# How to assess rangeland condition
# in semiarid ecosystems?

## The indicative value of vegetation
## in the High Atlas Mountains, Morocco

vorgelegt von

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# Abstract

The natural resource base of the world's drylands is under continuous threat, particularly due to immense population growth, climate and land use change. Since the majority of these ecosystems are used as rangelands for domestic livestock, forage is (beneath drinking water) one of the most required ecosystem goods. For local land users as well as policy-makers it is crucial to quantify the actual supply of forage and try to predict potential limitations in the future. Ecological indicators as easily interpretable surrogates for complex ecological processes play an important role to assess rangeland condition. However, in highly stochastic arid and semiarid ecosystems it is still a challenge to identify reliable indicators detecting anthropogenic change against a background of natural variability.

The present dissertation investigates three currently discussed rangeland indicators and their significance along a steep gradient of natural variability in southern Morocco. The research was conducted on four altitudinal levels along the southern slopes of the High Atlas Mountains. The transect represents a steep aridity gradient stretching from arid climate in the Basin of Ouarzazate to subhumid climate in the high mountain areas.

First, the production (ANPP) and rain-use efficiency (RUE) of the vegetation was analyzed by means of an ecological field experiment comparing grazed, 1 year and 7 years rested vegetation. It revealed that ANPP and RUE are suitable and relatively 'fast' indicators to quantify the actual supply of forage, but not to detect long-term and irreversible degradation processes. For that, the new parameters $ANPP_{rel}$ and $RUE_{rel}$ are suggested, which standardize the production on the amount of initial biomass. In contrast to ANPP and RUE, they focus on the vitality of perennial forage plants which is altered on a longer time scale and allows a better comparison across ecosystems.

Second, plant functional types (PFT) were tested as indicators. Particularly response groups and response traits were assembled to quantify grazing impact. In contrast to the initial goals of PFT research, those indicators were shown to be locally limited, since their predictive value was strongly influenced by resource

stochasticity (aridity). It is deduced that using response groups and response traits for range assessment in arid and semiarid ecosystem is only reliable if their application is restricted to the local scale.

Third, this work examines the local ecological knowledge of nomadic land-users in the research area. An interdisciplinary study among herdsmen of a local Berber fraction discovered that the 'reliability' of plants and pastures functions as a local indicator which influences local range management. The 'reliability'-concept integrates several spatial and temporal scales. It provides a new opportunity to quantify anthropological information and to compare it to ecological data.

The present work depicts an important milestone for the application of ecological indicators in range assessment. It is essential for land users and policy-makers to choose the appropriate indicator level not only to economize costs and manpower, but also to reduce bias in indication processes. A combination of several hierarchically operating indicators is suggested for arid and semiarid ecosystems, for example measures of ANPP/RUE to quantify actual forage supply of pastures and $ANPP_{rel}/RUE_{rel}$ to detect areas affected by long-term degradation. Results of this work further build a data base for two different vegetation models.

In the context of rapid climate and land use change we cannot afford further debates whether environmental changes have been caused by human impact or are just an impression of natural variability. My work shows the potential and limits of three ecological indicators under semiarid climate. It thus provides the framework for an appropriate application that allows an indication of human impact against a background of resource variability.

# Zusammenfassung

Die natürlichen Ressourcen in den Trockengebieten der Erde sind durch das anhaltende Bevölkerungswachstum sowie durch den Klima- und Landnutzungs-wandel bedroht. Da ein Großteil dieser Ökosysteme als Weideflächen genutzt wird, ist die Ressource „Futter" neben Trinkwasser eine der meistgefragten Ökosystem-Güter (ecosystem good). Es ist sowohl für lokale Landnutzer als auch für örtliche Entscheidungsträger unerlässlich, das aktuelle Futterangebot quantitativ bestimmen und eine potentielle Ressourcenverknappung in der Zukunft vorhersagen zu können. Dabei spielen ökologische Indikatoren als einfache Zeigerwerte für komplexe ökologische Prozesse eine wichtige Rolle. Da aride und semiaride Ökosysteme durch eine natürliche Unberechenbarkeit der Ressourcen gekennzeichnet sind, ist es jedoch immer noch eine große Herausforderung Indikatoren zu benennen, die vor diesem Hintergrund der natürlichen Ressourcenvariabilität zuverlässig anthropogene Umwelt-veränderungen anzeigen.

In der hier vorgelegten Arbeit wird die Wirkungsweise dreier aktuell angewandter Weideindikatoren entlang eines steilen Umweltgradienten in Südmarokko untersucht. Die Forschungsarbeiten wurden auf vier Höhenstufen am Südhang des Hohen Atlas Gebirges durchgeführt. Dieses Transekt stellt gleichzeitig einen Ariditätsgradienten dar und erstreckt sich vom ariden Becken von Ouarzazate bis in die subhumiden Hochgebirgsregionen des zentralen Hohen Atlas.

In einem ersten Schritt wurden die Biomasseproduktion (ANPP) und die Regennutzungseffizienz (RUE) der Vegetation mithilfe eines Feldexperimentes untersucht, bei dem beweidete Flächen, 1 Jahr geschonte und 7 Jahre geschonte Flächen miteinander verglichen wurden. Die Studie ergab, dass ANPP und RUE geeignete und relativ schnell reagierende Indikatoren darstellen um das aktuelle Futterangebot einer Weide zu messen, sie jedoch nicht geeignet sind, um langfristige irreversible Degradationsprozesse aufzuzeigen. Für diese Anwendung werden $ANPP_{rel}$ (relative Biomasseproduktion) und $RUE_{rel}$ (relative Regennutzungseffizienz) als neue Parameter vorgeschlagen, die die Biomasse-produktion bzw. Regennutzungseffizienz auf die Menge der produzierenden Biomasse standardisieren. Im Gegensatz zu ANPP und RUE stellen diese neuen

Indikatoren die Vitalität ausdauernder Weidepflanzen in den Vordergrund und machen es so möglich, Weidezustände zwischen verschiedenen Ökosystemen zu vergleichen.

Im zweiten Teil wurde der Indikatorwert von Pflanzenfunktionstypen getestet (PFT), insbesondere der sogenannter 'response groups' (Gruppe von Pflanzenarten, die dieselbe Reaktion auf Störung, z.B. Beweidung zeigen) bzw. 'response traits' (Gruppe von Pflanzenmerkmalen, die dieselbe Reaktion auf Störung zeigen). Ursprünglich war das Ziel der PFT-Forschung arten- und damit gebietübergreifende Indikatoren zu finden. Unsere Studie zeigte aber, dass die Anwendung von 'response groups' und 'response traits', um den Einfluss von Beweidung auf die Vegetation in semiariden Gebieten zu messen, nur räumlich beschränkt möglich ist, da die Güte dieser Indikatoren stark von der Aridität des jeweiligen Standortes abhing.

Der letzte Teil widmet sich dem lokalen Wissen von Nomaden im Untersuchungsgebiet. Die interdisziplinäre Studie fand mithilfe des Wissens von Hirten eines örtlichen Berberstammes heraus, dass die 'Verlässlichkeit' von Pflanzen bzw. Weiden einen lokalen Indikator darstellt, der das Wirtschaften der Nomaden entscheidend beeinflusst. Das 'Verlässlichkeits'-Prinzip ist ein integrativer Ansatz, der auf verschiedenen räumlichen und zeitlichen Ebenen angewendet werden kann. Es stellt eine neue Möglichkeit dar, ethnologische Informationen in Zahlen zu fassen und sie so mit ökologischen Daten zu vergleichen.

Die vorgelegte Arbeit stellt einen entscheidenden Meilenstein hin zur sachgemäßen Anwendung von ökologischen Indikatoren bei der Weidebeurteilung dar. Für Landnutzer und lokale Entscheidungsträger ist es bei der Wahl des passenden Indikatorlevels nicht nur wichtig, Kosten und Personal zu sparen sondern auch systematische Fehler bei der Indikation zu reduzieren. Deshalb wird in dieser Arbeit eine Kombination aus mehreren Indikatoren vorgeschlagen, um Umweltveränderungen, die auf verschiedenen hierarchischen Ebenen ablaufen, erkennen zu können. Im Zuge des raschen Klima- und Landnutzungswandels können wir es uns nicht länger leisten, lange Debatten zu führen, ob vergangene Umweltveränderungen in semiariden Gebieten natürlichen oder anthropogenen Ursprungs waren. Diese Arbeit zeigt sowohl das Potential als auch die Beschränkungen dreier ökologischer Indikatoren zur Weidebeurteilung in semiariden Gebieten. Sie ist damit die Vorraussetzung für

ihre sachgemäße Anwendung und macht es möglich, den Einfluss von Beweidung auf die Vegetation unabhängig von der natürlichen Ressourcen-variabilität zu messen.

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# 1 General introduction

## 1.1 The world's drylands

Drylands have been considered as the 'unappreciated gift' of nature (UNDP 2008b). They are characterized by an aridity index value of less than 0.65, that means annual potential evapotranspiration exceeds annual precipitation by a minimum factor of 1.5 (Middelton & Thomas 1997). Additionally, rainfall variability is very high both on the spatial and temporal scale. Drylands comprise more than 40 % of the earth's land surface and 65 % of the African continent (Fig. 1.1). More than one third of the world's total population, approximately 2.5 billion people, actually inhabit drylands (MEA 2005). The highest population growth rates were experienced in the 1990s (UNDP 2008a).
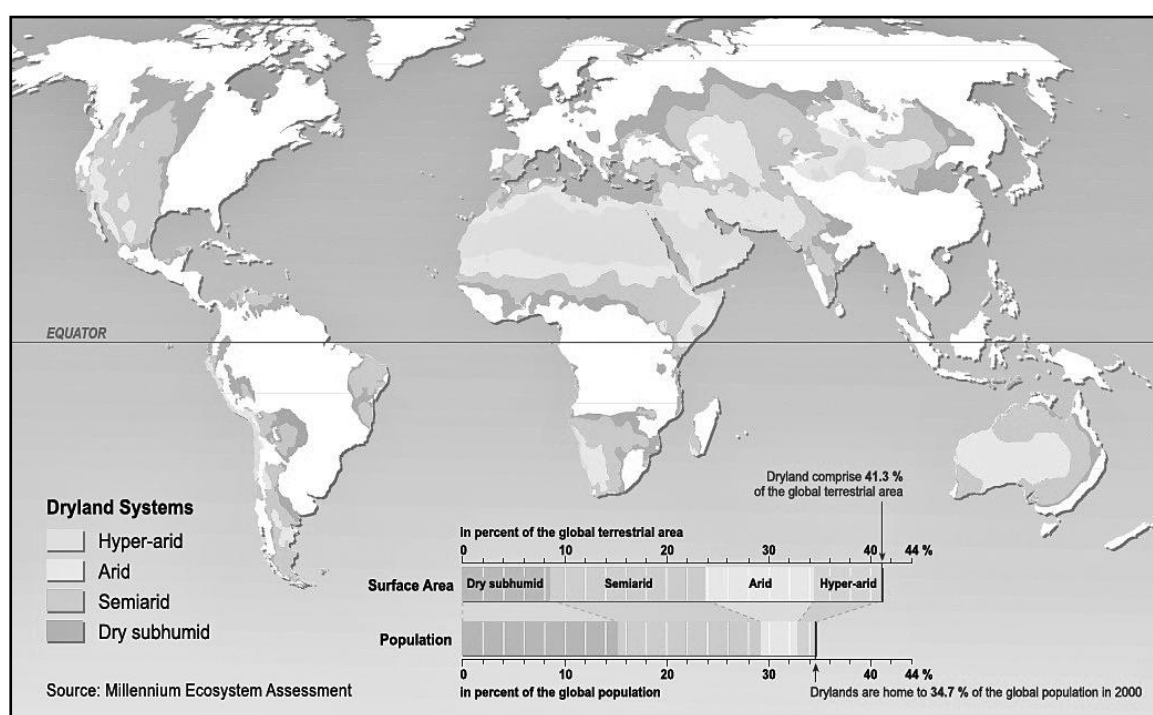
**Fig. 1.1** Location and classification of the world's dryland systems according to the MEA (2005). The greyscale represents the aridity zone from hyper-arid (light grey) to dry subhumid areas (dark grey).

The majority of drylands is used as pastures for domestic livestock (Darkoh 2003). Depending on aridity (Fig. 1.1), pastoral use is either the sole type of human land use or complemented by extensive rain-fed cropping and forestry (Darkoh 2003). Pastoralism is defined as a production system in which 50 % or

more of the household gross revenue comes from livestock or livestock-related activities (Niamir-Fuller 1998). Extensive pastoral production takes place on about 25 % of the world's land area and provides about one tenth of the global meat production. It supports between 100 and 200 million households and comprises herds of nearly a billion head of camel, cattle and smaller livestock (Gertel & Breuer 2007).

Drylands are vast but sparsely inhabited areas. Nomadism and transhumance are the most common land use practices. While nomadism is characterized by high mobility without any fixed abode (e. g. Saharan nomads), transhumance indicates a highly mobile production system where people and herds move between definite seasonal bases (e.g. herders in the High Atlas Mountains, Morocco) (Niamir-Fuller 1998). Little is known about the economic contribution of mobile pastoralists to the agricultural GDP (Gross Domestic Product) of a country. However, in some African countries, pastoralism in general contributes up to 84 % (Niger) to the agricultural GDP (Hatfield & Davies 2006).

The natural resource base of drylands is under continuous threat, particularly due to the immense population growth, climate and land use change. Throughout the world, human population growth is expanding the areas of settlement in arid lands and creating new demands for water. The population of arid lands is increasing at a rate much faster than the global average and is becoming increasingly urbanized. The growth of the urban fraction in drylands is projected to increase to around 52 % by 2010 and to 60 % by 2030 (MEA 2005).

Drylands are expected to undergo significant climate changes, but there is considerable variability and uncertainty in these estimates between different scenarios. For Africa, regional models project for the period 2080-2099 a temperature increase between 3 °C and 4 °C compared to 1980-1999. For the same period, precipitation is expected to decrease in most of the dryland areas by 20 % to 40 %, while tropical and eastern Africa are expected to future increases (Boko *et al.* 2007). For a majority of drylands, rainfall variability will additionally increase. Both population growth and climate change are important drivers for ongoing land use changes in drylands. These include the expansion of agricultural land, increasing sedentarization of mobile pastoralists, intensification of livestock production, overgrazing, tremendous migration, and urbanization (Foley *et al.* 2005).

Population growth, climate and land use change do and will further contribute to the loss of ecosystem services in drylands. Ecosystem services comprise all components of nature, which are directly enjoyed, consumed, or used to yield human well-being (Boyd & Banzhaf 2007). The Millennium Ecosystem Assessment (Safriel & Adeel 2005) categorized ecosystem services into supporting services (soil, nutrients, primary production), regulating services (water and climate regulation), provisioning services (food, fibre, fuel, freshwater), and cultural services (cultural identity, spiritual service).

The loss of ecosystem services is related to land degradation and desertification in drylands. In the broader sense, degradation determines an irreversible decline in land quality caused by human activities. In ecological research, however, degradation is often limited to the supporting services of ecosystems and measured as decrease in net primary production (Bai *et al.* 2008). According to this definition and an observation period from 1981 to 2003, the southern parts of Africa were most severely affected by degradation, accounting for 13 % of the global degrading area and 18 % of lost global net primary production (Bai *et al.* 2008).

Since drylands are subjected to high variability, e.g. in net primary production, even without human land use, it is unlikely to describe degradation processes by a succession of stable states. The latter is known from typical climax communities, for example temperate forests (Begon *et al.* 2006). However, ecologists and stakeholders ask how to assess the condition of a dryland system and want to quantify its vulnerability to future environmental or human impact. Resilience is a concept that is able to describe this condition. Since the 1970s, vigorous discussions have been going on how to define and how to assess resilience, in particular of arid and semiarid ecosystems. Recently, two main concepts emerged which define resilience either as the magnitude of perturbation which is needed to change a system to an alternative state (Holling 1973) or as the speed of recovery from perturbation (Holling 1973; McCann 2000; Steiner *et al.* 2006). In this context, one advantage of the resilience concept is that it cannot only be applied to ecosystems but similarly to socio-ecological systems and socio-economic systems (Carpenter 2001; Holling 2001).

Land use practices that maintain the resilience of an ecosystem are characterized to be sustainable. Sustainability is one of the major development goals all over

the world. Therefore, it is a great task to achieve and discuss new methodological approaches that help us to quantify the resilience of dryland systems.

## 1.2 Dryland vegetation and its 'memory' character

The present work focuses on dryland vegetation. Drylands are predominantly used as rangelands, thus vegetation is part of an important ecosystem service as it supports forage for livestock production. Apart of drinking water, forage is one of the most quested ecosystem goods in drylands. Ecosystem goods include the 'big four' - food, forage, fuel, and fibre - as well as timber, many pharmaceuticals, industrial products, and their precursors (Daily *et al.* 1997; Van Lynden & Kuhlmann 2002).

As an ecosystem good, vegetation is directly interesting for local land users who aim to quantify the actual supply of forage and try to predict and cope with potential limitations in the future (Daily *et al.* 1997). The assessment of rangeland condition is thus one central element of their risk-management (Bollig & Göbel 1997).

Since ecosystems have the capacity to store water, carbon, and nitrogen in various pools, mainly in vegetation and soil, these pools provide a kind of ecosystem memory (Peterson 2002; Schwinning *et al.* 2004; Wiegand *et al.* 2004; Faber *et al.* 2005). This memory accumulates information on both past climate conditions, e.g. precipitation history, and land use, e.g. grazing regime. Schwinning et al. (2004) state that the system's memory of precipitation history can last at least several decades, indicated for example by the amount and composition of soil organic matter (Austin *et al.* 2004) or the vegetation composition by different functional types of plants (Reynolds *et al.* 2004).

The present research is focused on vegetation patterns and soil conditions in drylands for two reasons: First, vegetation and soil have an indicative value due to their memory function. They are capable to report past impacts of climate and land use. And second, information on dryland vegetation is in great demand because it is used as forage for livestock production. Local land users as well as politicians share our interest to quantify its present and future supply.

## 1.3   Range ecology

### *1.3.1 Overview*

Rangelands are not exclusively found in arid and semiarid regions, but there are large conceptual and spatial overlaps between drylands and rangelands. The dynamic processes shaping dry rangelands are particularly complex. Various interactions occur between climatic constraints, e.g. the amount and pulsing of rainfall, edaphic conditions, the history of land use, and the actual land use pressure (Milchunas & Lauenroth 1993; Ellis 1994; Snyman 1998; Swinton *et al.* 2007). These multiple interactions need to be understood in a fundamental way to provide a basis for a sustainable range management.  It is the principal purpose of range ecology to gain this understanding (Behnke *et al.* 1993). Range ecology is an interdisciplinary field of research that combines classical concepts and methods of vegetation ecology with the anthropocentric objectives of range management (Schulte 2002). These classical approaches are recently complemented by remote sensing techniques and anthropological methods. The most important methods of range ecology are presented in the next section.

All approaches serve the development of effective instruments to assess rangeland condition. Range ecology aims to describe the recent state of a pasture and the consequences of human land use. It equally compares and evaluates the sustainability of various management practices (Schulte 2002). The present dissertation addresses these typical issues of range ecology.

Range ecology research is linked to application since it may result in management strategies or strategies for the rehabilitation of overused rangelands (Garden & Dowling 2003; Sayre & Fernandez-Gimenez 2003; Weltz *et al.* 2003; IRC 2008). An additional task for range ecologists is to attend such rehabilitation measures and to quantify their success (Harrison & Shackleton 1999; van der Merwe & Kellner 1999; Kessler & Thomas 2006).

### *1.3.2 Methods in range ecology*

There are several methods used in range ecology. Some belong to the classical set of vegetation ecology methods, i.e. range monitoring, range assessment, and range experiments. Some were increasingly adopted from other disciplines, such as remote sensing, ecological modeling, and from anthropology.

*1.3.2.1   Classical methods of vegetation ecology*

*Range monitoring* is used to determine trends in range ecosystems by repeat sampling. It is generally conducted at permanent sampling sites in order to minimize confounding factors (MFR 1998). According to the objective of range monitoring different parameters can be sampled (Breckenridge *et al.* 1995), for example the composition of plant species (Carignan & Villard 2002; Buckland *et al.* 2005), phytomass (Franklin *et al.* 2008), or visible soil erosion (Herrick 2000).

*Range assessments* are evaluations made by comparing measurements from one sampling time against standards or objectives. This desired state or condition of the range is also known as benchmark. The definition of benchmarks is one major challenge in range ecology, because they vary between different areas and strongly depend upon the relevant group of land users (Friedel 1991). To approach local benchmarks or to estimate the extent of occurring changes due to livestock grazing, range ecologists often investigate gradients of either grazing history or actual grazing pressure (Beever *et al.* 2003; Landsberg *et al.* 2003; Adler & Hall 2005; Getzin 2005; Smet & Ward 2006). In this method, spatial changes are assumed to infer temporal dynamics caused by grazing impact. This assumption is known as space-for-time substitution (Pickett *et al.* 1989; Hooper & Dukes 2004). Range assessments are often conducted by observing conditions across broad areas of rangelands. So, sampling methods tend to be less rigorous than range monitoring methods (MFR 1998). For that, range assessment needs generally applicable plant indicators that may even be employed by non-scientifics (Friedel 1997; Hardy *et al.* 1999; Ludwig *et al.* 2004). Such indicators can focus on vegetation patterns like single species, plant composition, or biomass production and abiotic range conditions like soil texture, soil organic matter, or erosion (Beever *et al.* 2003; Niemi & McDonald 2004; Albon *et al.* 2007). A general overview about ecological indicators, related problems, and indicators used in this work is given in chapter 2.

For a functional understanding of grazing-dependent vegetation changes, there is a need to assess vegetation condition in relation to known rates of grazing intensity. *Manipulative experiments* fulfil this demand by simulating certain levels of grazing impact and giving the possibility to monitor vegetation response. Manipulation is achieved by controlling the stocking rate of a pasture

(enclosure), artificial removal of plants or plant parts, or by excluding grazing herbivores for a certain period of time (exclosure).

In the past years, numerous dryland studies applied fixed stocking rates to analyse the impact of grazing on vegetation and soil (Greenwood *et al.* 1997; Fynn & Connor 2000; Todd & Hoffman 2000; Bester & Reed 2003; Reed *et al.* 2003; Rothauge *et al.* 2004). Defoliation and removal experiments (clipping) are very time-consuming, however, these methods guarantee to control most of the plant-influencing factors (Abdelmagid *et al.* 1987; Jacobs & Schloeder 2003; Bazot *et al.* 2005; Alhamad & Alrababah 2008). Since the control of stocking rates and removal experiments are very cost-intensive and/or personnel-intensive, they were often applied over a short time period only. But dryland vegetation and soil are known to show very slow response to altered conditions (Dregne 2002).

Exclosure experiments may be conducted over a long time interval with a minimum effort. To a certain extent exclosure experiments help to reconstruct a range condition before the onset of herbivory. Changes in vegetation composition, structure, and physiognomy can be studied. During the past years long-term exclosures have been frequently applied in dryland systems (Gabriel *et al.* 1998; Valone *et al.* 2002; Kraaij & Milton 2006; Firincioglu *et al.* 2007; Manier & Hobbs 2007). It is equally worth to investigate exclosure experiments over a short time, for example during one vegetation period. Short-term exclosures are often smaller (cages) than long-term exclosures, sometimes even movable (Omer *et al.* 2006). They are particularly used to quantify differences in biomass production between grazed and excluded sites (McNaughton *et al.* 1996; Adler *et al.* 2005; McCulley 2005).

### 1.3.2.2   *New interdisciplinary approaches*

During the last decade, remote sensing methods became more and more important to answer questions of range ecology. Remote sensing has three main advantages: even remote locations are easily accessible, data is provided two-dimensional and on broad scales, vegetation processes may be observed on a long time scale (Roughgarden *et al.* 1991). That is why remote sensing is widely used to assess the impact of climate and land use change and why it is a powerful tool to communicate research results with policy-makers.

Remote sensing data is accessed via satellite observation of the earth's surface. Radiation from different parts of the electromagnetic spectrum is reflected from the earth and can be detected by various satellites. Radiation data is analysed and

can be transformed into two-dimensional images and maps (Wessels *et al.* 2007). Recent ecological studies highlighted the relevance of the Normalised Difference Vegetation Index (NDVI) as a remote sensing tool linking vegetation to animal performance (Pettorelli *et al.* 2005). The NDVI is calculated as a ratio (-1.0 - 1.0) from data of near-infrared and red light spectra which are reflected by vegetation. It allows drawing conclusions about the amount and photosynthetic activity of vegetation (Turner *et al.* 2003). NDVI data are available with a spatial resolution up to 250 m and a temporal resolution between 10 and 30 days intervals. Most of the ecological remote sensing studies investigated the impact of climate and land use on primary production (Jobággy *et al.* 2002; Scurlock *et al.* 2002; Blanco 2008; De la Maza *et al.* 2009; Herrmann *et al.* 2009). Since NDVI data are available as time series, they were used in modeling approaches and to forecast future changes of vegetation cover. For example, Scanlon *et al.* (2002) developed a model for savanna ecosystems. An empirical model using NDVI calculations to estimate vegetation dynamics in southern Morocco is currently in preparation (Fritzsche 2009).

Ecological modeling of ecosystem goods such as food and forage in relation to climate and land use change is a very new approach in ecology. It allows analysing the relationships between different actors in an ecosystem or social-ecological system, to quantify their impact, and to run (sometimes impossible but scientifically interesting) scenarios (Wainwright & Mulligan 2004). Depending on the research question of the model, it may provide forecasts, for example the forage production of rangelands according to different management scenarios. The present work builds (together with an anthropological study) the data base for the grazing model BUFFER, which is currently in preparation. It investigates the question how nomadic management strategies are connected to forage ressources in southern Morocco (Drees *et al.* 2009a; Drees *et al.* 2009b).

Range ecology analyses the impact of human land use practices on the environment. Ecologists can thus benefit from social sciences, particularly from those sub-sections in anthropology that exclusively study human's relation to nature. Local people can offer alternative insights and often have implicit knowledge of interrelated stochastic and deterministic processes (Eisold *et al.* 2009). In drylands, anthropologic research is particularly interested in mechanisms how local land users cope with the unpredictability of resources,

how mobile pastoralists perceive and evaluate their environment, and what kind of management they practise (Homewood & Rodgers 1984; Oba & Lusigi 1987; de Bruijn & van Dijk 1999; Adriansen 2005; Davies & Hatfield 2007; Rachik 2007). Investigating local ecological knowledge is one promising approach to address these questions. Range ecology may benefit from local knowledge, since it provides an alternative source of information from a knowledge base which has accumulated over long times of observation (Johnson 1992; Huntington 2000; Brook & McLachlan 2008). It may help to identify new paradigms to understand the relationship between range, herds, and herd management (Tengoe & Belfrage 2004; Fazey *et al.* 2006; Chalmers & Fabricius 2007; Katjiua & Ward 2007).

The present work focuses on range assessment, in particular on ecological indicators that help to assess range conditions. In this context classical and new methods of range ecology are applied and critically discussed. For example, permanent exclosures and short-term exclosures are used by means of a field experiment to assess biomass production. This section is closely related to a remote sensing study in the same area. Plant functional types are investigated as one type of indicator and local ecological knowledge is analysed to benefit from the insights of mobile pastoralists. The entire research given in this thesis contributes to an ecological model, which is currently in preparation.

# 2 The methodological framework

## 2.1 Ecological indicators

Since the beginning of mankind, humans use easily interpretable surrogates, today known as 'indicators', for complex processes in order to detect and predict environmental changes. Indicators serve to assess environmental conditions and are often used as early-warning signal for dangerous trends in nature (Niemi & McDonald 2004). For that, ecological indicators for changing climate and land use processes are currently in great demand by scientists, environmental managers, and policy-makers. Following the definition of Niemi & McDonald (2004), ecological indicators are defined as "measurable characteristics of the structure (…), composition (…), or function (…) of ecological systems". They are measurable on the genetic, population, community, and on the landscape level and are often derived from field measurements.

Ecological indicators should simplify nature's complexity. However, their application requires some preliminary consideration. First, ecological indicators differ according to their objective, i.e. whether they are used to assess environmental conditions, for example in range assessment, or to identify causes of environmental change (Dale & Beyeler 2001). Second, it is crucial to apply indicators adapted to the temporal and spatial scale on which ecological information is desired. Indicator species, for example, allow drawing conclusions on the local scale, while measurements of aboveground net primary production (ANPP) are useful on the regional scale (Wessels *et al.* 2007). Third, indicating range condition is a question of sensitivity. It requires knowledge on the statistical variability and the precision of applied indicators. Fourth, rangeland indicators are part of the assessed ecosystem and thus not exclusively linked to the impact of herbivores. That is why linkages of the indicator to other environmental constraints, for example resource dependencies, have to be quantified. Fifth, it is useful to check whether the ecological indicator is cross-linked to economic or social indicators. This may increase its explanatory power and enables a broad application.

Apart of these considerations, there still exists a certain lack of understanding between scientists who develop complex indicators and environmental managers

and policy makers who need easily assessable indicators that are understood by the broad public (Schiller *et al.* 2001). Indicator science currently experiences a fascinating development which includes new insights from molecular biology, better computer technology, for example geographic information systems, better facilities for data management and remote sensing methods (Niemi & McDonald 2004). These approaches will contribute to improve the applicability of ecological indicators.

## 2.2   Indicators on several hierarchical levels

Ecological indicators, e.g. plant indicators for range assessment, operate on different hierarchical levels according to the spatial and temporal scale of application. Significance on the temporal scale is strongly affected by the regarded level, i.e. whether we assess plant individuals, populations, species or communities. The spatial level and temporal level in turn influence the sensitivity and statistical variability of rangeland indicators.

Particularly in highly variable arid and semiarid environments, it is certainly a trade-off to choose a range indicator that is fast and sensitive enough to detect changes in grazing impact and that remains predictable even under variable climatic constraints (Niemi & McDonald 2004). On the lowest level, the level of *individual plants*, indicators can be derived from phenotypic plasticity. For example, plants may individually respond to herbivory by inducible resistance mechanisms such as higher concentration of secondary metabolites or structural defense (Herms & Mattson 1992; Agrawal 2000; Callaway *et al.* 2003; Koricheva *et al.* 2004). Indicators operating on the individual plant level are maximum sensitive to changes of grazing impact and may react within one or a few vegetation periods.

Plant *characteristics* (traits), *plant species*, or *groups of plant species* are very slow and less sensitive indicators because they are altered by competition, selection and evolutionary processes. The oldest concepts of vegetation ecology focused on biodiversity on the species level. Species composition was compared of grazed and ungrazed sites or along gradients of different grazing intensity. This led to the concept of indicator species, which has recently risen much debate and criticism (Landres *et al.* 1988; Niemi *et al.* 1997; Carignan *et al.* 2002; Rolstad *et al.*

2002). The major disadvantages are: The application of indicator species is spatially limited by the occurrence of the chosen species and it is not likely to understand the world's ecosystems by developing models for the interaction between single species. There is a need to simplify this complexity. During the past decades, indicator species were more and more replaced by various functional aggregations (Cousins & Lindborg 2004). Plants are, for example, grouped by life form (Raunkiaer 1934), growth form (Chapin III 1993), or by their ecological strategy (Grime 1979). Grime describes a plant strategy as "a grouping of similar or analogous genetic characteristics which re-occurs widely among species or populations and causes them to exhibit similar ecology". Plant species using the same strategy are known as a Plant Functional Type (PFT). Because of their functional relation to ecosystem processes, PFTs were promoted as perfect indicators (Landsberg *et al.* 1999; McIntyre & Lavorel 2001; Vesk & Westoby 2001; Cadotte 2005; Ansquer 2009). Since the beginning of PFT research, PFTs were used for two different purposes and with varying success. Species are either grouped on the basis that they use the same resource (functional guilds) or they are grouped because of the same response to disturbance, e.g. grazing impact (response groups) (Gitay & Noble 1997). Guilds have become well-established as indicators to analyse ongoing trends in the context of climate change (Skarpe 1996; Díaz *et al.* 1999; Hely *et al.* 2006; Keith *et al.* 2007;). Response groups were assembled in many regions of the world often with the objective to serve as indicators for range assessment (Friedel 1991; McIntyre *et al.* 1995; Landsberg *et al.* 1999; Ludwig *et al.* 2004; Cousins & Lindborg, 2004; Lavorel *et al.* 2007; Hassani *et al*. 2008). The latest level of abstraction no longer applies functional groups of plant species, but directly addresses single plant characteristics (traits) and their functional background as indicators (McIntyre *et al.* 1999; Bullock *et al.* 2001; Reich *et al.* 2003; Diaz *et al.* 2004; Adler *et al.* 2005; De Bello *et al.* 2005; Diaz *et al.* 2007; Rusch *et al.* 2009). Generally, traits, species, and functional aggregations may be applied as indicators to detect changes in vegetation composition occurring within several vegetation periods up to decades and centuries. It is thus often indispensable in field studies to make use of the concept of space-for-time substitution (see chapter 1.3.2.1). Traits, species, and PFTs are slow-operating indicators, which stay rather predictable under certain variability of other environmental conditions. Spatially, indicator species are limited from the local up to the regional scale, while PFTs and functional traits may be applied on broader scales (Cousins & Lindborg 2004).

On the *community level*, plant indicators deal with entire populations no matter of species, traits or PFTs. These indicators may be applied on very large scales, for example to assess environmental conditions of whole regions or countries (Wessels *et al.* 2007). They may react very fast, but are equally used to detect long-term trends by means of time-series analyses. The most frequently applied measures include vegetation standing crop, aboveground net primary production (ANPP), and nowadays rain-use efficiency (RUE). Vegetation standing crop is determined as the total living plant biomass per area (in kg*ha$^{-1}$) for a given point of time (Gurevitch *et al.* 2006). Standing crop is frequently used as indicator for the impact of human land use from the local up to the regional scale (Shackleton *et al.* 1994; Phinn *et al.* 1996; Zimmermann *et al.* 2001). ANPP and RUE, i.e. ANPP in relation to the amount of fallen rain, became important indicators since remote sensing offered the possibility to easily access data about entire regions and even worldwide (see chapter 1.3.2.2). Primary production (ANPP) is usually measured in kg/ (ha*a), while RUE is assessed in kg/ (ha*year) per mm precipitation. So far, ANPP and RUE were applied to indicate human land use and grazing impact (Guevara *et al.* 1997; Hirata *et al.* 2005; Haberl *et al.* 2007), degradation and desertification (Snyman 1998; Holm *et al.* 2003; Wesche & Retzer 2005; Bai *et al.* 2008), or climate change (Bai *et al.* 2008; De la Maza *et al.* 2009). Standing crop, ANPP, and RUE are very fast reacting indicators that may detect changes from one vegetation period to the next. However, biomass and production indicators are criticised (Prince *et al.* 1998) for responding to a complex suite of environmental factors at the same time.

Local ecological knowledge is a very new indicator in the ecological context and implicitly includes information on several hierarchical levels of plant organisation. According to their requirements, local land users may apply very detailed indicators, for example plant attributes or plant species (Cunningham 1992; Hillyer *et al.* 2006; Camou-Guerrero *et al.* 2008;), or very broad indicators, for example a classification of entire pastures according to several quality issues, which is a process operating on the community level. Little is known about the context how local land users developed such indicators, but we assume that the sensitivity and the temporal scale on which local indicators detect environmental changes may be similar to those of comparable taxonomic levels of the mentioned scientific indicators.

## 2.3 The challenge

The most essential task for a good ecological indicator is detecting anthropogenic change against a background of natural variability (Niemi & McDonald 2004). Particularly in highly stochastic arid and semiarid ecosystems, it is still a challenge to find such indicators for range assessment. That is why choosing the appropriate level of indication is not only a question of costs and manpower (Niemi & McDonald 2004). For example, indicators on a high hierachic level (community level) are often loosely coupled to the primary effects which they are intended to detect. This may result in a slower response time, high natural variability and low sensitivity (Jenkins & Sanders 1992). In short, it increases bias. However, the significance of recently used rangeland indicators and the related sources of bias caused by natural variability in drylands are so far not well understood (Niemi *et al.* 2004).

# 3 Introduction to the research area

The Kingdom of Morocco, in Arab language المغرب المملكة (Al-Mamlaka al-Maġribiyya), is situated at the ultimate north-east of the African continent. It stretches from the street of Gibraltar in the north (latitude 36° N; longitude 6° W) to the Sahara desert in the south (latitude 22° N; longitude 20° W) and is characterized by various topographical gradients. The dominating mountain chains are the Rif Mountains along the north coast, the Middle and the High Atlas Mountains as well as the Anti-Atlas Mountains as the southernmost elevation. Morocco's highest peak is the Jebel Toubkal with 4,165 m situated in the southwest of the central High Atlas. The northern and western parts of the country comprise spacious coastal plains, whereas the southern parts are dominated by the dry alluvial plains of the Sahara basin. The investigation area of the present work limits to the northern catchment of the river Drâa situated at the southern slopes of the High Atlas Mountains (Fig. 3.1, Fig. 3.2).
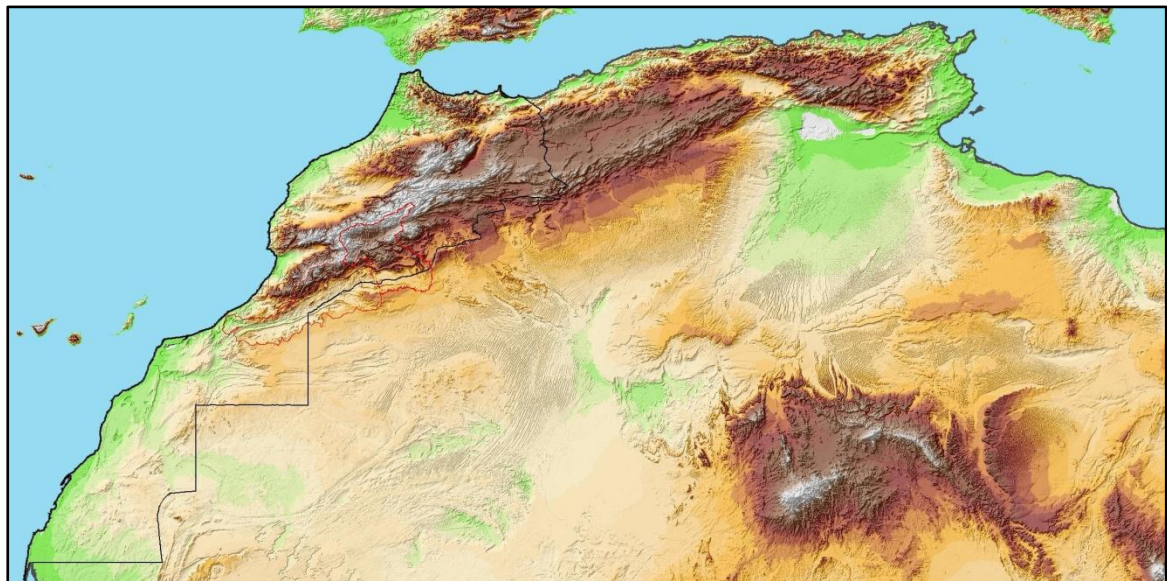


**Fig. 3.1** Topographical map of north eastern Africa and borders of the Moroccan country (dark grey line). The Drâa river catchment (light grey line) stretches from the High Atlas Mountains in the north to the Sahara in the south (for details see Fig. 3.2). The map is modified from Schulz & Judex (Eds) (2008)

This work was conducted within the framework of the IMPETUS project, an interdisciplinary research project for the efficient management of scarce water resources in West Africa. IMPETUS was active from 2000 to 2009 in Morocco and Benin and established a unique network for climate monitoring in both countries

(Schulz 2008a). In Morocco, the monitoring network comprised 13 study sites and extended along the altitudinal and aridity gradient from the top of the High Atlas Mountains (Jebel M'goun climate station at 3,850 m a.s.l.) to the Lake Iriki (421 m a.s.l.) at the Saharan border. It is due to this monitoring and to the work of numerous IMPETUS colleagues that it is possible to present most recent information on climate, geology, soil and vegetation. For my research it was a great advantage to have access to this data since it helped to quantify the impact of the abiotic environment on the vegetation. **Fig. 3.2** shows the northern part of the Drâa catchment, which was the investigation area of the present work.
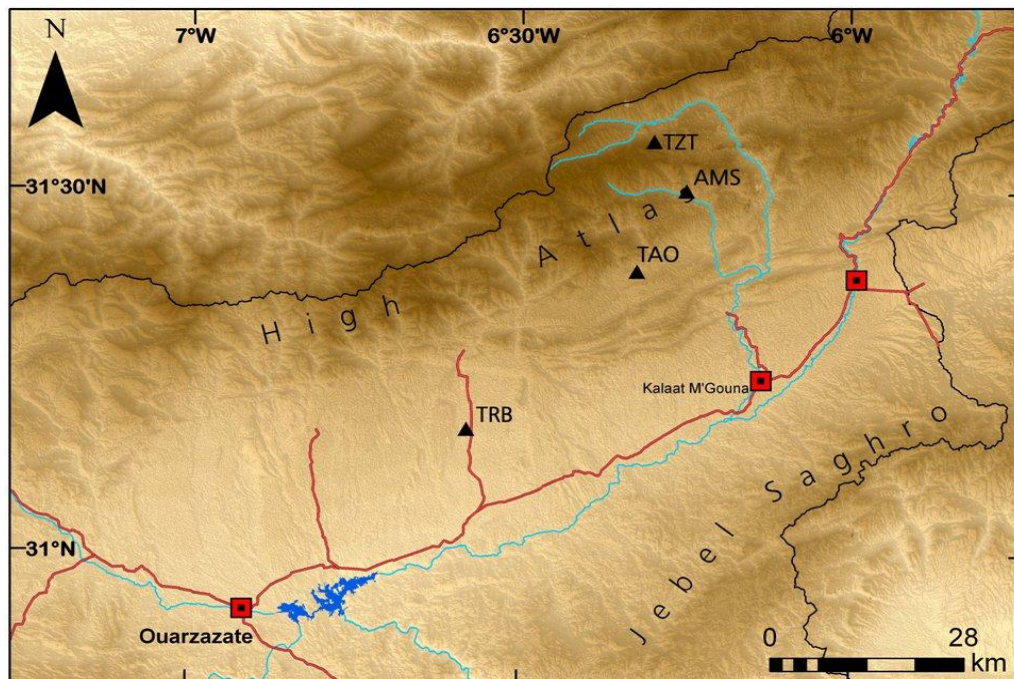


**Fig. 3.2** Topographical map of the research area with High Atlas Mountains in the north and the eastern chain of the Anti-Atlas (Jebel Saghro) in the south. Black lines indicate the limits of the Drâa river catchment. Ouarzazate is the province capital with approx. 57,000 inhabitants. ▲ indicate four of the IMPETUS study sites (*TRB* - Trab Labied 1,380 m a.s.l.; *TAO* - Taoujgalt 1,870 m a.s.l.; *AMS* - Ameskar 2250 m a.s.l.; *TZT* - Tizi n'Tounza 2,960 m a.s.l.) equipped with automatic weather stations and grazing exclosures since 2001. Topographical data derived from SRTM Digital Elevation Model, processing and cartography was made by Pierre Fritzsche.

