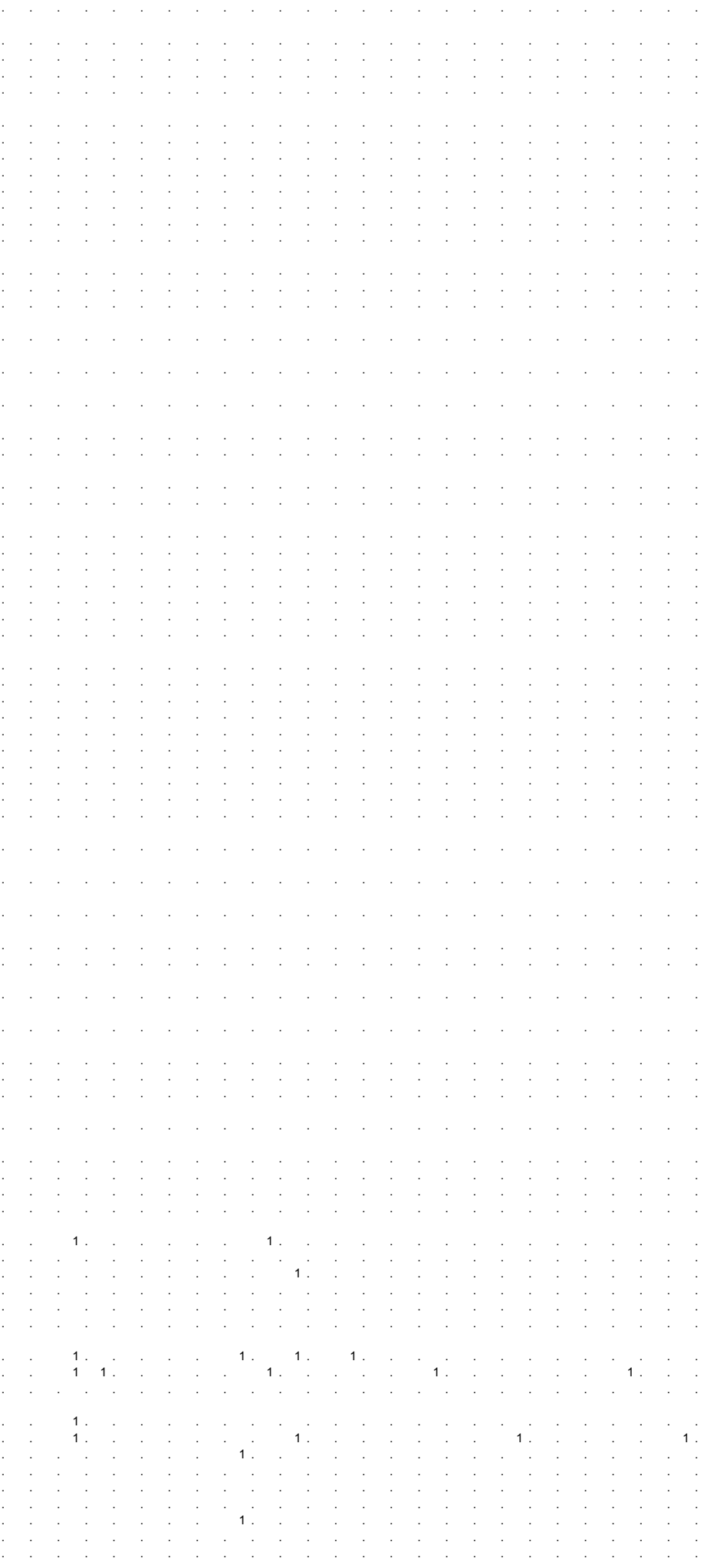
31	3076.0	20	2	19.78	22	21	31	24	18	39	200	10	0	50	0	27	32		8.20	0.240	3.2	
31	3028.0	20	2	29.41	16	14	31	24	18	39	180	8	0	5	0	25	28		UsI	7.80	0.087	4.0
31	5477.0	20	2	37.17	15	11	31	23	18	40	135	1	0	1	0	46	23		Su4	5.62	0.462	0.0
31	2886.0	20	2	20.10	17	12	31	24	18	39	90	4	0	5	0	10	27		Us	6.40	0.058	0.0
31	5469.0	20	2	33.63	18	14	31	23	18	40	0	0	0	0	0	25	10		Su4	6.80	0.234	0.0
31	7037.0	20	2	26.00	10	10	31	21	18	34	180	6	0	0	0	40	25		SI	5.55	0.800	0.0
31	6930.0	20	2	15.72	14	13	31	21	18	27	90	22	0	0	0	30	5		SI	6.03	0.210	0.0
31	5472.0	20	2	19.69	18	15	31	23	18	40	0	0	0	1	0	15	17		Su4	7.00	0.592	-
31	6908.0	20	2	15.90	12	12	31	21	18	27	315	17	0	0	0	20	70		SI	6.33	2.800	0.0
31	4681.4	20	2	37.11	14	13	31	25	18	39	0	13	0	0	0	-	-			7.64	0.053	0.0
30	9730.0	20	1	11.50	10	9	31	16	18	45	315	5	30	0	0	-	60		rocky	-	-	0.0
30	9729.0	20	1	13.80	8	8	31	16	18	45	225	2	30	0	0	-	40		rocky	-	-	0.0
30	7224.0	20	1	13.50	9	8	31	56	19	1	0	0	0	0	15	10		Su2	7.86	0.310	4.0	
30	9733.0	20	1	11.70	5	4	31	11	18	46	292	1	5	0	0	5	5		Su2	7.35	0.050	0.0
30	7223.0	20	1	15.85	9	9	31	56	19	2	0	0	0	0	0	10	1		Su2	7.26	0.350	0.0
30	7222.0	20	1	22.00	9	8	31	56	19	2	0	0	0	0	0	15	1		Su2	6.95	0.140	0.0
30	7167.0	20	1	16.71	14	14	31	26	18	33	220	7	0	0	0	20	20		SI	5.50	0.050	0.0