The area was chosen with respect to local land use practices. Several pastoral-nomadic groups practice annual transhumance along this altitudinal gradient using pastures in the Basin of Ouarzazate or the Jebel Saghro in winter time and High Atlas pastures in summer (see chapter 3.4). The Dades river is the only permanently flowing river in the area. It has its origin in the High Atlas

Mountains and was once the most important affluent of the river Drâa. Today it discharges into the reservoir Mansour-Eddahbi close to Ouarzazate.

## 3.1  Climate

Like other Maghreb countries, Morocco experiences subtropical climate. The main precipitation period is winter and spring. Climate ranges from moderate at the coastal side influenced by maritime atlantic and mediterranean weather systems over subhumid mountain climates in the High Atlas, to hot and dry steppe and desert climates at the northern boundary of the Sahara (Born *et al.* 2008b). Mean annual precipitation may exceed 1000 mm in the Rif Mountains. However, in the southern parts of the country and in our research area it ranges from below 150 mm per year in the dry Basin of Ouarzazate up to maximum 800 mm per year on the top of the High Atlas Mountains (see Tab. 3.1, Fig. 3.3).

**Tab. 3.1** Location and bioclimate at the study sites along the High Atlas transect. *MAP* is the mean annual precipitation. The *Aridity index* is the ratio of annual precipitation to annual potential evapotranspiration following Middelton & Thomas (1997) and was calculated as a mean for the years 2001-2008. The *bioclimatic unit* follows Oldeland *et al.* (2008). *Q* is the pluviothermic ratio introduced by Emberger (1930). $T_{min}$ is the minimum temperature of the coldest month, $T_{max}$ the maximum temperature of the hottest month. The *growth period* gives the mean amount of days exceeding a mean daily temperature of 5°C. *calculated annual for the years 2000-2006 (January to December); **calculated for hydrological years 2001/02 -2007/08 (September to August)

| *Testsite* | TRB | TAO | AMS | TZT |
|---|---|---|---|---|
|  | Trab Labied | Taoujgalt | Ameskar | Tizi n'Tounza |
| *Location* |  |  |  |  |
| Altitude | 1,380 m a.s.l. | 1,870 m a.s.l. | 2,250 m a.s.l. | 2,960 m a.s.l. |
| Latitude | 31°10′ | 31°23′ | 31°29′ | 31°34′ |
| Longitude | 6°34′ | 6°19′ | 6°14′ | 6°17′ |
| *Bioclimate* |  |  |  |  |
| MAP* | 124 mm | 170 mm | 285 mm | 363 mm |
| Aridity index | 0.07 | 0.17 | 0.28 | 1.25 |
| Bioclimatic unit | arid cool | arid cold | semiarid cold | subhumid cold |
| Q** | 25.6 | 37.3 | 52.7 | 64.5 |
| $T_{min}$ coldest month** | 9.2 °C | 3.2 °C | 3.7 °C | -2.2 °C |
| $T_{max}$ hottest month** | 30.7 °C | 25.5 °C | 23.4 °C | 16.5 °C |
| Growth period** | 350 days | 280 days | 305 days | 183 days |

Considerable amounts of precipitation in the High Atlas fall in form of snow, persisting more than five months around 4,000 m altitude and rarely up to some

weeks on altitudes between 2,000 m and 3,000 m (Schulz 2006). In the High Atlas, precipitation is temporally distributed over one main period in winter (unimodal) while rain falls over two seasons (autumn and spring) in the southern parts of our research area (bimodal) (Schulz 2008b). Potential evapotranspiration is very high all over the research area, thus the area can be described as dryland system (see chapter 1.1).
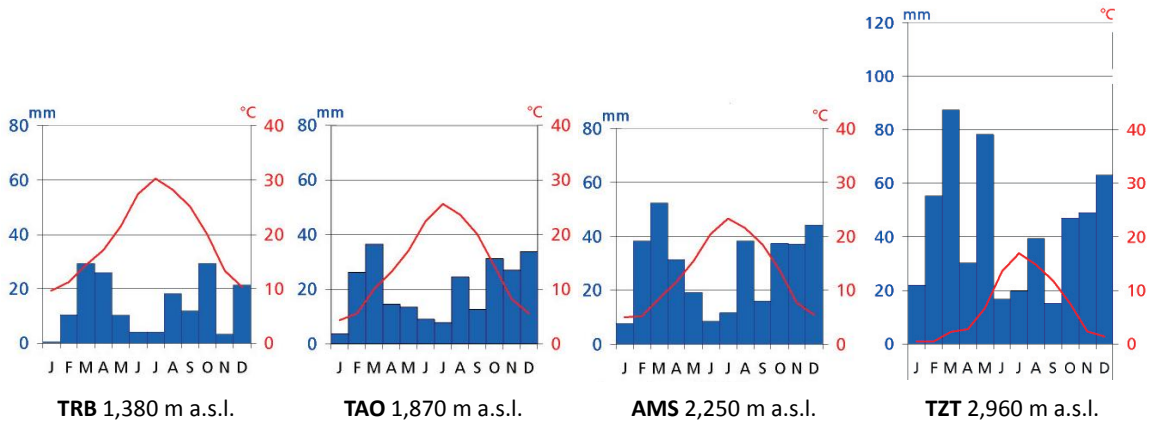


**Fig. 3.3** Climate diagrams for the investigated study sites: TRB - Trab Labied; TAO - Taoujgalt; AMS - Ameskar; TZT - Tizi n'Tounza. Bars indicate the amount of precipitation in mm (left axis), lines indicate temperature in °C (right axis). Mean annual precipitation, location and bioclimatic patterns are given in Tab. 3.1. Source of the diagrams: modified from (Schulz 2008a)

Highly variable rainfall is one major characteristic of dryland climates. Following Knippertz *et al.* (2003), the whole research area can be assigned to the 'Atlas region', one of three homogeneous regions of rainfall variability in Morocco. Rainfall variability can be determined by means of the Standardized Precipitation Index (SPI). The SPI, first presented by McKee *et al.* (1993), standardizes the annual amount of rainfall to the long-term mean at a certain location (Fig. 3.4). Thus, the SPI provides a reliable tool to detect dry and wet periods as well as to compare rainfall variability between different regions. Fig. 3.4 presents the SPI for the years 1900 to 2006 in the Atlas region (Born *et al.* 2008a).

Since the mid 1980s precipitation in the Atlas region has been above the average for most of the years. During the hydrological years 2001/02, 2002/03, and 2003/04 the region experienced a dry period. In the year 2006/07, when the presented work started, rainfall has been above the average.
The mean annual temperature in the Maghreb countries rises since the mid of the 20th century. Regional model results predict a further increase between 2 °C and

3 °C until 2050 and a decrease of precipitation between 10 % and 20 % (Paeth *et al.* 2009). In this context heavy and destructive rainfall events will increase.
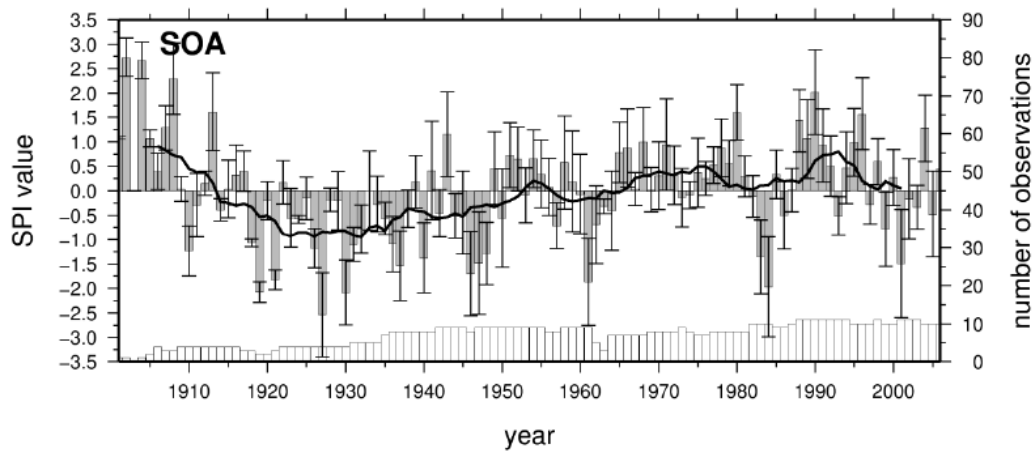


**Fig. 3.4** Standard Precipitation Index (SPI) for the years 1900 to 2006 in the Atlas region. Grey bars indicate the SPI values with standard deviation for the hydrological year (September - August). Positive values indicate hydrological years wetter than the long-term mean, negative values indicate drier years. White bars show the number of weather stations providing available rainfall data. Source: Born *et al.* (2008a)

## 3.2  Geology and soil properties

Northwest Africa is situated on one of the world's oldest land masses, the West African Craton. However, Morocco's geological evolution is very complex. The north of Morocco experienced several phases of continental building and break-up, while the southern parts remained more or less stable during the last  one billion years (Michard *et al.* 2008). The investigation area represents a transition zone between the geologically young mountain chain of the Central High Atlas and the old Anti-Atlas which is of proterozoic and palaeozoic origin. The High Atlas Mountains were formed during the Alpine orogeny in the Tertiary, and until now there is a continuing uplift. High Atlas and Anti-Atlas are separated by an important tectonic lineament - the South-Atlas-Fault  (Ennih & Liégeois 2008). It builds the northern border of the Basin of Ouarzazate, a vast molasse basin which accumulates clastic sediments since the Mesozoic. These sediments are very porous and account for the low water-holding capacity of the underground.

Up to now, Cavallar (1950) presented the only soil map for Morocco. However, a detailed description of the soils in the Drâa catchment is currently finished (Klose

2009). The following information derive from this work. Soils in the research area are generally shallow with a high proportion of skeleton  and a low organic matter content. They show high carbonate contents; and pH ranges between alkaline and neutral.

The Basin of Ouarzazate (**Fig. 3.2**, TRB) is characterized by quaternary sediments and soil of the types Kastanozem, Chernozem, and Regosol. The latter are untypical for the given dry climate since they represent steppe soils which are rich in organic matter. Soils of the sedentary basins are mostly of encrusted horizons and show eroded surfaces. With increasing altitude and along the South-Atlas-Fault, foothills of limestone, sandstone as well as silt- and limestone arise. The intramountainous basin of Taoujgalt (**Fig. 3.2**, TAO) is situated north of these foothills and soil types are comparable to those of the Ouarzazate basin. Above 2,000 m a.s.l. limestone, cristalline and sandstone predominate as bedrock material. Cambisols, Calcisols, and Luvisols are found in the jurassic limestone areas (**Fig. 3.2**, AMS). They are usually very shallow soils, sceletic, highly disturbed by erosion and covered by Juniper forests. The highest Atlas parts that are still covered by vegetation (**Fig. 3.2**, TZT) are characterized by high mountain and steppe soils (Kastanozem, Chernozem, Leptosol, Luvisol) on calcareous rocks and stony surfaces.

## 3.3  Flora

Morocco is situated at a point of intersection between the Holarctic and the Palaeotropic floristic kingdom. Vegetation combines elements of the mediterranean, saharo-arabic, irano-turanic, and the ibero-mauric flora. In terms of plant species and endemic plants, Morocco is one of the richest countries in the Mediterranean (Médail & Quézel 1997). More than 4200 species are described including some 20 % of endemic plants. The Middle Atlas and the High Atlas are fascinating centres of biodiversity with 300 endemic plant species only in the High Atlas Mountains  (Enriques-Barroso & Gómez Campo 1991).

The vegetation in the research area can be classified into three main ecological regions  (Benabid: 'écoregion') according to their succession along the High Atlas altitudinal gradient (Fig. 3.5) (Benabid 2000; Oldeland 2004; Finckh & Poete 2008).

## *3.3.1 Hammada and Artemisia steppes*

The ecoregion of *Hammada* and *Artemisia* steppes can be found from 1,200 m a.s.l. up to 2,000 m a.s.l. and they are characterized by less than 200 mm of annual rainfall.

The dry regs in the Basin of Ouarzazate are characterized by the sparse vegetation of the Saharan *Hammada*-semidesert (Fig. 3.5 A) dominated by dwarf shrubs such as *Farsetia occidentalis* and *Hammada scoparia* and by a few annual species like *Stipa capensis*. The azonal vegetation, for example in wadis, is rich in spiny phanerophytes and chamaephytes such as *Ziziphus lotus* and *Zilla spinosa ssp. macroptera*. Around water-sources, villages, and other intensively used, nitrogen-enriched locations, depleted erms of *Peganum harmala* can be found (Le Houérou 2001), including annual and perennial nitratophilous forbs like *Malva parviflora* and spiny or repellent shrubs like *Astragalus armatus ssp. armatus*.

The higher located plateaus and the intramountainous basin of Taoujgalt are covered by *Artemisia* steppes (Fig. 3.5 B). *Artemisia* steppes widely occur from Spain to Afghanistan and are estimated to cover an area of 10 million ha in North Africa (Le Houérou 2001). In our research area *Artemisia herba-alba*, *Artemisia mesatlantica*, *Teucrium mideltense*, and several *Thymus* species are the dominating dwarf-shrubs. Depending on rainfall in spring, *Artemisia* steppes can be covered by many different annual forbs and grasses like *Bromus rubens*, *Linaria micrantha*, *Sideritis montana*, *Ranunculus falcatus*, *Glaucium corniculatum*. Artemisia steppes are appreciated as rangelands. Particularly in the surroundings of villages, perennial forbs and grasses with high forage values like *Stipa parviflora* are merely found or only growing under the protection of dwarf shrubs (own observation).

It is currently discussed if *Hammada* and *Artemisia* steppes can be regarded as primary vegetation in the area. Le Houérou (2001) proposes that most of the present-day steppes are 'secondary' and derived from a dry, open forest which was degraded to perennial bunch grass steppes and further to *Artemisia* steppes and *Hammada* steppes. Forests probably consisted of tree species such as *Pinus halepensis*, *Tetraclinis articulata*, *Juniperus phoenicea*, *Pistacea lentiscus* that are currently very rare. The alfa grass (*Stipa tenacissima*), now rather rare except of some populations west of our research area (Oldeland 2004), probably dominated perennial bunch grass steppes.
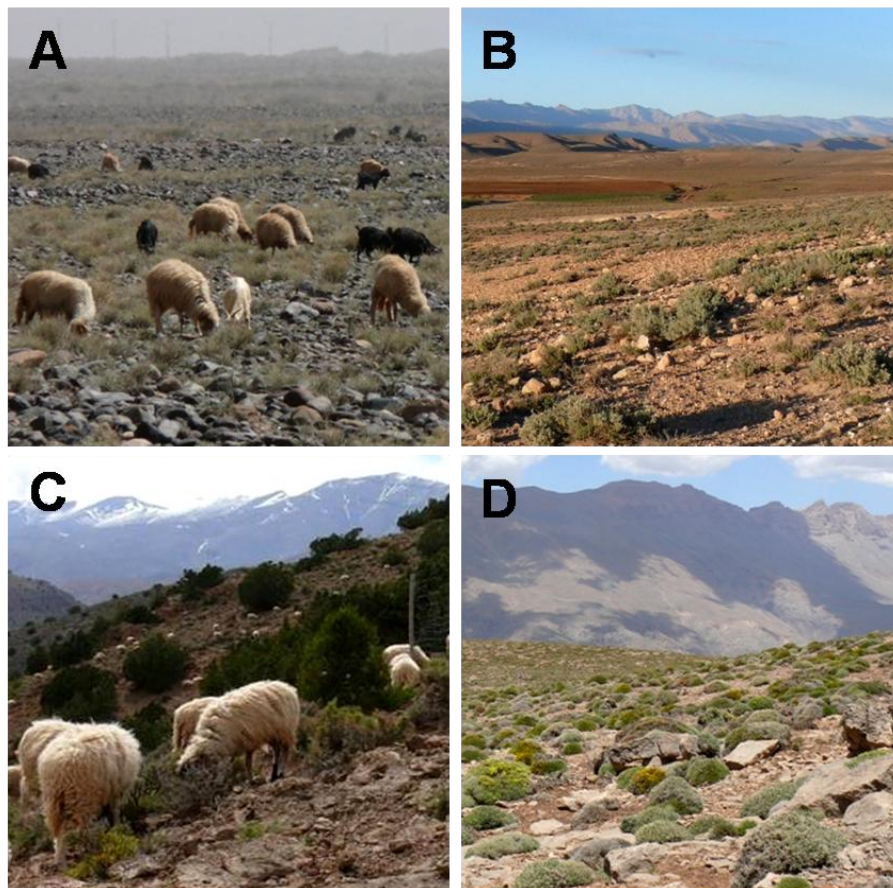
**Fig. 3.5** Vegetation types along the High Atlas transect: **A** - Hammada steppe; **B** - Artemisia steppe; **C** - Juniper woodsteppe; **D** - oromediterranean shrubland

Le Houérou states that alfa grass steppes built a belt of more than 8 million km² between the Saharan and the Mediterranean vegetation during the 19th century. The idea that arid and semiarid Morocco has been widely covered by forests which have been degraded by human land use are shared by many ecologists (Emberger 1939; Quézel & Barbero 1990; Benabid & Fennane 1994; Puigdefabregas & Mendizabal 1998; Oldeland 2004).

Nowadays, this view has been criticised as an environmental narrative and product of environmental policies during the Moroccan colonial period (Davis 2005). Following Davis the deforestation hypothesis favoured imperial interests over indigenous interests and helped to dispossess Moroccans from their lands and livelihoods. Even in the post-colonial era the deforestation hypothesis is still alive and frequently applied in form of potential vegetation maps. The present work will not take part in this debate, since the temporal scope is shorter and biodiversity is a minor subject.

### *3.3.2 Juniper woodsteppes*

From 2,000 m a.s.l. to approximately 2,500 m a.s.l. open sclerophyllous forests of *Juniperus phoenicea* and *Juniperus thurifera* occur (Fig. 3.5 C). Other tree species such as *Juniperus oxycedrus, Rhamnus oleioides, Quercus rotundifolia, Buxus balearica,* and *Fraxinus dimorpha* are rarely found or limited to shadowy and remote locations. Juniper trees are associated with dwarf shrub species of the *Artemisia* steppes and with other chamaephytes like *Cladanthus scariosus* and *Genista scorpius ssp. myriantha*. The Juniper zone is characterized by steep slopes, shallow soils and intense erosion. Plant growth depends to a great extent on slope exposition and on efficient attachment to the ground. Hemicryptophytic plants thus often grow in rock crevices or under the protection of chamaephytes and Juniper trees.

### *3.3.3 Oromediterranean shrubland*

Above 2,500 m a.s.l. the landscape is dominated by oromediterranean shrublands (Fig. 3.5 D). Abiotic conditions are so extreme that the growth of trees is no more possible. Plants of this altitudinal level cope with frost events all over the year, daily temperature differences up to 30 °C, strong winds and heavy erosion (Oldeland 2004). Vegetation is dominated by cushion-like xerophytic and often thorny shrubs such as *Alyssum spinosum, Bupleurum spinosum, Cytisus scoparius ssp. balansae, Erinacea anthyllis, Vella mairei,* and *Astragalus ibrahimianus*. They are associated with dwarf shrubs of the genus *Arenaria*. Hemicryptophytic forbs can be found in and between the shrub species. For example, *Veronica rosea* and *Iberis sempervirens* grow within the cushion shrubs. Perennial grasses such as *Helictotrichon filifolium, Festuca hystrix,* and other *Festuca* species colonize around the shrubs. And rosette species are found on the bare ground either individually like *Centaurea josiae, Raffenaldia primuloides* or in form of large flat aggregations like *Catananche caespitosa* or the endemic species *Centaurea takredensis*.

## 3.4  Society and land use

Unlike many underdeveloped countries in sub-Saharan Africa, Morocco is recently classified by the UN as a country of the 'Middle Human Development Group' (UNDP 2008). In 2008 Morocco generated a GDP (Gross Domestic Product) of 86.4 billion US $ and thus made the 61st place in the world compared

to Germany with 3,667.5 billion US $ on rank 4 (IMF 2009). For 2009 the total population of Morocco was estimated 34.8 million (CIA 2009). Currently population growth rates decrease because of emigration and declining natality. Morocco's population is very unevenly distributed throughout the country with 61 % of the people living on only 13 % of the territory. While population density in the western cities may reach more than 1,000 inhabitants/ km², the arid and less developed provinces in the south figure very low population densities, for example less than 5 to 50 inhabitants/ km² in our research area (Lanjouw 2004). Morocco's official language is Arabic. However, more than 40 % of the population are speaking one of three Berber dialects as their mother language. In the province of Ouarzazate 98 % speak the Berber dialect Tashelhijt (Oldeland 2004), which is up to now neither written nor taught in school. Since alphabetism means to read and write the Arabic language, the analphabetism rate, particularly in rural areas, among women, and elderly people, is very high (HCP 2007). The southern provinces additionally cope with high rates of unemployment, for example 13.1 % in the greater area Souss-Massa-Drâa  and estimated 20 % in the province Ouarzazate.

Besides some 10 % of urban population (Fig. 3.6 A), most of the inhabitants of the province Ouarzazate live in rural areas and practice subsistence agriculture. Only 1.4 % of the land in the research area is suitable for irrigated agriculture (Oldeland 2004) (Fig. 3.6 B). Depending on altitude and aridity, the main crops of the oases in the Basin of Ouarzazate are date, wheat, and alfalfa, while barley, maize and vegetables are



**Fig. 3.6** Land use in the research area: **A** - urban use in the city of Ouarzazate; **B** - irrigated agriculture with date palm, almond trees and wheat near Anguelz; **C** - rangelands, here with dromedaries in the Basin of Ouarzazate

grown in mountain oases. Additional production of apple, apricot, almond, and olives occur (Heidecke & Schmidt 2008; Kirscht 2008). However, the great majority of land is used by sedentary and nomadic pastoralists as rangelands for livestock production (Fig. 3.6 C). Livestock mainly consists of small domestic animals like sheep and goats. Mules are widely used for transport purposes, dromedaries are typically kept as pack animals by pastoral nomads (Heidecke & Roth 2008). The present work focuses on range management and particularly on the vast terrains used by pastoral nomads. Nomadism at the southern slopes of the High Atlas means transhumance, i.e. households and herds move between definite seasonal bases (Niamir-Fuller 1998). Several fractions of mobile pastoralists (a subcategory of the term 'tribe') such as the *Ait Aafane*, *Ait Zekri*, *Ait Toumert*, *Ait Mgoun*, practice transhumance along parallel corridors, each more or less orientated in north-south direction using pastures of high and low altitudes (IAV 2003). The interdisciplinary part of this study concentrates on the fraction Ait Toumert. Their transhumance cycle is described as an example for the High Atlas transhumance system. Information derives from studies of the Agricultural Insitute in Rabat, Morocco (IAV 2003), a diploma thesis of Birgit Kemmerling (2008) and own observations.

During the summer months, the Ait Toumert use rangelands in the High Atlas Mountains, often above 2,600 m a.s.l. far from villages and settlements. These summer pastures are exclusively used by this group. Shelters and caves are reused every year but not necessarily by the same household. At the beginning of autumn herds and herders move to transition pastures between 2,000 m a.s.l. and 2,600 m a.s.l. approximately. In the case of the Ait Toumert, transition pastures are located on the high plateau of Asselda which is shared with nomads of the Ait Zekri fraction. Depending on weather conditions, nomads move down on winter pastures in November or December. Near winter pastures comprise the near mountain chains around 1,800 m altitude. Far winter pastures are situated in the Basin of Ouarzazate and on the Jebel Saghro (Fig. 3.2). Compared to summer pastures, winter pastures stretch across a vast terrain, but are communally used with nomads of several fractions. Normally winter pastures are used until February or March, when herds move back to the transition pastures. During spring time the access to the summer pastures is regulated by a local institution, the so called 'Agdal' (Genin *et al.* 2005; Genin 2008). The Agdal is set every year by an assembly of local users, who determine the exact date when nomadic herds

are allowed to move to summer pastures (Ilahiane 1999). In the last years, the Agdal on Ait Toumert summer pastures opened between end of May and the beginning of June.



**Fig. 3.7** Nomadic family of the Ait Toumert fraction in front of their cave dwelling on the high plateau of Asselda in May 2008

The presented transhumance cycle is a normative one that is not only altered by weather phenomena and forage supply of the pastures. Socio-economic factors like herd size, financial situation, affinity to sedentary members of the family, and other factors also play an important role for mobility decisions (Kemmerling 2008; Kemmerling *et al.* 2009).

Pastoralists and sedentary people affect the vegetation in the research area in many ways. The main sources of impact are livestock grazing and the exploitation of fire wood and timber. Grazing herbivores destroy plant biomass by feeding and trampling and lead to a tremendous change of environmental conditions, for example by input of nitrogen and by facilitating erosion processes. While sedentary pastoralists often own little herds up to a few tens heads, herd sizes of nomads range between 50 and several hundreds of heads. However, the impact of many little herds leaving and returning each day to the same village exceeds the grazing pressure of nomadic herds which is a more extensive form of land use. The collection of fire wood is an exclusive task of women and specialized according to its purpose. For example *Artemisia herba-alba* is collected for baking bread and for cooking while *Genista scorpius ssp. myriantha* is used for

special rituals. Juniper trees are in great demand as long-lasting fire wood, but mainly in house building (Oldeland 2004).

# 4 Structure of this work

The present work wants to investigate the relationship between rangeland indicators on different hierarchical levels and their significance along a steep gradient of natural variability. Three approaches will be introduced, tested and critically discussed. Each type of rangeland indicator, showing the response of the vegetation to disturbance (grazing impact), is tested on four altitudinal levels in the High Atlas Mountains, Morocco. Water is the most limiting resource for plant growth in this area and the natural variability of water supply increases from subhumid high mountain areas to arid lowland basins (see chapter 3).

The first section analyses the indicative value of the parameters aboveground net primary production (ANPP) and rain-use efficiency (RUE). ANPP and RUE are widely used to indicate degradation on large spatial scales. However, there is a debate ongoing about the significance of these indicators. Thus it is worth to test the predictive value of ANPP and RUE along the Moroccan gradient of resource variability. The question is investigated by a 4 x 3 full factorial field experiment (4 altitudinal levels, 3 levels of grazing impact) quantifying and comparing biomass production on pastures, in short-term exclosures, and long-term exclosures (see chapter 0).

In the second part, plant functional types will be tested as indicators for range condition. More than 20 years of research on grazing response groups and grazing response traits resulted in a multitude of indicators, but they were often restricted to local application. There is increasing evidence that changes in resource availability are an essential source of bias which limits the application of response groups and response traits as rangeland indicators on the spatial scale (Coughenour 1985; De Bello *et al.* 2005; Rusch *et al.* 2009). Moroccan plant species on four altitudinal levels are assembled to grazing response groups (according to a catalogue of plant traits relevant to tolerate or avoid biomass losses through grazing) by means of multivariate statistics. The indicative value of response groups and response traits is tested along gradients of different grazing intensity. Response groups and traits are applied as one type of slow-working indicator.

Third, local ecological knowledge of herdsmen is questioned in order to find local criteria of range assessment. Unlike science analysing nature's complexity

fraction by fraction, local knowledge integrates information on several hierarchical levels (Berkes *et al.* 1998; Pierotti & Wildcat 2002). Natural variability is surely a part of it, too. It is thus not the question if resource variability alters the indicative value of local range assessment criteria. We rather ask whether local criteria can be transformed in ecologically measurable parameters and how these parameters are in turn influenced by the natural variability of water resources.

Summarizing, this work examines the significance of three currently discussed rangeland indicators (ANPP, plant functional types, local knowledge) and their dependence on different levels of natural resource variability. Indicators operating on different spatial and temporal scales are explicitly combined. It is asked which type of indicator is best applied for which purpose and which is most independent from background changes in resource availability.

# ANPP and rain-use efficiency

ANPP and rain-use efficiency
in semiarid rangelands:
Are they good indicators
of rangeland degradation?

# Abstract

The rain-use efficiency (RUE) – defined as the ratio of aboveground net primary production (ANPP) to corresponding precipitation –has like ANPP often been used to detect land degradation, for example resulting from grazing impact in semiarid rangelands. However, ANPP and therefore RUE are known to vary along resource and disturbance gradients. We conducted an integrated field experiment along both types of gradients on the southern slope of the High Atlas Mountains, Morocco, to disentangle four potentially influencing factors on ANPP and RUE: (1) climatic aridity and (2) soil condition representing resource gradients, (3) grazing as one prior disturbance, and (4) the amount of initial standing crop. Grazing analyses were based on a threefold exclosure design comparing grazed, 1 year and 7 years rested vegetation. Our results show that biomass accumulates the longer the vegetation is protected from grazing and with increasing altitude. ANPP and RUE peak for *Artemisia* steppe vegetation but do not show recovery on any altitudinal level. The standardization of ANPP and RUE on the amount of initial standing crop ($ANPP_{rel}$, $RUE_{rel}$) led to statistical equality of production along the gradient. At *Hammada* semidesert degradation could be detected as a decline in $ANPP_{rel}$ from 7 to 1 year rested sites.

Concluding, we recommend specifying which functional mechanism underlying a decline in ANPP or RUE is described as degradation. We suggest restricting degradation to irreversible long-term processes caused by changes in abiotic site conditions or in vegetation composition. They can be separated from short-term and often reversible changes in vegetation density (1) by using temporal exclosures to assess the full amount of ANPP at a grazed site and (2) by calculating $ANPP_{rel}$ or $RUE_{rel}$ that standardize production or rain-use efficiency to the amount of initial standing crop.

# 5 ANPP and rain-use efficiency

## 5.1  Introduction

The world's primary production provides the energy for all other trophic levels and is the basis of ecosystem functioning (McNaughton *et al.* 1989). In this context, the term degradation has always been defined from an anthropocentric point of view and specific for a certain land use perspective (Hambler *et al.* 2007). The latter determined the magnitude, severity, causes, and effects of observed degradation processes. However, there is a consensus that degradation is associated with a long-term decline in production, either in primary (Bai *et al.* 2008b) or in secondary production (Milton *et al.* 1994). Monitoring aboveground net primary production (ANPP) and rain use efficiency (RUE, production per millimetre of fallen rain) of the vegetation, in particular with the help of remote sensing techniques, is therefore regarded as a promising tool to indicate land degradation, both on a large spatial and temporal scale (Le Houérou 1984; Aronson 1993; Diouf & Lambin, 2001; Hein 2006; Swemmer *et al.* 2007). Because a decline in ANPP can occur as a result of environmental changes as well as changes in density and the relative growth rate of the vegetation (Milton *et al.* 1994), we have to consider which of these functional mechanisms is measured when assessing degradation.

Vegetation density and growth rate are influenced by a complex suite of limiting resources, such as water and nutrient availability in space and time, and by disturbances, such as recent and historical grazing pressure (Le Houérou 1984; Wiegand *et al.* 2004). As ANPP and RUE were already recognized as 'lumped' parameters (Prince *et al.* 1998), i.e. complex aggregations that are difficult to interpret functionally, various authors (Retzer 2006; Wessels *et al.* 2007; Bai *et al.* 2008a) have drawn the conclusion that ANPP and RUE alone are inappropriate as indicators for ecosystem health or degradation. Instead, we have to detect the functional mechanisms related to degradation. The goal of the present study is to disentangle interacting effects of resource availability and disturbance on ANPP and RUE. We investigated the limiting factors (1) climatic aridity and (2) soil conditions representing gradients of resource availability in combination with (3) grazing pressure representing a disturbance gradient. As a fourth factor, we studied the effects of (4) initial standing crop on ANPP and RUE, which is an

integral of resource availability and disturbance impact over time (Wiegand *et al.* 2004; Müller *et al.* 2007).

## 5.1.1 Climatic aridity

Climatic aridity determines the available water resources in a given region and is measured as the ratio of annual precipitation to annual potential evapotranspiration (Middelton & Thomas 1997). Many studies of arid and semiarid rangelands document a positive relationship between ANPP and mean annual precipitation (Le Houérou *et al.* 1988; Sala *et al.* 1988; Paruelo *et al.* 1999; Yahdjian & Sala 2006), while RUE first increases, then declines along precipitation gradients (Huxman *et al.* 2004; Bai *et al.* 2008a). Aridity gradients are also found in combination with altitudinal gradients. For example Hansen *et al.* (2000) showed for different vegetation types in Yellowstone National Park (USA) that ANPP declines with increasing altitudinal levels because temperature limits growth periods. Our study investigates ANPP and RUE following an aridity gradient along altitude reaching from arid climate in the Basin of Ouarzazate to subhumid climate in the High Atlas Mountains, Morocco. As altitude represents a complex gradient (Whittaker 1967a), changes in mean annual precipitation go along with changes in variability of rainfall, mean annual temperature and the length of the growing season.

## 5.1.2 Soil conditions

Soil affects phytomass production via the availability of several limiting resources for plant growth. Firstly, ANPP and RUE are particularly influenced by water availability (Noy-Meir 1973; Lauenroth *et al.* 1978; Le Houérou 1984; Sala *et al.* 1988; Burke *et al.* 1998), which is related to soil texture, soil depth as well as soil organic matter. Secondly, production is limited by nutrient availability which is (amongst other biogeochemical components) related to the nitrogen content (total N) of the soil (Vitousek & Howarth 1991; Schimel *et al.* 1997).

## 5.1.3 Grazing

Grazing is, besides fire, one of the most important disturbance types affecting vegetation composition and structure, and primary production in arid and

semiarid rangelands (Archibald *et al.* 2005; Belsky 1992). Studies across a wide variety of ecosystems indicate that ANPP is considerably reduced by grazing (Milchunas & Lauenroth 1993; Varnamkhasti *et al.* 1995; Guevara *et al.* 1997; van de Koppel *et al.* 2002;). Grazing influences RUE at least as much as aridity through its impact on range condition (Le Houérou 1984; Snyman & Fouche 1991). Consequently, spatial and temporal differences in ANPP and RUE have been widely used to identify land degradation, especially via broad-scale remote sensing studies (Paruelo 2000; Jobággy *et al.* 2002; Bai & Dent 2006; Bai *et al.* 2008b; Blanco 2008; Vlek *et al.* 2008). These studies measure ANPP in grazed regions as difference between standing crop at two different points in time, e.g. at the beginning and at the end of the growing season. However, if animals consume biomass during the investigation period, this method does not allow assessing the full amount of ANPP a grazed site is able to express. To avoid this artefact, we applied short-term exclosures (McNaughton *et al.* 1996; McCulley 2005; Adler *et al.* 2005) to protect the grazed sites from offtake during the investigation period.

## 5.1.4 Initial standing crop

Phytomass production of plant communities directly depends on the amount of standing crop that produces it (i.e. the interest rate on the capital; Begon *et al.* (2006). The standing crop, particularly of perennial plants, is highly variable along resource gradients and grazing gradients. It is an ecosystem's memory for predominant abiotic conditions, times of resource scarcity, and especially for its disturbance history (Wiegand *et al.* 2004). Thus, regarding ANPP and RUE along resource and disturbance gradients, it is useful to relate the amount of production to standing crop. In the past, similar measures were introduced as relative growth rate or ecosystem production efficiency (Reich *et al.* 1997). Le Houérou (1984), who first described RUE, concludes that "the RUE factor seems to be a useful tool for assessing the health and productivity of arid zone ecosystems, […] *but as a complement* to the biological efficiency factor (Barbour 1967)". Surprisingly many studies (Prince *et al.* 2007; Bai *et al.* 2008a; Muldavin *et al.* 2008) give functional interpretations for ANPP differences in space and time, but do not relate ANPP to standing crop biomass (but see Wiegand (2004)), who relate production to basal cover). Furthermore, the two terms 'production' and 'productivity' are often used by ecologists as synonyms for ANPP (Snyman 1998;

Knapp & Smith 2001; Huenneke *et al.* 2002; Swemmer *et al.* 2007). Following an economic point of view where productivity is defined as output per unit of input, we emphasise a distinction between biomass *production* (or ANPP) and the term *productivity* or relative ANPP (ANPP$_{rel}$), i.e. a primary production per unit of standing crop. As rain-use efficiency (RUE) is the ratio of ANPP to precipitation, relative rain-use efficiency (RUE$_{rel}$) can be similarly derived from ANPP$_{rel}$. With these measures we are able to distinguish, whether a decline in ANPP occurred as a result of decreasing vegetation density (often reversible processes) or of changes in abiotic site conditions as well as species composition (often irreversible, 'degradation').

We use data from a field study in the High Atlas Mountains, Morocco to analyze and differentiate between the impacts of limiting factors that affect ANPP and RUE of the vegetation. Our aim is to come to a functional interpretation of processes affecting the indicative value of these parameters, which have explicitly to be considered when ANPP and RUE differences are interpreted in terms of degradation.

## 5.2  Methods

### 5.2.1 Study sites

Our study was performed in the Moroccan province Ouarzazate at the southern slopes of the High Atlas Mountains. The region is characterized by a steep altitudinal gradient, including different landscapes such as the Basin of Ouarzazate in the south (1300 m asl.) and the peaks of the High Atlas Mountains (4000 m asl.) in the northern part. The altitudinal gradient is associated with an aridity gradient reaching from arid climate with less than 200 mm precipitation per year and high interannual variability to a subhumid climate in the highest mountain parts with an annual precipitation over 700 mm per year (Schulz 2008a).

We studied vegetation dynamics on four altitudinal levels (Fig. 5.1, Tab. 5.1) close to the following test sites, established by the IMPETUS (Integrated Approach to the Efficient Management of Scarce Water Resources in West Africa) project: Trab Labied (TRB), Taoujgalt (TAO), Ameskar (AMS) and Tizi n'Tounza (TZT).

In the following the altitudinal levels will be addressed by their vegetation type i.e. *Hammada* semidesert at TRB (desert); *Artemisia* steppe at TAO (steppe); *Juniper* woodsteppe at AMS (wood), and oromediterranean shrubland at TZT (shrub) (Tab. 5.1). Every test site is equipped with an automatic weather station and an approximately 400 m² grazing exclosure, both working since 2001.
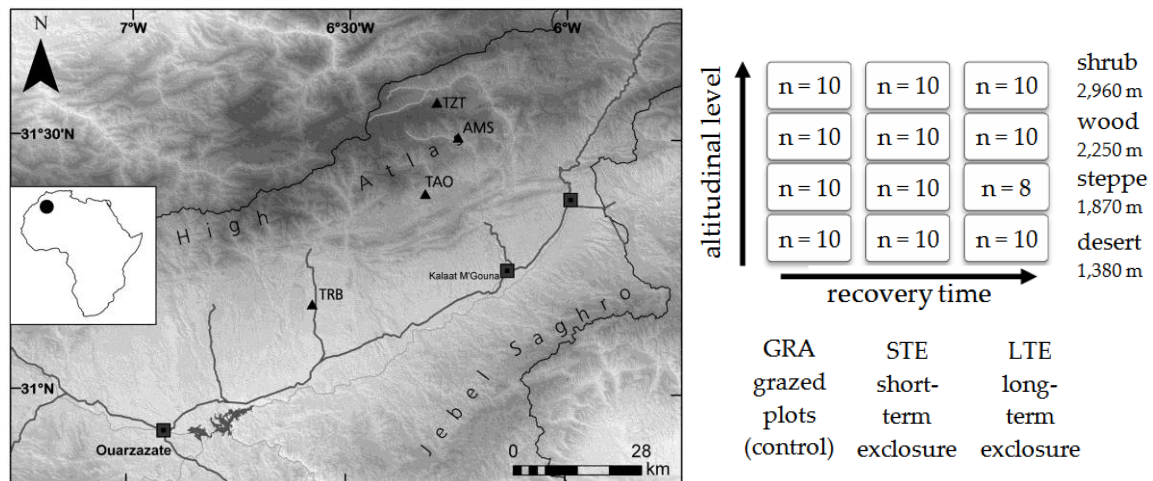


**Fig. 5.1** Map of investigation area and 4 x 3 full factorial sampling design. ▲ test sites on four altitudinal levels: TRB - desert at 1,380 m a.s.l.; TAO - steppe at 1,870 m a.s.l.; AMS - wood at 2,250 m a.s.l.; and TZT - shrub at 2,960 m a.s.l. On each altitudinal level three different treatments (replicates n = 10) were analysed: GRA - grazed plots; STE - short-term exclosures; and LTE - long-term exclosures

Tab. 5.1 gives an overview of location parameters and bioclimatic patterns of the four test sites. The entire study area has experienced a long grazing history. It has been used for centuries as pasture for livestock – mostly sheep and goats – both of sedentary and transhumant pastoralists (Barrow & Hicham 2000; Montés *et al.* 2002; Breuer 2007). The oromediterranean shrubland is exclusively used by nomadic livestock as a summer pasture (Kemmerling *et al.* 2009).

## 5.2.2 Experimental design

We conducted a 4 x 3 full factorial experiment (four altitudinal levels, three recovery time intervals) to measure standing crop (kg*ha$^{-1}$) of the vegetation. Aboveground net primary production (ANPP in kg*ha$^{-1}$*season$^{-1}$) and rain-use

efficiency (RUE in kg*ha$^{-1}$*season$^{-1}$*mm$^{-1}$) was assessed for two recovery time intervals (4 x 2 factorial design).

**Tab. 5.1** Location, bioclimate, and investigation period of the four different study sites along the High Atlas Mountain transect. *Testsite* shows map codes and local names of the study sites. *MAP* is the mean annual precipitation. The *Aridity index* is the ratio of annual precipitation to annual potential evapotranspiration following Middelton & Thomas (1997). *Bioclimatic unit* follows Oldeland *et al.* (2008). *Q* is the pluviothermic ratio introduced by Emberger (1930). *$T_{min}$* is the minimum temperature of the coldest month, *$T_{max}$* the maximum temperature of the hottest month. The *growth period* gives the mean amount of days exceeding a mean daily temperature of 5°C. The *vegetation type* is derived from a regional vegetation map (Finckh & Poete 2008). *Start and end of the investigation period* and the *precipitation* fallen during this time interval are also indicated. *calculated annually for the years 2000 – 2008 (01.01. to 31.12.); **calculated for the rain years 2001/02 – 2007/08 (01.09. to 31.08.)

| *Altitudinal level* | **Desert** | **Steppe** | **Wood** | **Shrub** |
|---|---|---|---|---|
| *Testsite* | TRB | TAO | AMS | TZT |
| | Trab Labied | Taoujgalt | Ameskar | Tizi n'Tounza |
| *Location* | | | | |
| Altitude | **1380 m asl.** | **1870 m asl.** | **2250 m asl.** | **2960 m asl.** |
| Latitude | 31°10′ | 31°23′ | 31°29′ | 31°34′ |
| Longitude | 6°34′ | 6°19′ | 6°14′ | 6°17′ |
| *Bioclimate* | | | | |
| MAP* | 124 mm | 170 mm | 285 mm | 363 mm |
| Aridity index* | 0.07 | 0.17 | 0.28 | 1.25 |
| Bioclimatic unit | arid cool | arid cold | semiarid cold | subhumid cold |
| Q** | 25.6 | 37.3 | 52.7 | 64.5 |
| $T_{min}$ coldest month** | 9.2 °C | 3.2 °C | 3.7 °C | -2.2 °C |
| $T_{max}$ hottest month** | 30.7 °C | 25.5 °C | 23.4 °C | 16.5 °C |
| Growth period** | 350 days | 280 days | 305 days | 183 days |
| Vegetation type | *Hammada* semidesert | *Artemisia* steppe | *Juniperus* woodsteppe | *Oromediterranean* shrubland |
| *Investigation period* | | | | |
| Begin | 02.09.2007 | 22.09.2007 | 13.09.2007 | 17.09.2007 |
| End | 04.04.2008 | 26.04.2008 | 08.10.2008 | 09.10.2008 |
| Precipitation | 170 mm | 246 mm | 424 mm | 522 mm |

We randomly installed 10 single square meters (= plots) at each of the four test sites for the following treatments: (1) LTE – long-term exclosure plots, located inside the grazing exclosure that has not been grazed since 2001; (2) STE – short-term exclosure plots, protected by a permanently installed wired cage from the beginning to the end of the experiment; and (3) GRA – grazed plots without protection. A triplet of grazed plots (GRA), long-term exclosure plots (LTE) and

short-term exclosure plots (STE) was used to differentiate between two kinds of grazing impact: a recent grazing offtake (or 'consumption' *sensu* Adler *et al.* (2005)) during the investigation period (GRA vs. STE), and a potential recovery from long-term grazing impact (STE vs. LTE). To reduce the effects of abiotic differences and spatial autocorrelation, plots were placed at a minimum distance of 3 m and a maximum distance of 100 m apart from each other. As the long-term exclosure plots are limited by the fenced area already used by an existing monitoring system, minimum distance between plots was partially less than 3 m.

The investigation period started in September 2007 at every altitudinal level and ended in April 2008 for desert and steppe vegetation, and in October 2008 for wood and shrub vegetation (Tab. 5.1). We applied different measuring periods, assuming the main growing season to end at the end of spring for the *Hammada* semidesert and the *Artemisi*a steppe, and in autumn for the *Juniper* woodsteppe and the oromediterranean shrubland (Schulz 2008b). An early onset of winter in October 2008 prevented us from finishing our measurements on long-term exclosure plots at the shrubland level; vegetation had been totally covered by snow. Here we alternatively used LTE measurements from end of June 2008.

## 5.2.3 Measurements

For data assessment on plant production we followed the sampling instructions of the Jornada Basin LTER program (Huenneke *et al.* 2001; Huenneke *et al.* 2002; Peters & Huenneke 2009), and measured diameter, height and cover of each perennial plant individual at least at the beginning and at the end of the experiment. To record peak standing crop of perennial herbs and perennial grasses, we additionally measured woodsteppe and shrubland vegetation in spring 2008. Annual plants were only assessed at the end of the experiment. Therefore we counted individuals, estimated the cover per species and measured maximum height as well as maximum diameter if several plants of the same annual species occurred on one square meter. For perennial plants, biomass was harvested individually (annual individuals pooled per species and m²) at the end of the experiment, oven-dried (24 h at 105 °C), and weighed. The data (at least of 10 individuals) were used to construct linear regressions on plant volume and, in contrast to Flombaum & Sala (2007), quadratic regressions on plant cover (0.23 < $r^2$ < 0.99). Because it was not possible to harvest directly on LTE-plots due to the

objectives of a long-term monitoring, regressions were set up for the most frequent perennial species within the LTE using plants from beneath the measured square meters. We used the data from 2007 and regressions to calculate the initial biomass at 2007 for each perennial plant individual and each perennial species on a plot. For the LTE plots, we also calculated the biomass for 2008, respectively.

To analyze soil conditions, the cover of blocks (> 60 cm), stones (> 20 cm), coarse grit (> 6 cm), fine grit (> 2 cm), and fine material (> 0.2 cm) on the plot surface was estimated. Five topsoil samples (0 – 5 cm) taken in each plot were mixed to a bulk sample (Ladd *et al.* 2009), separated in coarse grit, fine grit, and fine material and every fraction was weighed to obtain their mass proportion. Fine material was analyzed in the soil laboratory where the sand fraction was sieved. Silt and clay contents were determined by pipette analyses (Schlichting *et al.* 1995). PH was measured by a pH electrode and the carbonate content was determined by $CO_2$ gas volume using a Scheibler apparatus (Schlichting *et al.* 1995). Salinity was determined by measurements of electrical conductivity (Schlichting *et al.* 1995). Soil organic C and N content were measured by an automatic CN-analyser (EuroEA 3000, EuroVector CHNS-O Elemental Analyser). All together 25 soil parameters (10 traits for skeleton, 9 traits for soil texture, 6 chemical traits) were recorded.

## 5.2.4 ANPP and RUE calculation

To obtain aboveground net primary production (ANPP), we measured the positive increment of biomass for each species on a plot over the study time, and summed for all species on a plot (Milner & Hughes 1968; Huenneke *et al.* 2001; Scurlock *et al.* 2002). Apparent ANPP of GRA plots was calculated to quantify biomass consumption during the investigation period. Rain-use efficiency (RUE) was calculated as an index of ANPP per plot and precipitation during the investigation period, recorded by the weather stations on the experimental sites. We assessed the parameters relative ANPP ($ANPP_{rel}$) and relative RUE ($RUE_{rel}$) by relating total biomass production (annuals and perennials) to the standing crop of perennial plants recorded at the beginning of the experiment in 2007.

## *5.2.5 Statistical analyses*

We conducted an ANOVA (GLM) procedure to analyse the effects of altitude and recovery time on the following dependent variables: Standing crop 2008, ANPP, RUE, ANPP$_{rel}$, and RUE$_{rel}$. To meet the GLM assumptions such as normality distribution and homogeneity of variances, all data of dependent variables was $\log(x + 1)$-transformed and outliers (exceeding five times the mean) were eliminated. Kruskal-Wallis-tests were applied to check the significance of median differences between each of the 12 subjects (Fig. 5.2).

We used Principal Component Analyses (PCA) and Factor Analyses to reduce the 25 measured soil parameters to three main factors. One analysis was applied for all samples and one for every altitudinal level to subsume soil differences along the altitudinal gradient and between the different recovery time intervals, respectively. Three parameters (sand content and N content of the topsoil, soil cover of coarse grit) were identified as proxies for the main factors and changing soil conditions along the altitudinal gradient and included as covariates into the GLM. The resulting mixed model (ANCOVA) tested if the additional use of these continuous soil parameters influences the effect of the categories altitude and recovery time on ANPP, ANPP$_{rel}$, RUE, and RUE$_{rel}$.

## 5.3 Results

### *5.3.1 Standing crop*

We observed significant effects of the factors altitude and recovery time on the standing crop at the end of the experiment (Fig. 5.2, Tab. 5.2). At the beginning of the experiment, standing crop differed only along altitude (results not shown). In 2008, total biomass per ha increased with increasing altitude (p = 0.006). Highest median standing crop, 9314 kg DM/ha on short-term exclosures, was found for oromediterranean shrubland in the High Atlas Mountains (Tab. 5.3).
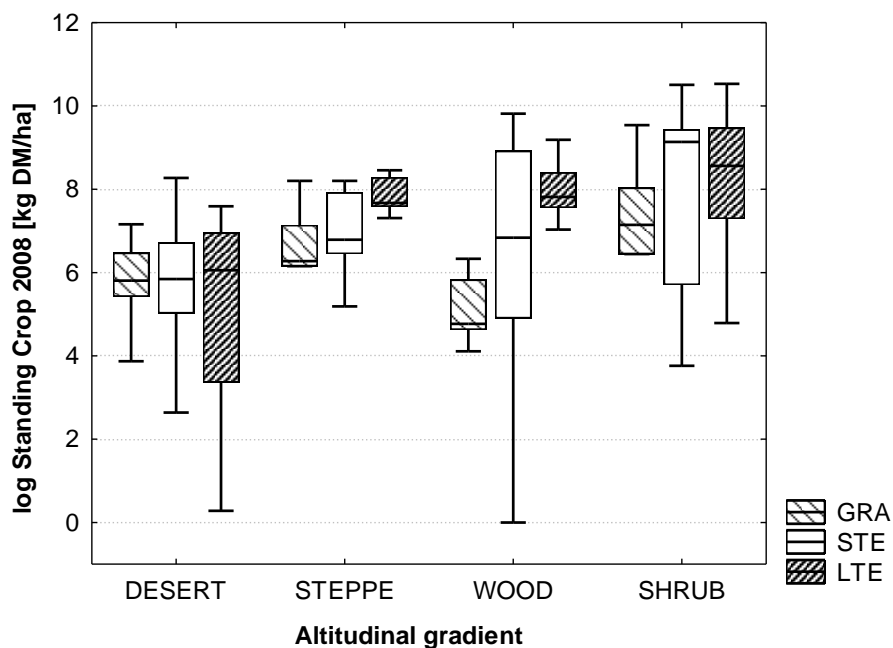


**Fig. 5.2** Standing crop along the altitudinal gradient and for grazed plots (GRA), short-term exclosures (STE) and long-term exclosures (LTE). Values are logarithmized for visual comparison. Boxes show medians and 25th to 75th percentiles, whiskers stand for the non-outlier ranges of the data. For descriptive statistics see Tab. 5.3.

The longer a grazed area had time to recover from grazing impact, the more biomass was accumulated (p = 0.031), e.g. for woodsteppe vegetation the biomass increase for grazed vs. short-term exclosures vs. long-term exclosures was 117, 565 and 2518 kg DM/ha, respectively (all data see Tab. 5.3). Shrubland vegetation showed a different trend: median standing crop on short-term exclosures was higher than on long-term exclosures.

During a recovery period of seven years, no interaction between the two factors was found, i.e. the increase of standing biomass did not differ along the altitudinal gradient.

**Tab. 5.2** ANOVA table showing the effects of altitude and recovery time on standing crop in 2008 (kg DM/ha). ** $p < 0.01$, * $p < 0.05$

| Predictor | dF | F | p |
|---|---|---|---|
| *Altitude* | 3 | 4.4 | 0.006** |
| *Recovery time* | 2 | 3.6 | 0.031* |
| Altitude x recovery time | 6 | 1.4 | 0.220 |
| Error | 106 | | |

Differences between grazed plots and short-term exclosures indicate the portion of biomass consumed by herbivores during the investigation period. However these differences were not significant for any altitudinal level (Kruskal-Wallis-test, $p > 0.05$).

Regarding the proportion of perennial biomass (Tab. 5.3), desert vegetation, in particular that on short-term exclosures (STE) had the lowest median percentage of standing crop (49.8 %). Wood and shrub vegetation of short-term or long-term exclosures only consisted of perennial plants, no matter if grazed or not.

**Tab. 5.3** Descriptive statistics for standing crop in 2008 [kg DM*ha$^{-1}$], and median proportion of perennial standing crop per altitudinal level and grazing treatment. GRA grazed plots; STE short-term exclosed plots; LTE long-term exclosed plots

| Altitudinal level | n | Median | Lower quartile | Upper quartile | Min | Max | % perennials |
|---|---|---|---|---|---|---|---|
| *desert* | | | | | | | |
| GRA | 10 | 335 | 226 | 647 | 47 | 1284 | 96.0 |
| STE | 9 | 331 | 151 | 423 | 2 | 948 | 49.8 |
| LTE | 10 | 437 | 28 | 1050 | 0 | 1978 | 95.3 |
| *steppe* | | | | | | | |
| GRA | 10 | 531 | 470 | 1261 | 47 | 3643 | 98.9 |
| STE | 10 | 889 | 630 | 2753 | 178 | 3644 | 95.3 |
| LTE | 8 | 2146 | 1964 | 3971 | 1492 | 4710 | 99.9 |
| *wood* | | | | | | | |
| GRA | 10 | 117 | 102 | 339 | 14 | 3206 | 100.0 |
| STE | 9 | 565 | 134 | 1832 | 0 | 18303 | 100.0 |
| LTE | 10 | 2518 | 1912 | 4458 | 1132 | 9790 | 100.0 |
| *shrub* | | | | | | | |
| GRA | 9 | 1075 | 629 | 2198 | 0 | 4023 | 100.0 |
| STE | 9 | 8786 | 300 | 11445 | 42 | 36558 | 100.0 |
| LTE | 10 | 5249 | 1466 | 13054 | 0 | 37462 | 100.0 |

## 5.3.2 ANPP and RUE

Aboveground net primary production and rain-use efficiency were influenced by altitude (Tab. 4). We observed a peak of median biomass production (903 kg DM/ha per period) and median rain-use efficiency (3.7 kg DM/ha per period * $mm^{-1}$) for the *Artemisia* steppe vegetation (Fig. 5.3). Furthermore, there was a slight increase of ANPP and RUE for most of the LTE plots, but the total outcome of the 7 years recovery period was not significant. In contrast, we observed a slight, non-significant decrease of median production and rain-use efficiency for the desert vegetation. We consistently calculated median and not mean values to account for high patch-scale heterogeneity of semiarid pastures (Huenneke *et al.* 2001; Augustine 2003).
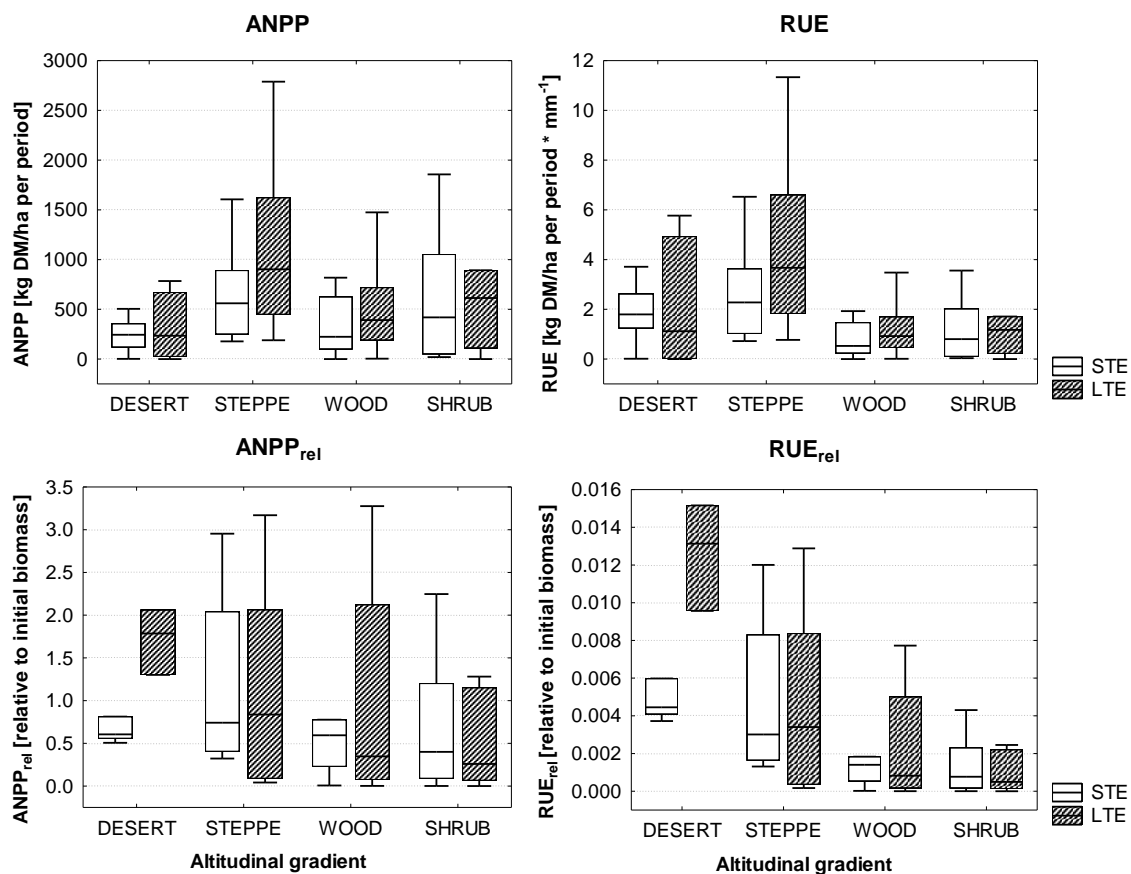


**Fig. 5.3** ANPP and RUE, relative ANPP (ANPPrel) and relative RUE (RUErel) along the altitudinal gradient and for previously grazed (STE) vs. recovered vegetation (LTE). Boxes show medians and 25th to 75th percentiles, whiskers stand for the non-outlier ranges of the data

### *5.3.3 ANPPrel and RUErel*

While total biomass production clearly was a function of altitude and thus climatic aridity, productivity ($ANPP_{rel}$) did not show such dependency (Tab. 5.4). ANPP was highest for *Artemisia* steppes, $ANPP_{rel}$ decreased with altitude. By relating ANPP not only to the amount of initial biomass but also to the amount of rain ($RUE_{rel}$), we could confirm the following trend: $RUE_{rel}$ decreased with altitude and thus decreasing aridity (Fig. 5.3). The more arid a site was the clearer we could observe higher productivity and higher relative RUE values at LTE sites in comparison to STE sites (Mann-Whitney U test, desert: $U = 21$, $p = 0.48$; steppe: $U = 30$, $p = 0.87$; wood: $U = 41$, $p = 0.74$; shrub: $U = 43$, $p = 0.87$). For example, previously grazed desert vegetation (STE) compared to 7 years recovered vegetation (LTE) converted 1 mm of fallen rain into a gain of 0.4 and 1.3 % (median) of its initial biomass, respectively (Fig. 5.3). Since these sites did not differ in median ANPP, but only in median $ANPP_{rel}$, we can reason that LTE sites had been covered by less perennial plant biomass at the beginning of the experiment than STE sites.

**Tab. 5.4** ANOVA table showing the effects of altitude and recovery on ANPP, RUE, $ANPP_{rel}$, and $RUE_{rel}$. ** $p < 0.01$, * $p < 0.05$

| Dependent Variable | Predictor | dF | F | p |
|---|---|---|---|---|
| ANPP | *Altitude* | *3* | *3.1* | *0.032\** |
| | Recovery | 1 | 0.2 | 0.622 |
| | Altitude x recovery | 3 | 0.2 | 0.873 |
| | Error | 67 | | |
| RUE | *Altitude* | *3* | *4.81* | *0.004\*\** |
| | Recovery | 1 | 0.36 | 0.549 |
| | Altitude x recovery | 3 | 0.36 | 0.780 |
| | Error | 67 | | |
| $ANPP_{rel}$ | Altitude | 3 | 0.9 | 0.456 |
| | Recovery | 1 | 0.0 | 0.989 |
| | Altitude x recovery | 3 | 0.6 | 0.622 |
| | Error | 60 | | |
| $RUE_{rel}$ | *Altitude* | *3* | *4.16* | *0.010\*\** |
| | Recovery | 1 | 0.17 | 0.681 |
| | Altitude x recovery | 3 | 1.72 | 0.173 |
| | Error | 60 | | |

## 5.3.4 Soil effect

PCA and factor analysis both revealed a major underlying gradient reflecting the change of soil properties with altitude (Eigenvalue E = 0.362). The environmental differences between plots belonging to the same altitudinal level (STE, LTE) were less important (Eigenvalues E ≤ 0.333). Three main parameters responsible for the soil gradient were sand content, N content and the cover of coarse grit on the plot surface. Both, the sand content and the cover of coarse grit decreased, while the N content of the topsoil increased with altitude (Fig. 5.4). Between STE and LTE plots, no differences could be detected (Fig. 5.4).

The inclusion of these soil parameters as covariables into the GLM analysis (ANCOVA) did not change the effect of altitude on ANPP (F = 3.2; p = 0.028*) and RUE (F = 5.95; p = 0.001**) (Tab. 5.5). ANPP rose with increasing sand and N content of the topsoil but decreased with an increasing soil cover with coarse grit. In contrast, RUE decreased with increasing sand content and the cover of coarse grit and increased with increasing N content in the topsoil. Only the percentage of coarse grit showed a dependency on the RUE (F = 4.76; p = 0.033*) of the vegetation (Tab. 5.1).

ANCOVA results for $ANPP_{rel}$ and $RUE_{rel}$ did not show any significant effect (Tab. 5.5), neither for the categorical factors altitude and recovery nor for the covariables sand content, N content, and percentage of coarse grit. Thus, if we statistically removed the effects of changing soil properties along the altitudinal gradient, $ANPP_{rel}$ and $RUE_{rel}$ became equal over all observed vegetation types. Like GLM, ANCOVA did not detect any significant differences for $ANPP_{rel}$ or $RUE_{rel}$ between grazed (STE) and 7 years recovered vegetation (LTE).
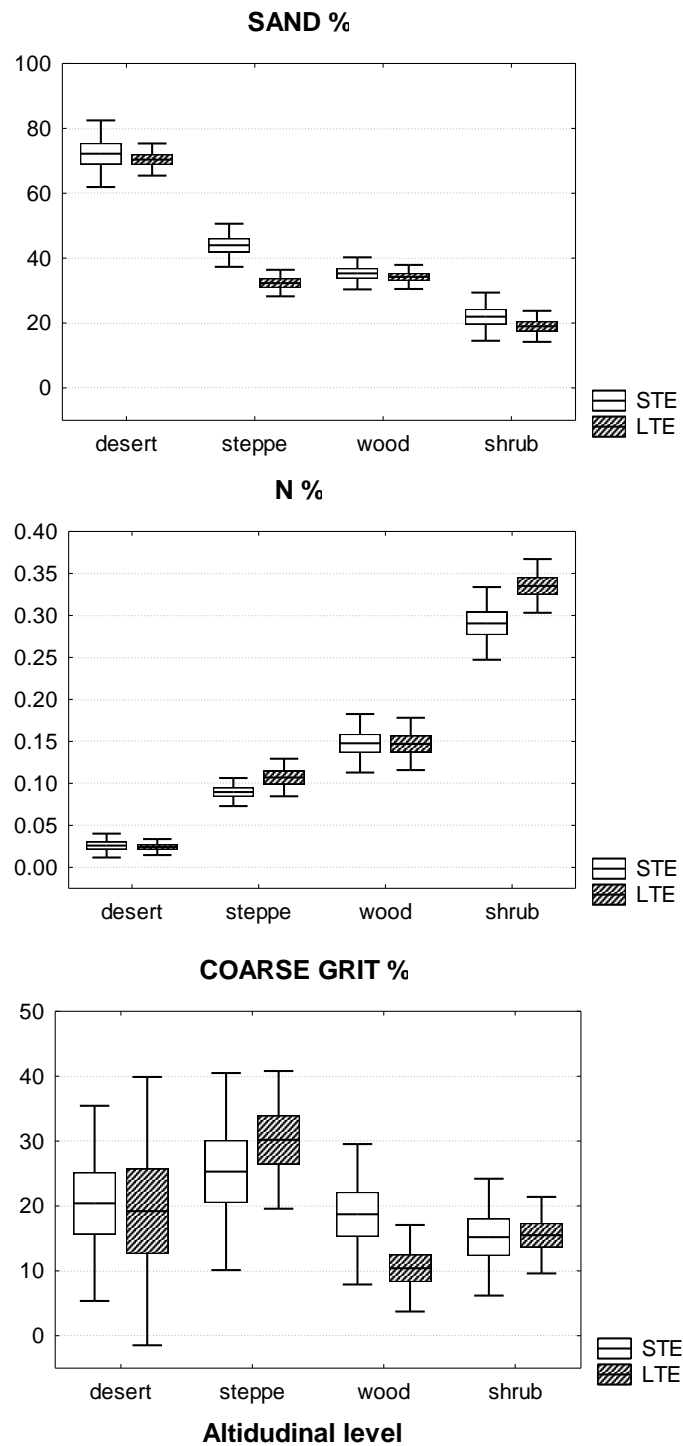
**Fig. 5.4** Means and standard deviations of the sand content (SAND), N content (N), and cover of coarse grit (COARSE GRIT) in percent of the topsoil for STE (short-term exclosure) and LTE (long-term exclosure) plots

**Tab. 5.5** ANCOVA table showing the effects of altitude, recovery and the covariates sand content (Sand), N content (N) of the topsoil, and the cover of coarse grit (Coarse grit) on ANPP, RUE, ANPP$_{rel}$, and RUE$_{rel}$. ** $p < 0.01$, * $p < 0.05$

| *Dependent Variable* | *Predictor* | *dF* | *F* | *p* |
|---|---|---|---|---|
| ANPP | Sand | 1 | 0.0 | 0.904 |
| | N | 1 | 0.7 | 0.391 |
| | Coarse grit | 1 | 2.7 | 0.103 |
| | *Altitude* | *3* | *3.2* | *0.028** |
| | Recovery | 1 | 0.9 | 0.352 |
| | Altitude x recovery | 3 | 0.4 | 0.779 |
| | Error | 64 | | |
| RUE | Sand | 1 | 0.55 | 0.461 |
| | N | 1 | 0.14 | 0.713 |
| | *Coarse grit* | *1* | *4.76* | *0.033** |
| | *Altitude* | *3* | *5.95* | *0.001*** |
| | Recovery | 1 | 0.18 | 0.677 |
| | Altitude x recovery | 3 | 0.40 | 0.753 |
| | Error | 64 | | |
| ANPP$_{rel}$ | Sand | 1 | 0.1 | 0.431 |
| | N | 1 | 0.1 | 0.797 |
| | Coarse grit | 1 | 2.3 | 0.151 |
| | Altitude | 3 | 0.4 | 0.976 |
| | Recovery | 1 | 0.3 | 0.722 |
| | Altitude x recovery | 3 | 1.3 | 0.805 |
| | Error | 57 | | |
| RUE$_{rel}$ | Sand | 1 | 0.10 | 0.758 |
| | N | 1 | 0.10 | 0.754 |
| | Coarse grit | 1 | 2.28 | 0.137 |
| | Altitude | 3 | 0.36 | 0.783 |
| | Recovery | 1 | 0.27 | 0.607 |
| | Altitude x recovery | 3 | 1.33 | 0.272 |
| | Error | 57 | | |

## 5.4 Discussion

Our results demonstrate how ANPP and RUE of the High Atlas vegetation were related to gradients of resource availability and disturbance. The factors (1) altitude and (2) soil condition were analysed as gradients of resource availability, (3) grazing as example for a disturbance gradient, and the factor (4) initial standing crop as an integral of resource availability and disturbance impact over time.

The amount of standing crop, biomass production (ANPP) and rain-use efficiency (RUE) along the High Atlas Mountains strongly depended on altitude. Grazing exclosure over seven years led up to a 4.5 fold biomass accumulation, depending on altitude. No recovery was found for primary production or rain-use efficiency. Relative ANPP (ANPP$_{rel}$) did not differ between altitudes. Relative RUE (RUE$_{rel}$) depended on changes of soil properties along the altitudinal gradient, since altitudinal differences diminished after soil effects had been included into the analysis. Highest differences in productivity (ANPP$_{rel}$) between STE and LTE sites were observed at *Hammada* semidesert.

## 5.4.1 Precipitation and temperature directly affected RUE

As we studied arid and semiarid ecosystems along the southern slope of the High Atlas Mountains, biomass production and rain-use efficiency of the vegetation are influenced by two interacting resource gradients due to aridity and altitude. Aridity limits the amount of available water for phytomass production. For example, ANPP and RUE decline towards low levels (desert, Fig. 5.3), where the ratio of precipitation to potential evapotranspiration (Aridity Index,Tab. 5.1) is lowest. Altitude represents a complex gradient. However, temperature plays an important role because it determines the growth period and thus limits biomass production. Towards high altitudinal levels (shrub, Fig. 5.3) the decline in ANPP and RUE was caused by increasingly limited growth periods, e.g. 183 days at the highest altitude. Both parameters, ANPP as well as RUE, peak at medium altitudinal levels with *Artemisia* steppe vegetation, medium annual precipitation (170 mm / year) and medium temperatures (minimum of 3.2 °C in the coldest and maximum of 25.5 °C in the warmest month) resulting in a growth period of 280 days (Tab. 5.1).

Our results support past findings, showing that production and rain-use efficiency of the vegetation decline towards more arid sites (Le Houérou *et al.* 1988; Yahdjian & Sala 2006; Bai *et al.* 2008a) and with higher altitudinal levels (Whittaker 1967b; Hansen *et al.* 2000). ANPP and RUE along the High Atlas Mountains transect were mainly influenced by this resource gradient because it either sets precipitation or temperature limits.

## 5.4.2 Soil conditions indirectly affected RUE

ANPP and RUE in our study area were most affected by soil characteristics that alter water availability, e.g. higher sand content of the topsoil at desert level accounted for a decrease in RUE. The nitrogen content (total N) of the topsoil changed with altitude and was thus less important as independent limiting resource (Tab. 5.5). The relationship between the coarse grit covering a soil surface and the measured rain-use efficiency can be explained by site-specific differences in pedogenesis. Compared to other sites, the site with the highest ANPP and RUE (*Artemisia* steppe) is characterized by a high proportion of grit which are calcareous concretions, and a smaller proportion of coarse skeleton. A functional relation to RUE was not found.

While $RUE_{rel}$ depended on altitude, the inclusion of soil parameters into the general linear model resulted in statistically equal $RUE_{rel}$ values in the investigation area (Tab. 5.4, Tab. 5.5). Thus, we deduce that soil differences (in particular those affecting water holding capacity) are responsible for changes in relative rain-use efficiencies (English *et al.* 2005).

## 5.4.3 ANPP and RUE

As expected we found that grazing led to a reduction of standing crop (O'Connor *et al.* 2001) while biomass strongly increased on excluded sites (Wesche & Retzer 2005). However, despite of seven years of grazing exclosure, ANPP and RUE of the vegetation were not able to recover.

In general, measurable ANPP differences between grazed and protected sites decrease with the length of their pastoral history (Milchunas & Lauenroth 1993). The investigated area at the southern slope of the High Atlas has been extensively grazed and transformed by nomadic herds for hundreds of years (Le Houérou 1980; Quézel & Barbero 1990; Le Houérou 2001), and in the last decades sedentary pastoralists increasingly use these rangelands, too. Thus, one explanation for the lack of ANPP or RUE recovery can be that differences between grazing treatments could not be detected by means of a seven years experiment. Another explanation takes methodological constraints into account. Absolute ANPP and RUE values can be contrasted for the *Artemisia* steppe level to data of Le Houérou (1974). For exclosure conditions we measured less ANPP (902 vs. 1044 kg DM/ha/year) and less RUE (3.66 vs. 4.75 kg DM/ha/year/mm) than in Algerian *Artemisia* steppe experiencing similar rainfall conditions (246 vs.

220 mm rain). In contrast, for grazed vegetation (STE) we measured higher ANPP (560 vs. 425 kg DM/ha/year) and higher RUE values (2.28 vs. 1.93 kg DM/ha/year/mm), even though the Moroccan grazing pressure (approx. 1 sheep or goat/ 2 ha following own observations) remarkably exceeded that in Algeria (1 sheep/ 8 ha). ANPP as well as RUE differences between grazed and excluded vegetation are smaller for the Moroccan case.

The studies differ in the way how ANPP was measured for grazed sites. In other studies, ANPP is still often  determined by measuring standing crop at the end of the vegetation period (Diouf & Lambin 2001; Holm *et al.* 2003; McCulley 2005). Similarly, remote sensing studies calculated ANPP by measuring NDVI at a certain point of time no matter of grazing offtake (Prince *et al.* 1998; Evans & Geerken 2004; Pettorelli *et al.* 2005; Hein 2006; Jafari *et al.* 2008; Vlek *et al.* 2008). Our study showed that these methods may underestimate standing crop. The full amount of production is not assessed on the grazed sites, but an ANPP reduced by locally occurring grazing pressure. Hence, RUE is underestimated, too.

For the Moroccan case, we quantified the bias of such an underestimation by calculating the difference between median ANPP of GRA sites, which is reduced by grazing during the investigation period, and median ANPP of STE sites (Tab. 5.6). Outside the short-term exclosures grazing animals consumed about 56 % (shrub) to 91 % (steppe) of total ANPP inside. Adler *et al.* (2005) performed a similar study using short-term exclosures at arid sagebrush steppe (USA) and measured 15 to 40 % of consumption depending on the site's distance from water.

**Tab. 5.6** Median percentage of ANPP consumed by livestock during the investigation period. Values are calculated by subtracting median ANPP of the GRA sites from that of STE sites

| Altitudinal level | % ANPP consumed by livestock |
| --- | --- |
| desert | 57.5 |
| steppe | 91.4 |
| wood | 71.5 |
| shrub | 56.3 |

These differences show that ANPP and thus RUE measured on GRA sites considerably depend on actual grazing pressure. If this factor is not quantified, RUE loses its indicative value for long-term and irreversible degradation processes. It primarily indicates the grazing pressure during the preceding

investigation period (presumably highly variable in space) which strongly affects vegetation density. However, density-dependent environmental changes are often short-term and reversible.

## 5.4.4 Initial standing crop is the ecosystem's memory

ANPP and RUE clearly depended on the amount of initial standing crop particularly where spatial differences in past resource availability, e.g. rainfall variability, and disturbances altered the distribution of standing crop. This was shown for ANPP which differed along the High Atlas transect. These differences were caused by underlying changes in initial biomass and not by an increased productivity of the plant individuals (Tab. 5.4). The system's memory (Wiegand *et al.* 2004) was mainly coupled to a build up of reserve biomass by perennial plants. Differences in the proportion of perennials therefore influenced the ANPP and RUE in a region. We therefore recommended the parameters $ANPP_{rel}$ and $RUE_{rel}$ to suppress the strong influence of perennial standing crop.

Comparing $ANPP_{rel}$ to 'ecosystem production efficiency' (Reich *et al.* 1997), which relates annual production to the mass of canopy foliage, $ANPP_{rel}$ has the advantage to include total plant biomass and to calculate with the initial biomass instead of that measured at harvest time. The first difference is important because plants, in particular those in arid and semiarid regions, are able to store energy in specialized tissues often situated at the plant basis as well as in aboveground or belowground woody parts (Müller *et al.* 2007; Owen-Smith 2008). Relating production to initial standing crop better describes the absolute gain in relation to already existing plant material. However, it is only indirectly accessible via backward-calculation (e.g. cover-biomass regressions) and thus a source of bias.

The most obvious influence of perennial plant biomass was seen at *Hammada* semidesert, where a larger proportion of perennials at the beginning of the experiment leaded to lower $ANPP_{rel}$ and $RUE_{rel}$ values at STE compared to LTE sites. By only regarding ANPP and RUE, this change or degradation process could not be detected. Degradation, i.e. the decline in productivity ($ANPP_{rel}$) on grazed sites (STE) could be caused by one of the following major functional mechanisms: either a qualitative change in vegetation or a dramatic change in site conditions due to grazing impact. Vegetation change could be due to altered species composition. For example grasses, forbs and perennials with a small proportion of woody biomass (e.g. *Farsetia occidentalis*) at LTE sites had been

replaced by less palatable stress tolerant woody perennials (e.g. *Hammada scoparia*) at STE sites. The fact, that stress-tolerant species benefit from grazing impact under arid conditions was in general shown by Grime (2001) and by Jauffret and Lavorel (2003) for the case of a Tunisian steppe ecosystem. Abiotic site conditions could affect the proportion of perennial biomass, for example a higher sand content of the soil at LTE sites would favour annual grass species (e.g. *Stipa capensis*) over woody perennial species.

Unlike ANPP and RUE, the parameters $ANPP_{rel}$ and $RUE_{rel}$ give an idea about the productive capacity of a habitat or what a plant community is able to accomplish/produce. $ANPP_{rel}$ and $RUE_{rel}$ are thus more appropriate than ANPP and RUE to describe long-term degradation processes, because they are independent from (frequently occurring and site specific) changes in vegetation density.

## 5.5  Conclusion

The rain-use efficiency was shown to be substantially influenced by resource as well as disturbance gradients due to grazing. Therefore ANPP/RUE were bad predictors for land degradation in the highly variable landscape along the southern slope of the High Atlas Mountains, Morocco. Local differences in water availability, temperature, and soil conditions strongly overlaid the effects of rangeland degradation on ANPP/RUE. In addition, ANPP/RUE of grazed sites were generally underestimated in the past due to methodological limitations, making it easy to declare heavily grazed sites as degraded land. We can face this problem by establishing short-term exclosures close to grazed plots to quantify grazing offtake, and calculate local conversion factors (Brenner 2009). These data may, for example, be used to adjust standing crop values measured by remote sensing in grazed areas.

Finally, ANPP/RUE are confounded by the amount of initial standing crop, which may vary in space and time independent from long-term degradation processes. To suppress the effects of initial standing crop on ANPP/RUE, we recommend the use of $ANPP_{rel}$ and $RUE_{rel}$.

As observed at *Hammada* semidesert, long-term degradation processes go along with hardly reversible changes in vegetation composition or in abiotic site conditions altering $ANPP_{rel}$, but not necessarily ANPP. $ANPP_{rel}$ and $RUE_{rel}$ provide useful tools to describe the capacity of an ecosystem to produce or convert rain into biomass independent from recently occurring vegetation density. They are thus crucial parameters for ecosystem modelling.

# Plant functional types

Inseparable impact
of grazing and stochastic resources
on plant functional traits
in southern Moroccan rangelands

# Abstract

Functional classifications (PFT – plant functional types) are widely seen as a promising tool to simplify the world's floristic complexity. So far, the plant's response along resource gradients is well understood, but functional adaptations to disturbance (e.g. grazing) are still challenging. However, such response groups are in great demand as indicators for rangeland condition. Since temporal unpredictability of resources favours similar plant adaptations as grazing impact, the predictive value of grazing response groups on a regional scale is problematic, particularly in arid and semiarid ecosystems. We investigated grazing response groups along a steep climate and altitudinal gradient along the southern slopes of the High Atlas Mountains, Morocco. First, 16 traits from the sectors life history, regeneration, morphology, and grazing defense of the 69 most abundant plant species were assessed and clustered by PCA into common trait syndromes. Second, the abundance of trait syndromes and, as a second approach, of single trait attributes was tested along consistent grazing gradients on every altitudinal level and subjected to CCA in order to filter additional environmental effects other than grazing impact. Climate and grazing impact were tested by ANOVA-based general linear models. We succeeded to identify grazing response groups and response traits for southern Moroccan pastures, but separately for every altitudinal level. Depending on altitude, heavy grazing favoured tolerance, temporal avoidance, or defense strategies. None of the selected plant traits showed an exclusive response to grazing; but all traits were related to aridity. We emphasize that, in the context of PFT research, temporal stochasticity of resources is a so far underestimated dimension of resource stress. Just like grazing it results in sudden biomass losses. Both impacts thus provoke the same adaptations in plants. We assume that a common core list of pure grazing response traits is unlikely to exist for arid and semiarid environments, irrespective of improved field methods or elaborated statistical approaches. Plant functional types are useful for classifications along resource gradients and as such easy to generalize. However, functional groups in regard to disturbance only make sense on the local scale.

# 6 Plant functional types

## 6.1 Introduction

Functional classifications or Plant Functional Types (PFT) have become widely accepted as a means to simplify the world's floristic complexity. PFTs are applied in vegetation modelling, for monitoring purposes, to estimate the effects of global change and altered land use management on vegetation distribution and ecosystem processes (Noble & Gitay 1996; Bonan *et al.* 2002; Boer & Smith 2003; Hely *et al.* 2006; Lavorel *et al.* 2007). Therefore many studies sought classification criteria that combine a high explanatory value, easy and standardized measurement options, and applicability across a wide range of environmental conditions at the same time. For a global review see Diaz *et al.* (2007). However, the more studies have been performed in order to find this 'holy grail' (Lavorel *et al.* 2007), the more classification approaches occurred.

Plants are energetically constrained in their performance for alternative functions, such as resource capture and conservation (Weiher *et al.* 1999; Lavorel & Garnier 2002). Consequently, trade-offs occur between possible plant adaptations, e.g. to altered resource availability (water, soil nutrients) or to disturbances such as grazing.