30	6931.0	20	1	15.95	19	19	31	21	18	27	0	0	0	0	0	-	50		SI	4.04	0.370	0.0
30	738.0	20	1	16.45	12	12	31	23	18	41	45	4	70	0	0	20	50		LS	4.82	0.420	0.0
30	2913.0	20	1	29.07	21	18	31	24	18	37	95	1	0	0	0	23	1		Ls2	7.06	0.129	0.0
30	6901.0	20	1	12.80	9	9	31	24	18	39	1	22	0	0	0	30	1		SI	5.97	0.970	0.0
30	2928.1	20	1	43.45	17	14	31	26	18	29	293	3	0	0	0	9	6		SI	6.68	0.114	0.0
29	7143.0	19	3	25.62	11	10	31	23	18	42	0	0	0	0	0	60	1		SI2	7.20	3.690	3.2
29	7107.0	19	3	22.05	8	8	31	18	18	47	0	0	0	0	0	25	1		Su	7.60	1.130	0.0
29	9740.0	19	3	15.20	5	4	31	15	18	38	0	0	0	0	0	-	-		-	-	-	0.0
29	7106.0	19	3	26.70	10	10	31	19	18	46	0	0	0	0	0	30	1		SI	8.23	0.420	4.0
29	9665.0	19	3	36.20	10	10	31	24	18	40	0	0	0	0	0	-	-		-	-	-	3.2
29	6943.0	19	3	7.07	9	7	31	9	18	39	337	5	0	0	0	20	1		SI	6.96	1.830	0.0
29	7147.0	19	3	23.51	9	7	31	22	18	42	0	0	0	0	0	40	1		SI	8.22	1.820	2.0
29	6935.0	19	3	26.63	13	12	31	13	18	35	0	0	0	0	0	30	20		SI	8.30	0.210	3.4
29	7034.0	19	3	27.75	9	9	31	24	18	31	0	0	0	0	0	30	-		SI	-	-	3.4
28	7146.0	19	3	39.12	12	10	31	22	18	42	0	0	0	0	0	50	10		SI	8.00	0.220	2.0
28	2909.1	19	2	64.14	24	16	31	26	19	52	0	0	0	0	0	38	2		L12	8.00	5.570	3.4
28	7225.0	19	2	14.20	9	8	31	56	19	1	0	0	0	0	0	10	1		Su	7.11	0.280	0.0
28	7038.0	19	2	27.75	13	11	31	10	18	33	0	0	0	0	0	40	5		SI	8.34	0.440	5.0