Following (Gitay & Noble 1997) plants can be functionally classified depending on whether they use the same resource (guilds) or show the same response to disturbances (groups). There exists a variety of studies showing how plants adapted along resource gradients, such as climate gradients (Leishman & Westoby 1992; Skarpe 1996; Díaz & Cabido 1997; Thuiller *et al.* 2004; Westoby & Wright 2006) and gradients of water or nutrient availability (Breshears & Barnes 1999; Sperry 2002; Ogle & Reynolds 2004; Schmidtlein 2004). But up to now, functional classifications according to the plant's adaptation to disturbances (response groups), e.g. grazing, still remain a challenging issue. Under disturbance we can subsume all mechanisms which limit the plant biomass by causing its partial or total destruction (Grime 1979). Assembling response groups depending on grazing intensity has been a major scientific goal of vegetation ecology, because response groups were assumed to be indicative for rangeland condition (Landsberg *et al.* 1999; Duckworth *et al.* 2000; Maestre & Escudero 2009). In terms of methodology, response groups often followed an *a priori*

classification such as growth form analyses (Aguiar *et al.* 1996; Sternberg *et al.* 2000; Pykälä 2004; Adler *et al.* 2005; Wang & Ni 2005). If not, they were assembled by means of multivariate analyses clustering plant traits and attributes to commonly occurring trait syndromes (Leishman & Westoby 1992; Wang & Ni 2005; Navarro *et al.* 2006; Ansquer *et al.* 2009). In this context it is still under discussion which adaptations or plant strategies are favourable under increasing grazing pressure.

Numerous models offer functional explanations for the distribution of plant characteristics along grazing gradients (Dyksterhuis 1949; Coley *et al.* 1985; Milchunas *et al.* 1988; Milchunas & Lauenroth 1993; Briske & Richards 1995; Briske 1996; Westoby 1998; Grime 2001). Following the global synthesis of Diaz *et al.* (2007), we are able to subsume these models under three cornerstones: productivity, frequency and magnitude of disturbance, and grazing history mainly determine the pool of plant characteristics (trait attributes) at a given site. Studies about the impact of these driving-forces for arid and semiarid ecosystems face a conceptual problem. Resource scarcity (also called 'stress' (Grime 2001) and 'adversity' (Southwood 1988)) and herbivory often favour the same functional adaptations. Increasing aridity means that plants have to cope with declining annual rainfall and at the same time with increasing rainfall variability which leads to temporal unpredictability of plant resources. Existing conceptual models see resource availability (stress) and disturbance as two different driving-forces (Southwood 1988; Briske 1996; Grime 2001; Ladd *et al.* 2009). In contrast to this, we emphasize that irregular spells of resource scarcity typical for arid environments and disturbances may have similar impact on plant individuals and will thus provoke the same functional response. This fact has been discussed for example by Milchunas *et al.* (1988) and Coughenour (1985), but exclusively for semiarid grasslands and not in the context of PFT classification. We can explain the impact of resource scarcity and disturbance under an economic point of view: physiologically it is rather similar whether a plant has to cope with a temporal lack of resources (e.g. water) or with a loss of photosynthetic tissue caused by herbivory. Both events reduce the plant's ability to fix energy. Compared to a financial shortage for example, it does not matter if one was confronted to an unexpected deficit, reduced income, or additional costs. In either case, plants have the same possibilities: to avoid or to compensate potential losses.

Compensation  is often described as tolerance strategy (Briske & Richards 1995; Agrawal 2000; Diaz *et al.* 2001; Milchunas & Noy-Meir 2002). Tolerance to grazing may be induced by a range of mechanisms such as increased photosynthetic rate or relative growth rate, increased branching, a pre-existing carbon storage, or the ability to reallocate stored compounds after damage (Strauss & Agrawal 1999; Owen-Smith 2008). Avoidance as a plant strategy can be further classified into temporal avoidance mechanisms and defense mechanisms. Temporal avoidance is mainly practised by fast growing species of the ruderal type (Grime 2001) which are able to persist most of the vegetation period in form of seed and avoid spells of predation. Defense mechanisms comprise chemical defense, for example by accumulation of flavonoids or toxins, and structural or mechanical defense by thorns, spines, sclerophylly, and squarrose growth (Cooper & Owen-Smith 1986; Strauss & Agrawal 1999; Milchunas & Noy-Meir 2002; Koricheva *et al.* 2004). Many plant adaptations have been interpreted as coping mechanisms against herbivory, but may similarly be interpreted as an adaptation to temporal resource stresses. For example short lifespan (Reich *et al.* 2003) and carbon storage in non-photosynthetic tissues (Noy-Meir 1973; Suzuki & Stuefer 1999) are profitable under conditions with highly variable water resources, and sclerophylly protects leaves from severe transpiration losses in dry periods (Turner 1994; Grubb 1998).

To investigate this problem, comparisons of grazing effects between regions with contrasting climates are needed (Diaz *et al.* 2007). However, comparisons have rarely been made. De Bello *et al.* (2005) and Adler *et al.* (2005) found, for example, that climatic constraints overruled the impact of grazing on plant traits. Considering the functional similarity in effects of disturbance and resource stochasticity on plant response, we assume that even the most stringent experimental design would fail to find exclusive adaptations to grazing at least in arid and semiarid environments.

For that reason, we conducted a study on plant functional traits and investigated two driving forces: resource availability (stress) and disturbance. In detail we focused on four grazing gradients along a steep altitudinal and aridity gradient at the southern slopes of the High Atlas Mountains, Morocco. The altitudinal gradient was chosen with respect to one main group of land users, thus grazing history as a third potential driving force (Milchunas & Lauenroth 1993) was kept constant. Grazing gradients were all established within the same range of grazing

intensities, starting with sites that had not been grazed for seven years and ending with heavily grazed sites close to human settlements. The following hypotheses were tested:

(1) Climate will predominantly select plant traits because it alters the spatial and temporal availability of water resources along the altitudinal gradient.

(2) Since temporal unpredictability of water resources and disturbance regime will affect trait assemblages in a similar way, we expect difficulties in disentangling one functional background from another. Exclusive response of plant traits to grazing will not occur.

## 6.2  Material and Methods

### *6.2.1 Investigation area*

The study was conducted along a steep altitudinal gradient at the southern slope of the High Atlas Mountains, Morocco. It is associated with an aridity gradient and reaches from arid lowland basins (1,200 m a.s.l.) with high rainfall variability to the subhumid peaks of the High Atlas Mountains (up to 4,071 m a.s.l.) (Schulz 2008) (Tab. 6.1). Vegetation along this gradient gradually changes from sparse *Hammada scoparia* semideserts (desert) to *Artemisia herba-alba* steppes (steppe), *Juniperus* woodsteppes (wood) and up to oromediterranean shrubland (shrub) in the highest mountain parts (Finckh & Poete 2008).

The entire study area has experienced a long grazing history. It has been used for centuries as pasture for livestock – mostly sheep and goats –  both of sedentary and transhumant pastoralists (Barrow & Hicham 2000; Montés *et al.* 2002; Breuer 2007). Our study sites are used by one main group of local land users, thus grazing history can be regarded as constant. In spring 2007, gradients of different grazing intensity were identified for each of the four vegetation types. Identification was made by observation of direct grazing indicators (dung, trampling, bare ground, distance to settlements, see Fig. 6.1, Tab. 6.6) and interviews with local people (Beever *et al.* 2003; Adler *et al.* 2005; Maestre & Escudero 2009). For every type the gradient consisted of four levels, congruently starting from sites that were not grazed for seven years (1 - grazing exclosure) up to sites exposed to a very high grazing pressure (4) close to a settlement (Tab. 6.1).

**Tab. 6.1** Location parameters and climatic conditions of 17 investigated sites along the High Atlas transect. ARID shows the mean annual precipitation in mm (in brackets) and the aridity index, i.e. the ratio of annual precipitation to annual potential evapo-transpiration following Middelton & Thomas (1997) calculated for the years 2000-2008 (01.01.-31.12.). VEG gives the length of the vegetation period as the mean amount of days exceeding a mean daily temperature of 5°C, calculated for the rain years 2001/02-2007/08 (01.09.-31.08.). Latitude (LAT), longitude (LONG) and altitude (ALT) are means of eight sample plots calculated for each level of grazing intensity

| SITE | ARID | VEG *(days)* | LEVEL | LOCALITY | LAT *(N)* | LONG *(W)* | ALT *(m)* |
|---|---|---|---|---|---|---|---|
| desert | 0.07 | 350 | 1 low | Grazing exclosure | 31°10'24" | 6°34'48" | 1362 |
| | (124) | | 2 | Pasture close to the exclosure | 31°10'20" | 6°34'45" | 1366 |
| | | | 3 | Close to nomad shelter | 31°08'40" | 6°34'08" | 1316 |
| | | | 4 high | Close to the village Tiliguite | 31°06'35" | 6°33'27" | 1278 |
| steppe | 0.17 | 280 | 1 low | Grazing exclosure | 31°23'13" | 6°19'22" | 1868 |
| | (170) | | 2 | Pasture close to the exclosure | 31°23'13" | 6°19'23" | 1866 |
| | | | 3 | Close to nomad shelter | 31°22'26" | 6°19'08" | 1816 |
| | | | 3 | Far from village Ait Khlifa | 31°24'28" | 6°15'51" | 1808 |
| | | | 4 high | Close to the village Ait Khlifa | 31°25'20" | 6°14'10" | 1802 |
| wood | 0.28 | 305 | 1 low | Grazing exclosure | 31°30'05" | 6°14'51" | 2243 |
| | (285) | | 2 | Pasture close to the exclosure | 31°30'06" | 6°14'51" | 2258 |
| | | | 3 | Close to nomad shelter | 31°29'54" | 6°15'54" | 2073 |
| | | | 4 high | Close to the village Ameskar | 31°30'21" | 6°16'03" | 2167 |
| shrub | 1.25 | 183 | 1 low | Grazing exclosure | 31°20'27" | 6°10'30" | 2985 |
| | (363) | | 2 | Extensively grazed plateau | 31°20'00" | 6°10'02" | 2991 |
| | | | 3 | Pasture close to the exclosure | 31°20'27" | 6°10'32" | 2976 |
| | | | 4 high | Close to nomad shelter | 31°20'25" | 6°10'44" | 2966 |

## 6.2.2 Trait catalogue and trait assessment

We selected 16 grazing-predictive plant traits by means of a literature review (Leishman & Westoby 1992; Pillar 1999; Weiher *et al.* 1999; Jauffret & Lavorel 2003; Pausas & Lavorel 2003; Cornelissen *et al.* 2003; Navarro *et al.* 2006). The assembled traits fell into four categories concerning plant's life history, regeneration, morphology, and grazing defense mechanisms (Tab. 6.2).

The given traits were selected due to the following functional considerations. Life history traits like lifetime and leaf phenology are generally associated with the plant's response to climate and play an important role to survive adverse conditions (tolerance, avoidance), and in terms of competitive vigour (Leishman & Westoby 1992; Pillar 1999). Regeneration traits are relevant to describe how grazed plant species avoid or compensate (tolerate) biomass losses (Weiher *et al.* 1999; Pausas & Lavorel 2003; Navarro *et al.* 2006). They include the reproduction type, regeneration period, flower height, dispersal mechanism, and resprouting ability. For example, the ability for vegetative reproduction after damage is one mechanism to compensate lost biomass, and flowers located near the ground level may prevent herbivores from reaching them. Morphological traits can be considered as adaptations to climate and to grazing. The position of dormant buds and orientation of main axes are characteristics associated to grazing avoidance (Navarro *et al.* 2006). The specific leaf area (SLA) is positively correlated to the plant's relative growth rate and tends to increase in resource-rich environments, thus SLA is known to be dominantly influenced by climate and less by grazing. Plant height, individual ground cover and the proportion of herbaceous biomass are related to the plant's competitive vigour and determines how grazing and climate stress can be tolerated or avoided (Cornelissen *et al.* 2003). Chemical protection, mechanical protection and sclerophylly can be considered relevant defense mechanisms of plant species against grazing (Pausas & Lavorel 2003; Navarro *et al.* 2006). However, spinescence and sclerophylly are also known to respond to climate (Cornelissen *et al.* 2003).

Trait attributes were assessed for 69 plant species (23, 21, 15 and 10 of desert, steppe, wood and shrub vegetation, respectively) during field studies and with the help of literature/local floras (Nègre 1961a; Nègre 1961b; Quézel & Santa 1962a; Quézel & Santa 1962b; Fennane *et al.* 1999; Ozenda 2004; Fennane *et al.*

2007). Unlike Tremlova and Münzbergova (2007), we combined categorical and measured traits in order to include a wide range of species and to cope with the

**Tab. 6.2** Trait catalogue with grazing relevant traits identified for 69 plant species along the altitudinal transect. Nomenclature of trait attributes follows an ordinal scale and ranks trait attributes from being least favourable (0) to most favourable (highest value) for grazing animals. In this context, favourableness is high if the attribute leads to increased palatability, the provision of forage on a broader spatial scale or on a longer time scale

| Plant traits | | Attributes |
|---|---|---|
| *Life history* | | |
| 1 | lifetime | 0 = annual; 1 = short perennial (< 10 years); 2 = long perennial (> 10 years) |
| 2 | leaf phenology | 0 = without leaves; 1 = leaves or whole plant only seasonal; 2 = evergreen |
| *Regeneration* | | |
| 3 | reproduction type | 0 = only sexual; 1 = predominantly vegetative; 2 = sexual and vegetative |
| 4 | regeneration period | 0 = without peak; 1 = Dec-Feb; 2 = Mar-May; 3 = Mar-Aug; 4 = Jun-Aug; 5 = Sep-Nov |
| 5 | flower height | 0 = above 2 m; 1 = at ground level; 2 = below 2 m but protected; 3 = like 2 but flowers unprotected |
| 6 | dispersal mechanism | 0 = autochorous; 1 = zoochorous short distance; 2 = zoochorous long distance; 3 = anemochorous |
| 7 | resprouting ability | 0 = no resprouting after grazing; 1 = resprouting possible |
| *Morphology* | | |
| 8 | bud position | 0 = under ground level/survival as seed; 1 = above 2 m; 2 = at ground level; 3 = below 2 m |
| 9 | axe orientation | 0 = without long axes (tuft, rosette); 1 = axes horizontal (creeping plant); 2 = axes vertical (plant erect) |
| 10 | specific leaf area (SLA) [m²/kg] | In classes: 0 = without leaves; 1 = max 3; 2 = max 6; 3 = max 9; 4 = max 12; 5 = > 12 |
| 11 | plant height [cm] | In classes: 0 = max 1; 1 = max 3; 2 = max 9; 3 = max 27; 4 = max 81; 5 = > 81 |
| 12 | individual ground cover [% of 1 m²] | In classes: 0 = max 0.3; 1 = max 1; 2 = max 3; 3 = max 9; 4 = max 27; 5 = > 27% |
| 13 | herbaceous biomass ratio [%] | In classes: 0 = max 20; 1 = max 40; 2 = max 60; 3 = max 80; 4 = > 80; 5 = totally herbaceous |
| *Grazing defense* | | |
| 14 | chemical protection | 0 = with secondary metabolites for grazing protection; 1 = without chemical protection |
| 15 | mechanical protection | 0 = with mechanical protection (thorns, spines, squarrose growth); 1 = without mechanical protection |
| 16 | sclerophylly | 0 = without leaves; 1 = hard-leaved; 2 = malacophyllous |

recent lack of sufficient ecological information on Moroccan plant species. Plant height, individual ground cover, specific leaf area (SLA) and herbaceous biomass ratio were assessed as the mean of 10 plant individuals measured for each species and along the whole grazing gradient. The SLA was assessed by picking 10 leaves of each plant individual, which were dried and weighed. The leaf surface was measured by scanning the leaves and calculating the surface area with the Software DatInf Measure ® 2.1. Herbaceous biomass ratio was obtained by harvesting the aboveground biomass. Woody and herbaceous biomass were separated, oven-dried (105 °C; 24 hours) and weighed. All assembled trait attributes resulted in a species × trait (S×T) matrix similar to that of Wang & Ni (2005) (Tab. 6.5, Appendix).

## 6.2.3 Vegetation plots along grazing gradients

To quantify the response of plant species to grazing intensity, we randomly installed eight independent vegetation plots per grazing intensity and on every altitudinal level i.e. at the same locations where we had sampled trait attributes (Tab. 6.1). Plots were sampled in spring 2008 and surveyed at the time of expected peak of vegetation development in the corresponding location. Each plot measured 5 × 5 m. We assessed the ground cover in percent of all vascular plant species, assigned them to life forms and measured their maximum height in cm. At the woodsteppe level, plot size was extended to an area of 20 × 20 m in order to assess the ground cover of *Juniperus* trees. A total of 195 species belonging to 136 genera and 37 families were recorded. Field work resulted in a plot × species (P×S) matrix (Wang & Ni 2005).

## 6.2.4 Environmental data

To analyse influencing soil conditions, the cover of blocks (> 60 cm), stones (> 20 cm), coarse grit (> 6 cm), fine grit (> 2 cm), and fine material (> 0.2 cm) on the plot surface was estimated. Five topsoil samples (0 – 5 cm) taken in each plot were mixed to a bulk sample (Ladd *et al.* 2009), separated in coarse grit, fine grit, and fine material and every fraction was weighed to obtain their mass proportion. Fine material was analysed in the soil laboratory where the sand fraction was sieved. Silt and clay contents were determined by pipette analyses

(Schlichting *et al.* 1995). PH was measured by a pH electrode and the carbonate content was determined by $CO_2$ gas volume using a Scheibler apparatus (Schlichting *et al.* 1995). Salinity was determined by measurements of electrical conductivity (Schlichting *et al.* 1995). Soil organic C and N content were measured by an automatic CN-analyser (EuroEA 3000, EuroVector CHNS-O Elemental Analyser). All together 25 soil parameters (10 parameters for skeleton, 9 parameters for soil texture, 6 chemical parameters) were recorded.

## 6.2.5 Data analysis

### 6.2.5.1 *Trait syndromes and response groups*
Our first step of analysis aimed to assemble grazing response groups. Therefore, we translated the S × T matrix into binary codes and then subjected it to Principal Component Analyses (PCA) to emerge common trait syndromes. We used the software CANOCO (version 4.5, (Ter Braak & Smilauer 2002)) and performed one PCA for each vegetation type. All analyses followed the default settings.

To quantify species' response to grazing intensity, we assigned all plant species which occurred on a plot to one trait syndrome according to vegetation type and life form. The P × T matrix was used to calculate the relative ground cover in percent for every trait syndrome. Abundance of trait syndromes along grazing gradients was tested using Kendall's rank correlation coefficient τ. Syndromes showing $τ > 0.04$ and $p < 0.05$ were selected as members of potential response groups (Tab. 6.3). Despite these criteria, we did not focus on trait syndromes showing an indefinite response along the gradient, but additionally included syndromes where we observed a hump-shaped response (nonlinear). Single ANOVA analyses on every altitudinal level tested whether grazing intensity can significantly predict the abundance of trait syndromes (Garnier *et al.* 2006). Unlike other authors (Pykälä 2004; De Bello *et al.* 2005; Tremlova & Münzbergova 2007), we generally did not perform regression analyses along grazing gradients, because the regarded grazing intensity levels followed an ordinal scale.

### 6.2.5.2 *Response of single trait attributes*
In a second step we directly focussed on the abundance of single trait attributes in order to evaluate if traits can be considered as a functional adaptation to aridity or reflect a grazing response. Here, analyses were performed using data

from the S × T matrix. Since the assessed 69 plant species accounted for more than 77 % of total vegetation cover, trait analyses allow drawing conclusions for the whole vegetation type. This procedure is equally applied by Garnier *et al.* (2006).

The P × T matrix was used to calculate the relative ground cover in percent for every trait attribute, e.g. those of creeping plants along grazing gradients. Relative cover values were arcsin-transformed (Gnanadesikan 1997) and subjected to GLM analyses. Analyses were based on factorial ANOVA and tested whether the climatic gradient, the disturbance gradient, or a combination of both influenced the abundance of certain trait attributes. Afterwards, we picked trait attributes that had been important to assemble response groups, and performed single ANOVA analyses on every altitudinal level. ANOVA tested whether grazing intensity can significantly predict the abundance of selected trait attributes.

### 6.2.5.3 *Trait syndromes and trait attributes in relation to environmental factors*

Both abundances, those of significant trait syndromes and selected trait attributes along grazing gradients were checked for the influence of changing environmental parameters by means of Canonical Correspondence Analyses (CCA). CCAs were performed for each vegetation type, respectively. As direct grazing-dependent parameters, we included the cover of bare ground (BARE, in %) and the intensity of trampling (TRAMPLE, in %) estimated for every vegetation plot (Fig. 6.1). Five of the most influencing environmental parameters were selected by PCA and factor analyses, separately for every altitudinal level. On all altitudinal levels the proportion of grit (SKELET, 2 mm – 6 cm), sand (SAND), organic carbon (C), and nitrogen (N) in the topsoil sample best characterized local environmental gradients. Additionally, the percentage of clay (CLAY) was chosen at desert, the percentage of carbonate (CACO3) at steppe, and the percentage of fine grit (SKE-GRIT) at woodsteppe level to account for local particularities.

Abundance data of trait syndromes and trait attributes were log (x + 1)-transformed. We only investigated trait attributes which were found to characterize the trait syndromes emerged from PCA. Further, we eliminated redundant attributes and those which did not occur on the given altitudinal level. Environmental parameters were included by forward selection procedure and

tested for significance by Monte Carlo permutation tests. We ran these analyses in CANOCO 4.5 (Ter Braak & Smilauer 2002).

As a result of CCA analyses, trait syndromes and trait attributes which predominantly reacted to environmental conditions unrelated to grazing, e.g. $CaCO_3$ content of the soil, were omitted from further analyses. We excluded trait syndromes and attributes showing no directed response (increase or decrease) to grazing. On some altitudinal levels, several trait syndromes showing the same response were pooled to one response group.

## 6.3 Results

### 6.3.1 Quantification of grazing intensity

We investigated the response of plant groups and plant traits along gradients of grazing intensity on four altitudinal levels in the High Atlas Mountains. Since no detailed information was available on the number of grazing animals, we quantified their visible impact on the soil surface in order to confirm the chosen grazing gradients (Fig. 6.1). This approach is similarly used by other authors (McIntyre *et al.* 1995; Beever *et al.* 2003; De Bello *et al.* 2005; Adler *et al.* 2005; Maestre & Escudero 2009).
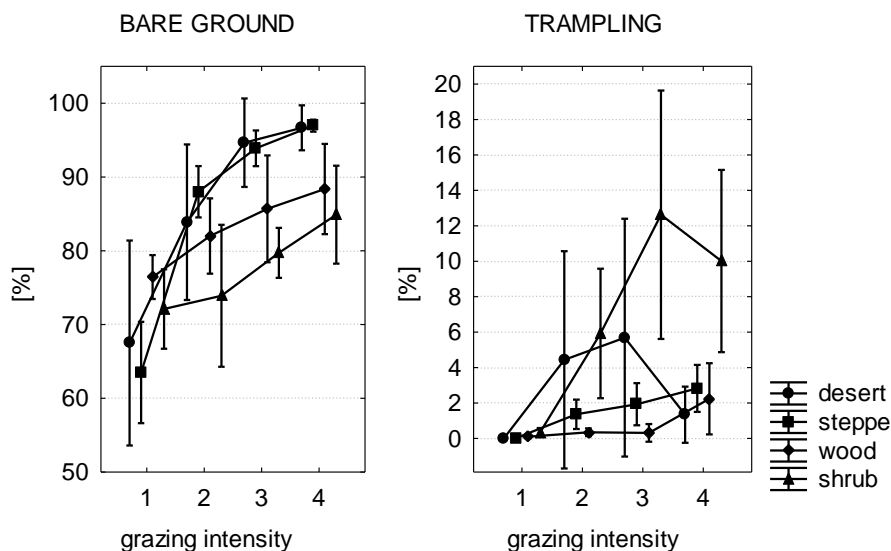


**Fig. 6.1** Percentage of bare ground and trampled surface (mean and standard deviation) as examples for variables indicating grazing pressure. Both increase from ungrazed sites (1) to heavily grazed sites (4) confirming the selected levels of grazing gradients. Note that the percentage of bare ground and the percentage of trampling locally differed in their response along the grazing gradient

On all altitudinal levels we observed an increase (Kendall's Tau, see Tab. 6.3) of faeces, trampling traces and the percentage of bare ground on the plots (Fig. 6.1); while the proportion of dead plant material decreased the more intensive a surface had been grazed.For desert and shrub vegetation, soil salinity significantly increased along the grazing gradients. At the steppe site, the organic C and N content decreased the more intensive a surface had been grazed. This was equally the case for the N content in the topsoil at woodsteppe level (Tab. 6.6).

## 6.3.2 Trait syndromes at four altitudinal levels

For every vegetation type, PCA analyses revealed a specific set of trait syndromes which generally depended on plant's lifetime (Tab. 6.3, general attributes). However, as the set of predominating species and thus trait attributes strongly varied along the altitudinal gradient, each vegetation type showed a unique set of trait syndromes (Tab. 6.3, separating attributes). This was equally observed along a climatic gradient in Spain (De Bello *et al.* 2005).

For *Hammada* semidesert, we observed three types of annuals (A, B, C), one type of short perennials (D), and two types of long perennial plants (E, F). Annuals differed in their position of flowers, SLA and chemical protection mechanisms. Long perennial plant species differed in their mean individual cover and the amount of herbaceous (palatable) biomass. Little shrub species (E) seemed to have a higher proportion of herbaceous biomass, while huge shrub species (F) had a higher proportion of woody biomass. Two of these trait syndromes were selected as possible response groups (Tab. 6.3,Fig. 6.2). First, we identified a group of annuals with high forage value and flowers that are well accessible for grazing herbivores (C), e.g. annual grasses like *Stipa capensis*. These plant species were negatively correlated to grazing impact ($\tau = -0.572$; $p = 0.000$). Despite no linear correlation to the grazing gradient ($\tau = 0.087$; $p = 0.484$), we picked out a second group of plant species (E), containing shrubs with little ground cover, but medium proportion of herbaceous biomass such as *Hammada scoparia*. This type of long perennial species was observed to increase towards the highest level of grazing intensity (Tab. 6.7, Appendix).

**Tab. 6.3** Trait syndromes with characterizing trait attributes along the altitudinal gradient. Abundances of trait syndromes along grazing gradients were tested for linear correlation using Kendall's rank correlation coefficient $\tau$. Trait syndromes with $\tau > 0.4$ and $p < 0.05$ (bold) were selected to build up response groups, which are marked as *decreasers and ***invaders (Dyksterhuis 1949). See also Fig. 6.2. Whether the abundance of a trait syndrome depended on grazing gradients, was also tested by single ANOVAs, for results see Tab. 6.7 (Appendix)

| Trait syn-drome | General attributes | Separating attributes | Example of plant species | Kendall's correlation coefficient | |
|---|---|---|---|---|---|
| | | | | $\tau$ | $p$ |
| *Hammada* **semidesert** | | | | | |
| A | Annual | Little cover; flowers well accessible; chemical protection | *Cleome africana* | 0.247 | 0.047 |
| B | | Creeping plant; flowers at ground level; low forage value (SLA < 9) | *Paronychia arabica* | 0.348 | 0.005 |
| C* | | Flowers well accessible, high forage value (SLA > 9 m²/kg) | *Stipa capensis* | **-0.572** | **0.000** |
| D | Short perennial | Buds at ground level; 80 – 100 % herbaceous | *Stipagrostis obtusa* | -0.238 | 0.055 |
| E | Long perennial | Little cover (< 27 %); medium proportion of herbaceous biomass (> 40 %) | *Hammada scoparia* | 0.087 | 0.484 |
| F | | Big cover (> 27 %); small proportion of herbaceous biomass (< 40 %) | *Zilla spinosa* | 0.057 | 0.645 |
| *Artemisia* **steppe** | | | | | |
| A*** | Annual | Little cover (< 0.3 %); thin leaves (SLA > 12 m²/kg) | *Bromus rubens* | **0.559** | **0.000** |
| B*** | | Rosettes; thicker leaves (SLA < 12 m²/kg) | *Glaucium corniculatum* | **0.776** | **0.000** |
| C*** | Short perennial | Creeping plant | *Helianthemum crocceum* | **0.418** | **0.000** |
| D | | Rosette or tuft | *Stipa parviflora* | 0.319 | 0.004 |
| E* | Long perennial | Flowering in autumn | *Artemisia herba-alba* | **-0.468** | **0.000** |
| F | | Flowering in spring/summer | *Thymus satureioides* | 0.313 | 0.004 |
| *Juniperus* **woodsteppe** | | | | | |
| A | Annual | 100 % herbaceous biomass | *Schismus barbatus* | -0.050 | 0.685 |
| B | Short perennial; | Up to 100 % herbaceous biomass | *Telephium imperati* | 0.383 | 0.002 |
| C | creeping plant | 60 -80 % herbaceous biomass | *Asperula cynanchica* | -0.032 | 0.794 |
| D | Short perennial; | Little rosettes (Cover < 0.3 %) | *Centaurea gattefossei* | 0.151 | 0.224 |
| E* | rosette or tuft | Medium cover (< 3 %) | *Dactylis glomerata* | **-0.536** | **0.000** |

| | | | | | |
|---|---|---|---|---|---|
| F* | | Big cover (< 9 %); thick leaves; anemochorous | *Carlina brachylepis* | **-0.431** | **0.001** |
| G* | Long perennial | Little: < 27 cm high | *Santolina africana* | **-0.490** | **0.000** |
| H*** | | Medium: < 81 cm high | *Genista scorpius* | **0.499** | **0.000** |
| I | | Tall: > 81 cm high; without leaves | *Juniperus phoenicea* | -0.023 | 0.854 |
| **Oromediterranean shrubland** | | | | | |
| A*** | Annual | 100 % herbaceous biomass | *Minuartia funckii* | **0.672** | **0.000** |
| B | Short perennial | Tuft; flowers high and unprotected; less than 100 % herbaceous biomass | *Helictotrichon filifolium* | -0.151 | 0.224 |
| C*** | | Rosette; flowers at ground level; 100 % herbaceous biomass | *Centaurea josiae* | **0.422** | **0.001** |
| D | Long perennial | Little: < 9 cm high; hard leaves; medium proportion of herbaceous biomass (< 60 %) | *Astragalus ibrahimianus* | -0.323 | 0.009 |
| E | | Tall: > 9 cm high; soft leaves; small proportion of herbaceous biomass (< 40 %) | *Alyssum spinosum* | -0.092 | 0.461 |

*Artemisia herba-alba* steppe vegetation consisted of two types of annual species (A, B), differing by individual cover, SLA and growth form. There were further two types of short perennials, creeping (C) and non-creeping (D) species, and two types of long perennial plant species, differing by their flowering time (E, F). While A, B, and C increased in their abundance along the grazing gradient (Tab. 6.3, Fig. 6.2), plant species of syndrome E strongly decreased ($\tau$ = -0.47; p = 0.000). For *Juniperus* woodsteppe we observed nine trait syndromes: annuals (A), five types of short-perennials (B, C, D, E, F), and three types of long perennial plant species (G, H, I). Short perennials differed in growth form, proportion of herbaceous biomass and individual ground cover. Long perennial species mainly differed in vegetative height.

Correlation analysis revealed four potential response groups (Tab. 6.3). Two syndromes of short perennial plant species (E, F) characterized as tuft (*Dactylis glomerata ssp hispanica*) or rosettes and by individual cover values from 1 – 9 dm². Some of these plant species were anemochorous such *Carlina brachylepis*. This trait syndrome decreased in abundance along the grazing gradient (Tab. 6.3, Fig. 6.2). Another decreasing group (G) consisted of little shrub species like *Santolina africana* ($\tau$ = -0.49; p = 0.000). Contrarily, tall shrubs (H; mean height 27

cm < h < 81 cm) like *Genista scorpius ssp myriantha* increased along the grazing gradient ($\tau = 0.499$; $p = 0.000$).

Oromediterranean shrub vegetation consisted of annual plants (A), two types of short perennials (B, C) differing by growth form and their position of flowers, and further two types of perennial plant species with a long lifetime. The latter are divided in little hard-leaved shrubs (D) and taller soft-leaved shrubs (E) having only little proportion of herbaceous biomass. Two of these types were identified to correlate along the grazing gradient.
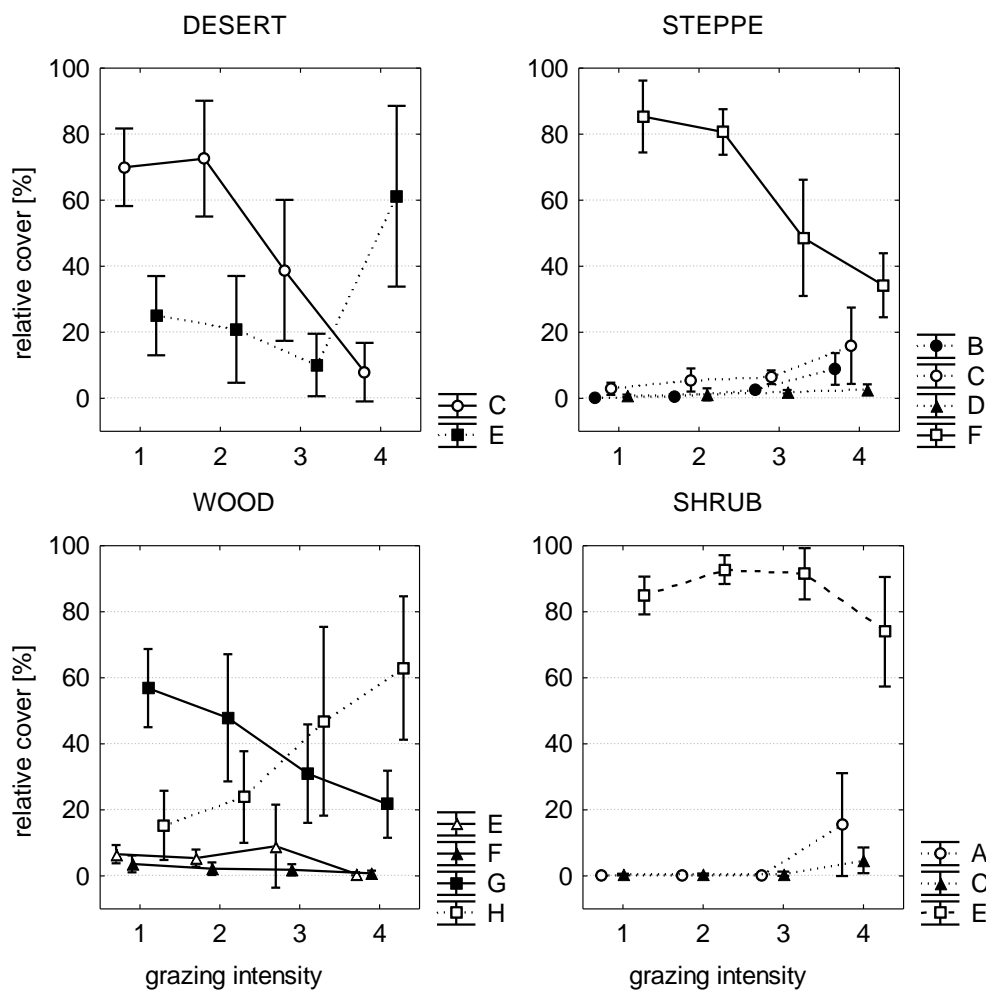


**Fig. 6.2** Response (relative ground cover in %, mean and 95 % confidence interval) of selected trait syndromes along grazing gradients (1 - not grazed for 7 years; 4 - high grazing intensity). Decreasers, increasers and invaders are shown by solid, dashed and dotted lines, respectively (Dyksterhuis 1949). Trait syndromes are sorted by lifespan: O/● annual species; Δ/▲ short perennial species; □/■ long perennial species. We only plotted trait syndromes correlating to grazing intensity ($p < 0.05$; $\tau > 0.4$) except one group of steppe annuals (Tab. 6.3; A) which showed an intermediate response. For desert and shrub vegetation, groups of long perennial species (Tab. 6.3; E) were added which did not meet correlation criteria but represented an increaser group

Annual species (A) like *Minuartia funckii* were rare but increased towards the highest level of grazing intensity ($\tau$ = 0.672; p = 0.000). Short perennial species, characterized by a rosette growth form and flowers located at the ground level also increased ($\tau$ = 0.422; p = 0.001). Since predominant cushion-like shrub species like *Alyssum spinosum* did not show a linear but a hump-shaped trend along the grazing gradient (Fig. 6.2), their abundance could not be described by linear correlation analyses.

However, this trait syndrome decreased towards higher grazing intensities (Fig. 6.2). As a first approach, we show the response of selected trait syndromes using the classification of Dyksterhuis (1949), who described plant response groups along grazing gradients as decreasers, increasers (most abundant at medium grazing pressure) and invaders (continuously increasing with grazing pressure).

## 6.3.3 Abundance of trait syndromes related to underlying environmental gradients

CCA analyses showed the following relationships between relative abundances of trait syndromes and environmental parameters at each altitudinal level (Fig. 6.3). Detailed information on Eigenvalues and explained variances are listed in Tab. 6.8 (Appendix), results of forward selection and Monte Carlo permutation tests in Tab. 6.9 (Appendix).

For semidesert pastures, CCA identified two major environmental gradients characterizing the distribution of trait syndromes on vegetation plots. The first axis explained 44.9 % of the variance of trait syndrome-environment-correlations (Eigenvalue E = 0.667) and reflected a gradient of nutrient availability from low to high N and C content of the topsoil. The second axis was correlated to the proportion of grit (SKELET), sand (SAND) and bare ground (BARE) and explained another 35.4 % of variance in the dataset (E = 0.762). Ungrazed ($\square$, level 1) and heavily grazed (+, level 4) plots were well separated by the second axis, showing an increase of bare ground (BARE) on the plots. The soil of intensively grazed sites (O, level 3) showed the highest proportion of clay and N; moderately grazed sites ($\Delta$, level 2) slightly differed from ungrazed sites. In general, the abundance of trait syndromes on *Hammada* semidesert pastures was most influenced by soil texture (SKELET - percentage of grit, $\lambda$ = 0.05; F = 3.28; p = 0.02) and grazing intensity (BARE - cover of bare ground, $\lambda$ = 0.04; F = 2.39;

p = 0.04). Regarding the relationship between trait syndromes and environment, there was mainly syndrome C which clearly depended on grazing intensity. Plant species of syndrome C were most abundant on sites with little cover of bare ground (BARE, ungrazed, moderately grazed), but their abundance also depended on the sand content of a site (SAND). The abundances of the syndromes A and B positively correlated to the clay content of the topsoil (CLAY), the percentage of grit (SKELET) and the cover of bare ground (BARE) at a site. D became more and E, F less abundant on intensively trampled sites (TRAMPLE). However, this grazing dependent parameter correlated with the C and N content (C, N) of the soil. Thus, we were not able to distinguish if these groups (A, B, D, E, F) showed a response to grazing intensity or to environmental constraints (Le Houérou 2001).

For steppe pastures, CCA revealed a dominant gradient of soil texture (SAND, SKELET), nutrient availability (C, N) and grazing intensity (BARE, TRAMPLE) for the first axis. It explained 75.0 % of the trait syndrome-environment-correlations (E = 0.807). The second axis accounted for another 14.6 % of the variance (E = 0.536) and was correlated to the lime content (CACO3) of the soil. Plots of different grazing intensity levels were ordered along the first axis with ungrazed plots (□, level 1) showing highest N and C contents (N, C) in the topsoil and heavily grazed sites (+, level 4) showing the largest cover of bare ground (BARE), highest trampling intensity (TRAMPLE), highest proportion of grit (SKELET) and sand (SAND) in the topsoil. For every level of grazing intensity, there were sites with high and low lime content (CACO3).

For *Artemisia* steppe pastures, grazing intensity (BARE - proportion of bare ground, $\lambda = 0.05$; F = 14.73; p = 0.00) most influenced the abundance of trait syndromes. Abundances of trait syndromes A, B, C and E most correlated with the first axis, thus representing the best grazing indicators. A is located close to the point of origin, thus we expect a slight increase along the grazing gradient. B and C increased the more a site had been grazed, but also with increasing sand content (SAND) of the soil. The relative abundance of E is well correlated to the first axis. Plants of that type strongly decrease along the grazing gradient and with decreasing N content (N) of the soil. The abundance of the syndromes D and F was more correlated to the second CCA axis (CACO3, lime content), thus these groups were less appropriate to predict grazing intensity.

At woodsteppe level, CCA ordered the occurring trait syndromes and plots along a first axis correlated to the cover of bare ground, the grit and the C

content of the soil (46.4 % explained variance, E = 0.502) and along a second axis which correlated to trampling intensity, sand and N content as well as to the percentage of grit in the soil (37.6 % explained variance, E = 0.699). Heavily grazed sites (+, level 4) were either more trampled or showed a higher proportion of bare ground, additionally soil contained more grit and sand than less intensively grazed sites. Moreover, the topsoil at ungrazed sites (□, level 1) compared to grazed sites contained more C and N. Grazing intensity was more correlated to the second than to the first axis. Trampling intensity (TRAMPLE) showed the only significant effect on the abundances of trait syndromes ($\lambda = 0.04$; F = 2.49; p = 0.04). Trait syndromes such as B, D and I highly loaded on the first axis associated to the grit and C content of the soil. Like the syndromes A, C and G which were rarely correlated to grazing intensity, they all reflect bad grazing indicators. The abundances of E and F were negatively correlated to trampling intensity (TRAMPLE) on the plots; they decreased along the grazing gradient. In contrast, H became more abundant with increasing grazing intensity and increasing sand content of the soil (SAND). These three groups may serve as grazing indicators.
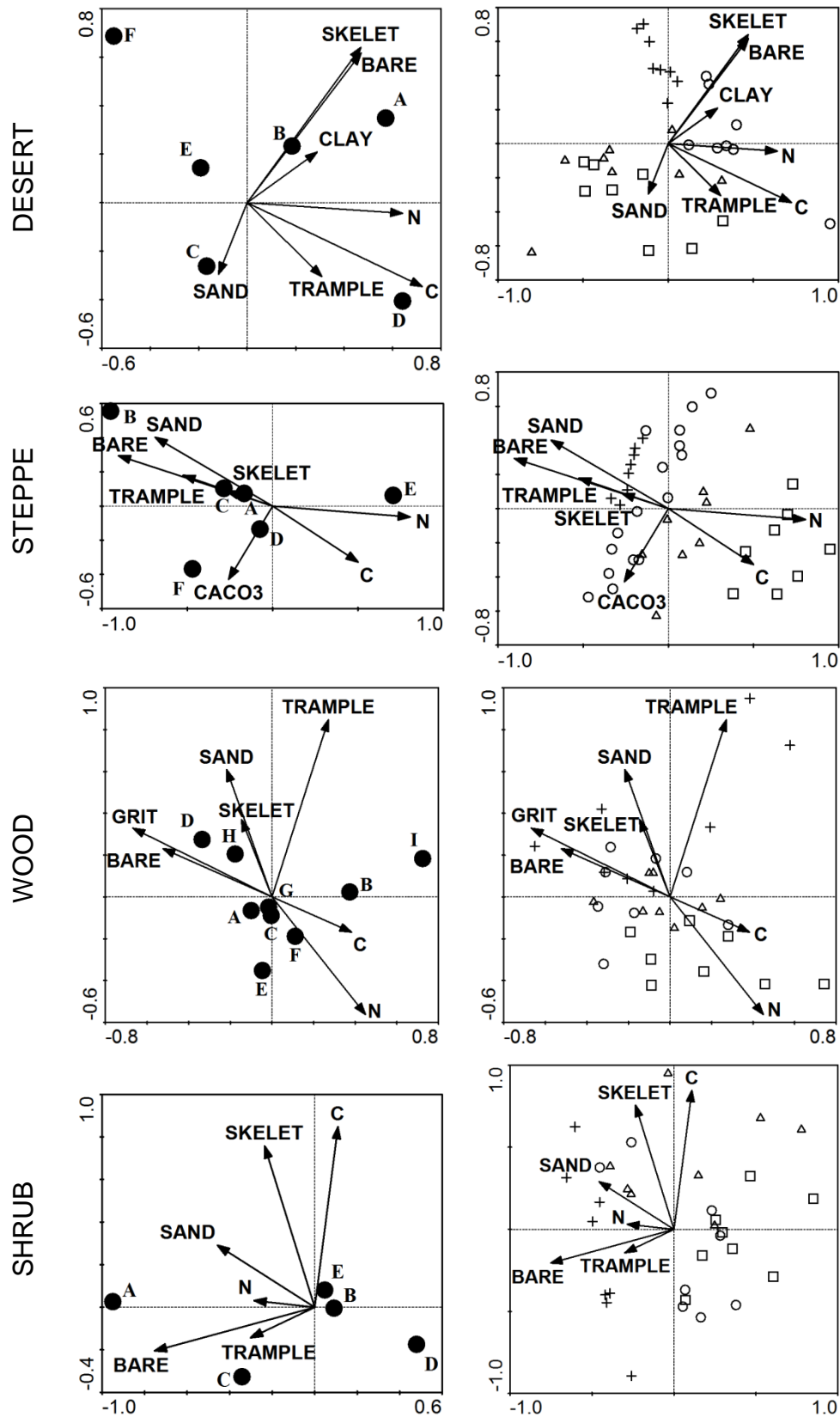
**Fig. 6.3** CCA results for the relationship between grazing dependent parameters (BARE, TRAMPLE), environmental variables (C, CACO3, CLAY, GRIT, N, SAND, SKELET), and the relative abundance of trait syndromes (A – I, see Tab. 6.3) at each of the four

investigated altitudinal levels. The second column of joint plots shows the affiliation of single plots to grazing intensity levels (□ level 1, not grazed; Δ level 2, moderately grazed; O level 3, intensively grazed; + level 4, heavily grazed) and the relationship to grazing dependent parameters and environmental variables. Joint plots always show the first (horizontal) and second (vertical) CCA axis. For Eigenvalues and statistical information see Tab. 6.8 and Tab. 6.9 (Appendix). Legend for grazing dependent variables: BARE percentage of bare ground; TRAMPLE trampling intensity. Legend for environmental variables: C proportion of organic carbon in the topsoil; CACO3 proportion of calcium carbonate in the topsoil; CLAY proportion of clay in the topsoil; GRIT mass percent of fine grit (diameter 0.2 – 2 cm) in the topsoil sample; N proportion of nitrogen in the topsoil; SAND proportion of sand in the topsoil; SKELET mass percent of soil skeleton (all components with diameter > 0.2 cm) in the topsoil sample

For oromediterranean shrubland, CCA ordered the identified trait syndromes and vegetation plots along two main axes: the first axis was correlated to grazing intensity (BARE, cover of bare ground) and the sand content (SAND) of the soil and explained 84.1 % of the trait syndrome-environment-correlations (E = 0.777). The second axis correlated to the C content (C) and the percentage of grit (SKELET) in the topsoil and explained another 12.6 % of the variance in the dataset (E = 0.657). Heavily grazed sites (+, level 4) showed the highest percentage of bare ground (BARE) and trampling intensity (TRAMPLE), less intensively grazed sites (□, Δ, O) strongly varied in environmental conditions such as sand (SAND) and C content (C) as well as the percentage of grit (SKELET) in the topsoil.

At oromediterranean shrubland pastures, relative abundance of trait syndromes was most influenced by grazing intensity (BARE – cover of bare ground, $\lambda = 0.08$; F = 8.49; p = 0.00), but also significantly influenced by nutrient availability (N – N content, $\lambda = 0.04$; F = 4.63; p = 0.01) and soil texture (SKELET – percentage of grit, $\lambda = 0.03$; F = 3.89; p = 0.02).

Plant species of the trait syndromes A and C most obviously profited from increased grazing pressure as their abundance correlated to the cover of bare ground (BARE) and trampling intensity (TRAMPLE). Groups B and E were closely located to the diagram's point of origin, showing only a slight decrease the more intensive a site had been grazed. The abundance of D is negatively correlated to the sand content of the soil (SAND), thus it is difficult to distinguish whether plant species of trait syndrome D became more abundant as a result of protection from grazing or as a result of altered soil texture.

## 6.3.4 Response of trait attributes at four altitudinal levels

Trait attributes were tested for their predictive value along the climatic gradient and along grazing gradients by means of ANOVA-based general linear models. See Tab. 6.10 (Appendix) for statistical information whether altitude or grazing predominantly influenced the relative abundance of trait attributes. Single ANOVA analyses regarding grazing impact separately at each altitudinal level were calculated for a selection of trait attributes (Tab. 6.11, Appendix), which had been identified by PCA analyses that identified the above-named trait syndromes (Tab. 6.3). Results referring to this selection of traits (lifetime, bud position, flower height, regeneration period, orientation of main axes, SLA, height, cover, herbaceous biomass, chemical protection) will be presented here.

*Lifetime & bud position.* Plant's lifetime and the position of dormant buds clustered the investigated species at all altitudinal levels into three main groups: annual (plants with buds under ground level or surviving as seed), short perennial (buds at ground level) and long perennial plant species (buds well accessible). These groups equal Raunkiaer's life forms (Raunkiaer 1934). The first group mainly contains therophytes, because geophytes were rarely found in our research area. The second group were mainly hemicryptophytes and the last group integrates chamaephytes and, to a little extent, phanerophytes.

Lifetime (and thus bud position) was observed as a trait being more influenced by altitude than by grazing intensity (e.g. for annual plants $p_{altitude} = 0.00$; $p_{grazing} = 0.08$). The relative abundance of annual plants decreased with altitude while long living plant species increased. Along grazing gradients, annual plants slightly increased at steppe and shrub level the more intensively a pasture had been grazed. At desert and wood level we observed the contrary trend.

*Flower height.* The height of inflorescences, particularly if flowers are well accessible to grazing animals, was an important trait characterizing trait syndromes at most of the vegetation types except shrub level (Fig. 6.4). Plants protecting their inflorescences, e.g. at the ground level or by means of thorns, increased the more intensive a site had been grazed. Plant species with flowers at the ground level were most abundant on desert pastures, while those protecting their flowers by thorns increased towards higher altitudinal levels (wood, shrub).
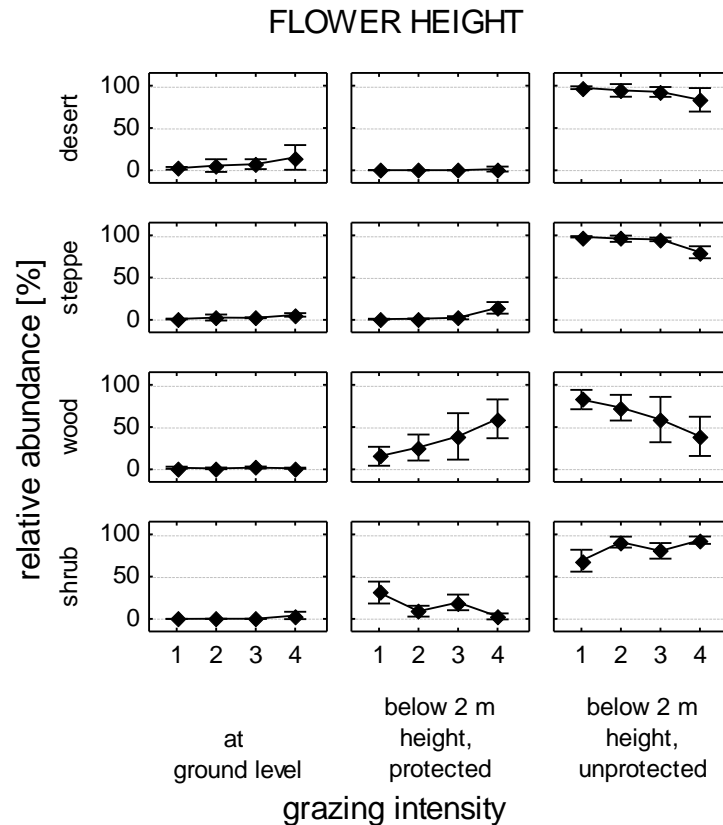
FLOWER HEIGHT



**Fig. 6.4** Relative abundance of plant species (in %, mean and standard deviation) differing in flower height in relation to grazing gradients (1 ungrazed; 4 heavily grazed) and for every altitudinal level (desert, steppe, wood, shrub)

*Regeneration period.* The regeneration period, here assessed as flowering time, played a major role for the distinction of shrub species in *Artemisia* steppes. The trait was generally strongly correlated to the altitudinal gradient with most of the spring flowering species at desert level, summer flowering species increasing along altitude, and a peak of autumn flowering species at steppe level. At *Artemisia* steppe level, spring and summer flowering species increase while autumn flowering species decrease the more intensive a pasture had been grazed. The same is true for *Juniperus* woodsteppe pastures.

*Orientation of main axes.* One trait which was important to classify annuals and short perennial plant species on every altitudinal level was the orientation of the plant's main axes (Fig. 6.5). GLM analyses revealed that prostrate plant species were generally most abundant at medium altitudinal levels (steppe, wood) and increased along the grazing gradients at desert and steppe level. Summarizing, the orientation of main axes, e.g. the abundance of prostrate plant species, is a good predictor for grazing intensity, but its predictive value is restricted to *Hammada* semidesert and *Artemisia* steppe pastures.

ORIENTATION OF MAIN AXES
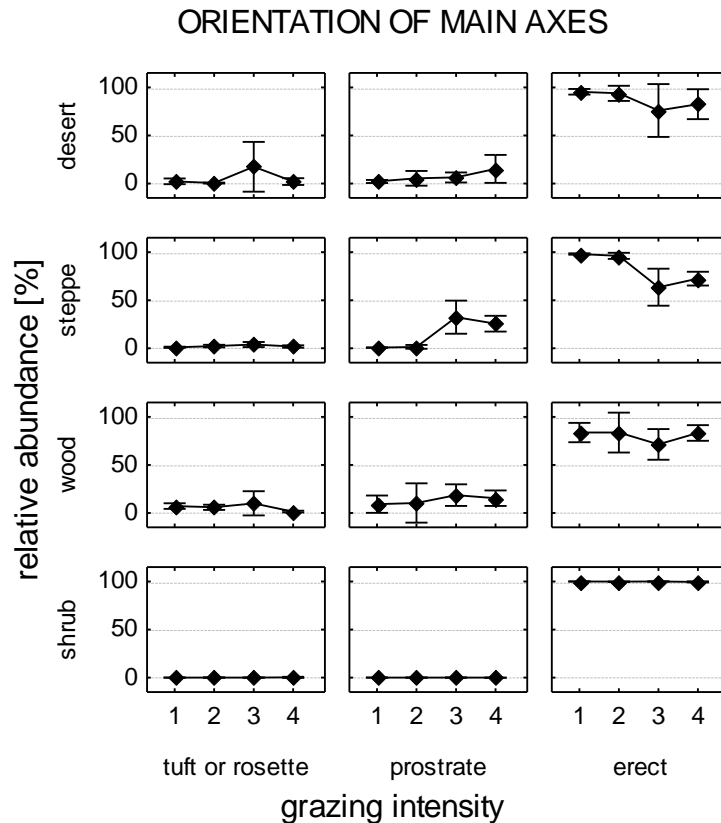


**Fig. 6.5** Relative abundance of plant species (in %, mean and standard deviation) differing in the orientation of main axes in relation to grazing gradients (1 ungrazed; 4 heavily grazed) and for every altitudinal level (desert, steppe, wood, shrub)

*SLA.* For assembling trait syndromes, the specific leaf area (SLA) was mainly important at desert and steppe level and to separate annual species with large thin leaves (SLA high; grasses) from those with little thicker leaves (SLA low; rosette species, water-storing tissues). Generally regarding the trait SLA at desert level, chenopod shrubs without leaves (*Hammada scoparia*) increased, plant species with SLA < 3 m²/kg (*Farsetia occidentalis*) and SLA 6 to 9 m²/kg decreased (*Stipa capensis*, *Morettia canescens*), while species with SLA 3 to 6 m/kg (*Peganum harmala*) increased with intensification of grazing. The increased abundance of such nitratophilous forbs (annual and perennial) as well as spiny, repellent, and/or toxic plants near water sources, villages, and towns in northern Africa is known as a zone called 'depleted erms of *Peganum harmala'* (Le Houérou 2001). At steppe level plant species with low and high SLA increased (3 to 6 m²/kg, e.g. *Glaucium corniculatum* and 9 to 12 m²/kg, e.g. *Bromus rubens*) while plants with medium SLA (6 to 9 m²/kg, e.g. *Artemisia* species, *Thymus satureioides*) decreased.
*Height.* The plant's vegetative height played a major role for distinguishing groups of long perennial plant species at woodsteppe and oromediterranean

shrubland level. While dwarf shrubs (mean height < 27 cm, *Artemisia* species) decreased with intensification of grazing at woodsteppe level, tall shrubs (27 to 81 cm high, *Genista scorpius*) became more abundant. At oromediterranean shrubland pastures we observed the contrary trend. Little plant species (mean height < 27 cm, *Raffenaldia primuloides*, *Astragalus ibrahimianus*) increased while tall shrub species (27 to 81 cm, *Vella mairei*) slightly decreased along the grazing gradient.

*Cover.* The mean individual ground cover helped to distinguish between different groups of annuals at desert and steppe level, groups of short perennial species at woodsteppe level, and separated long perennial plant species at desert level. For desert vegetation, little plant species (cover < 0.3 dm², *Pallenis hierochuntica*) decreased, while larger species increased along the grazing gradient, in particular shrubs like *Zilla spinosa* (mean cover 9 to 27 dm²). At steppe level, plants smaller than 3 dm² (herbs) and larger than 9 dm² (shrubs like *Othonna maroccana*) increased the more intensively a pasture had been grazed, while plant species with individual covers from 3 to 9 dm² decreased (dwarf shrubs, *Artemisia* species). At woodsteppe level all plants smaller than 9 dm² decrease while large shrubs (*Genista scorpius*) increase along the grazing gradient.

*Herbaceous biomass.* Except for steppe vegetation, the proportion of herbaceous (palatable) biomass of a plant species was an important trait to separate different groups of perennial species. At desert level, shrub species with less than 40 % of herbaceous biomass (*Zilla spinosa*) increased, while more palatable species (herbaceous biomass > 40 %, *Farsetia occidentalis*) decreased the more a pasture had been grazed. At woodsteppe level, we observed the opposite – less palatable species (herbaceous biomass < 40 %, *Juniperus phoenicea*, *Helianthemum pergamaceum*) decreased and species with more than 40 % of herbaceous biomass (*Telephium imperati*) increased. At shrub level we mainly detected a replacement of woody species by entirely herbaceous species along the grazing gradient.

*Chemical protection.* Whether plant species possessed a mechanism of chemical protection against herbivores mainly played a role for annual plants on desert pastures. There, plants with chemical protection mechanisms increased the more a pasture had been grazed. On the other altitudinal levels we observed the contrary trend (steppe, shrub) or no distinct response of the trait (wood). Generally, plants possessing chemical protection mechanisms increased along the altitudinal gradient, too.

***Sclerophylly.*** This trait helped to distinguish different groups of long perennial plant species at woodsteppe and shrub level. Hard-leaved plants generally increased along the altitudinal gradient while species without leaves mainly occurred on desert pastures, and soft-leaved species decreased along altitude. At woodsteppe level we observed a slight but not significant decrease of hard-leaved plants along the grazing gradient. On oromediterranean shrubland pastures hard-leaved plants peaked at medium grazing intensities, while soft-leaved plants were most abundant at ungrazed and heavily grazed sites.

## 6.3.5 Response of trait attributes and underlying environmental gradients

CCA analyses showed the following relationships between relative abundances of trait attributes and environmental parameters at each altitudinal level (Fig. 6.6). Detailed information on Eigenvalues and explained variances are listed in Tab. 6.12 (Appendix), results of forward selection and Monte Carlo permutation tests in Tab. 6.13 (Appendix). Here, we want to focus on trait attributes favoured or penalized by grazing impact as well as trait attributes getting more abundant as a response to altered soil parameters. For each altitudinal level, CCA ordered the given vegetation plots along the first axis according to grazing intensity, from heavily grazed sites (+, level 4) on the left to ungrazed sites (□, level 1) on the right side.

For semidesert pastures, heavily grazed sites are found on the bottom left and ungrazed sites on the upper right side. Intensively grazed sites (○, level 3, upper left) showed highest N and C content of the topsoil and highest trampling intensity. Under these conditions thin-leaved (sla4) and short-perennial plant species (time1) were most abundant. On heavily grazed sites (+, level 4), we observed the highest clay content (CLAY) in the topsoil, what favoured long-perennial plant species (time2), prostrate growth (axes1), early spring-flowering (flower1), species without leaves (sla0) as well as those with a little proportion of herbaceous biomass.
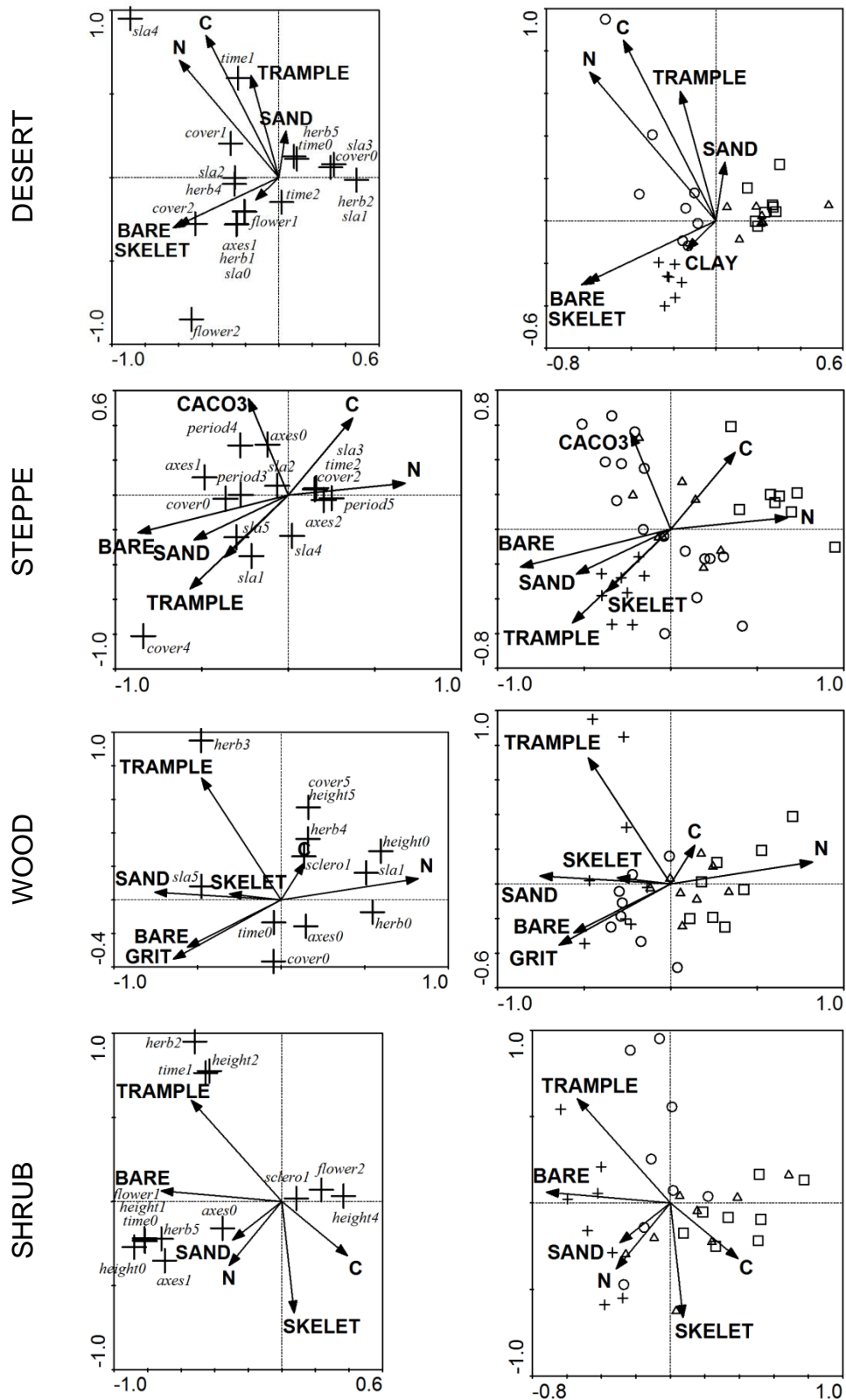
**Fig. 6.6** CCA results for the relationship between grazing dependent parameters (BARE, TRAMPLE), environmental variables (C, CACO3, CLAY, GRIT, N, SAND, SKELET) (for a legend see Fig. 6.3), and the relative abundance of selected trait attributes (for labels see Tab. 6.2) at each of the four investigated altitudinal levels. The second column of joint plots shows the affiliation of single plots to grazing intensity levels (□ level 1, not grazed;

Δ level 2, moderately grazed; O level 3, intensively grazed; + level 4, heavily grazed) and the relationship to grazing dependent parameters and environmental variables. Joint plots always show the first (horizontal) and second (vertical) CCA axis. For Eigenvalues and statistical information see Tab. 6.12 and Tab. 6.13 (Appendix)

At *Artemisia* steppe level, heavily grazed sites (bottom left) showed highest trampling intensity while ungrazed sites (right) correlated to highest N contents of the soil. Intensively grazed sites (O, level 3, upper left) built an exception. Here the soil contained more $CaCO_3$ than at other sites and species of rosette or tuft growth (axes1) were more abundant. Long-perennials (time2), autumn-flowering species (period5), and those with medium cover (cover2) were most abundant on ungrazed (□, level 1) and moderately grazed sites (Δ, level 2) with better nutrient availability (N). Large plants (cover4), thin-leaved (sla5) as well as thick-leaved (sla1) species were favoured on heavily grazed sites (+, level 4) and correlated to highest trampling intensity (TRAMPLE).

Among plots on *Juniperus* woodsteppe pastures, most trampled sites were located in the upper left side of the diagram favouring perennial species with a medium proportion of herbaceous biomass (herb3). Hard-leaved species (sclero1) and those with a high proportion of herbaceous biomass (herb4) were most abundant on sites with high C content of the soil (□, level 1; Δ, level2). Little (height0) species and those with thick leaves (sla1) were favoured at ungrazed sites (□, level 1) and by higher N content of the soil. At sandy sites thin-leaved (sla5) plant species were most abundant.

At oromediterranean woodsteppe level, short perennial plant species (time1) of medium height (height2) and a little proportion of herbaceous biomass (herb2) were most abundant on intensively trampled sites. Grazing exclosure (□, level 1) favoured higher shrubs (height4), hard-leaved (sclero1) plant species and those with well accessible, but protected flowers (flower2). At heavily grazed sites (+, level 4) with higher sand and N content of the topsoil, prostrate herbs (axes1, herb5) of little height (height1), annual species (time0) and those with their flowers at the ground level (flower1) were most abundant.

## 6.4 Discussion

### *6.4.1 Response groups and their functional background*

In the preceding section we assembled plant species to trait syndromes according to their characteristics (trait attributes) in terms of adaptation to grazing (PCA). Afterwards we tested the response of these trait syndromes along grazing gradients (ANOVA) and related their abundance to environmental variables (CCA). Trait syndromes which predominantly reacted to environmental conditions unrelated to grazing, e.g. $CaCO_3$ content of the soil, and syndromes showing no directed response (increase or decrease) were omitted from further analyses. Our results provide little evidence that similar response groups can be assembled across a wide range of climatic conditions. We rather observed the following groups for every single altitudinal level along the steep High Atlas Mountain transect.

At *Hammada* semidesert we identified one main response group (syndrome C) that decreased in relative abundance along the grazing gradient. It contained annual grasses (e.g. *Stipa capensis*) and annual herbs (e.g. *Leysera leyseroides*) that had no chemical protection, well accessible flowers and a high forage value (SLA > 9 m²/kg). This group is disadvantaged by grazing, because such plants invest temporally occurring water and nutrient resources into fast growth and a high ratio of leaf area to leaf mass instead of avoiding herbivory. In low resource environments, however, grazed species with chemical or structural defense mechanisms against herbivores and an efficient use of scarce resources are more successful (Coley *et al.* 1985; Herms & Mattson 1992).

For *Artemisia* steppe pastures we combined the trait syndromes A, B, and C to one response group of invaders *sensu* Dyksterhuis (1949). This group contained all annual plant species (e.g. *Schismus barbatus*, *Bromus rubens*, *Androsace maxima*, *Filago spec*, *Glaucium corniculatum*) and short perennials of prostrate growth (e.g. *Helianthemum crocceum*, *Erodium guttatum*). Annuals are well adapted to heavy grazing by a strategy of temporal avoidance. Their competitive success is based on a rapid acquisition of resources as long as environmental conditions (water, nutrients) were favourable (Grime 2001). Short-perennials benefit from prostrate growth which makes leaves and shoots less accessible to herbivores (Noy-Meir *et al.* 1989). The second response group at steppe level (E) was a group of decreasers which contained long perennial and evergreen plant species flowering at the end of the vegetation period (*Artemisia*

species). Oba et al. (2001) showed in semiarid East Africa that a similar dwarf-shrub species (*Indigofera spinosa*) tolerated light and even severe grazing, but if grazing occurred throughout the year (like on level 4, close to the village), biomass losses could no longer be balanced and dwarf-shrubs were outcompeted by faster growing species.

At woodsteppe level three possible response groups were identified. The trait syndromes E and F can be combined to one response group of short perennial plant species of medium cover (0.3 < cover < 9 dm²) growing erect (e.g. *Carlina brachylepis*), as tuft (e.g. *Dactylis glomerata ssp hispanica*), or little subshrub (e.g. *Helianthemum pergamaceum*). These species decreased along the grazing gradient since they have a high forage value and their competitive vigour is low outside the protection of higher shrub species. These long perennial shrub species (syndrome G, e.g. *Artemisia species*, *Teucrium mideltense*, *Santolina africana*) could provide refuge and thus avoidance of herbivory (Milchunas & Noy-Meir 2002), but equally decrease along the grazing gradient. The group is very similar to syndrome E at *Artemisia* steppe level, thus we suggest the same functional explanation. The third response group at woodsteppe level comprises trait syndrome H, i.e. large shrubs up to 81 cm of mean height (*Genista scorpius ssp myriantha*) increasing along the grazing gradient. In this case, we suppose that not plant size was favoured by grazing, but the species increased as a result of phosphorous accumulation close to the settlements. We have no data on the P content of soils, however this fact was regularly observed in semiarid ecosystems (Turner 1998; Dougill *et al.* 1999). Jauffret *et al.* (2003) pointed out that North-African calcareous soils are often nutrient-deficient (Osman *et al.* 1991; Ewing 1999) favouring nitrogen-fixing legumes if enough phosphorous is available.

For oromediterranean shrubland pastures we suggest one response group of invaders, which combined trait syndrome A and C, i.e. annual species (e.g. *Minuartia funckii*) and short perennials of rosette growth (e.g. *Raffenaldia primuloides*, *Taraxacum atlanticum*, *Centaurea takredensis*). However, this group showed no steady increase, but abruptly appeared at heavily grazed sites (+, level 4). Both, annuals and rosette plants benefitted from heavy grazing as it created open, N-rich habitats. Annuals were advantaged by a temporal avoidance strategy (Milchunas & Noy-Meir 2002) while rosette plants avoid herbivory by protecting their leaves close to the ground level (Klimesova *et al.* 2008). The most dominant group of cushion-like xerophytes (syndrome E, e.g. *Alyssum spinosum*)

is not identified as grazing indicators, as their relative abundance did not change considerably along the grazing gradient.

## 6.4.2 Response traits and their functional background

For CCA analyses grazing impact was quantified with the help of the variables 'proportion of bare ground' (BARE) and 'trampling intensity' (TRAMPLE). However, trait attributes correlating to these variables often differed in their response, i.e. certain attributes were more abundant on trampled sites (short perennial species at desert and shrub level), others on sites with a high cover of bare ground (annual species at wood and shrub level). Despite these differences, we could find similarities in trait attributes favoured or disadvantaged by grazing impact. Like for response groups, climatic constraints played a major role for the abundance of trait attributes along grazing gradients, i.e. adaptations on desert pastures always differed from those on High Atlas pastures (steppe, wood, and shrub). At the *Hammada* semidesert level less palatable, long perennial shrub species, often without leaves were advantaged by grazing while the abundance of annual species declined. Similar findings were made by Jauffret & Lavorel (2003) for arid steppe pastures in southern Tunisia. The strategy is generally known for heavily grazed sites of low resource environments, where species with chemical or structural defense mechanisms against herbivory and an efficient (but slow) use of scarce resources outcompete fast growing species (Coley *et al.* 1985; Herms & Mattson 1992).

Heavy grazing at steppe, wood, and shrub pastures led to a higher abundance of little plants, either with extremely thick (sla1) or thin (sla5) leaves. These are mostly annuals, for example annual grasses (thin leaves, e.g. *Bromus rubens*) or prostrate leaf-succulent species (thick leaves, e.g. *Herniaria cinerea*). Annuals mostly practise a strategy of temporal avoidance which is related to high relative growth rate and high SLA values (Westoby 1998). Long perennial species most profited from grazing exclosure, and larger (cover) as well as higher species became more abundant the less arid a site was. Grazing exclosure protected the vegetation from disturbance and led to a slight accumulation of nutrients, which was similarly shown by Su et al. (2005). Since High Atlas pastures (steppe, wood, and shrub) also received more precipitation, the habitats could be described as resource-rich environments. Such habitats favour growth-dominated processes in plant physiology, i.e. allocation of resources is given

priority and the availability of carbon for the support of secondary metabolism (chemical defense) and structural defense decreases (Herms & Mattson 1992).

## 6.4.3 Synopsis: Response groups and response traits put to the test

Summarizing, the presented response groups may locally serve as grazing indicators in the High Atlas region. They can be applied to simplify and extrapolate information on vegetation composition for future modelling approaches treating questions of land use and grazing impact in the area (Drees *et al.* 2009). However, response groups are limited to the occurring vegetation type, thus their indicative value in other semiarid ecosystems is problematic, since we could merely find common principles in plant's response to grazing for all altitudinal levels.

Instead of dealing with response groups (Kleyer 1999; Landsberg *et al.* 1999; McIntyre & Lavorel 2001; Jauffret & Lavorel 2003; Navarro *et al.* 2006), many studies directly investigated the response of single plant characteristics (traits) to grazing (Cingolani *et al.* 2005; Westoby & Wright 2006; Mouillot *et al.* 2007; Kühner & Kleyer 2008; Ansquer *et al.* 2009). However, the same principles were found. Plant's adaptations along resource gradients were easily demonstrated (Leishman & Westoby 1992; Thuiller *et al.* 2004; Westoby & Wright 2006), but adaptations along disturbance gradients strongly depended on resource availability. This led to response traits with an applicability limited to the local scale (Adler *et al.* 2004; De Bello *et al.* 2005). For example, Adler *et al.* (2004) observed that plants with grazing defense mechanisms and low forage quality benefitted from grazing in Patagonia, but only in dry areas. De Bello *et al.* (2005) investigated a climatic gradient in the Mediterranean, but without the advantage of comparable grazing history for all sites. Like in the High Atlas region this study identified useful grazing response traits at the local scale, which were not transferable from one climatic region to another. Only 2 out of 11 listed plant traits in de Bello's study showed an exclusive response to grazing impact; all other traits were both predictive in terms of climate or for climate and grazing at the same time (De Bello *et al.* 2005). For the Moroccan case the same comparison is even more obvious (Tab. 6.4). We exclusively selected traits consistently named to have a clear response to grazing and chose a stringent experimental design. But none of the investigated plant traits showed an exclusive response to grazing. In most of the cases, relative abundance of traits

depended on both parameters aridity and grazing. Their impacts were hard to separate (Tab. 6.4). Annual grasses, for example were found to indicate heavily grazed sites for most of the High Atlas pastures. However, the temporal avoidance strategy of annual grasses appears to be the best adaptation to the temporal unpredictability of water resources in undisturbed desert environments. We are thus not able to describe annual grasses and their characteristics as indicator for heavily grazed sites, because their indicative value depends on aridity.

We consider these findings to be of little surprise. To our knowledge, all approaches treating climate and grazing gradients simoultaneously were realized in arid and semiarid ecosystems. Here, the predictive value of grazing response

**Tab. 6.4** Response of plant traits to increasing aridity (*Aridity*) and increasing grazing impact (*Grazing*). For reasons of clarity the table only shows categorical traits and for every trait the response of one single attribute, i.e. that with the highest ordinal value. The highest value represents a plant characteristic that makes a species most favourable for grazing herbivores (see Tab. 6.2). The given response summarizes GLM results of Tab. 6.10 (Appendix): + significant response ($p < 0.05$); - no significant response ($p > 0.05$). None of the investigated plant traits was observed to exclusively respond to grazing (including those which are not listed here, but in Tab. 6.10, Appendix)

| Trait | | Attribute | | Response to | | |
|-------|--|-----------|--|-------------|--|--|
| no. | Description | no. | Description | Aridity | Grazing | Aridity x Grazing |
| *Life history* | | | | | | |
| 1 | lifetime | 2 | long perennial | + | + | + |
| 2 | leaf phenology | 2 | evergreen | + | + | + |
| *Regeneration* | | | | | | |
| 3 | reproduction type | 2 | sexual + vegetative | + | + | - |
| 5 | flower height | 3 | well accessible flowers | + | + | + |
| 6 | dispersal mechanism | 3 | anemochorous | + | + | + |
| 7 | resprouting ability | 1 | exists | + | + | + |
| *Morphology* | | | | | | |
| 8 | bud position | 3 | well accessible buds | + | + | + |
| 9 | axe orientation | 2 | erect growth | + | + | - |
| *Grazing defense* | | | | | | |
| 14 | chemical protection | 1 | does not exist | + | - | + |
| 15 | mechanical protection | 1 | does not exist | + | + | + |
| 16 | sclerophylly | 2 | malacophyllous plant | + | + | + |

traits strongly varied along the climate gradient due to great differences in the spatial and temporal availability of water resources. Temporal unpredictability can be seen as additional 'stress' and has a similar impact on plant strategies than grazing. We thus emphasize a definition of stress that is slightly different from those presented in the literature (Grime 1979; Southwood 1988; Herms & Mattson 1992; Ladd *et al.* 2009). We want to underline that resource stress does not only mean to cope with a lower level of resources but, particularly for water in arid regions, an additional increase of variability and temporal scarcity because of unpredictable pulsing of the resource (Chesson *et al.* 2004; Huxman *et al.* 2004; Ogle & Reynolds 2004; Craine 2005). This is the reason why temporal unpredictability displays an own dimension of resource stress and affects plant strategies such like grazing. Both periodically result in partial or total loss of biomass and provide selection pressures to avoid or compensate (tolerate) such losses (Coughenour 1985; Milchunas *et al.* 1988).

It is thus impossible to separate a plant's response to grazing impact from that to temporal water scarcity, because selection affects the same functional mechanisms. Pure grazing response groups or response traits applicable for a wide range of arid and semiarid regions are thus a stillborn child. We can assemble such groups or identify response traits in order to indicate range condition, but they will always function on a local scale only.

## 6.5 Conclusion

Our case study in southern Morocco showed response groups and response traits applicable to indicate range condition. However, the emerged groups and traits are of local interest and cannot be extrapolated to other regions. In our opinion, a common core list of grazing response traits is not realistic, particularly for arid and semiarid ecosystems. Even if we developed further statistical approaches (Mouillot *et al.* 2007; Kühner & Kleyer 2008; Rusch *et al.* 2009) and improved field methods, we will not succeed. In regions with highly stochastic resource availability, e.g. water and nutrients, temporal unpredictability of resources and disturbance have a comparable impact on plants resulting in similar adaptations. Namely those plant traits which enable the plant to avoid or to compensate sudden biomass losses or losses of energy are thus hard to interpret as grazing adaptations.

Plant functional types are useful to classify plants along resource gradients, and such classifications may be extrapolated to other regions. However, functional groups indicating the plant's response to disturbance only make sense on the local scale.