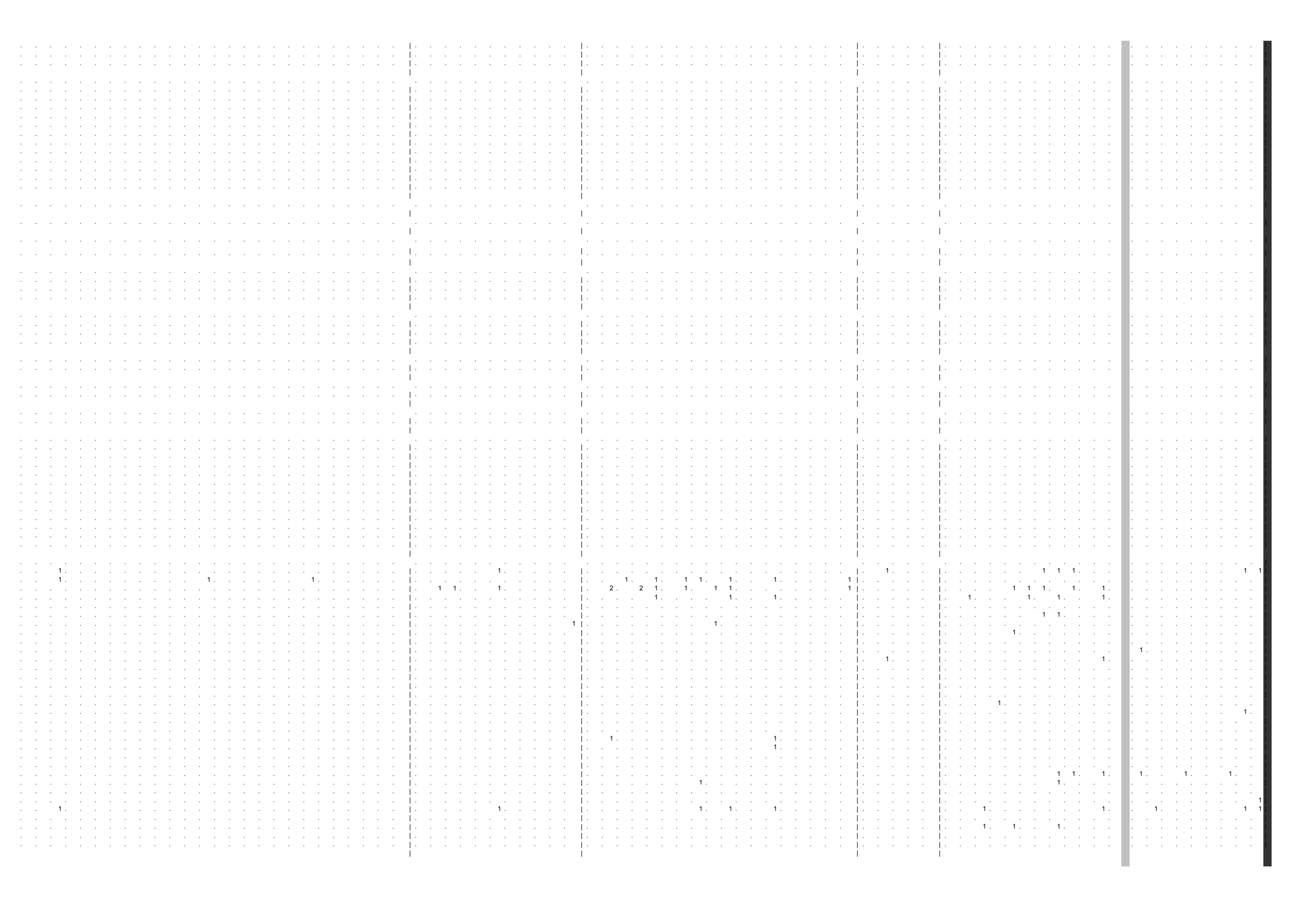


Thesium sp. (Schulte 93529 HGB)																																
D																																
Cladoraphis spinosa (L.f.) S.M.Phillips																																
Bromus pectinatus Thunb.																																
Wiborgia sericea Thunb.																																
Euphorbia burmannii E.Mey. ex Boiss.																																
E																																
Ruschia cf. ruschiana (Schulte 93302 HBG)																																
Helichrysum micropoides DC.																																
Ruschia excedens L.Bolus																																
Wahlenbergia annularis A.DC.																																
Osteospermum pinnatum (Thunb.) Norl.																																
Vanzijlia annulata (A.Berger) L.Bolus																																
Schismus barbatus (Loefl. ex L.) Thell.																																
Senecio arenarius Thunb.																																
F																																
Ruschia sp. (Schmiedel 104621 HBG)																																
Drosanthemum curtophyllum L.Bolus																																
Stipagrostis obtusa (Deille) Nees																																
G																																
Stipagrostis namaquensis (Nees) De Winter																																
H																																
Ruschia robusta L.Bolus																																
I																																
Ruschia versicolor L.Bolus																																
J																																
Leipoldtia calandra (L.Bolus) L.Bolus																																
Ruschia lisabelliae L.Bolus																																
K																																
Cephalophyllum parvibracteatum (L.Bolus) H.E.K.Hartmann																																
Hallianthus planus (L.Bolus) H.E.K.Hartmann																																
L																																
Brownanthus ciliatus (Aiton) Schwantes																																
Ruschia spinosa (L.) Dehn																																
Rhinephyllum macradenium (L.Bolus) L.Bolus																																
Arenifera stylosa (L.Bolus) H.E.K.Hartmann																																
Tylecodon wallichii (Harv.) Tölken																																
Eriocephalus ericoides (L.f.) Druce																																
Cheiridopsis cigarettifera (A.Berger) N.E.Br.																																
M																																
Psilocaulon leptarthron (A.Berger) N.E.Br.																																
Tripteris clandestina Less.																																
Euphorbia mauritanica L.																																
Drosanthemum sp. (Schmiedel 104614 HBG)																																
Euphorbia exilis L.C.Leach																																
Aridaria noctiflora (L.) Schwantes ssp. noctiflora																																
Euphorbia muricata Thunb.																																