## 6.6 Appendix

**Tab. 6.5** Species × trait matrix of 69 plant species and their trait attributes. Species are in alphabetical order. Plant traits and trait attributes are encoded according to Tab. 6.2. *Fam* is the plant's family (Bor - Boraginaceae, Cap - Capparaceae, Car - Caryophyllaceae, Che - Chenopodiaceae, Cis - Cistaceae, Com - Compositae, Cru - Cruciferae, Cup - Cupressaceae, Eup - Euphorbiaceae, Fab - Fabaceae, Ger - Geraniaceae, Lam - Lamiaceae, Lil - Liliaceae, Pap - Papaveraceae, Pla - Plantaginaceae, Plu - Plumbaginaceae, Poa - Poaceae, Pri - Primulaceae, Rub - Rubiaceae, Umb - Umbelliferae, Zyg- Zygophyllaceae). *LF* is the life form according to Raunkiaer (T - therophyte, GEO - geophyte, H - hemicryptophyte, CH - chamaephyte, P - phanerophyte). *Veg.type* is the vegetation type, where the trait attributes were sampled

| No. | *Genus* | *Species* | Author | Fam | LF | Veg. type | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|-----|---------|-----------|--------|-----|-----|------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 72 | *Aaronsohnia* | *pubescens* | (Desf.) Bremer & Humphries | Com | T | desert | 0 | 1 | 0 | 2 | 3 | 3 | 0 | 0 | 1 | 2 | 1 | 2 | 5 | 0 | 1 | 2 |
| 106 | *Alyssum* | *spinosum* | L. | Cru | CH | shrub | 2 | 1 | 0 | 4 | 3 | 0 | 1 | 3 | 2 | 1 | 3 | 4 | 1 | 1 | 0 | 2 |
| 104 | *Androsace* | *maxima* | L. | Pri | T | steppe | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 2 | 4 | 1 | 0 | 5 | 1 | 1 | 2 |
| 8 | *Artemisia* | *herba-alba* | Asso. | Com | CH | steppe | 2 | 2 | 0 | 5 | 3 | 0 | 1 | 3 | 2 | 3 | 3 | 3 | 1 | 0 | 1 | 2 |
| 9 | *Artemisia* | *mesatlantica* | Maire | Com | CH | steppe | 2 | 2 | 0 | 5 | 3 | 0 | 1 | 3 | 2 | 3 | 3 | 3 | 1 | 0 | 1 | 2 |
| 116 | *Asperula* | *cynanchica* | L. | Rub | H | wood | 1 | 1 | 2 | 2 | 3 | 0 | 1 | 2 | 1 | 3 | 2 | 1 | 3 | 0 | 1 | 2 |
| 125 | *Astragalus* | *ibrahimianus* | Maire | Fab | CH | shrub | 1 | 1 | 2 | 3 | 2 | 1 | 1 | 3 | 2 | 1 | 2 | 3 | 2 | 1 | 0 | 2 |
| 103 | *Astragalus* | *cf. tribuloides* | Del. | Fab | H | steppe | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 1 | 2 | 1 | 1 | 5 | 1 | 1 | 2 |
| 101 | *Bromus* | *rubens ssp. eu-rubens* | Maire | Poa | T | steppe | 0 | 1 | 0 | 2 | 3 | 0 | 0 | 0 | 2 | 4 | 2 | 1 | 5 | 1 | 1 | 2 |
| 120 | *Bupleurum* | *cf. atlanticum* | Murb. | Umb | CH | wood | 1 | 1 | 2 | 4 | 3 | 0 | 1 | 2 | 0 | 2 | 2 | 3 | 2 | 0 | 1 | 1 |
| 121 | *Bupleurum* | *fruticescens* ssp. *spinosum* | (Gouan) O. Bolos & Vigo | Umb | CH | shrub | 2 | 2 | 0 | 4 | 2 | 0 | 1 | 3 | 2 | 2 | 3 | 3 | 1 | 0 | 0 | 2 |
| 86 | *Carduncellus* | *duvauxii* | Batt. | Com | H | desert | 1 | 1 | 0 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 5 | 1 | 0 | 1 |
| 111 | *Carlina* | *brachylepis* | (Batt.) Meusel & Kästner | Com | H | wood | 1 | 1 | 0 | 3 | 2 | 3 | 1 | 2 | 2 | 2 | 2 | 2 | 5 | 1 | 0 | 1 |
| 110 | *Centaurea* | *gattefossei* | Maire | Com | H | wood | 1 | 1 | 0 | 2 | 1 | 3 | 1 | 2 | 0 | 2 | 1 | 1 | 5 | 0 | 1 | 2 |
| 123 | *Centaurea* | *josiae* | Humbert | Com | H | shrub | 1 | 1 | 0 | 4 | 1 | 3 | 1 | 2 | 0 | 2 | 1 | 1 | 5 | 0 | 1 | 2 |

| | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16 | *Cladanthus* | *scariosus* | (Ball.) Oberpr. & Vogt | Com | CH | wood | 2 | 1 | 0 | 4 | 3 | 0 | 1 | 3 | 2 | 4 | 3 | 4 | 1 | 0 | 1 | 2 |
| 78 | *Cleome* | *africana* | Boc. | Cap | T | desert | 0 | 1 | 0 | 2 | 3 | 0 | 0 | 0 | 2 | 2 | 3 | 2 | 5 | 0 | 1 | 2 |
| 126 | *Cytisus* | *purgans ssp. balansae* | (Boiss.) Maire | Fab | CH | shrub | 2 | 1 | 0 | 3 | 3 | 0 | 1 | 3 | 2 | 4 | 3 | 4 | 1 | 0 | 0 | 1 |
| 113 | *Dactylis* | *glomerata ssp. hispanica* | (Roth) Nyman | Poa | H | wood | 1 | 1 | 2 | 3 | 3 | 0 | 1 | 2 | 0 | 4 | 2 | 2 | 2 | 1 | 1 | 2 |
| 98 | *Echium* | *velutinum ssp. velutinum* | Coincy | Bor | T | steppe | 0 | 1 | 0 | 2 | 3 | 1 | 0 | 0 | 2 | 2 | 1 | 0 | 5 | 0 | 0 | 2 |
| 271 | *Erinacea* | *anthyllis* | Link | Fab | CH | shrub | 2 | 1 | 0 | 3 | 3 | 0 | 1 | 3 | 2 | 4 | 3 | 4 | 1 | 0 | 0 | 1 |
| 7 | *Erodium* | *guttatum* | (Desf.) Willd. | Ger | H | steppe | 1 | 1 | 0 | 2 | 3 | 3 | 1 | 2 | 1 | 2 | 1 | 1 | 5 | 1 | 1 | 2 |
| 115 | *Erucastrum* | *leucanthum* | Cosson & Durieu | Cru | H | wood | 1 | 1 | 0 | 2 | 3 | 0 | 1 | 2 | 0 | 2 | 2 | 1 | 5 | 0 | 1 | 2 |
| 82 | *Eryngium* | *ilicifiolium* | Lam. | Umb | T | desert | 0 | 1 | 0 | 2 | 2 | 3 | 0 | 0 | 0 | 3 | 2 | 1 | 5 | 0 | 0 | 1 |
| 107 | *Euphorbia* | *spec.* | | Eup | H | shrub | 1 | 1 | 0 | 4 | 3 | 1 | 0 | 2 | 2 | 3 | 3 | 4 | 3 | 0 | 1 | 2 |
| 95 | *Euphorbia* | *sulcata* | Loisel. | Eup | T | steppe | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 2 | 5 | 2 | 0 | 5 | 0 | 1 | 2 |
| 41 | *Fagonia* | *glutinosa* | Delile | Zyg | T | desert | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 5 | 0 | 0 | 2 |
| 80 | *Farsetia* | *occidentalis* | B.L. Burtt. | Cru | CH | desert | 2 | 1 | 0 | 2 | 3 | 0 | 1 | 3 | 2 | 1 | 3 | 4 | 2 | 0 | 1 | 2 |
| 94 | *Filago* | *spec.* | L. | Com | T | steppe | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 5 | 1 | 0 | 2 |
| 112 | *Genista* | *scorpius ssp. myriantha* | (Ball) Maire | Fab | CH | wood | 2 | 2 | 0 | 2 | 2 | 0 | 1 | 3 | 2 | 3 | 4 | 4 | 2 | 0 | 0 | 2 |
| 129 | *Glaucium* | *corniculatum      ssp. corniculatum* | (L.) J.H. Rudolph | Pap | T | steppe | 0 | 1 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 5 | 0 | 1 | 2 |
| 27 | *Hammada* | *scoparia* | (Pomel) Il'in | Che | CH | desert | 2 | 0 | 0 | 5 | 3 | 0 | 1 | 3 | 2 | 0 | 3 | 4 | 1 | 0 | 1 | 0 |
| 93 | *Helianthemum* | *crocceum ssp. crocceum* | (Desf.) Pers. | Cis | CH | steppe | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 2 | 5 | 1 | 1 | 1 |
| 118 | *Helianthemum* | *pergamaceum* | Pomel | Cis | CH | wood | 1 | 1 | 0 | 2 | 3 | 0 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 |
| 122 | *Helictotrichon* | *filifolium* | (Lag.) Henrard | Poa | H | shrub | 1 | 1 | 2 | 4 | 3 | 2 | 1 | 2 | 0 | 1 | 2 | 2 | 5 | 1 | 0 | 1 |
| 91 | *Herniaria* | *cinerea* | DC. | Car | T | steppe | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 5 | 0 | 1 | 2 |
| 99 | *Hordeum* | *murinum ssp. leporinum* | (Link) Asch. & Gr. | Poa | T | steppe | 0 | 1 | 0 | 2 | 3 | 2 | 0 | 0 | 2 | 5 | 2 | 1 | 5 | 1 | 1 | 2 |
| 75 | *Ifloga* | *spicata* | (Forssk.) Sch. Bip. | Com | T | desert | 0 | 1 | 0 | 2 | 3 | 0 | 0 | 0 | 2 | 4 | 1 | 0 | 5 | 1 | 1 | 2 |
| 11 | *Juniperus* | *phoenicea* | L. | Cup | P | wood | 2 | 2 | 0 | 4 | 3 | 2 | 1 | 3 | 2 | 0 | 5 | 5 | 1 | 0 | 1 | 1 |
| 92 | *Lactuca* | *spec.* | | Com | H | steppe | 1 | 1 | 0 | 4 | 3 | 3 | 1 | 2 | 0 | 4 | 2 | 2 | 5 | 0 | 1 | 2 |
| 32 | *Launaea* | *arborescens* | (Batt.) Maire | Com | CH | desert | 2 | 1 | 0 | 2 | 2 | 3 | 1 | 3 | 2 | 2 | 4 | 5 | 1 | 0 | 0 | 2 |
| 79 | *Limonium* | *sinuatum ssp. bonduellei* | (Lestib.) Sauvage & Vindt | Plu | T | desert | 0 | 1 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 5 | 1 | 1 | 2 |
| 109 | *Lotus* | *eriosolen* | (Maire) Mader & Poslech | Fab | H | wood | 1 | 2 | 2 | 2 | 1 | 0 | 0 | 2 | 1 | 3 | 2 | 2 | 5 | 1 | 1 | 2 |

| No. | Genus | species | Author | Fam | LF | Habitat | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 83 | *Medicago* | *laciniata* | (L.) Miller | Fab | T | desert | 0 | 1 | 0 | 2 | 1 | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 5 | 1 | 1 | 2 |
| 90 | *Minuartia* | *funckii* | (Jordan) Graebner | Car | T | steppe | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 2 | 5 | 1 | 0 | 5 | 1 | 1 | 2 |
| 85 | *Morettia* | *canescens* | Boiss. | Cru | H | desert | 1 | 2 | 0 | 2 | 1 | 0 | 1 | 2 | 1 | 3 | 0 | 3 | 5 | 1 | 0 | 2 |
| 77 | *Notoceras* | *bicorne* | (Aiton) Amo | Cru | T | desert | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 2 | 5 | 0 | 1 | 2 |
| 10 | *Othonna* | *maroccana* | (Batt.) Jeffrey | Com | CH | steppe | 2 | 2 | 0 | 2 | 3 | 3 | 1 | 3 | 2 | 2 | 4 | 4 | 3 | 0 | 1 | 2 |
| 117 | *Pallenis* | *spinosa* | L. | Com | H | wood | 1 | 1 | 0 | 3 | 3 | 3 | 1 | 2 | 0 | 3 | 2 | 1 | 5 | 0 | 1 | 2 |
| 73 | *Pallenis* | *hierochuntica* | (Michon) Greuter | Com | T | desert | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 5 | 0 | 1 | 2 |
| 100 | *Paronychia* | *chlorothyrsa* | Murb. | Car | H | steppe | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 1 | 3 | 1 | 1 | 5 | 0 | 1 | 2 |
| 74 | *Paronychia* | *arabica ssp. longiseta* | Batt. | Car | T | desert | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 5 | 0 | 1 | 2 |
| 76 | *Peganum* | *harmala* | L. | Zyg | CH | desert | 1 | 1 | 2 | 2 | 3 | 0 | 1 | 2 | 2 | 2 | 4 | 4 | 5 | 0 | 1 | 2 |
| 87 | *Plantago* | *ciliata* | Desf. | Pla | T | desert | 0 | 1 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 5 | 0 | 1 | 2 |
| 108 | *Polycarpon* | *polycarpoides* | (Biv.) Jahandiez & Maire | Car | H | wood | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 4 | 2 | 1 | 5 | 1 | 1 | 2 |
| 124 | *Raffenaldia* | *primuloides* | Godron | Cru | H | shrub | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 5 | 0 | 1 | 2 |
| 84 | *Salvia* | *aegyptiaca* | L. | Lam | CH | desert | 1 | 2 | 0 | 2 | 3 | 0 | 1 | 2 | 0 | 2 | 1 | 2 | 4 | 0 | 1 | 2 |
| 89 | *Salvia* | *verbenaca* | L. | Lam | H | steppe | 1 | 1 | 0 | 2 | 3 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 5 | 0 | 1 | 2 |
| 14 | *Santolina* | *africana* | Jord. & Fourr. | Com | CH | wood | 2 | 1 | 0 | 4 | 3 | 3 | 1 | 3 | 2 | 2 | 3 | 4 | 0 | 0 | 1 | 2 |
| 69 | *Schismus* | *barbatus ssp. calycinus* | (L.) Maire & Weiller | Poa | T | desert | 0 | 1 | 0 | 2 | 3 | 3 | 0 | 0 | 2 | 4 | 2 | 1 | 5 | 1 | 1 | 2 |
| 102 | *Stipa* | *parviflora* | Desf. | Poa | H | steppe | 1 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 5 | 1 | 1 | 2 |
| 70 | *Stipa* | *capensis* | Thunb. | Poa | T | desert | 0 | 1 | 0 | 2 | 3 | 3 | 0 | 0 | 2 | 3 | 1 | 0 | 5 | 1 | 1 | 2 |
| 71 | *Stipagrostis* | *obtusa* | (Del.) Nees | Poa | H | desert | 1 | 1 | 2 | 2 | 3 | 3 | 1 | 2 | 0 | 2 | 1 | 1 | 5 | 1 | 1 | 2 |
| 119 | *Telephium* | *imperati* | L. | Car | H | wood | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 1 | 3 | 1 | 2 | 4 | 0 | 1 | 2 |
| 96 | *Teucrium* | *mideltense* | (Batt.) Humbert | Lam | CH | steppe | 2 | 2 | 0 | 4 | 3 | 3 | 1 | 3 | 2 | 2 | 3 | 3 | 0 | 0 | 1 | 2 |
| 97 | *Thymus* | *satureioides ssp. satureioides* | Cosson | Lam | CH | steppe | 2 | 2 | 2 | 4 | 3 | 0 | 1 | 3 | 1 | 3 | 2 | 3 | 1 | 0 | 1 | 2 |
| 88 | *Urginea* | *noctiflora* | Batt. & Trab. | Lil | GEO | desert | 0 | 1 | 2 | 2 | 3 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 5 | 0 | 1 | 2 |
| 130 | *Vella* | *mairei* | Humbert | Cru | CH | shrub | 2 | 1 | 0 | 3 | 2 | 0 | 1 | 3 | 2 | 2 | 4 | 4 | 1 | 0 | 0 | 2 |
| 81 | *Zilla* | *spinosa ssp. macroptera* | (Cosson) Maire & Weiller | Cru | CH | desert | 2 | 1 | 0 | 2 | 2 | 0 | 1 | 3 | 2 | 2 | 4 | 4 | 1 | 0 | 0 | 2 |

**Tab. 6.6** Correlation of grazing intensity levels and observed grazing dependent parameters. * indicates significant correlations. *Faeces* denotes the dung cover [%] of grazing animals (sheep, goats, mules), *trampling* was estimated as trampled area in %, *bare ground*, i.e. all surface without plants, was estimated in %, *dead material* denotes the cover of dead plants on a plot in %, *pH, salinity, C,* and *N* content derived from analyses of the topsoil

| | N | Kendall's rank correlation coefficient | | |
| --- | --- | --- | --- | --- |
| | | τ | Z | p |
| *Hammada* **semidesert** | | | | |
| Faeces* | 32 | 0.34 | 2.74 | 0.006* |
| Trampling* | 32 | 0.31 | 2.53 | 0.011* |
| Bare ground* | 32 | 0.61 | 4.93 | 0.000* |
| Dead material* | 32 | -0.55 | -4.44 | 0.000* |
| PH | 32 | -0.21 | -1.68 | 0.094 |
| Salinity* | 32 | 0.33 | 2.69 | 0.007* |
| C | 32 | 0.23 | 1.83 | 0.068 |
| N | 32 | 0.22 | 1.74 | 0.081 |
| | | | | |
| *Artemisia* **steppe** | | | | |
| Faeces* | 40 | 0.48 | 4.36 | 0.000* |
| Trampling* | 40 | 0.61 | 5.51 | 0.000* |
| Bare ground* | 40 | 0.78 | 7.11 | 0.000* |
| Dead material* | 40 | -0.60 | -5.47 | 0.000* |
| PH | 40 | 0.10 | 0.94 | 0.345 |
| Salinity | 40 | -0.21 | -1.88 | 0.060 |
| C* | 40 | -0.31 | -2.85 | 0.004* |
| N* | 40 | -0.43 | -3.94 | 0.000* |
| | | | | |
| *Juniperus* **woodsteppe** | | | | |
| Faeces* | 32 | 0.49 | 3.97 | 0.000* |
| Trampling* | 32 | 0.53 | 4.26 | 0.000* |
| Bare ground* | 32 | 0.50 | 4.05 | 0.000* |
| Dead material* | 32 | -0.63 | -5.06 | 0.000* |
| PH | 32 | -0.20 | -1.61 | 0.106 |
| Salinity | 32 | 0.18 | 1.46 | 0.143 |
| C | 32 | 0.11 | 0.85 | 0.397 |
| N* | 32 | -0.58 | -4.64 | 0.000* |
| | | | | |
| **Oromediterranean shrubland** | | | | |
| Faeces* | 32 | 0.80 | 6.44 | 0.000* |
| Trampling* | 32 | 0.54 | 4.32 | 0.000* |
| Bare ground* | 32 | 0.45 | 3.66 | 0.000* |
| Dead material* | 32 | -0.39 | -3.13 | 0.002* |
| PH | 32 | -0.06 | -0.52 | 0.606 |
| Salinity* | 32 | 0.51 | 4.11 | 0.000* |
| C | 32 | -0.14 | -1.11 | 0.269 |
| N | 32 | 0.09 | 0.70 | 0.483 |

**Tab. 6.7** Response of trait syndromes (ANOVA) along grazing gradients tested separately for every altitudinal level. Significant dependencies are marked with *; changes in abundance of the regarded trait syndromes are given as: 'decrease'/'increase' – trait syndrome decreases/increases in abundance the more intensive a site had been grazed; 'independent' – no directed response to grazing impact; 'hump' – hump-shaped response to grazing impact, showing a peak in abundance at medium grazing intensity levels. Nomenclature of trait syndromes follows Tab. 6.3

| Altitudinal level | Trend along grazing gradient | F | p |
|---|---|---|---|
| *Hammada* **semidesert** | | | |
| A* | independent | 5.1 | 0.01 |
| B* | increase | 3.4 | 0.03 |
| C* | decrease | 20.0 | 0.00 |
| D* | independent | 6.7 | 0.00 |
| E* | increase | 8.9 | 0.00 |
| F | independent | 1.1 | 0.35 |
| | | | |
| *Artemisia* **steppe** | | | |
| A* | increase | 11.1 | 0.00 |
| B* | increase | 30.9 | 0.00 |
| C* | increase | 4.9 | 0.01 |
| D* | increase | 8.9 | 0.00 |
| E* | decrease | 9.9 | 0.00 |
| F* | increase | 4.5 | 0.01 |
| | | | |
| *Juniperus* **woodsteppe** | | | |
| A* | hump | 4.0 | 0.02 |
| B* | increase | 3.7 | 0.02 |
| C | independent | 0.8 | 0.53 |
| D* | increase | 3.9 | 0.02 |
| E* | decrease | 4.3 | 0.01 |
| F* | decrease | 3.3 | 0.04 |
| G* | decrease | 6.7 | 0.00 |
| H* | increase | 6.0 | 0.00 |
| I | independent | 0.3 | 0.83 |
| | | | |
| *Oromediterranean* **shrubland** | | | |
| A* | increase | 13.6 | 0.00 |
| B | independent | 0.8 | 0.49 |
| C* | increase | 12.2 | 0.00 |
| D* | decrease | 8.7 | 0.00 |
| E* | hump | 5.1 | 0.01 |

**Tab. 6.8** CCA results for the relationship between abundances of trait syndromes and correlating grazing dependent parameters and environmental variables. Eigenvalues and the cumulative explained variance are given for trait syndrome-environment-correlations

| Altitudinal level | CCA - axis | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| *Hammada* **semidesert** | | | | |
| Eigenvalue | 0.667 | 0.762 | 0.560 | 0.440 |
| Cumulative explained variance | 44.9 | 80.3 | 92.0 | 98.3 |
| *Artemisia* **steppe** | | | | |
| Eigenvalue | 0.807 | 0.536 | 0.483 | 0.343 |
| Cumulative explained variance | 75.0 | 89.6 | 96.7 | 98.6 |
| *Juniperus* **woodsteppe** | | | | |
| Eigenvalue | 0.502 | 0.699 | 0.755 | 0.558 |
| Cumulative explained variance | 46.4 | 74.0 | 88.5 | 95.8 |
| **Oromediterranean shrubland** | | | | |
| Eigenvalue | 0.770 | 0.657 | 0.311 | 0.111 |
| Cumulative explained variance | 84.1 | 96.7 | 99.8 | 100.0 |

**Tab. 6.9** Summary of CCA forward selection results for the relationship between the abundance of trait syndromes and grazing dependent parameters (BARE, TRAMPLE) as well as environmental variables (C, N, SKELET, SAND, CLAY, CACO3, GRIT). The term $\lambda$ describes the additional variance each variable explains at the time when it was included into the model. F and p values derived from Monte Carlo permutation tests. * marks significant impact of that variable on the given altitudinal level

| Altitudinal level | Conditional Effects | | | |
|---|---|---|---|---|
| | Var. N | $\lambda$ | p | F |
| *Hammada* **semidesert** | | | | |
| C | 8 | 0.06 | 0.06 | 3.44 |
| SKELET* | 5 | 0.05 | 0.02* | 3.28 |
| BARE* | 3 | 0.04 | 0.04* | 2.39 |
| N | 9 | 0.02 | 0.25 | 1.32 |
| SAND | 6 | 0.01 | 0.41 | 1.01 |
| TRAMPLE | 4 | 0.02 | 0.45 | 0.74 |
| CLAY | 7 | 0.00 | 0.86 | 0.35 |
| *Artemisia* **steppe** | | | | |
| BARE* | 3 | 0.05 | 0.00* | 14.73 |
| N | 9 | 0.00 | 0.06 | 2.31 |
| C | 8 | 0.01 | 0.16 | 1.64 |
| SAND | 6 | 0.01 | 0.05 | 2.43 |

| | | | | |
|---|---|---|---|---|
| CACO3 | 7 | 0.00 | 0.21 | 1.53 |
| SKELET | 5 | 0.00 | 0.40 | 0.95 |
| TRAMPLE | 4 | 0.01 | 0.73 | 0.54 |

***Juniperus* woodsteppe**

| | | | | |
|---|---|---|---|---|
| GRIT | 6 | 0.03 | 0.08 | 2.36 |
| TRAMPLE* | 4 | 0.04 | 0.04* | 2.49 |
| BARE | 3 | 0.01 | 0.20 | 1.41 |
| C | 8 | 0.02 | 0.25 | 1.36 |
| SAND | 7 | 0.01 | 0.44 | 0.86 |
| N | 9 | 0.01 | 0.45 | 0.81 |
| SKELET | 5 | 0.01 | 0.56 | 0.64 |

**Oromediterranean shrubland**

| | | | | |
|---|---|---|---|---|
| BARE* | 3 | 0.08 | 0.00* | 8.49 |
| N* | 8 | 0.04 | 0.01* | 4.63 |
| SKELET* | 5 | 0.03 | 0.02* | 3.89 |
| C | 7 | 0.01 | 0.36 | 1.06 |
| SAND | 6 | 0.00 | 0.59 | 0.63 |
| TRAMPLE | 4 | 0.00 | 0.92 | 0.18 |

**Tab. 6.10** Results of ANOVA-based general linear models (GLM) analysing the effect of altitude and grazing on the abundance of trait attributes. Significant dependencies are marked in **bold**. Nomenclature of traits and trait attributes follows Tab. 6.2

| Trait | | | | **Trait attribute** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0 | | 1 | | 2 | | 3 | | 4 | | 5 | | |
| | d.f | F | p | F | p | F | p | F | p | F | p | F | p |
| **lifetime** | | | | | | | | | | | | | |
| Intercept | 1 | 608.1 | 0.0 | 278.0 | 0.00 | 7302. | 0.00 | | | | | | |
| Altitude | 3 | 216.4 | **0.0** | 23.8 | 0.00 | 207.5 | **0.00** | | | | | | |
| Grazing | 3 | 2.3 | 0.0 | 7.7 | 0.00 | 7.5 | **0.00** | | | | | | |
| Alt x Graz | 9 | 11.5 | **0.0** | 8.0 | 0.00 | 18.1 | **0.00** | | | | | | |
| **leaf** | | | | | | | | | | | | | |
| Intercept | 1 | 141.1 | 0.0 | 3665. | 0.00 | 4245. | 0.00 | | | | | | |
| Altitude | 3 | 138.3 | **0.0** | 389.2 | **0.00** | 900.5 | **0.00** | | | | | | |
| Grazing | 3 | 34.4 | **0.0** | 4.2 | **0.01** | 12.0 | **0.00** | | | | | | |
| Alt x Graz | 9 | 34.2 | **0.0** | 26.9 | **0.00** | 11.0 | **0.00** | | | | | | |
| **reproduction** | | | | | | | | | | | | | |
| Intercept | 1 | 4812. | 0.0 | | | 111.4 | 0.00 | | | | | | |
| Altitude | 3 | 14.2 | **0.0** | | | 14.2 | **0.00** | | | | | | |
| Grazing | 3 | 9.1 | **0.0** | | | 9.1 | **0.00** | | | | | | |
| Alt x Graz | 9 | 2.0 | 0.0 | | | 2.0 | 0.05 | | | | | | |
| **regeneration period** | | | | | | | | | | | | | |
| Intercept | | | | | | 1416. | 0.00 | 816.9 | 0.00 | 328.9 | 0.00 | 569.7 | 0.00 |

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Altitude | | | | | | 242.0 | **0.00** | 417.0 | **0.00** | 42.4 | **0.00** | 117.1 | **0.00** |
| Grazing | | | | | | 4.2 | **0.01** | 9.5 | **0.00** | 2.2 | 0.10 | 3.4 | **0.02** |
| Alt x Graz | | | | | | 21.5 | **0.00** | 11.2 | **0.00** | 3.1 | **0.00** | 14.1 | **0.00** |

**flower**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | | | | 264.5 | 0.00 | 409.4 | 0.00 | 5977. | 0.00 | | | | |
| Altitude | | | | 17.2 | **0.00** | 74.1 | **0.00** | 34.6 | **0.00** | | | | |
| Grazing | | | | 10.7 | **0.00** | 4.3 | **0.01** | 9.3 | **0.00** | | | | |
| Alt x Graz | | | | 1.9 | 0.06 | 9.1 | **0.00** | 5.8 | **0.00** | | | | |

**dispersal mechanism**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 3692. | 0.0 | 81.3 | 0.00 | 105.2 | 0.00 | 618.2 | 0.00 | | | | |
| Altitude | 3 | 72.1 | **0.0** | 21.4 | **0.00** | 23.4 | **0.00** | 119.1 | **0.00** | | | | |
| Grazing | 3 | 4.8 | **0.0** | 7.2 | **0.00** | 1.0 | 0.40 | 13.8 | **0.00** | | | | |
| Alt x Graz | 9 | 8.5 | **0.0** | 1.4 | 0.20 | 1.8 | 0.07 | 12.3 | **0.00** | | | | |

**resprouting**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 689.0 | 0.0 | 9941. | 0.00 | | | | | | | | |
| Altitude | 3 | 216.7 | **0.0** | 216.7 | **0.00** | | | | | | | | |
| Grazing | 3 | 2.8 | **0.0** | 2.8 | **0.04** | | | | | | | | |
| Alt x Graz | 9 | 16.2 | **0.0** | 16.2 | **0.00** | | | | | | | | |

**bud**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 608.1 | 0.0 | | | 284.8 | 0.00 | 7873. | 0.00 | | | | |
| Altitude | 3 | 216.4 | **0.0** | | | 34.0 | **0.00** | 230.1 | **0.00** | | | | |
| Grazing | 3 | 2.3 | **0.0** | | | 6.2 | **0.00** | 6.4 | **0.00** | | | | |
| Alt x Graz | 9 | 11.5 | **0.0** | | | 9.3 | **0.00** | 19.7 | **0.00** | | | | |

**axe orientation**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 135.8 | 0.0 | 149.1 | 0.00 | 4043. | 0.00 | | | | | | |
| Altitude | 3 | 14.3 | **0.0** | 17.8 | **0.00** | 19.5 | **0.00** | | | | | | |
| Grazing | 3 | 4.2 | **0.0** | 9.1 | **0.00** | 7.5 | **0.00** | | | | | | |
| Alt x Graz | 9 | 2.3 | **0.0** | 2.7 | **0.01** | 1.8 | 0.08 | | | | | | |

**SLA**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 71.7 | 0.0 | 266.7 | 0.00 | 544.1 | 0.00 | 1672. | 0.00 | 407.5 | 0.00 | 126.4 | 0.00 |
| Altitude | 3 | 28.7 | **0.0** | 82.6 | **0.00** | 0.6 | 0.61 | 219.2 | **0.00** | 107.7 | **0.00** | 33.7 | **0.00** |
| Grazing | 3 | 7.9 | **0.0** | 8.8 | **0.00** | 5.6 | **0.00** | 7.1 | **0.00** | 9.9 | **0.00** | 24.3 | **0.00** |
| Alt x Graz | 9 | 7.8 | **0.0** | 15.3 | **0.00** | 9.5 | **0.00** | 13.8 | **0.00** | 7.7 | **0.00** | 10.5 | **0.00** |

**plant**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 23.2 | 0.0 | 424.4 | 0.00 | 281.1 | 0.00 | 1864. | 0.00 | 174.8 | 0.00 | 10.7 | 0.00 |
| Altitude | 3 | 0.9 | 0.4 | 150.8 | **0.00** | 30.4 | **0.00** | 90.5 | **0.00** | 58.2 | **0.00** | 10.5 | **0.00** |
| Grazing | 3 | 0.0 | 0.9 | 4.2 | **0.01** | 18.7 | **0.00** | 9.0 | **0.00** | 4.7 | **0.00** | 0.3 | 0.84 |
| Alt x Graz | 9 | 2.5 | **0.0** | 15.1 | **0.00** | 4.5 | **0.00** | 12.1 | **0.00** | 5.6 | **0.00** | 0.3 | 0.98 |

**cover**

| | df | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 472.6 | 0.0 | 320.9 | 0.00 | 137.8 | 0.00 | 1957. | 0.00 | 1143. | 0.00 | 10.7 | 0.00 |
| Altitude | 3 | 246.8 | **0.0** | 31.8 | **0.00** | 16.8 | **0.00** | 437.3 | **0.00** | 186.7 | **0.00** | 10.5 | **0.00** |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Grazing | 3 | 19.6 | **0.0** | 10.6 | **0.00** | 3.5 | **0.02** | 27.6 | **0.00** | 18.1 | **0.00** | 0.3 | 0.84 |
| Alt x Graz | 9 | 32.7 | **0.0** | 6.4 | **0.00** | 4.9 | **0.00** | 4.1 | **0.00** | 3.5 | **0.00** | 0.3 | 0.98 |

**herbaceous biomass**

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | 1 | 98.2 | 0.0 | 3290. | 0.00 | 232.8 | 0.00 | 8.4 | 0.00 | 3.9 | 0.05 | 1075. | 0.00 |
| Altitude | 3 | 37.4 | **0.0** | 192.7 | **0.00** | 87.4 | **0.00** | 3.1 | **0.03** | 1.1 | 0.36 | 222.8 | **0.00** |
| Grazing | 3 | 25.9 | **0.0** | 1.8 | 0.16 | 1.4 | 0.26 | 3.0 | **0.03** | 1.4 | 0.26 | 5.9 | **0.00** |
| Alt x Graz | 9 | 10.2 | **0.0** | 16.0 | **0.00** | 7.5 | **0.00** | 1.1 | 0.39 | 1.0 | 0.45 | 18.5 | **0.00** |

**chemical**

| | | | | | |
|---|---|---|---|---|---|
| Intercept | 1 | 4281. | 0.0 | 864.1 | 0.00 |
| Altitude | 3 | 59.5 | **0.0** | 59.5 | **0.00** |
| Grazing | 3 | 0.5 | 0.6 | 0.5 | 0.68 |
| Alt x Graz | 9 | 20.2 | **0.0** | 20.2 | **0.00** |

**mechanical protection**

| | | | | | |
|---|---|---|---|---|---|
| Intercept | 1 | 859.5 | 0.0 | 3959. | 0.00 |
| Altitude | 3 | 174.5 | **0.0** | 174.5 | **0.00** |
| Grazing | 3 | 3.7 | **0.0** | 3.7 | **0.01** |
| Alt x Graz | 9 | 12.1 | **0.0** | 12.1 | **0.00** |

**sclerophyll**

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Intercept | 1 | 141.1 | 0.0 | 332.7 | 0.00 | 2941. | 0.00 |
| Altitude | 3 | 138.3 | **0.0** | 94.9 | **0.00** | 51.9 | **0.00** |
| Grazing | 3 | 34.4 | **0.0** | 2.2 | 0.09 | 2.9 | **0.04** |
| Alt x Graz | 9 | 34.2 | **0.0** | 5.3 | **0.00** | 11.8 | **0.00** |

**Tab. 6.11** Response of selected trait attributes (ANOVA) along grazing gradients tested separately for every altitudinal level. Traits are abreviated by their number (Tab. 6.2): 1 - lifetime; 4 - regeneration period; 5 - flower height; 8 - bud position; 9 - axe orientation; 10 - SLA; 11 plant height; 12 - individual cover; 13 - herbaceous biomass; 14 - chemical protection; 16 - sclerophylly. The nomenclature of trait attributes follows Tab. 6.2. Significant dependencies are marked in **bold**; changes in abundance of the regarded trait attributes are given above the F and p values: 'decrease'/'increase' – trait attribute decreases/increases in abundance the more intensive a site had been grazed; 'independent' – no directed response to grazing impact; 'hump' – hump-shaped response to grazing impact, showing a peak in abundance at medium grazing intensity levels; 'extreme' – trait attributes being most abundant at ungrazed and heavily grazed sites

*Hammada semidesert*

| Trait n° | Trait attribute | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | | 1 | | 2 | | 3 | | 4 | | 5 | |
| | F | p | F | p | F | p | F | p | F | p | F | p |
| 1 | **decrease** | | independent | | **increase** | | | | | | | |
| | 8.38 | **0.00** | 7.32 | **0.00** | 16.95 | **0.00** | | | | | | |

| Trait n° | 0 | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| 8 | **decrease** 8.38 **0.00** | | independent 7.32 **0.00** | **increase** 16.95 **0.00** | |
| 9 | independent 2.64 0.07 | increase 2.37 0.09 | decrease 2.01 0.14 | | |
| 5 | | increase 2.24 0.11 | increase 1.46 0.25 | **decrease** 3.62 **0.03** | |
| 10 | **increase** 31.74 **0.00** | **decrease** 8.97 **0.00** | **increase** 7.38 **0.00** | **decrease** 29.63 **0.00** | independent 7.58 **0.00** |
| 12 | **decrease** 29.18 **0.00** | **increase** 7.24 **0.00** | increase 2.77 0.06 | decrease 1.85 0.16 | **increase** 8.41 **0.00** |
| 13 | | **increase** 31.95 **0.00** | **decrease** 8.97 **0.00** | independent 0.96 0.42 | **decrease** 15.33 **0.00** |
| 14 | **increase** 14.52 **0.00** | **decrease** 14.52 **0.00** | | | |

*Artemisia steppe*

| Trait n° | 0 | | 1 | | 2 | | 3 | | 4 | | 5 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | p | F | p | F | p | F | p | F | p | F | p |
| 1 | **increase** 11.05 | **0.00** | **increase** 16.05 | **0.00** | **decrease** 21.80 | **0.00** | | | | | | |
| 8 | **increase** 11.05 | **0.00** | | | **increase** 16.05 | **0.00** | **decrease** 21.80 | **0.00** | | | | |
| 4 | | | | | **increase** 20.55 | **0.00** | **increase** 10.90 | **0.00** | increase 1.64 | 0.20 | **decrease** 8.47 | **0.00** |
| 9 | hump 1.11 | 0.36 | **increase** 8.04 | **0.00** | **decrease** 6.33 | **0.00** | | | | | | |
| 10 | | | **increase** 10.14 | **0.00** | **increase** 3.61 | **0.02** | **decrease** 8.45 | **0.00** | **increase** 3.96 | **0.02** | **increase** 8.92 | **0.00** |
| 12 | **increase** 8.39 | **0.00** | **increase** 8.96 | **0.00** | **increase** 13.73 | **0.00** | **decrease** 21.24 | **0.00** | increase 1.67 | 0.19 | | |

*Juniperus woodsteppe*

| Trait n° | 0 | | 1 | | 2 | | 3 | | 4 | | 5 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | p | F | p | F | p | F | p | F | p | F | p |
| 1 | **hump** 4.59 | **0.01** | **decrease** 4.72 | **0.01** | **increase** 4.54 | **0.01** | | | | | | |
| 8 | **hump** 4.59 | **0.01** | | | **decrease** 4.72 | **0.01** | **increase** 4.54 | **0.01** | | | | |
| 9 | **decrease** 3.48 | **0.03** | increase 1.63 | 0.20 | independent 1.19 | 0.33 | | | | | | |
| 10 | independent 0.24 | 0.87 | independent 0.38 | 0.77 | **decrease** 7.66 | **0.00** | increase 2.74 | 0.06 | hump 2.74 | 0.06 | independent 0.40 | 0.75 |
| 11 | independent 0.97 | 0.42h | independent 2.61 | 0.07 | independent 1.36 | 0.27 | **decrease** 7.45 | **0.00** | **increase** 5.79 | **0.00** | independent 0.24 | 0.87 |
| 12 | hump 1.75 | 0.18 | **decrease** 4.11 | **0.02** | **decrease** 3.77 | **0.02** | **decrease** 5.46 | **0.00** | **increase** 6.12 | **0.00** | independent 0.24 | 0.87 |
| 13 | **decrease** 22.32 | **0.00** | decrease 1.38 | 0.27 | **increase** 4.84 | **0.01** | increase 1.56 | 0.22 | independent 0.60 | 0.62 | **increase** 4.51 | **0.01** |
| 16 | | | decrease 0.48 | 0.70 | increase 0.48 | 0.70 | | | | | | |

*Oromediterranean shrubland*

| Trait n° | 0 | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|

| | F | p | F | p | F | p | F | p | F | p | F | p |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | **increase** | | increase | | **decrease** | | | | | | | |
| | 20.96 | **0.00** | 1.89 | 0.15 | 6.78 | **0.00** | | | | | | |
| 8 | **increase** | | | | **increase** | | decrease | | | | | |
| | 20.96 | **0.00** | | | 3.63 | **0.02** | 19.11 | **0.00** | | | | |
| 9 | increase | | increase | | **decrease** | | | | | | | |
| | 2.79 | 0.06 | 2.22 | 0.11 | 4.40 | **0.01** | | | | | | |
| 5 | | | **increase** | | **decrease** | | **increase** | | | | | |
| | | | 16.09 | **0.00** | 14.62 | **0.00** | 9.56 | **0.00** | | | | |
| 11 | **increase** | | **increase** | | increase | | **hump** | | **decrease** | | | |
| | 4.03 | **0.02** | 16.53 | **0.00** | 1.98 | 0.14 | 3.62 | **0.03** | 6.31 | **0.00** | | |
| 13 | | | **decrease** | | independent | | | | | | **increase** | |
| | | | 6.78 | **0.00** | 1.88 | 0.16 | | | | | 19.21 | **0.00** |
| 16 | | | **hump** | | **extreme** | | | | | | | |
| | | | 8.58 | **0.00** | 8.58 | **0.00** | | | | | | |

**Tab. 6.12** CCA results for the relationship between abundances of selected trait attributes and correlating grazing dependent parameters and environmental variables. Eigenvalues and the cumulative explained variance are given for trait attribute-environment-correlations

| Altitudinal level | CCA - axis | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| *Hammada* **semidesert** | | | | |
| Eigenvalue | 0.914 | 0.821 | 0.483 | 0.609 |
| Cumulative explained variance | 49.0 | 78.9 | 87.4 | 93.8 |
| *Artemisia* **steppe** | | | | |
| Eigenvalue | 0.800 | 0.673 | 0.736 | 0.457 |
| Cumulative explained variance | 61.7 | 82.2 | 92.5 | 97.2 |
| *Juniperus* **woodsteppe** | | | | |
| Eigenvalue | 0.781 | 0.581 | 0.686 | 0.622 |
| Cumulative explained variance | 41.0 | 73.8 | 86.0 | 92.2 |
| **Oromediterranean shrubland** | | | | |
| Eigenvalue | 0.672 | 0.642 | 0.505 | 0.428 |
| Cumulative explained variance | 61.9 | 90.9 | 97.4 | 99.1 |

**Tab. 6.13** Summary of CCA forward selection results for the relationship between the abundance of selected trait attributes and grazing dependent parameters (BARE, TRAMPLE) as well as environmental variables (C, N, SKELET, SAND, CLAY, CACO3, GRIT). The term $\lambda$ describes the additional variance each variable explains at the time when it was included into the model. F and p values derived from Monte Carlo permutation tests. *marks significant impact of that variable on the given altitudinal level

| Altitudinal level | Conditional Effects | | | |
|---|---|---|---|---|
| | Var. N | $\lambda$ | p | F |
| *Hammada* **semidesert** | | | | |
| N* | 9 | 0.06 | 0.00 | 4.97 |
| SKELET* | 5 | 0.04 | 0.00 | 3.43 |
| BARE* | 3 | 0.03 | 0.02 | 2.90 |
| C | 8 | 0.01 | 0.15 | 1.64 |
| TRAMPLE | 4 | 0.02 | 0.13 | 1.50 |
| SAND | 6 | 0.01 | 0.24 | 1.26 |
| CLAY | 7 | 0.01 | 0.47 | 0.90 |
| | | | | |
| *Artemisia* **steppe** | | | | |
| BARE* | 3 | 0.04 | 0.00 | 9.50 |
| CACO3 | 7 | 0.00 | 0.05 | 2.20 |
| TRAMPLE | 4 | 0.01 | 0.23 | 1.32 |
| SAND | 6 | 0.00 | 0.25 | 1.27 |
| N | 9 | 0.01 | 0.33 | 1.11 |
| C | 8 | 0.01 | 0.01 | 4.05 |
| SKELET | 5 | 0.00 | 0.56 | 0.80 |
| | | | | |
| *Juniperus* **woodsteppe** | | | | |
| N* | 9 | 0.03 | 0.02 | 3.62 |
| TRAMPLE* | 4 | 0.03 | 0.02 | 3.41 |
| C | 8 | 0.01 | 0.16 | 1.55 |
| GRIT | 6 | 0.01 | 0.16 | 1.54 |
| BARE | 3 | 0.01 | 0.23 | 1.31 |
| SAND | 7 | 0.01 | 0.30 | 1.07 |
| SKELET | 5 | 0.00 | 0.37 | 0.93 |
| | | | | |
| **Oromediterranean shrubland** | | | | |
| BARE* | 3 | 0.04 | 0.00 | 4.40 |
| N* | 8 | 0.03 | 0.02 | 3.47 |
| TRAMPLE* | 4 | 0.02 | 0.03 | 2.74 |
| SKELET | 5 | 0.01 | 0.13 | 1.91 |
| C | 7 | 0.01 | 0.57 | 0.68 |
| SAND | 6 | 0.00 | 0.36 | 1.08 |

# Local ecological knowledge

Seeking reliability as local insurance
What can we learn
from southern Moroccan nomads?

# Abstract

Coping with environmental variability is one major issue for all human land users in arid and semiarid ecosystems. Livestock production and thus people's livelihood mainly depend on strategies that are able to stabilize or buffer the highly variable production of forage resources. Range ecologists particularly identified perennial plant species to buffer rainfall variability because they accumulate biomass over time (fodder storage) as well as energy in special storage tissues (vitality). We hypothesize that a sustainable land use system should (1) have indicators to perceive the buffering capacity of a pasture and (2) apply an adapted range management in order to preserve these buffering mechanisms. To test our hypothesis, we conducted a case study on local knowledge among the Ait Toumert pastoralists in southern Morocco. The study compares the local perception of pasture quality to the actually offered amount and production of forage resources. Therefore, we first recorded the local valuation of forage plant species in contrast to their ecological performance and revealed that Ait Toumert herdsmen value perennial plant species much more than short living herbaceous species. This is in line with our assumption that perennials buffer rainfall variability and thus represent a more reliable forage resource.

In a second step, we observed by means of an ecological field experiment that the proportion of perennial plants (e.g. dwarf shrubs and perennial grasses) in forage biomass (standing crop) and forage production (ANPP) increased from lowland winter pastures to highly mountainous summer pastures. The Ait Toumert grazing area thus can be seen as a gradient of reliability. The experiment revealed that a rest period without grazing over seven years led to increased vitality (ANPP) of chamaephytes but decreased the vitality of short-living plant species.

Since Ait Toumert pastoralists seek reliability and adapt their mobility decisions to the given reliability gradient in order to ensure their livelihood, they concurrently care for some kind of ecological insurance, because they sustain the capacity of their pastures to buffer rainfall variability. Our study explicitly contributes making local knowledge accessible for ecological research, because reliability depicts a term which can be quantified by anthropological as well as ecological methods.

# 7 Local ecological knowledge

## 7.1 Introduction

### 7.1.1 Dryland pastures buffer rainfall variability

The world's dryland areas are characterized by low annual rainfall and evapotranspiration exceeding precipitation most of the year. Rainfall variability is typically high both on the spatial and temporal scale (De la Maza *et al.* 2009). Since aboveground net primary production (ANPP) in these areas is widely driven by rainfall, phytomass is a highly unpredictable natural resource for human land use. Despite of harsh climatic constraints, livestock of more than 30 million people directly depends on rangeland production there (Ellis 1994).

Recent rangeland ecology intensively studied the transformation of variable rainfall into phytomass, and several mechanisms were identified that stabilize pasture production (ANPP) in drylands (Enfors & Gordon 2007; Müller *et al.* 2007a; Morris *et al.* 2008; Owen-Smith 2008).

First, rainfall variability can be buffered abiotically (hydrologically), for example on sites experiencing low above-ground and below-ground water losses, or having a water surplus due to lateral water transport (van de Koppel *et al.* 2002). Second, variability of rainfall can be biotically buffered; and particularly perennial plant species account for this mechanism (Morris *et al.* 2008). Biotical buffers operate at two different levels. At the pasture level, perennial species are able to accumulate biomass over several vegetation periods. Pastures with a high density of perennial species thus better provide forage even in times of forage scarcity. Biomass accumulation is measurable as perennial standing crop.

Another mechanism acts at the individual plant level. Unlike annual plants, perennial species, e.g. perennial grasses, are able to accumulate energy in specialized storage tissues such as stems and roots. This energy stock can be reallocated to support production for example at the beginning of the vegetation period (Müller *et al.* 2007a; Owen-Smith 2008), and thus increases the vitality of the plant. Increased vitality of perennial plant individuals sums up to better growth of the whole pasture, since a pasture is regarded as a community of plant individuals and under the assumption that competition effects are neglected. This condition of a pasture is here determined as the 'vitality' of the pasture and

exclusively refers to the energy stocks accumulated by perennial plants. We know that accumulated energy in specialized storage tissues, also called reserve biomass, is essential to build up herbaceous biomass. Thus, the vitality of plants is closely related to their productivity (Noy-Meir 1982). In this paper we make use of this relationship and apply aboveground net primary production (ANPP) of perennial species as an indirect measure for the vitality of a pasture.

Both, accumulation of biomass (increased standing crop) and accumulation of energy (increased ANPP) can be understood as a type of insurance capital on the community level, which becomes crucial in times of rainfall scarcity (Enfors & Gordon 2007).

## 7.1.2 Measuring the buffering capacity

The biotic buffering potential has already been addressed implicitly by Raunkiaer's life forms (Raunkiaer 1934). According to the location of the plant's growth-point during seasons of adverse conditions, Raunkiaer distinguished between phanerophytes (P, woody perennials, buds highly above the ground), chamaephytes (CH, buds on persistent shoots max. 20 cm above the ground, e.g. dwarf shrubs), hemicryptophytes (H, perennial forbs and grasses with buds at the soil surface), and therophytes (T) surviving the unfavourable season in form of seed, amongst others. Annual plants (therophytes) have no capacity to buffer interannual rainfall variability, because they only accumulate negligible amounts of biomass and energy in their seeds.

## 7.1.3 Range management and local knowledge

Range management can modulate the buffering capacity of a pasture. While intensive and untimely grazing typically results in a decline of ANPP of perennial plants (Paruelo *et al.* 2008), moderate grazing – like other moderate levels of disturbance – often increases ANPP due to positive effects on plant vitality (Milton & Dean 2000). Land users further influence pastures by a mobility adapted to rainfall variability which may lead to the accumulation of perennial plant biomass for livestock nutrition (Wiegand *et al.* 2004).

Range ecologists implemented the given abiotic and biotic buffer mechanisms in criteria to assess pasture quality. For example, high quality pastures providing forage during scarce times were consequently defined as key

resource areas (Illius & O'Connor 1999; Ngugi & Conant 2008; Prins *et al.* 2008; Scholte & Brouwer 2008). However, past studies showed that scientific quality criteria can strongly differ from those applied by local land users (Bollig & Schulte 1999; Moritz & Tarla 1999; Reed *et al.* 2008). Local people can offer alternative insights and often have implicit knowledge of interrelated stochastic and deterministic processes (Eisold *et al.* 2009). In recent years the interest on such knowledge increased, partly due to the recognition that local knowledge can substantially contribute to a sustainable use of natural resources (Berkes 2000; Fernandez-Gimenez 2000; Oba *et al.* 2000; Oba *et al.* 2003; Oba & Kaitira, 2006). Although such knowledge has been frequently assessed (Lalonde 1993; Moritz & Tarla 1999; Berkes *et al.* 2000; Ford & Martinez 2000; Byers *et al.* 2001; Adams 2004; Barrera-Bassols *et al.* 2006; Camou-Guerrero *et al.* 2008; Anadón *et al.* 2009), it was neither related to general principles (Niamir-Fuller 1998) nor were these principles linked to ecological field data.

## 7.1.4 The case study in southern Morocco

In our case study we attempt to match local criteria for pasture quality with forage resources in the area. We want to analyze if and how local land users perceive ecological differences in the buffering capacity of their pastures and how they are able to take advantage of these buffer mechanisms.

Here, we investigated traditional criteria of pasture quality (local indicators) among the Ait Toumert herdsmen in southern Morocco. Criteria were implicitly assessed in an interdisciplinary study by recording local valuation of forage plant species and contrasting it to their ecological performance on pastures. We hypothesize that the Ait Toumert herdsmen have developed criteria - comparable to those of their scientific colleagues - to assess pasture condition, and that they implicitly include these criteria into range management in order to sustain the capacity of their pastures to buffer rainfall variability. We ask, which criteria are used by local herdsmen and how does their use contribute to a sustainable range management in the High Atlas region?

## 7.1.5 The Ait Toumert and their pastoral area

The nomadic fraction of the Ait Toumert comprise 29 households (Kemmerling *et al.* 2009) which regularly exploit a vast pastoral area situated in the Moroccan

province of Ouarzazate at the southern slope of the High Atlas Mountains (Fig. 7.1). The region is characterized by a steep altitudinal gradient stretching from the Basin of Ouarzazate in the south (1,300 m a.s.l.) to the peaks of the High Atlas Mountains (4,000 m a.s.l.) in the northern part. The altitudinal gradient is associated with an aridity gradient from arid climate with less than 200 mm precipitation per year and high interannual variability to a subhumid climate in the highest mountain parts with an annual precipitation up to 700 mm per year (Schulz 2008) (Tab. 7.1). Along this gradient, four different vegetation zones can be distinguished. The most arid sites (Fig. 7.1, TRB) are covered by Hammada semidesert; Artemisia steppes succeed (Fig. 7.1, TAO) dominated by dwarf shrubs and perennial grasses. Steeper mountainous parts are covered by Juniper woodsteppes (Fig. 7.1, AMS) and oromediterranean shrubland (Fig. 7.1, TZT), the latter dominated by long-living, cushion-like xerophytes (Benabid & Fennane 1994; Finckh & Poete 2008).
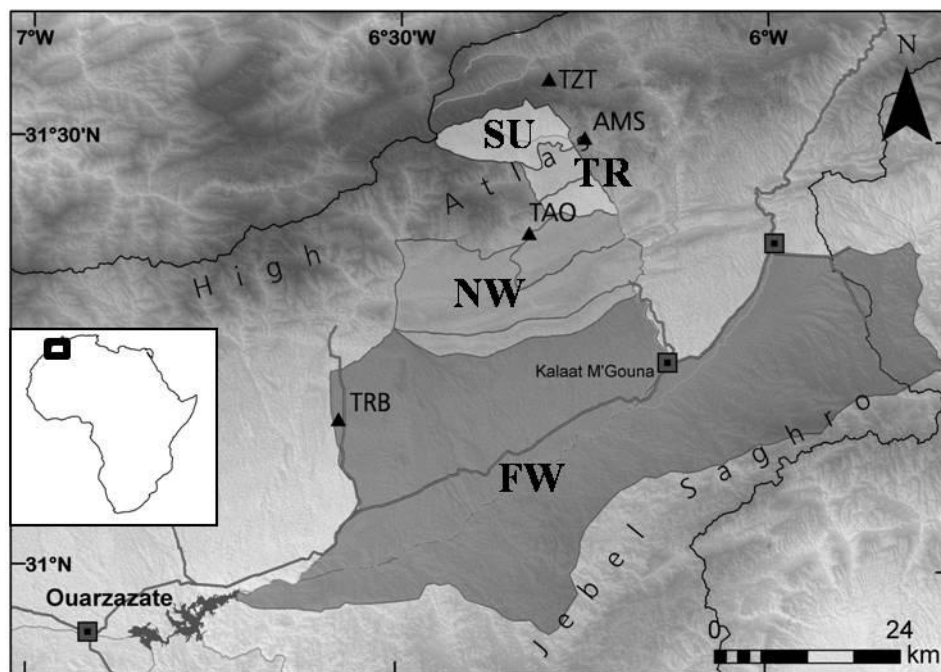


**Fig. 7.1** Study area with Ait Toumert pastures. Pasture types were derived from mental maps developed by local informants: **FW** far winter pasture, **NW** near winter pasture, **TR** transition pasture, **SU** summer pasture. ▲ Corresponding experimental sites: Tizi n'Tounza (TZT); Ameskar (AMS); Taoujgalt (TAO); Trab Labied (TRB). Cartography and processing by Pierre Fritzsche.

The Ait Toumert practice an annual transhumance cycle using the *Hammada* and *Artemisia* steppes as winter pastures (FW and NW, 1,300 to 2,000 m a.s.l.) and the

oromediterranean shrubland (TZT) as summer pastures (SU 2,600 to 3,200 m a.s.l.). Transition pastures (2,000 to 2,600 m a.s.l.) are occupied in spring and autumn (Fig. 7.1, Tab. 7.1). The large winter pastures, characterized by a high spatial and temporal heterogeneity of natural resources, are shared with at least two neighbouring fractions (Breuer 2007). Among the Ait Toumert, sheep and goats are the most abundant livestock species.

**Tab. 7.1** Pasture types and climatic conditions at experimental sites. *MAP* is the mean annual precipitation. The *Aridity index* is the ratio of annual precipitation to annual potential evapotranspiration (Middelton & Thomas 1997). Both parameters were calculated for the years 2001-2008 based on data from weather stations installed at the experimental sites (Fig. 7.1)

| *Pasture type* | **FW** | **NW** | **TR** | **SU** |
|---|---|---|---|---|
| | far winter pasture | near winter pasture | transition pasture | summer pasture |
| *Experimental site* | TRB | TAO | AMS | TZT |
| | Trab Labied | Taoujgalt | Ameskar | Tizi n'Tounza |
| Altitude | 1,380 m a.s.l. | 1,870 m a.s.l. | 2,250 m a.s.l. | 2,960 m a.s.l. |
| | 124 mm | 170 mm | 285 mm | 363 mm |
| Aridity index | 0.07 | 0.17 | 0.28 | 1.25 |

## 7.2  Material and Methods

Our methodological approach was twofold: in a first interdisciplinary study we assessed local criteria of range assessment. In a second experimental part we quantified pasture resources and pasture production in order to analyze the ecological background and functional explanation of such criteria.

### 7.2.1 Interdisciplinary part: Local range assessment

*7.2.1.1  Assessment of herdsmen's knowledge and ecological performance of forage plants*
Local ecological knowledge on forage plants was recorded by means of the free-list technique (Chambers 1994). It provides information on the local valuation (salience) of items from a certain cultural domain (here: forage species). The salience of a given species is determined by the frequency of its nomination in all free-lists, and by its rank in each list (Borgatti 1999; Sutrop 2001). The free-list technique was chosen as an effective method to gain quantitative data that can be transferred to scientific codes (Eisold *et al.* 2009). We separately questioned 17

informants (14 from pastoral-nomadic households and three from households who are sedentary in first generation) to name all forage plants of both sheep and goats. Interviews were conducted by visiting the pastoral-nomads at their current housing or on pastures (Kemmerling *et al.* 2009).

To compare local ecological knowledge on forage plants to related scientific ecological knowledge, data on the species' ecological performance were collected. The ecological performance depicts the relative success of a plant species on the Ait Toumert pastures. For that, species ground cover was visually estimated on vegetation plots. Species frequency was calculated as the number of plots where a certain plant species occurred. In each of the four main pasture types (Fig. 7.1), species cover values were recorded on 24 plots with a size of 25 m² each. Vegetation plots were randomly positioned within a radius of 3 to 5 km from existing climate stations. For far winter pastures and transition pastures, additional plots were assessed at more remote locations frequented by Ait Toumert herds (Imlil plains, high plateau of Asselda). We generally kept a minimum distance of 10 m between the plots to avoid spatial autocorrelation, and chose locations with regard to comparable site conditions such as soil type and water availability. In total 96 plots were sampled.

### 7.2.1.2 *Calculating the cognitive salience index (CSI) to compare local and ecological knowledge*

The comparison of local and scientific knowledge on forage plants is done with an ethno-ecological method allowing a quantitative comparison. The formal match of both data sets required a relation of vernacular species names to scientific names (Eisold *et al.* 2009). We only used plant species mentioned by at least two informants for rank correlation (Trabut 2006), and identified scientific and vernacular names of these plants. In the case of forage plants only known by their vernacular name, informants were asked to collect specimens for a taxonomic identification. Forage plants where the Berber name was unknown were collected within the grazing area of the Ait Toumert. Their vernacular name was then obtained in interviews with pastoral-nomadic informants. Additionally, ethnobotanical publications on Moroccan plant species were consulted (IAV 2002; Beloud 2002; Bennana 2004). In total, 79 from 109 items (72 %) mentioned more than once by the informants were identified, and 59 % of the species occurring more than once on the vegetation plots were assigned to an Ait Toumert vernacular (see Tab. 7.3, Appendix).

For a rank correlation of ecological and anthropological data, we used the Cognitive Salience Index (CSI).

$$CSI = S/N \times mP$$

This weighted rank computes the salience (S) of an item with a frequency parameter (F), the number of informants (N), and the mean position (mP) of an item (Sutrop 2001). It was originally developed for free-list data. To contrast the two data sets by means of their corresponding CSI values, three individual parameters were set as analogous:

**Tab. 7.2** Analogous parameters for ecological and anthropological CSI calculation

| Parameter | Value for ecological CSI | Value for anthropological CSI |
|---|---|---|
| N (sample size) | Number of vegetation plots | Number of interview partners |
| mP (mean position) | Mean rank of a species due to its coverage on each plot | Mean rank of a species in each free-list |
| F (frequency) | Species' frequency on all plots (F > 2) | Species' frequency in all free-lists (F > 2) |

Ecological and anthropological CSI values were contrasted by correlation and regression analysis. Further, we assigned plant species to life forms according to Raunkiaer (see Tab. 7.3, Appendix) and calculated the mean CSI percentage for every life form in the Ait Toumert pastoral area.

## 7.2.2 Experimental part: Assessing forage production

### 7.2.2.1 *Experimental conditions*

In order to assess the amount of forage and forage production, we conducted a twofold exclosure experiment at four sites representing the four pasture types (FW far winter pasture, NW near winter pasture, TR transition pasture, and SU summer pasture) used by Ait Toumert herds (Fig. 7.1). From September 2007 to October 2008 data on forage biomass and forage production were assessed on the different pasture types. Experimental sites have been established in 2001 by the IMPETUS project (Integrated Approach to the Efficient Management of Scarce Water Resources in West Africa). They were equipped with an automatic weather station and a 400 m² permanent grazing exclosure. In September 2007 we

randomly installed 10 single square meters (= plots) at each of the four experimental sites for the following treatments: (1) LTE – long-term exclosure plots, located inside the grazing exclosure that thus have not been grazed since 2001 and (2) STE – short-term exclosure plots, protected by a permanently installed wired cage from the beginning to the end of the experiment. STE were used to prevent an underestimation of ANPP due to grazing offtake during the investigation period (see chapter 5.2.2).

We followed the sampling instructions of the Jornada Basin LTER program (Huenneke *et al.* 2001; Peters & Huenneke 2009), and measured diameter, height, and cover of each perennial plant individual at least at the beginning and at the end of the experiment. Annual plants were only assessed at the end of the experiment. Therefore we counted individuals, estimated the cover per species and measured maximum height as well as maximum diameter if several plants of the same annual species occurred on one square meter. For perennial plants, biomass was harvested individually (annual individuals pooled per species and m²) at the end of the experiment, oven-dried (24 h at 105 °C), and weighed. The data was used to construct linear regressions on plant volume and quadratic regressions on plant cover ($0.23 < r^2 < 0.99$). Inside the long-term exclosure it was not possible to harvest perennial plant species directly on the plots. Instead, regressions were constructed based on data of individuals beneath the measured square meters.

### 7.2.2.2 *Calculating standing crop and production*

Standing crop in kg DM/ha was directly obtained by harvesting at the end of the experiment for short-term exclosure plots. At long-term exclosure plots perennial standing crop was calculated with the help of cover-biomass regressions. For annual plants standing crop was set analogous with ANPP.

To measure forage production (ANPP) of perennial plants, we calculated the initial biomass in 2007 for each individual and each species on a plot using cover-biomass regressions and measurement data of 2007. ANPP was calculated as the positive increment of biomass for each species and summed for all species (annuals and perennials) on a plot over the study time (Milner & Hughes 1968; Huenneke *et al.* 2001; Scurlock *et al.* 2002). Species were assigned to one of five life forms (T, H, GEO, CH, P). Standing crops of all species were aggregated by lifeform and plot. Production data was calculated, respectively. Since life form standing crop and life form production on plot level were non-normally

distributed for any pasture type, results were aggregated with the help of medians and quartiles. We applied Kruskal-Wallis tests to compare standing crop as well as production per life form between the four pasture types.

To quantify how the ANPP of different life forms changed during seven years of grazing exclosure, we contrasted median values of life form ANPP measured in STE to those measured in LTE and calculated the change in percent for every pasture type.

# 7.3 Results

## 7.3.1 *Interdisciplinary part: Local valuation vs. ecological performance of forage plants*

Both anthropological CSI values ($CSI_{anthro}$) and ecological CSI values ($CSI_{eco}$) were normally distributed (Kolmogorov-Smirnov $p < 0.01$; $CSI_{anthro}$ $d = 0.30$; $CSI_{eco}$ $d = 0.27$). We found a weak positive linear relationship between the ecological performance and the local valuation of forage plants (Fig. 7.2 A) ($CSI_{anthro} = 0.63 \cdot CSI_{eco}$; $R^2 = 0.356$; $p < 0.001$). The more frequent and dominant a plant species was the more it was valued by local herdsmen.

Furthermore, life forms differed in their contribution to total CSI values (Fig. 7.2 B). Long living plant species such as phanerophytes and chamaephytes (CH) were more valued by local herdsmen than their mean ecological performance would imply.
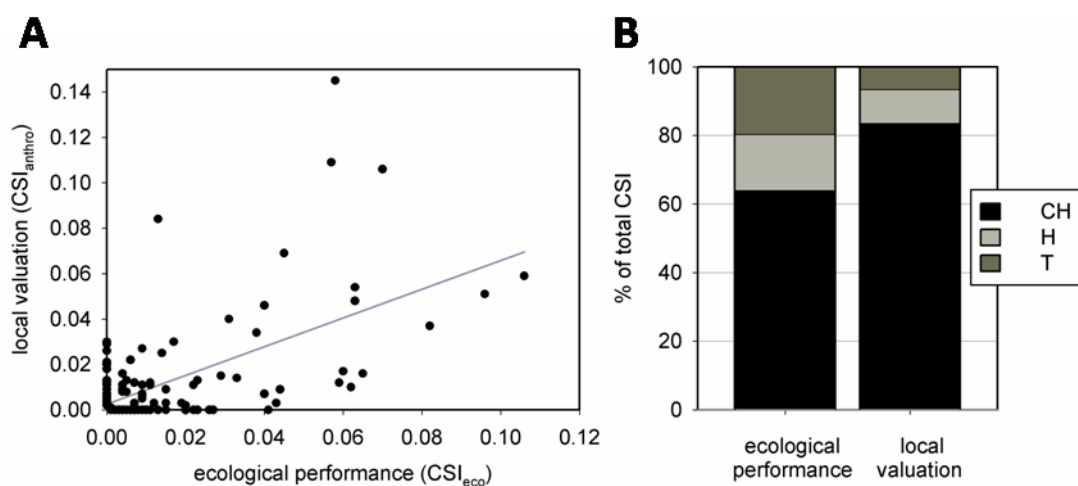


**Fig. 7.2 A** Ecological performance of forage plant species compared to their local valuation. The grey line represents the calculated regression $CSI_{anthro} = 0.63 \cdot CSI_{eco}$ ($R^2 = 0.356$; $F = 79.571$; $p < 0.001$) **B** Contribution (mean %) of different life forms to total CSI compared for ecological performance vs. local valuation of forage plants. Chamaephytes and phanerophytes (CH) are more valued by local herdsmen than they occur on vegetation plots; the opposite is true for short-living plants such as hemicryptophytes (H) and therophytes (T).

Conversely, short-living plant species such as hemicryptophytes (H) and therophytes (T) were on average more frequently found on pastures than they had been named by local herdsmen (see Tab. 7.3, Appendix). However, CSI

differences between ecological performance and local valuation of a life form were only significant for therophytes (t-test; t = -2.96; p < 0.01).

## 7.3.2 Experimental part I: Standing crop of Ait Toumert pastures

Standing crop of lifeforms differed between the regarded pasture types (Fig. 7.3). While median amount of chamaephytes increased from far winter pastures (FW 53 kg/ha) to summer pastures (SU 9256 kg/ha), median standing crop of therophytes decreased (FW 159 to SU 0 kg/ha). Standing crop of hemicryptophytes such as perennial grasses and forbs peaked on transition pastures (TR 112 kg/ha).
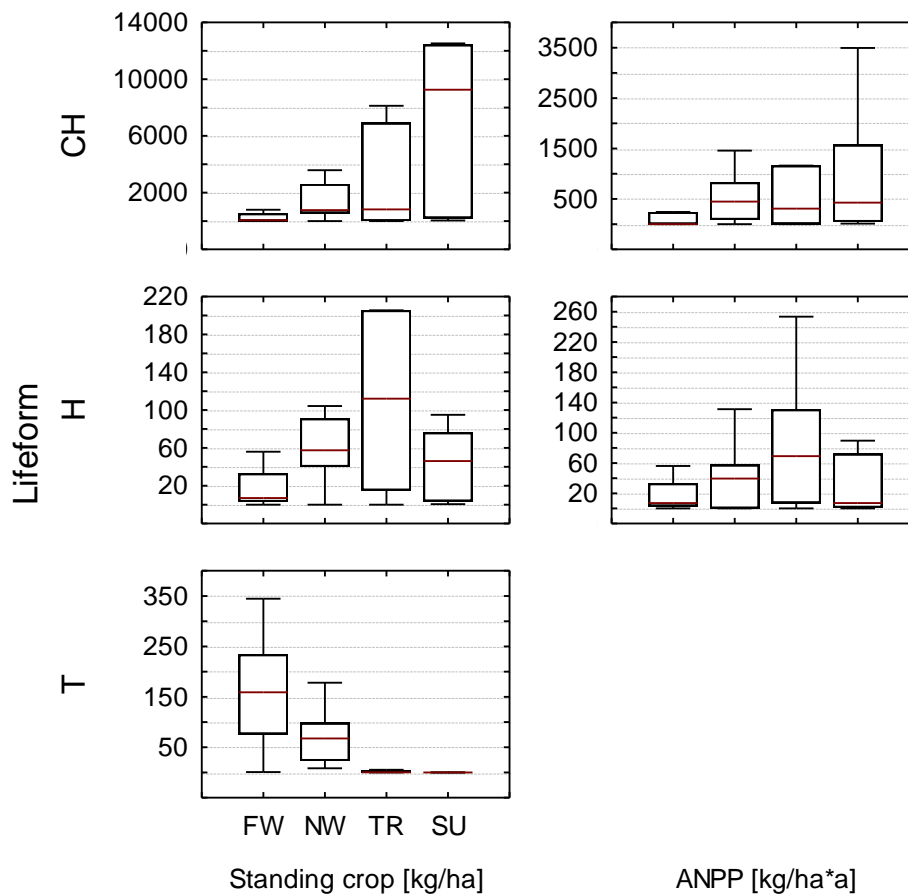


**Fig. 7.3** Standing crop [kg/ha] and ANPP [kg/ha*a] per life form (CH chamaephytes; H hemicryptophytes; T therophytes) for the different pasture types (FW far winter pasture; NW near winter pasture; TR transition pasture; SU summer pasture). Standing crop and ANPP are shown as medians with quartiles (box) and outlier ranges (whiskers). Because ANPP of annual plants (T) equals standing crop, it is not separately shown.

Kruskal-Wallis tests revealed significant differences for chamaephytes between summer and far winter pastures (p < 0.05) and for therophytes between High Atlas pastures (summer and transition pasture) and winter pastures (near and far) (FW vs. TR p < 0.01; FW vs. SU p < 0.001; NW vs. TR p < 0.05; NW vs. SU p < 0.01).

### 7.3.3 Experimental part II: Forage production (ANPP) related to life forms

ANPP of chamaephytes, hemicryptophytes, and therophytes differed depending on pasture type (Fig. 7.3). For chamaephytes median ANPP was highest for near winter pastures (NW 447 kg/ha per period) and lowest for far winter pastures (FW 1 kg/ha per period). Like standing crop, median ANPP of hemicryptophytes peaked for transition pastures with 69 kg/ha per year. The only significant changes along altitude were observed for therophytes whose ANPP decreased from far winter pastures to summer pastures (FW 159 to SU 0 kg/ha per year) (see standing crop).

### 7.3.4 Experimental part III: ANPP of life forms changed during seven years of grazing exclosure

For grazed sites, ANPP per lifeform is shown in Fig. 7.3. In contrast, Fig. 7.4 compares median ANPP per life form of grazed and 7 years recovered vegetation in order to quantify how life form vitality changed on different pasture types. The most pronounced change in ANPP was observed on far winter pastures, where chamaephytic production on LTE was more than 400-fold higher than that on STE (increase of 4226 %, Fig. 7.4). However, this considerable change merely occurred due to high ANPP variability between STE plots and because of a considerable change in the abiotic conditions due to grazing exclosure.

On near winter pastures (NW) and transition pastures (TR), chamaephytic production increased during seven years of grazing exclosure by 100 % and 90 %, respectively (Fig. 7.4). The production of hemicryptophytes and therophytes generally decreased except for summer pastures, where hemicryptophytic production increased (increase of 260 %) within the grazing exclosure.
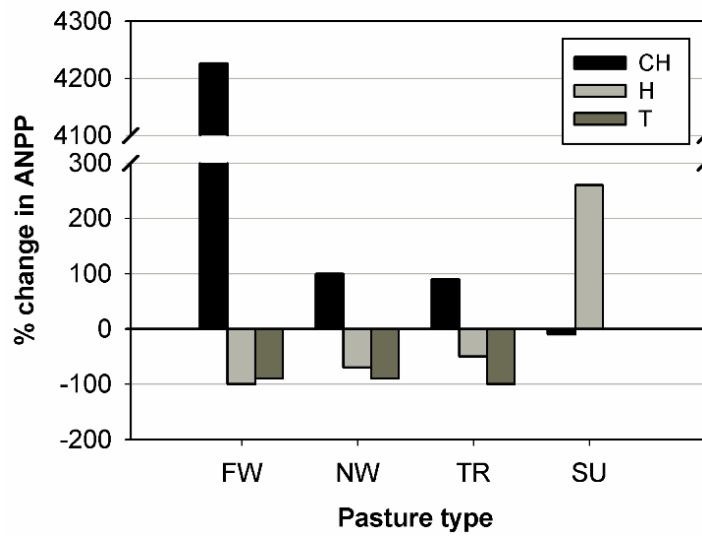
**Fig. 7.4** Change [%] in life form ANPP during 7 years of grazing exclosure. CH chamaephytes; H hemicryptophytes, T therophytes

## 7.4 Discussion

Our study revealed that Ait Toumert herdsmen value forage resources by quality and quantity. One key element contributing to their local valuation was the lifetime of forage plants i.e. perennial species were much more appreciated than annual and other short living herbaceous species. Concurrently, the experiment showed that the higher a pastoral area was situated in the High Atlas Mountains, the more the total amount of forage and forage production depended on long living plant species like chamaephytes. In addition, the change of ANPP during a seven years exclosure experiment differed between life forms and along altitude. Mainly chamaephytes benefited from grazing exclosure, in particular those on winter and transition pastures. At the same time the contribution of therophytes to total ANPP declined for each pasture type.

### *7.4.1 Interdisciplinary output: Reliability serves as local criterion for pasture quality*

The Ait Toumert pastoralists have a complex understanding of the quality and availability of natural resources in space and time, a notion which is known from other heterogeneous environments as well (Angassa & Oba 2008; Reed *et al.* 2008). Since perennial forage plants were much more valued by herdsmen than annual species, we aimed to understand what makes perennial species more valuable in local perception. Our results can be seen in the context of coping with environmental variability (Owen-Smith 2008). Species which can accumulate forage and energy, i.e. perennial species, are able to buffer the effects of rainfall variability on available forage. This buffering ability is especially important for periods of forage scarcity, either within the year or in times of drought. For the Ait Toumert pastoralists, a high grazing value of a certain species or pasture is thus not only determined by a high production of forage, but also by a predictable availability of forage. This is congruent to other studies from arid rangelands (Reed & Dougill 2002; Eisold *et al.* 2009). We thus conclude that *reliability* of plants and pastures is a major criterion applied by Moroccan pastoral-nomads to cope with their spatially heterogeneous and temporally highly variable environment (Kemmerling *et al.* 2009).

## 7.4.2 *Experimental output I: How Ait Toumert pastures differ in their quality*

Since reliability seems to be one main local criterion, we interpret the findings of our exclosure experiment with regard to how reliable actually offered forage resources are in the area. While forage production on winter pastures predominantly relied on annual and short living herbaceous plants (T, H), transition and summer pastures as well as their production were dominated by long living perennial plants (CH). Though, the pastoral area of the Ait Toumert stretches along a gradient of reliability of available forage and forage production. The most reliable forage resources are found on the top of the High Atlas Mountains for the summer pastures where 98 % of total standing crop and 90 % of forage production were provided by chamaephytes. Pastures with a high proportion of chamaephytes buffer intraannual and interannual rainfall variability by accumulating standing crop which can function as fodder storage (Enfors & Gordon 2007). In addition, chamaephytic and hemicryptophytic plants accumulate energy in specialized storage tissues (Müller *et al.* 2007a; Owen-Smith 2008), which buffers the impact of rainfall variability on forage production (ANPP), in particular on transition and near winter pastures. In contrast, far winter pastures are less reliable forage resources than summer pastures because more than half of the forage production was supplied by annual species. Such kind of forage (T) strongly depends on magnitude, regionalism, and pulsing of precipitation (Kaiser 2001; Huxman *et al.* 2004; Ogle & Reynolds 2004). Therophytes neither accumulate biomass nor energy, are not able to buffer rainfall variability and thus display a less reliable forage resource for the Ait Toumert.

## 7.4.3 *Experimental output II: Rest period changed life form ANPP*

Comparing life form ANPP of grazed and rested sites, we observed that seven years of grazing exclosure doubled the vitality (ANPP) of long-living perennial plant species, particularly chamaephytes on near winter and transition pastures, while ANPP of annual plants and the vitality of most of the hemicryptophytes declined. Thus, even if the vitality of a whole pasture (measured as ANPP) during an average rain year does not change during a certain rest time, a rest time can shift the proportion of perennials in standing crop offering a greater buffer capacity and thus making a pasture more reliable.

### 7.4.4 *How pastoralists invest into the buffering capacity of their pastures*

Ait Toumert herdsmen apparently seek reliability. It is applied as local criterion for pasture quality and influences their mobility decisions (Kemmerling *et al.* 2009). Apart of minimizing economical risk, using pastures along a gradient of reliability is considerably useful as ecological insurance (Quaas & Baumgärtner 2008). Since herds do not graze the same patch of vegetation all the time, transhumance can contribute to the vitality of the pastures by preserving natural storage tissues of perennial plant individuals. In addition, nomads use the highly productive summer and transition pastures more frequently than winter pastures, which also represents an investigation into the vitality (ANPP) of the pasture because grazing animals mainly consume the surplus of biomass production. Furthermore nomads invest into the fodder storage of their pastures, for example by using less productive far winter pastures only in years with high precipitation. Not only on far winter pastures, but everywhere where the vegetation receives rain but is not grazed at the same time, it can regrow and accumulate fodder storage (Müller *et al.* 2007b).

Ait Toumert herdsmen implicitly support the mechanisms of increased plant vitality and accumulation of fodder storage, and thus maintain the capacity of their pastures to buffer rainfall variability.

## 7.5  Conclusion

We found that Ait Toumert nomads in southern Morocco seek reliability. It is one major local criterion to assess pasture quality, or in detail the buffering capacity of their pastures. Assessing the reliability of pastures is advantageous for the nomads as they practise transhumance along a reliability gradient of forage resources. By adapting their mobility subject to the amount of rainfall and to the specific buffering capacity of each pasture type, they sustain both the capacity of the vegetation to build up a surplus of standing crop (fodder storage) and to build up an energy stock which maintains or enhances the vitality (ANPP) of perennial plant individuals even under grazing conditions.

Because reliability depicts a term which is assessable by anthropological methods and ecologically measurable as the proportion of perennial plant species, this study contributes to make local knowledge accessible for ecological research. Further studies are needed to investigate such functional relationships

between local valuation and ecosystem function of environmental components as well. It will surely prepare us to future challenges of climate and land use change.

# 7.6 Appendix

**Tab. 7.3** Plant species with vernaculars named by Ait Toumert herdsmen and/or occurring on vegetation relevés in alphabetical order. Family and life form*s* (P phanerophyte; CH chamaephyte, H hemicryptophyte, GEO geophyte, T therophyte) are given according to (Fennane *et al.* 1999; Fennane *et al.* 2007). The pasture type (like in Fig. 7.1, *SU* summer pasture, *TR* transition pasture, *NW* near winter pasture, *FW* far winter pasture) states where the species mainly occurred following own observations. $CSI_{eco}$ gives the salience index calculated for the ecological performance of forage plants, $CSI_{anthro}$ the salience index calculated from free-lists. Plant family names are abbreviated as follows: *Ana* Anacardiaceae, *Ama* Amaranthaceae, *Apo* Apocynaceae, *Ber* Berberidaceae, *Bor* Boraginaceae, *Bux* Buxaceae, *Cap* Capparaceae, *Cam* Campanulaceae, *Car* Caryophyllaceae, *Che* Chenopodiaceae, *Cis* Cistaceae, *Com* Compositae, *Con* Convolvulaceae, *Cru* Cruciferae, *Cup* Cupressaceae, *Dip* Dipsacaceae, *Eph* Ephedraceae, *Eup* Euphorbiaceae, *Fab* Fabaceae, *Ger* Geraniaceae, *Jun* Juncaceae, *Lam* Lamiaceae, *Lil* Liliaceae, *Mal* Malvaceae, *Ole* Oleaceae, *Pap* Papaveraceae, *Pla* Plantaginaceae, *Plu* Plumbaginaceae, *Poa* Poaceae, *Pol* Polygonaceae, *Pri* Primulaceae, *Ran* Ranunculaceae, *Res* Resedaceae, *Rha* Rhamnaceae, *Rut* Rutaceae, *Scr* Scrophulariaceae, *Sol* Solanaceae, *Tam* Tamaricaceae, *Umb* Umbelliferae, *Zyg* Zygophyllaceae

| Species | Fam | CSI eco | Life form | Pasture type | Vernacular | CSI anthro |
|---|---|---|---|---|---|---|
| **(1) Identified items named by herdsmen and occuring on vegetation plots** | | | | | | |
| **(1a) identified species** | | | | | | |
| Ajuga iva (L.) Schreber | Lam | 0.001 | H | T | Ouchen N'Tougoura | 0.001 |
| Alyssum spinosum L. | Cru | 0.096 | CH | SU | Tifssite N'Ilghman | 0.051 |
| Arenaria pungens Lag. | Car | 0.004 | CH | SU | Awizra | 0.009 |
| Astragalus ibrahimianus Maire | Fab | 0.013 | CH | SU | Touchkt | 0.084 |
| Bupleurum fruticescens ssp spinosum (Gouan) O. Bolos & Vigo | Umb | 0.058 | CH | SU | Adolfssa | 0.145 |
| Centaurea josiae Humbert | Com | 0.007 | H | SU | Tamzoght N'Tili | 0.012 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Cytisus purgans ssp balansae (Boiss.) Maire | Fab | 0.106 | CH | SU | Azmroy | 0.059 |
| Dactylis glomerata ssp hispanica (Roth) Nyman | Poa | 0.009 | H | TR | Mtidert | 0.005 |
| Echinops spinosus L. | Com | 0.004 | H | FW | Tasskra | 0.008 |
| Echium velutinum ssp velutinum Coincy | Bor | 0.020 | T | TR | Ils N'Azgar | 0.002 |
| Erinacea anthyllis Link | Fab | 0.063 | CH | SU | Tardma | 0.048 |
| Farsetia occidentalis B.L. Burtt. | Cru | 0.033 | CH | FW | Tamjoute | 0.014 |
| Filago spec | Com | 0.015 | T | TR | Atou N'Tidad | 0.003 |
| Genista scorpius ssp myriantha (Ball) Maire | Fab | 0.045 | CH | TR | Ouchfoud | 0.069 |
| Hordeum murinum ssp leporinum (Link) Asch. & Gr. | Poa | 0.012 | T | TR | Tizmi N'Ighardayan | 0.003 |
| Malva parviflora L. | Mal | 0.005 | T | FW (NW) | Tibdadde N'Imkssawne | 0.013 |
| Minuartia funckii (Jordan) Graebner | Car | 0.043 | T | NW | Tizikart | 0.003 |
| Morettia canescens Boiss. | Cru | 0.017 | H | FW | Taliwaghte | 0.030 |
| Othonna maroccana (Batt.) Jeffrey | Com | 0.009 | CH | TR | Alzaz | 0.027 |
| Pallenis hierochuntica (Michon) Greuter | Com | 0.006 | T | FW | Tet N'Tili | 0.022 |
| Peganum harmala L. | Zyg | 0.005 | CH | FW (NW) | L'Hermel | 0.008 |
| Reseda phyteuma ssp phyteuma L. | Res | 0.009 | T | NW (FW) | Irkajdi | 0.006 |
| Santolina africana Jord. & Fourr. | Com | 0.011 | CH | TR | Akchrire | 0.012 |
| Schismus barbatus ssp calycinus (L.) Maire & Weiller | Poa | 0.062 | T | FW (NW) | Tarazore | 0.010 |
| Scorzonera undulata ssp alexandrina (Boiss.) Maire | Com | 0.004 | GEO | TR | Tiliwite | 0.016 |
| Stipa capensis Thunb. | Poa | 0.038 | T | FW (NW) | Tizmi | 0.034 |
| Teucrium maleconianum Maire | Lam | 0.007 | CH | TR | L'Hercha | 0.003 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Teucrium mideltense (Batt.) Humbert | Lam | 0.023 | CH | TR | Tairarte | 0.013 |
| Vella mairei Humbert | Cru | 0.031 | CH | SU | Mijou | 0.040 |
| **(1b) identified groups** | | | | | | |
| Aphyllous shrubs group | | 0.082 | CH | FW | Assay | 0.037 |
|   Ephedra nebrodensis Guss. | Eph | | CH | FW | | |
|   Hammada scoparia (Pomel) Il'in | Che | | CH | FW | | |
| Artemisia group | | 0.267 | CH | TR (NW) | Izri | 0.181 |
|   Artemisia herba-alba Asso. | Com | | CH | TR (NW) | | |
|   Artemisia mesatlantica Maire | Com | | CH | TR (NW) | | |
| Asteraceae group | | 0.009 | H | FW/SU | Tiliwite Moughou | 0.011 |
|   Catananche caespitosa Desf. | Com | | H | SU | | |
|   Launaea arborescens (Batt.) Maire | Com | | CH | FW | | |
| Asteracean herbs group | | 0.044 | H | NW (FW) | Tifangrit | 0.009 |
|   Lactuca spec | Com | | H | NW (TR) | | |
|   Launaea nudicaulis (L.) Hook.f. | Com | | T | FW | | |
| Bromus group | | 0.040 | T | TR | Ilssgdid | 0.007 |
|   Bromus rubens ssp eu-rubens Maire | Poa | | T | TR | | |
|   Bromus tectorum L. | Poa | | T | TR | | |
| Creeping herbs group | | 0.059 | T | FW (NW) | Latar N'Outbir | 0.012 |
|   Astragalus cf tribuloides Del. | Fab | | H | NW | | |
|   Fagonia glutinosa  Del. | Zyg | | H | FW | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Herniaria cinerea DC. | Car | | T | NW | | |
| Paronychia arabica ssp longiseta Batt. | Car | | T | FW | | |
| Erodium group | | 0.019 | T | NW | Tizarzay N'Tamada | 0.003 |
| Erodium cicutarium (L.) L'Hér. | Ger | | T | NW | | |
| Erodium guttatum (Desf.) Willd. | Ger | | H | NW | | |
| Erodium laciniatum (Cav.) Willd. | Ger | | T | NW | | |
| Euphorbia group | | 0.009 | H | SU (TR) | Tanogha | 0.007 |
| Euphorbia megaatlantica Ball | Eup | | H | SU | | |
| Euphorbia spec. | Eup | | H | TR | | |
| Euphorbia sulcata Loisel. | Eup | | T | NW | | |
| Helianthemum group | | 0.022 | CH | NW | Asserghzem | 0.011 |
| Helianthemum crocceum ssp crocceum (Desf.) Pers. | Cis | | CH | NW | | |
| Helianthemum leptophyllum Dunal | Cis | | CH | NW | | |
| Helianthemum lippii (L.) Dum.-Courset | Cis | | CH | FW | | |
| Juniperus group | | 0.063 | P | TR | Adghomam | 0.054 |
| Juniperus phoenicea L. | Cup | | P | TR | | |
| Juniperus thurifera L. | Cup | | P | TR | | |
| Lamiaceae group | | 0.004 | CH | FW | Ouzghyale | 0.011 |
| Lavandula spec. | Lam | | CH | | | |
| Salvia aegyptiaca L. | Lam | | CH | | | |
| Medicago group | | 0.060 | T | FW (NW) | Lfessat N'Igddad | 0.017 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Medicago laciniata (L.) Miller | Fab | | T | FW | | |
| Medicago polycerata L. | Fab | | T | NW | | |
| Ononis group | | 0.015 | CH | FW (TR) | Afzdad | 0.009 |
| Ononis atlantica Ball | Fab | | CH | TR | | |
| Ononis natrix ssp prostrata (Br.-Bl. & Wilczek) Sirj. | Fab | | CH | FW | | |
| Poaceae group | | 0.057 | H | SU | Akftou | 0.109 |
| Festuca cf elatior L. | Poa | | H | SU | | |
| Festuca ovina L. | Poa | | H | SU | | |
| Helictotrichon filifolium (Lag.) Henrard | Poa | | H | SU | | |
| Rosette group (Basin) | | 0.040 | T | FW (NW) | Awerdal | 0.046 |
| Erysimum incanum ssp mairei (Sennen & Mauricio) Nieto Fel. | Cru | | T | NW | | |
| Limonium sinuatum ssp bonduellei (Lestib.) Sauvage & Vindt | Plu | | T | FW | | |
| Moricandia arvensis (L.) DC. | Cru | | T | FW | | |
| Plantago ciliata Desf. | Pla | | T | FW | | |
| Plantago ovata Forsskal | Pla | | T | FW | | |
| Rosette group (High Atlas) | | 0.011 | H | SU | Ankach | 0.011 |
| Centaurea gattefossei Maire | Com | | H | TR | | |
| Jurinea humilis DC. | Com | | H | SU | | |
| Raffenaldia primuloides Godron | Cru | | H | SU | | |
| Spiny desert shrub group | | 0.014 | CH | FW | Assgher | 0.025 |
| Acanthorrhinum ramosissimum (Coss. & Dur.) Rothm. | Scr | | CH | FW | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Convolvulus trabutianus Schweinf. & Muschler | Con | | CH | FW | | |
| Zilla spinosa ssp macroptera (Cosson) Maire & Weiller | Cru | | CH | FW | | |
| Stipa group | | 0.029 | H | TR | Taworgha | 0.015 |
| Stipa barbata Desf. | Poa | | H | TR | | |
| Stipa parviflora Desf. | Poa | | H | TR | | |
| Thistle group | | 0.065 | H | TR (FW) | Karzi | 0.016 |
| Carduncellus duvauxii Batt. | Com | | H | FW | | |
| Carlina brachylepis (Batt.) Meusel & Kästner | Com | | H | TR | | |
| Thymus group | | 0.070 | CH | TR | Azoukni | 0.106 |
| Thymus algeriensis Boiss. & Reuter | Lam | | CH | TR | | |
| Thymus satureioides ssp satureioides Cosson | Lam | | CH | TR | | |