Asparagus suaveolens Burch.																																
Salsola sp. (Schmiedel 93117 HBG)																																
Stipa capensis Thunb.																																
N																																
Ruschia patulifolia L.Bolus																																
O																																
Drosanthemum roseatum (N.E.Br.) L.Bolus																																
P																																
Cephalophyllum framesii L.Bolus																																
Q																																
Ruschia stricta L.Bolus var. turgida L.Bolus																																
Antimima komkansica (L.Bolus) H.E.K.Hartmann																																
R																																
Drosanthemum decudum H.E.K. Hartmann & Bruckmann																																
S																																
Drosanthemum hispidum (L.) Schwantes																																
T																																
Melolobium candicans (E.Mey.) Eckl. & Zeyh.																																
Hermannia cuneifolia Jacq.																																
Tribolium echinatum (Thunb.) Renvoize																																
U																																
Ruschia subsphaerica L.Bolus																																
V																																
Aridaria serotina L.Bolus																																
Ruschia sp. (Bartels 93268 HBG)																																
Tripteris hyoseroides DC.																																
Antimima intervallaris (L.Bolus) H.E.K.Hartmann																																
W																																
Crassula columnaris Thunb. ssp. prolifera Friedrich																																
Senecio aloides DC.																																
Crassula deceptor Schönland & Baker f.																																
Sarcocornia xerophila (Toelken) A.J.Scott																																
Bulbine sedifolia Schltr. ex Poelln.																																
Bulbine mesembryanthemoides Haw.																																
X																																
Drosanthemum diversifolium L.Bolus																																
Argyroderma fissum (Haw.) L.Bolus																																
Phyllobolus spinuliferus (Haw.) Gerbaulet																																
Y																																
Argyroderma delaetii C.A.Maass																																
Cephalophyllum spissum H.E.K.Hartmann																																
Othonna intermedia Compton																																
Zygophyllum teretifolium Schltr.																																
Cephalophyllum caespitosum H.E.K.Hartmann																																
Adromischus marianiae (Marloth) A.Berger																																
Diplosoma luckhoffii (L.Bolus) Schwantes ex Ihlenf.																																
Cephalophyllum staminodosum L.Bolus																																
Conophytum subfenestratum Schwantes																																

Phyllobolus sinuosus (L.Bolus) Gerbaulet		
Brunsvigia radula (Jacq.) Aiton		
Pharnaceum elongatum (DC.) Adamson		
AY		
Antimima sp. (Schmiedel 104874 HBG)		
Suaeda sp. (Schmiedel 102015 HBG)		
Adenoglossa decurrens (Hutch.) B.Nord.		
Lithops meyeri L.Bolus		
Octopoma connatum (L.Bolus) L.Bolus		
Galenia crystallina (Eckl. & Zeyh.) Fenzl		
Antimima sp. (Schmiedel 102039 HBG)		
Cheiridopsis acuminata L.Bolus		
Arenifera pillansii (L.Bolus) Herre		
Conophytum maughanii N.E.Br. ssp. latum (Tischer) S.A.Hammer		
Nelia pillansii (N.E.Br.) Schwantes		
Ruschia paucipetala L.Bolus		
Crassula subaphylla (Eckl. & Zeyh.) Harv. var. subaphylla		
AZ		
Ruschia leucosperma L.Bolus	1.	1.
BA		
Cephalophyllum regale L.Bolus		
BB		
Aspazoma amplectens (L.Bolus) N.E.Br.		5.
Leipoldtia klaverensis L.Bolus		
BC		
Eberlanzia cyathiformis (L.Bolus) H.E.K.Hartmann		
Leipoldtia laxa L.Bolus		
Ceraria fruticulosa H.Pearson & Stephens		
Ruschia atrata L.Bolus		
BD		
Schlechteranthus hallii L.Bolus		
Euphorbia gummifera Boiss.		
Conophytum gratum (N.E.Br.) N.E. Br.		
Galenia dregeana Fenzl ex Sond.		
BE		
Brownanthes pubescens (N.E.Br. ex C.A.Maass) Bullock		
Ruschia inconspicua L.Bolus		
BF		
Brownanthes schlichtianus (Sond.) Ihlenf. & Bittrich		
Prenia tetragona (Thunb.) Gerbaulet		
BG		
Cheiridopsis robusta (Haw.) N.E.Br.		
Euphorbia ephedroides E.Mey. ex. Boiss.		
BH		
Sarcocaulon crassicaule Rehm		
Crassula grisea Schönland		
Euphorbia decussata E.Mey. ex Boiss.		
Trachyandra muricata (L.f.) Kunth		
Othonna obtusiloba Harv.		
Cephalophyllum numeesense H.E.K.Hartmann		
Anacampseros papyracea E.Mey. ex Fenzl ssp. namaensis Gerbaulet		
Crassula expansa Dryand. ssp. expansa		
Tetragonia reduplicata Welw. ex Oliv.		
Zygophyllum prismatocarpa E.Mey. ex Sond.		
Salsola sp. (Schmiedel 5030 HBG)		
Triptaris microcarpa Harv. ssp. septentrionalis (Norl.) B.Nord.		
Portulacaria pygmaea Pillans		
BI		
Asparagus capensis L. var. capensis		1.
Zygophyllum cordifolium L.f.	1.	1
Atriplex lindleyi Moq. ssp. inflata (F.Muell.) Paul G.Wilson	1.	1
Salsola zeyheri (Moq.) Bunge	1	1
Tetragonia fruticosa L.	1.	1
Crassula tomentosa Thunb. var. tomentosa		1.
Phyllobolus trichotomus (Thunb.) Gerbaulet		1.
Tetragonia verrucosa Fenzl	1.	1.
Drosanthemum cf. muirii (L. Bolus)	1.	1.
Hypertelis salsoloidea (Burch.) Adamson		1.
Lampranthus watermeyerii (L.Bolus) N.E.Br.		1.
Crassula subaphylla (Eckl. & Zeyh.) Harv. var. virgata (Harv.) Toelken	1.	1.
Crassula elegans Schönland & Baker f.		1.
Rhynchosidium pumilum (L.f.) DC.		1.
Othonna protecta Dinter		1.
Gazania lichtensteinii Less.		1.
Oxalis pes-caprae L.		1.
Anacampseros namaquensis H.Pearson & Stephens		1.
Triptaris oppositifolia (Aiton) B.Nord.		1.
Hoplophyllum spinosum DC.		1.
Pteronia glabrata L.f.	1.	
Triptaris sinuata DC. var. sinuata		1.
Psilocaulon dinteri (Engl.) Schwantes	1	1
Haworthia arachnoidea (L.) Duval		1.
Antimima watermeyerii (L.Bolus) H.E.K.Hartmann	1	1
Galenia fruticosa (L.f.) Sond.		1.
Jacobsenia kolbei (L.Bolus) L.Bolus & Schwantes		1.
Crassula expansa Dryand. ssp. pyriformis (Compton) Toelken		1.
Didelta carnosus (L.f.) Aiton	1.	1
Berkheya fruticosa (L.) Ehrh.		1.
Tylecodon reticulatus (L.f.) Tölken	1.	1.
Crassula muscosa L. var. muscosa		1.
Eriocaulon namaquensis M.A.N. Müller		1.

for non-diagnostic species see synoptic table





1. 1. 1.

1. 1. 1.

2. 1. 2. 1. 1. 1. 1. 1. 1. 1.

1. 1.

1. 1. 1. 1. 1. 1. 1. 1.

1. 1.

1.

1.

1.

1.

1. 1.

1. 1. 1.

1.

1.

1. 1. 1. 1. 1.

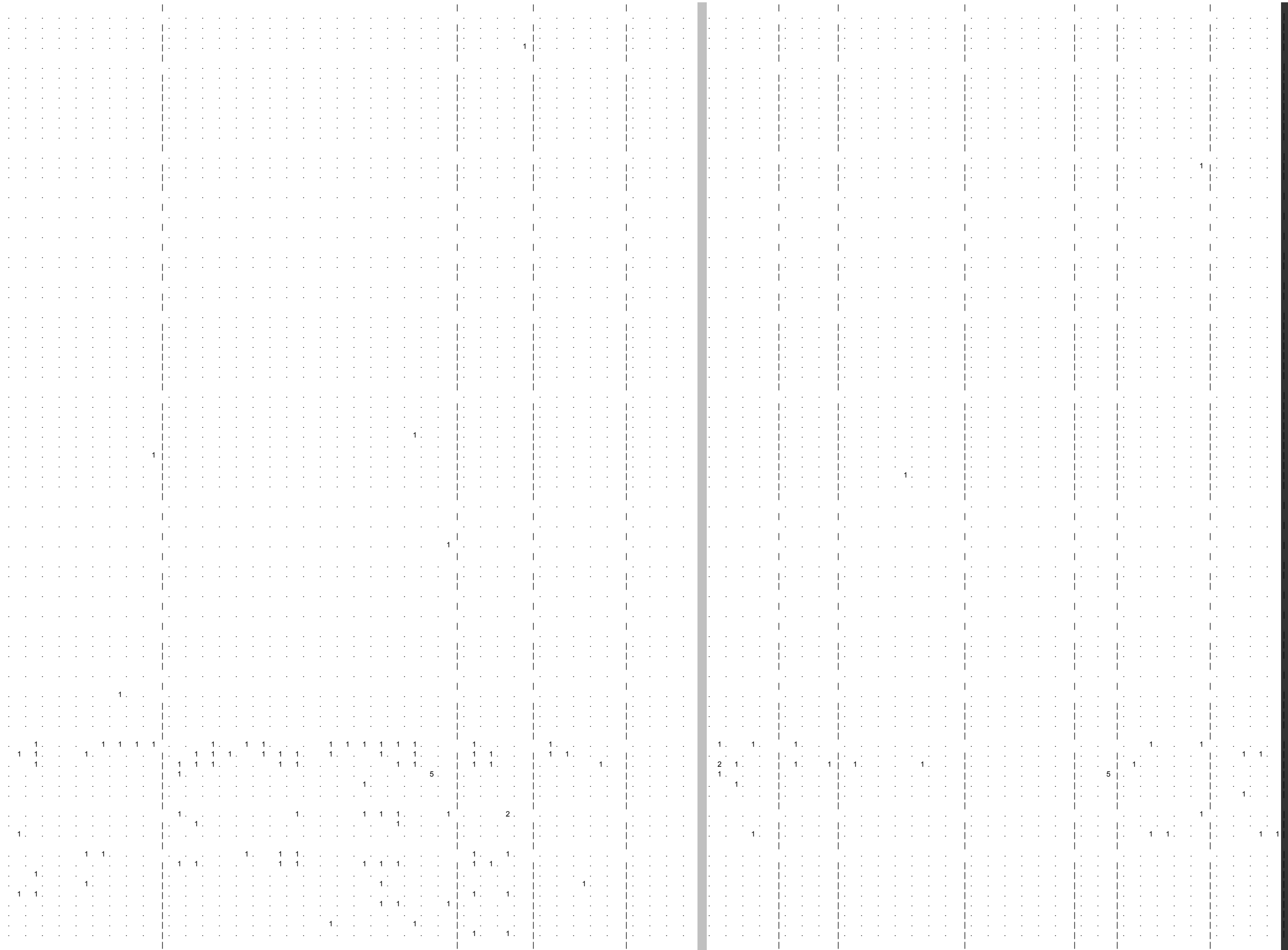
1.

1. 1. 1.

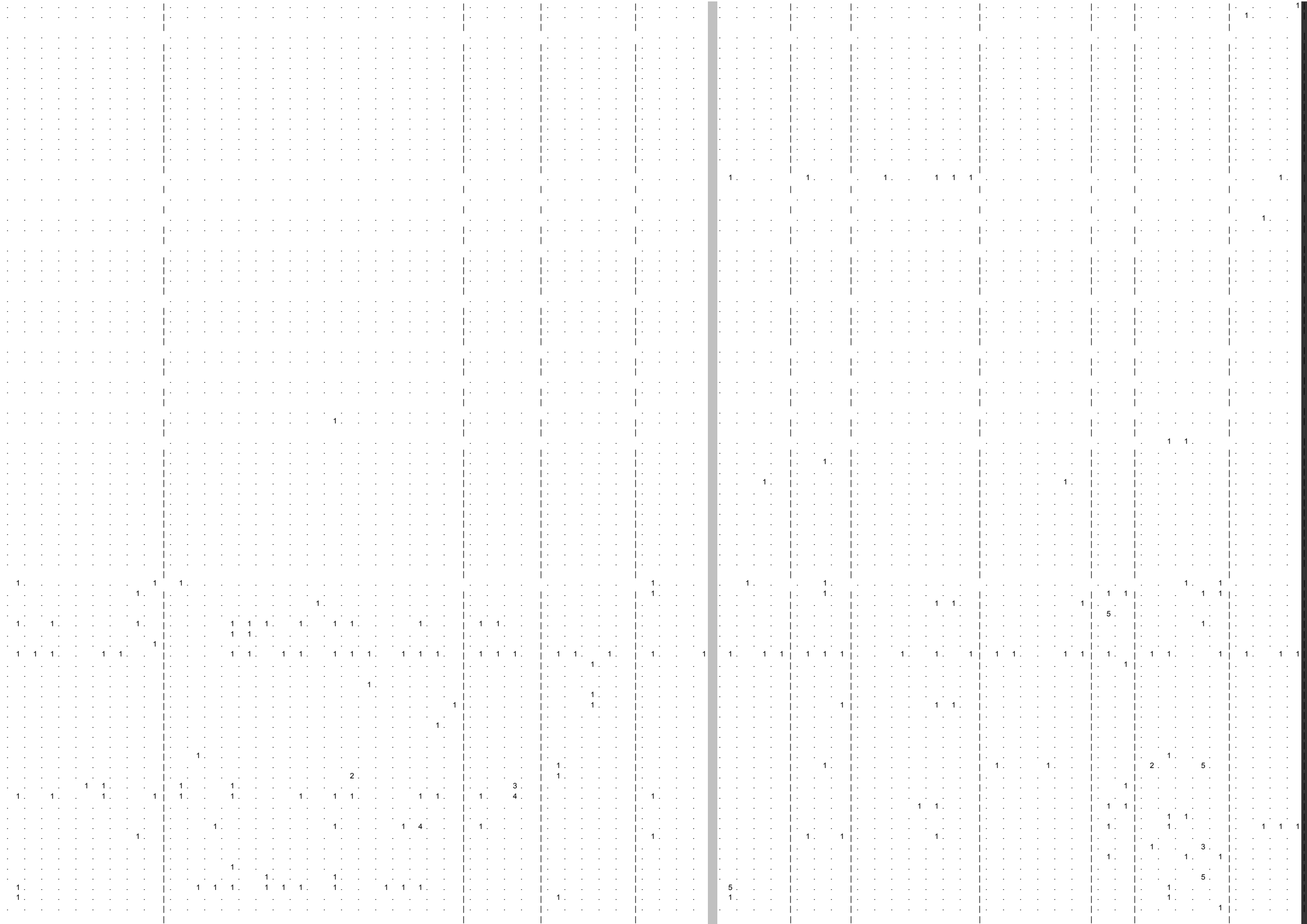
1. 1. 1. 1.

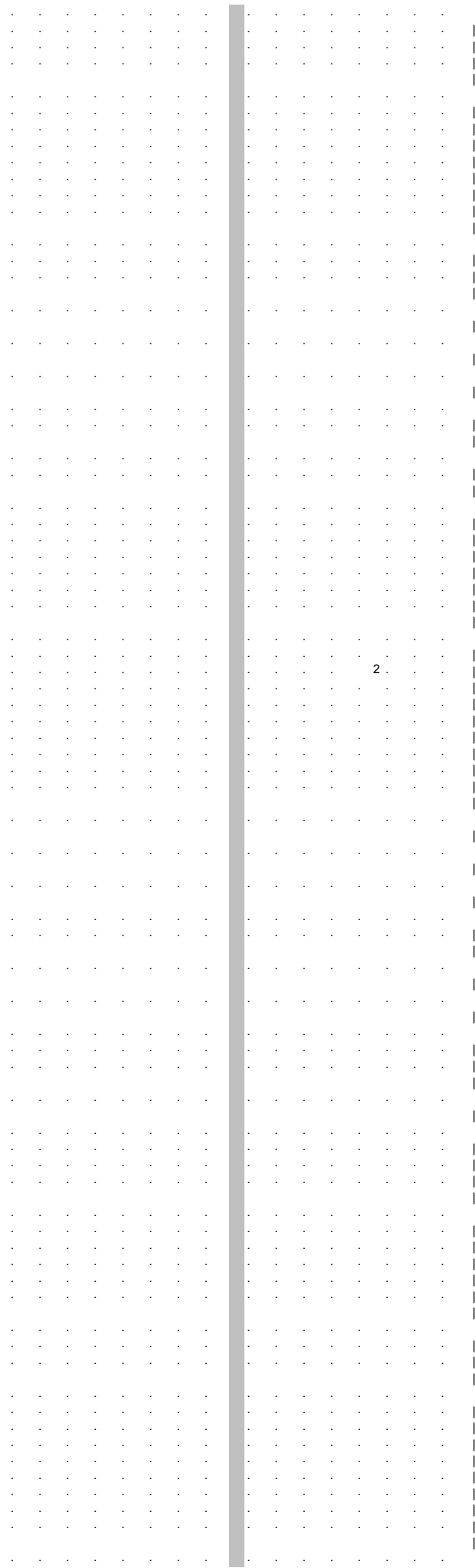
1.

1. 1.

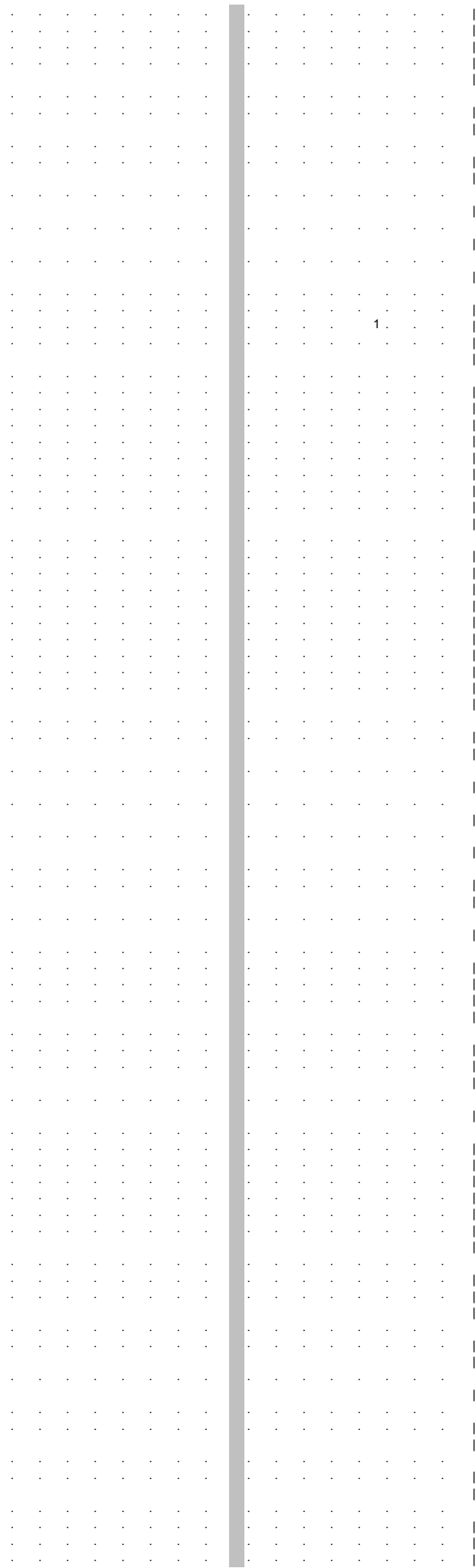


This image shows a large grid of dots, similar to a dot grid paper. The grid is divided into several vertical columns by dashed lines. A prominent vertical grey bar runs down the right side of the grid. Scattered throughout the grid are small numbers, including 1, 2, 3, 4, 5, 6, and 7. These numbers are often placed at the intersections of the grid lines. The numbers are distributed across the grid, with some appearing in clusters and others in isolation. The overall layout is sparse and appears to be a template or a collection of data points.





2



1.