**(2) Identified items named by herdsmen not occuring on vegetation plots**

**(2a) identified species**

| | | | | | | |
|---|---|---|---|---|---|---|
| Adenocarpus bacquei Batt. & Pitard | Fab | 0.000 | CH | NW | Ageltem | 0.018 |
| Aristida caerulescens Desf. | Poa | 0.000 | H | FW | Aghifoufe | 0.011 |
| Astragalus gombo Bunge | Fab | 0.000 | CH | FW | Awachkid | 0.004 |
| Atriplex halimus L. | Ama | 0.000 | CH | FW | Armass | 0.013 |
| Berberis hispanica Boiss. & Reuter | Ber | 0.000 | CH | TR | Isknass | 0.007 |
| Bupleurum cf atlanticum Murb. | Umb | 0.000 | CH | TR | Azazer | 0.018 |
| Buxus balearica Lam. | Bux | 0.000 | CH | TR | Tylouloute | 0.004 |
| Capparis spinosa L. | Cap | 0.000 | CH | TR | Iraz | 0.020 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Carthamus fruticosus Maire | Com | 0.000 | CH | TR | Idzghi | 0.029 |
| Chenopodium ambrosioides L. | Che | 0.000 | T | FW | Lmkhanza | 0.007 |
| Cladanthus scariosus (Ball.) Oberpr. & Vogt | Com | 0.000 | T | FW | Ifanzi N'Oudad | 0.009 |
| Evax pygmaea (L.) Brot. | Com | 0.000 | P | FW | Imtess | 0.018 |
| Fraxinus xanthoxyloides (G. Don) DC. | Ole | 0.000 | T | TR (NW) | Isk Waghad | 0.026 |
| Juncus spec | Jun | 0.000 | T | FW | Agou | 0.021 |
| Medicago truncatula Gaertn. | Fab | 0.000 | T | TR | Tazzoumerte | 0.002 |
| Mentha pulegium L. | Lam | 0.000 | H | NW | Timija | 0.007 |
| Mentha rotundifolia L. | Lam | 0.000 | H | TR | Flyou | 0.005 |
| Nerium oleander L. | Apo | 0.000 | P | FW | Alili | 0.004 |
| Reseda phyteuma ssp phyteuma L. | Res | 0.000 | T | TR | Moukhridd | 0.007 |
| Rhamnus lycioides ssp atlantica (Murb.) Jahandiez & Maire | Rha | 0.000 | CH | TR | Tassloukht | 0.030 |
| Rhus pentaphylla (Jacq.) Desf. | Ana | 0.000 | P | FW | Rman N'Oudad | 0.006 |
| Rumex bucephalophorus L. | Pol | 0.000 | T | TR | Tassmoumte | 0.005 |
| Ruta cf chalepensis L. | Rut | 0.000 | CH | TR | Awermi | 0.009 |
| Salsola vermiculata L. | Che | 0.000 | CH | FW | Tassra | 0.011 |
| Solanum nigrum L. | Sol | 0.000 | T | NW | Adyle N'Ouchen | 0.006 |
| Tamarix spec | Tam | 0.000 | P | FW | Tamaite | 0.013 |
| Withania adpressa (Coss.) Batt. | Sol | 0.000 | CH | FW | Hjijou | 0.003 |
| Ziziphus lotus (Linn.) Desf. | Rha | 0.000 | CH | FW | Azgar | 0.012 |

**(2b) identified groups**

| | | | | | | |
|---|---|---|---|---|---|---|
| Brassicaceae group | | 0.000 | CH | TR | Tazzelft | 0.013 |
| Matthiola maroccana Coss. | Cru | | T | FW | | |
| Notoceras bicorne (Aiton) Amo | Cru | | T | FW | | |
| Glaucium group | | 0.000 | H | FW | Azmou | 0.004 |
| Erucastrum leucanthemum Cosson & Durieu | Cru | | H | TR | | |
| Glaucium corniculatum ssp corniculatum (L.) J.H. Rudolph | Pap | | T | NW | | |

**(3) Items occuring on vegetation plots but not named by herdsmen**

| | | | | | | |
|---|---|---|---|---|---|---|
| Aaronsohnia pubescens (Desf.) Bremer & Humphries | Com | 0.005 | T | FW | | 0.000 |
| Adonis microcarpa DC. | Ran | 0.008 | T | NW | | 0.000 |
| Alyssum minutum DC. | Cru | 0.005 | T | TR (NW) | | 0.000 |
| Alyssum serpyllifolium Desf. | Cru | 0.015 | CH | SU | | 0.000 |
| Anacyclus pyrethrum (L.) Cass. | Com | 0.008 | T | SU | | 0.000 |
| Androsace maxima L. | Pri | 0.011 | T | TR | | 0.000 |
| Asperula cynanchica L. | Rub | 0.006 | H | TR | | 0.000 |
| Astragalus caprinus L. | Fab | 0.004 | H | NW | | 0.000 |
| Atractylis delicatula Batt. & Chev. | Com | 0.006 | T | FW | | 0.000 |
| Biscutella didyma L. | Cru | 0.002 | T | NW | | 0.000 |
| Boraginaceae | Bor | 0.005 | T | TR (NW) | | 0.000 |
| Bufonia tenuifolia ssp tenuifolia L. | Car | 0.041 | T | TR (NW) | | 0.000 |
| Calendula aegyptiaca Desf. | Com | 0.004 | T | FW | | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| Callipeltis cucullaria (L.) Stev | Rub | 0.001 | T | TR (NW) | 0.000 |
| Campanula filicaulis Durieu | Cam | 0.004 | H | NW (TR) | 0.000 |
| Capsella bursa-pastoris (L.) Medicus | Cru | 0.001 | T | SU | 0.000 |
| Carduncellus spec | Com | 0.026 | H | TR | 0.000 |
| Carum proliferum Maire | Umb | 0.002 | H | SU | 0.000 |
| Centaurea pungens Pomel. | Com | 0.003 | H | FW | 0.000 |
| cf Helianthemum | Cis | 0.002 | H | TR | 0.000 |
| Chenopodium ambrosioides L. | Che | 0.007 | T | SU | 0.000 |
| Cichoria spec | Com | 0.008 | H | TR (SU) | 0.000 |
| Cirsium cf syriacum (L.) Gaertn. | Com | 0.002 | T | SU | 0.000 |
| Cleome africana Boc. | Cap | 0.009 | T | FW | 0.000 |
| Crepis hookeriana Ball | Com | 0.004 | T | TR | 0.000 |
| Crucianella hirta Pomel. | Rub | 0.001 | T | NW | 0.000 |
| Ctenopsis cynosuroides (Desf.) R. Garcia | Poa | 0.009 | T | NW | 0.000 |
| Cynodon dactylon (L.) Pers. | Poa | 0.003 | H | FW | 0.000 |
| Dianthus cintranus Boiss. & Reuter | Car | 0.004 | CH | TR | 0.000 |
| Echinaria capitata (L.) Desf. | Poa | 0.013 | T | TR (NW) | 0.000 |
| Eryngium ilicifiolium Lam. | Umb | 0.003 | T | FW | 0.000 |
| Erysimum incanum ssp mairei (Sennen & Mauricio) Nieto Fel. | Cru | 0.002 | T | NW | 0.000 |
| Festuca  hystrix Boiss. | Poa | 0.011 | H | SU | 0.000 |
| Helianthemum ledifolium (L.) Miller | Cis | 0.007 | T | NW | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| Hippocrepis cf monticola Lassen | Fab | 0.005 | H | TR (NW) | 0.000 |
| Hohenackeria exscapa (Steven) Koso-Pol. | Umb | 0.007 | T | TR (NW) | 0.000 |
| Iberis sempervirens L. | Cru | 0.005 | CH | SU | 0.000 |
| Ifloga spicata (Forssk.) Sch. Bip. | Com | 0.002 | T | FW | 0.000 |
| Lamium amplexicaule L. | Lam | 0.005 | T | SU | 0.000 |
| Leysera leyseroides (Desf.) Maire | Com | 0.005 | T | FW (NW) | 0.000 |
| Liliaceae | Lil | 0.003 | GEO | TR (NW) | 0.000 |
| Linaria micrantha (Cav.) Hoffm. & Link | Scr | 0.003 | T | TR (NW) | 0.000 |
| Lomelosia stellata (L.) Raf. | Dip | 0.001 | T | TR | 0.000 |
| Lotus cf thomsonii Oliver | Fab | 0.010 | H | TR | 0.000 |
| Lotus eriosolen (Maire) Mader & Poslech | Fab | 0.002 | H | TR | 0.000 |
| Marrubium deserti (De Noé) Cosson | Lam | 0.003 | CH | FW | 0.000 |
| Oryzopsis caerulescens (Desf.) Richter | Poa | 0.002 | H | TR | 0.000 |
| Paronychia chlorothyrsa Murb. | Car | 0.023 | H | NW | 0.000 |
| Phagnalon spec | Com | 0.004 | H | TR | 0.000 |
| Picris hispanica (Willd.) P.D. Sell | Com | 0.027 | H | TR (NW) | 0.000 |
| Plantago afra L. | Pla | 0.005 | T | NW | 0.000 |
| Polycarpon polycarpoides (Biv.) Jahandiez & Maire | Car | 0.020 | H | TR | 0.000 |
| Polycnemum fontanesii Durieu & Moq. | Che | 0.002 | H | TR | 0.000 |
| Ranunculus falcatus ssp incurvus (Steven) Maire & Weiller | Ran | 0.005 | T | TR (NW) | 0.000 |
| Rochelia disperma (L. fil.) C. Koch | Bor | 0.004 | T | TR (NW) | 0.000 |

| | | | | | |
|---|---|---|---|---|---|
| Salvia verbenaca L. | Lam | 0.006 | H | TR | 0.000 |
| Sedum spec | Car | 0.002 | H | TR | 0.000 |
| Sideritis montana ssp ebracteata (Asso) Murb. | Lam | 0.003 | T | TR (NW) | 0.000 |
| Silene filipetala Litard. & Maire | Car | 0.009 | H | TR (NW) | 0.000 |
| Stipagrostis obtusa (Del.) Nees | Poa | 0.004 | H | FW | 0.000 |
| Taraxacum atlanticum Pomel | Com | 0.022 | H | SU | 0.000 |
| Telephium imperati L. | Car | 0.002 | H | TR | 0.000 |
| Teucrium musimonum Humbert | Lam | 0.009 | CH | TR | 0.000 |
| Urginea noctiflora Batt. & Trab. | Lil | 0.010 | GEO | FW | 0.000 |
| Veronica rosea Desf. | Scr | 0.013 | H | SU | 0.000 |

# 8 Synopsis

It seems that the description of drylands as an 'unappreciated gift' of nature is not only meant with regard to the inhabitants. From the scientific perspective dryland ecosystems have equally been disregarded. Many ecological concepts once developed for temperate regions have been successively applied on drylands and now emerge to be problematic (Behnke *et al.* 1993). Promising approaches of ecological indication, for example, often failed in highly stochastic environments (Prince *et al.* 1998; De Bello *et al.* 2005). The present work was assigned to test and evaluate currently discussed rangeland indicators in relation to a steep environmental gradient of arid and semiarid ecosystems in southern Morocco. It aimed to examine how the predictive value of (1) production and rain-use efficiency, (2) plant functional types, and (3) local knowledge as indicators depend on different levels of resource variability. The following sections will summarize pros and cons for each of the tested indicators and will give suggestions for their application. Afterwards, range conditions along the High Atlas transect are compared between the different indicator approaches.

## 8.1  Indicators put to the test

### 8.1.1 Biomass production (ANPP) and rain-use efficiency (RUE)

Since ANPP and RUE are easily measurable by remote sensing techniques and across broad spatial scales, they have become widely applied indicators for land degradation (Bai *et al.* 2008b). In this work ANPP and RUE were locally assessed by clipping experiments in order to critically evaluate their predictive value. The study revealed two potential sources of bias: (1) field studies comparing grazed and protected sites often underestimate ANPP at grazed sites due to measuring artefacts, which leads to the identification of 'threatened areas' that are not affected by long-term degradation but rather exposed to high grazing pressure. (2) ANPP measured by remote sensing and thus RUE are lumped parameters that may be low as a result of a reduction of vegetation density (temporarily high grazing pressure), of altered soil conditions such as reduced water-holding capacity, and of naturally occurring gradients in standing crop. For example, vegetation on sandy soils is not necessarily more degraded than vegetation on loamy soils, it only shows lower ANPP and RUE because of unfavourable

conditions of soil water availability. Hence, it is suggested to differentiate between ANPP/RUE indicating the actual range condition and $ANPP_{rel}/RUE_{rel}$ indicating long-term degradation processes. ANPP and RUE help to state the actual range condition by quantifying the supply of the ecosystem good 'forage'. But they are not likely to draw conclusions about the causes of low forage supply. For that, $ANPP_{rel}$ and $RUE_{rel}$ are more suitable since they are not biased by differences in initial standing crop. A comparison between ANPP/RUE and $ANPP_{rel}/RUE_{rel}$ can detect whether forage supply at a site is low because of low vegetation density (often reversible) or because of a declined ability of individual plants or the plant community to produce biomass (often irreversible). It is the difference between production and productivity or the difference between the interest and the interest rate of the capital.

Summarizing, ANPP and RUE were found to react on a shorter time scale than $ANPP_{rel}/RUE_{rel}$. All parameters are technically applicable up to the regional scale. However, they are strongly influenced by local and short-term differences of grazing pressure, soil, and the amount of initial biomass (Le Houérou *et al.* 1988; Allcock & Hik 2003; Wiegand *et al.* 2004; Blanco 2008). To make use of these indicators and the great advantages of remote sensing, I thus suggest to use ANPP and RUE only in combination with local field studies. These may be conducted in limited key areas to quantify the impact of actual grazing pressure, plant-soil interactions, and the effect of local differences in initial biomass. Grazing pressure can be locally quantified as percent of 'consumed production' and included in form of a correction factor for the ANPP values measured by remote sensing (Brenner 2009). Soil effects can be statistically removed, if local changes in soil conditions are quantified. ANPP is related to the initial biomass of an ecosystem like the interest to the capital (Begon *et al.* 2006). To face the effect of changes in initial biomass, this work proposed to use $ANPP_{rel}$ and $RUE_{rel}$ in addition to ANPP and RUE to describe and compare different aspects of range condition.

## 8.1.2 Plant functional types (PFT)

One of the initial goals of PFT research was getting simple ecological indicators independent from the species level and thus applicable by a broad public and on a larger spatial scale (McIntyre *et al.* 1995; Friedel 1997; Landsberg *et al.* 1999;

Ansquer *et al.* 2009). In the present work, response groups and response traits were identified as indicators for grazing impact along an aridity gradient in the High Atlas Mountains. The study showed that such indicators are limited to the local scale, since changes in the variability of resources (here water) and grazing impact provoked similar plant adaptations (Coughenour 1985; Milchunas *et al.* 1988). Thus, huge differences have been observed, for example between plant traits indicating high grazing pressure in semidesert ecosystems versus mountain ecosystems.

Response groups and response traits are indicators that react on a longer time scale than ANPP or RUE (Niemi & McDonald 2004). Since their predictive value was strongly influenced by resource stochasticity, these indicators are in my opinion unreliable for range assessment in arid and semiarid ecosystems. The application should be limited to the local scale. However, this is contradictory to the original aims of PFT research.

## 8.1.3 Local ecological knowledge

Since local herdsmen have means or criteria to assess the condition of potential pastures, their local ecological knowledge has an indicative value that is worth to access for scientific purposes (Fernandez-Gimenez 2000; Angassa & Oba 2008; Reed *et al.* 2008). Direct comparisons, however, have rarely been made because there was a lack of methods matching ecological data with data on herdsmen's knowledge which has often been assessed by anthropologists. The present work explicitly makes use of local ecological knowledge of the *Ait Toumert* herdsmen on forage plants and discovers that the 'reliability' of plants and pastures functions as a kind of local indicator (see section 7.4.1).

Compared to ANPP and plant functional types, one major advantage of the 'reliability'-concept is its integrative character on spatial and temporal scales. A single plant species can be valued as 'reliable', because it is long-perennial, buffers rainfall variability and thus represents a 'reliable' forage resource even in times of forage scarcity. But also whole pastures can be considered as 'reliable' if they contain many of 'reliable' plant species and/or plants in a good condition (vitality). Since the 'reliability' of plants was linked to the plant's life form, this study confirmed the significance of a very new method quantifying one aspect of

local knowledge and linking it to ecological research (Eisold *et al.* 2009). However, additional studies are necessary to question what factors other than ecological ones influence the 'reliability' of plants and pastures in the local view. There is some evidence that further utilization purposes such as fire wood or medical use may play a role as well as the toxicity of certain plants (IAV 2002; IAV 2003).

## 8.2  Rangeland condition in the area

Despite this work focused on methodological issues, the following section aims to shortly summarize and compare the results of the indicator approaches presented. Note that results are derived from point information gathered in the pasture areas close to the IMPETUS climate stations. I caution against a spatial extrapolation of these data. Tab. 8.1 shows an overview of the results presented in the chapters 5 to 7.

**Tab. 8.1** Range condition according to the indicators applied in the presented work. For each approach information is limited to plot samples assessed at grazed sites close the IMPETUS climate stations, which approximately stretched across an area of 1 to 5 ha depending on the applied methods (see section 5.2.2 for ANPP/RUE/ANPPrel/RUErel approach, section 6.2.3 for PFT approach, and section 7.2.2 for local knowledge approach). Note that results are not absolute, but represent range condition in relation to that of the nearby grazing exclosure (see chapter 1.3.2.1).

| Altitudinal level | Type of indicator | | | |
|---|---|---|---|---|
| | ANPP & RUE | $ANPP_{rel}$ & $RUE_{rel}$ | PFT | Local knowledge |
| Hammada semidesert (1,380 m a.s.l.) | no measurable decline in forage supply | degraded | no measurable grazing impact | least reliable pastures |
| Artemisia steppe (1,870 m a.s.l.) | great decline in forage supply | degradation not measurable | little grazing impact | medium reliable pastures |
| Juniperus woodsteppe (2,250 m a.s.l.) | little decline in forage supply | degradation not measurable | medium grazing impact | medium reliable pastures |
| Oromediterranean shrubland (2,960 m a.s.l.) | little decline in forage supply | degradation not measurable | no measurable grazing impact | most reliable pastures |

For each approach, the pasture condition refers to the condition inside a seven years grazing exclosure on the same pasture type, i.e. the location under the most favourable conditions and which was comparable with respect to abiotic site conditions. The grazing exclosure thus served as a benchmark (see chapter 2.1). Most of the approaches identify oromediterranean shrubland pastures to be most reliable or in good condition (Tab. 8.1). This might either reflect less intensive grazing pressure or - on the contrary - that regeneration processes take too long as to be detected within seven years of grazing exclosure. Further, semidesert pastures were identified to be least reliable or degraded by two types of indicators. Apart of these common aspects, the applied indicator approaches differ significantly in their results. The PFT approach, for example, indicates the most obvious grazing impact at *Juniperus* woodsteppe pastures, little impact on *Artemisia* steppe pastures, and no measurable differences between exclosures and grazed sites at semidesert and shrubland pastures. Differences in the results between the ANPP/RUE and the $ANPP_{rel}$/$RUE_{rel}$ approach are most interesting. For example, *Artemisia* steppe pastures are identified to show the most obvious decline in forage supply (ANPP) compared to the nearby grazing exclosures. However, degradation in the sense of reduced productivity of the site ($ANPP_{rel}$) could not be detected (see section 8.1.1).

Summarizing, $ANPP_{rel}$ and $RUE_{rel}$ were the least sensitive indicators. They reacted slower than ANPP and RUE. Since ANPP, RUE, $ANPP_{rel}$, and $RUE_{rel}$ all showed high variability on the local scale, they are more likely to be applied on the regional scale, for example to compare range conditions between different altitudinal levels. PFT indicators were limited to the local scale and showed less variability than ANPP between the sampled plots. PFTs are most suitable to detect differences in grazing impact within one ecosystem, but not to compare range conditions between different systems. The 'reliability' concept as integrative approach is not limited to a certain spatial scale. However, in this work a regional gradient of 'reliability' along the High Atlas slopes was shown quantifying the change in ANPP of perennial plant species.

## 8.3   In short - what is new?

This work represents a substantial progress for the debate on ecological indicators in drylands since it contributes four major aspects.

First, ANPP$_{rel}$ and RUE$_{rel}$ are newly introduced parameters to indicate range condition on large spatial scales. Depending on research question, i.e. whether one is interested in the actual supply of forage resources or to detect areas affected by long-term degradation processes, it is suggested to use ANPP and RUE for the first purpose or ANPP$_{rel}$ and RUE$_{rel}$ for the second purpose. ANPP$_{rel}$ and RUE$_{rel}$ are complementary or even more appropriate indicators to detect range degradation, because they are not biased by regional differences in standing crop (see section 8.1.1).

Second, the application of response groups and response traits was shown to be locally limited, since grazing and stochasticity of resources had similar impacts on plant characteristics. If these indicators are applied along gradients of resource stochasticity, i.e. across arid and semiarid ecosystems, it is no longer possible to separate between the two impacts and see grazing as the sole trigger of plant traits.

Third, a part of the local knowledge of herdsmen was quantified and thus prepared to be contrasted to ecological data. This led to the integrative concept of 'reliability'. The 'reliability' of plants and pastures is a new local indicator and assessable by either anthropological or ecological methods.

Forth, it is emphasized that indicators have to be combined in order to achieve a detailed and credible range assessment. Particularly indicators operating on different hierarchical levels are suitable to fulfil this task. While indicators using species, functional groups or traits may provide detailed information within an ecosystem, production-dependent indicators such as ANPP and RUE allow comparisons across ecosystems. It is a challenge for the future to combine the right indicators to monitoring systems, which provide appropriate scientific information for management decisions on different hierarchical levels (Niemi & McDonald 2004; Danz *et al.* 2005).

## 8.4 Benefit and application of results

Results of the presented work, in particular those of the first section, provide input for related studies such as a remote sensing approach in the same region (Fritzsche 2009). The vegetation model MOVEG-DRÂA, which aims to describe vegetation dynamics for the whole Drâa catchment, is currently under construction. On the base of NDVI time series (see section 1.3.2.2) and data on abiotic site conditions, it provides two-dimensional information with a resolution

of 250 m on the past, present, and future condition of the vegetation. In particular, it calculates vegetation cover, biomass production (ANPP), and the leaf area index (LAI). By means of climate scenarios these parameters may be projected for the southern Moroccan region until 2050. The results of the presented work are the main source of ground trith data for standing crop and ANPP that are available for this area. They are used to calibrate model functions that transform NDVI data into ANPP. Additionally results are used for a final validation of the model results. MOVEG-DRÂA will be finished in 2009 and results will be presented in form of a dissertation by Pierre Fritzsche, Geographical Institute, Bonn (Germany).

Together with anthropological information about the Ait Toumert and their herd management (Kemmerling 2008), this work builds the database for the grazing model BUFFER. The ecological-economic model treats the concept of key resource areas (Illius & O'Connor 2000) which are crucial for the sustainability of pastoral systems on the regional scale, because they provide reliable forage for livestock. Taking the Ait Toumert as a good-practise example, it is asked how pastoral nomadic range management strategies influence local key resources (Drees *et al.* 2009). This work contributes to the model in two different ways: It first provides the initial condition of pastures in the research area, a kind of starting point for the model. Second, it contributes functional relationships between plants, grazing herbivores, rainfall, and biomass production that result in rules driving the model. For example, the rain-use efficiency is used to quantify how plant growth of different life forms is altered by grazing impact. Modeling is still in progress and will provide first results in 2010 (for the conceptual framework see (Drees *et al.* 2009)).

Arid and semiarid ecosystems are highly complex. Thus it is promising to address selected questions of range ecology to ecological models, not in order to rebuild the reality, but to understand functional relationships between the biotic and abiotic actors in rangeland systems (Wiegand *et al.* 2000; Tews *et al.* 2006; Jeltsch *et al.* 2008). Ecological models treating plant populations have become crucial for research as well as for policy-makers, particularly because they are able to predict the impact of environmental changes on the ecosystem good 'forage'. In doing so, they need empirical information, first to be included as rules and parameters into the model and second as independent data for validation

purposes (Clark *et al.* 2001). However, many ecological models suffer a lack of appropriate information. In the case of the presented work, research was planed from the outset for the application in an ecological model. For example, all data assessment followed a full-factorial design treating the interplay between resource-dependencies and grazing impact. The study was restricted to a single group of land users. Vegetation composition was not only investigated on the species level, but described by functional assemblages of plants (PFT, life forms). There was a close collaboration with remote sensing research in order to extrapolate point information (plots) to the two-dimensional scale. These strategies help to provide adequate empirical information which is easy to introduce into an ecological model and functional relations that can be transformed in mathematical rules.

## 8.5 Future prospects

This thesis aimed a functional understanding of ecological indicators and their use in semiarid ecosystems. I succeeded to evaluate three recently applied rangeland indicators in southern Morocco and contributed new aspects concerning their applicability (section 8.3). However, this work won't finish without some suggestions for future investigations.

Since several disciplines worked together in southern Morocco in the context of the IMPETUS project, it would be promising to prepare an interdisciplinary view on rangelands in the region. Maps of potential rangeland classifications could for example be achieved. It would be interesting to compare between a meteorological classification (according to the variability of rainfall), an ecological classification (following the PFT composition), a classification according to the NDVI signal, and a classification made by local land users (reliability).

Additional application of $ANPP_{rel}$ and $RUE_{rel}$ in other dryland areas seems a promising goal to test this new rangeland indicator on large spatial scales. In the future it is generally crucial to further investigate ecological indicators, their sensitivity and their reliability in drylands (Dregne 2002; MEA 2005). There is a need for reliable indicators stating the present and the future supply of food, forage, fuel, and fibre (Daily *et al.* 1997; Daily 1997), particularly in dryland zones where climate and land use change tremendously alter the capacity of ecosystems to provide these goods and services (Safriel & Adeel 2005;

UNDP 2008). Gradients of aridity, such as they are found in most of the mediterranean climate zones of the earth, are particularly suitable to test the predictability of ecological indicators in relation to changing natural variability (Scholes *et al.* 2002; Blanco 2008; Bai *et al.* 2008a). In the context of rapid climate and land use change we cannot afford further debates which environmental changes in the past have been of anthropogenic and which of natural origin. We need sensitive and reliable indicators that are able to separate between the two. They will surely help to detect precarious changes in our environment - which is the basis for sustainable management decisions in the future.

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# References

Abdelmagid, A. H., Trlica, M. J. & Hart, R. H. (1987). Soil and vegetation responses to simulated trampling. *Journal of Range Management*, 40, 303-306.

Adams, B. (2004). African savannas: Global narratives and local knowledge of environmental change. *African Affairs*, 103, 690-692.

Adler, P. B., Milchunas, D. G., Lauenroth, W. K., Sala, O. E. & Burke, I. C. (2004). Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology*, 41, 653-663.

Adler, P. B. & Hall, S. A. (2005). The development of forage production and utilization gradients around livestock watering points. *Landscape Ecology*, 20, 319-333.

Adler, P. B., Milchunas, D. G., Sala, O. E., Burke, I. C. & Lauenroth, W. K. (2005). Plant traits and ecosystem grazing effects: comparison of US sagebrush steppe and Patagonian steppe. *Ecological Applications*, 15, 774-792.

Adriansen, H. K. (2005). Pastoral mobility: a review. *Nomadic Peoples*, 9, 207-214.

Agrawal, A. A. (2000). Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends in Plant Science*, 5, 309-313.

Aguiar, M. R., Paruelo, J. M., Sala, O. E. & Lauenroth, W. K. (1996). Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe. *Journal of Vegetation Science*, 7, 381-390.

Albon, S. D., Brewer, M. J., O'Brien, S., Nolan, A. J. & Cope, D. (2007). Quantifying the grazing impacts associated with different herbivores on rangelands. *Journal of Applied Ecology*, 44, 1176-1187.

Alhamad, M. N. & Alrababah, M. A. (2008). Defoliation and competition effects in a productivity gradient for a semiarid mediterranean annual grassland community. *Basic and Applied Ecology*, 9, 224-232.

Allcock, K. G. & Hik, D. S. (2003). What determines disturbance-productivity-diversity relationships? The effect of scale, species and environment on richness patterns in an Australian woodland. *Oikos*, 102, 173-185.

Anadón, J. D., Giménez, A., Ballestar, R. & Pérez, I. (2009). Evaluation of local ecological knowledge as a method for collecting extensive data on animal abundance. *Conservation Biology*, in press.

Angassa, A. & Oba, G. (2008). Herder perceptions on impacts of range enclosures, crop farming, fire ban and bush encroachment on the rangelands of Borana, Southern Ethiopia. *Human Ecology*, 36, 201-215.

Ansquer, P., Duru, M., Theau, J. P. & Cruz, P. (2009). Functional traits as indicators of fodder provision over a short time scale in species-rich grasslands. *Annals of Botany*, 103, 117-126.

Archibald, S., Bond, W. J., Stock, W. D. & Fairbanks, D. H. K. (2005). Shaping the landscape: Fire-grazer interactions in an African savanna. *Ecological Applications*, 15, 96-109.

Aronson, J. (1993). Restoration, rehabilitation of degraded ecosystems in arid and semi-arid lands. *Restoration Ecology*, 8-17.

Augustine, D. J. (2003). Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem. *Plant Ecology*, 167, 319-332.

Austin, A. T., Yahdjian, L., Stark, J. M., Belnap, J., Porporato, A., Norton, U., Ravetta, D. A. & Schaeffer, S. M. (2004). Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, 141, 221-235.

Bai, Y., Wu, J., Xing, Q., Pan, Q., HUANG, J., Yang, D. & Han, X. (2008). Primary production and rain use efficiency across a precipitation gradient on the Mongolia Plateau. *Ecology*, 89, 2140-2153.

Bai, Z. G. & Dent, D. L. (2006). Global assessment of land degradation and improvement: Pilot study in Kenya. *ISRIC - World Soil Information* Wageningen, Netherlands.

Bai, Z. G., Dent, D. L., Olsson, L. & Schaepman, M. E. (2008). Global assessment of land degradation and improvement. 1. Identification by remote sensing. *ISRIC - World Soil Information* Wageningen, Netherlands.

Barbour, M. G. Ecological patterns in the physiological ecology of desert shrub Larrea divaricata. 1967. Duke University, Durham, USA.
Ref Type: Thesis/Dissertation

Barrera-Bassols, N., Zinck, J. A. & Van Ranst, E. (2006). Symbolism, knowledge and management of soil and land resources in indigenous communities: Ethnopedology at global, regional and local scales. *CATENA*, 65, 118-137.

Barrow, C. J. & Hicham, H. (2000). Two complimentary and integrated land uses of the western High Atlas Mountains, Morocco: The potential for sustainable rural livelihoods. *Applied Geography*, 20, 369-394.

Bazot, S., Mikola, J., Nguyen, C. & Robin, C. (2005). Defoliation-induced changes in carbon allocation and root soluble carbon concentration in field-grown Lolium perenne plants: do they affect carbon availability, microbes and animal trophic groups in soil? *Functional Ecology*, 19, 886-896.

Beever, E. A., Tausch, R. J. & Brussard, P. F. (2003). Characterizing grazing disturbance in semiarid ecosystems across broad scales, using diverse indices. *Ecological Applications*, 13, 119-136.

Begon, M., Townsend, C. R. & Harper, J. L. (2006). *Ecology - from individuals to ecosystems*. Oxford, UK: Blackwell Publishing.

Behnke, R. H., Scoones, I. & Kerven, C. (1993). *Range ecology at disequilibrium - new models of natural variability and pastoral adaption in African savannas*. London, UK: Overseas Development Institute.

Behnke, R. H. & Scoones, I. (1993). Rethinking range ecology: Implications for rangeland management in Africa. In R. Behnke, I. Scoones & C. Kerven (Eds) *Range ecology at*

*disequilibrium - new models of natural variability and pastoral adaption in African savannas* (pp. 1-30). London: Overseas Development Institute.

Beloud, A. (2002). Plantes Sahariennes.

Belsky, A. J. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science,* 3, 187-200.

Benabid, A. & Fennane, M. (1994). Connaissances sur la végétation du Maroc: Phytogéographie, phytosociologie et séries de végétation. *Lazaroa,* 14, 21-97.

Benabid, A. (2000). *Flore et écosystèmes du Maroc: Évaluation et préservation de la biodiversité.* Paris, France: Ibis Press.

Bennana, A. (2004). La toponymie amazighe en Afrique du Nord.

Berkes, F., Kislalioglu, M., Folke, C. & Gadgil, M. (1998). Exploring the basic ecological unit: ecosystem-like concepts in traditional societies. *Ecosystems,* 1, 409-415.

Berkes, F., Colding, J. & Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications,* 10, 1251-1262.

Bester, F. V., Van Eck, J. A. J., Kölling, H. & Van Rooyen, B. (2003). The influence of stocking rate on the distribution of individual grass species in the sward. *Spotlight on Agriculture,* 74, 1-2.

Blanco, L. J. (2008). Grazing effect on NDVI across an aridity gradient in Argentina. *Journal of Arid Environments,* 72, 764-776.

Boer, M. & Smith, M. S. (2003). A plant functional approach to the prediction of changes in Australian rangeland vegetation under grazing and fire. *Journal of Vegetation Science,* 14, 333-344.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Medany, M., Osman-Elasha, B., Tabo, R. & Yanda, P. (2007). Africa. In M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. Van der Linden & C. E. Hanson (Eds) *Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel of climate change* (pp. 433-467). Cambrigde, UK: Cambridge University Press.

Bollig, M. & Göbel, B. (1997). Risk, uncertainty and pastoralism: An introduction. *Nomadic Peoples,* 1, 5-21.

Bollig, M. & Schulte, A. (1999). Environmental change and pastoral perceptions: degradation and indigenous knowledge in two African pastoral communities. *Human Ecology,* 27, 493-514.

Bonan, G. B., Levis, S., Kergoat, L. & Oleson, K. W. (2002). Landscapes as patches of plant functional types: An integrating concept for climate and ecosystem models. *Global Biogeochemical Cycles,* 16, 1-30.

Borgatti, S. (1999). Elicitation techniques for cultural domain analysis. In J. Schensul, M. LeCompte, B. K. Nastasi & S. Borgatti (Eds) *Enhanced ethnographic methods: Audiovisual*

*techniques, focused group interviews, and elicitation techniques* (pp. 115-151). Walnut Creek, USA: AltaMira Press.

Born, K., Fink, A. H. & Paeth, H. (2008). Dry and wet periods in the northwestern Maghreb for present day and future climate conditions. *Meteorologische Zeitschrift*, 17, 533-551.

Born, K., Piecha, K. & Fink, A. (2008). Shifting climate zones in the northwestern Maghreb. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research Results 2000-2007* (pp. 13-14). Department of Geography, University of Bonn, Germany.

Boyd, J. & Banzhaf, S. (2007). What are ecosystem services? The need for standardized environmental accounting units. *Ecological Economics*, 63, 616-626.

Breckenridge, R. P., Kepner, W. G. & Mouat, D. A. (1995). A process for selecting indicators for monitoring conditions of rangeland health. *Environmental Monitoring and Assessment*, 36, 45-60.

Brenner, J. Ecological indicators for grazing pressure and degradation in drylands: Lessons from two arid pastures in southern Morocco. 2009. Cologne, Germany, University of Cologne, Botanical Institute.
Ref Type: Thesis/Dissertation

Breshears, D. D. & Barnes, F. J. (1999). Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: A unified conceptual model. *Landscape Ecology,* 14, 465-478.

Breuer, I. (2007). Livelihood security and mobility in the High Atlas Mountains. In J. Gertel & I. Breuer (Eds) *Pastoral Morocco: globalizing scapes of mobility and insecurity* (pp. 165-179). Wiesbaden, Germany: Reichert.

Briske, D. D. & Richards, J. F. (1995). Plant responses to defoliation: A physiological, morphological and demographic evaluation. In D. Bedunah & R. E. Sosebee (Eds) *Wildland Plants: Physiological Ecology and Developmental Biology* (pp. 635-710). Denver, USA: Society for Range Management.

Briske, D. D. (1996). Strategies of plant survival in grazed systems: A functional interpretation. In F. D. I. Hodgson & A. W. Illius (Eds) *The ecology and management of grazed systems* (pp. 37-67). Wallingford, UK: CAB International.

Brook, R. K. & McLachlan, S. M. (2008). Trends and prospects for local knowledge in ecological and conservation research and monitoring. *Biodiversity and Conservation,* 17, 3501-3512.

Buckland, S. T., Magurran, A. E., Green, R. E. & Fewster, R. M. (2005). Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 243-254.

Bullock, J. M., Franklin, J., Stevenson, M. J., Silvertown, J., Coulson, S. J., Gregory, S. J. & Tofts, R. (2001). A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, 38, 253-267.

Burke, I. C., Lauenroth, W. K., Vinton, M. A., Hook, P. B., Kelly, R. H., Epstein, H. E., Aguiar, M. R., Robles, M. D. & Aguilera, M. O. (1998). Plant-soil interactions in temperate grasslands. *Biogeochemistry*, 42, 121-143.

Byers, B., Cunliffe, R. & Hudak, A. (2001). Linking the conservation of culture and nature: A case study of sacred forests in Zimbabwe. *Human Ecology*, 29, 187-218.

Cadotte, M. & Fukami, T. (2005). Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecology Letters*, 8, 548-557.

Callaway, R. M., Pennings, S. C. & Richards, C. L. (2003). Phenotypic plasticity and interactions among plants. *Ecology*, 84, 1115-1128.

Camou-Guerrero, A., Reyes-Garcia, V., Martinez-Ramos, M. & Casas, A. (2008). Knowledge and use value of plant species in a Rarámuri community: A gender perspective for conservation. *Human Ecology*, 36, 259-272.

Carignan, V. & Villard, M. A. (2002). Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment*, 78, 45-61.

Carpenter, S. R. (2001). From metaphor to measurement: Resilience of what to what? *Ecosystems*, 4, 765-781.

Cavallar, W. Esquisse préliminaire de la carte des sols du Maroc. 1950. Rabat, Morocco, Direction de l'Agriculture, du Commerce et des Forêts du Maroc. Division de l'Agriculture et de l'Elevage.
Ref Type: Map

Chalmers, N. & Fabricius, C. (2007). Expert and generalist local knowledge about land-cover change on South Africa's wild coast: can local ecological knowledge add value to science? *Ecology and Society*, 12, 10-[online] URL: http://www.ecologyandsociety.org/vol12/iss1/art10/.

Chambers, R. (1994). Participatory rural appraisal (PRA): Analysis of experience. *World Development*, 22, 1253-1268.

Chapin III, F. S. (1993). Functional role of growth forms in ecosystem and global processes. In J. R. Ehleringer & C. B. Field (Eds) *Scaling physiological processes: Leaf to globe* (pp. 287-312). San Diego, USA: Academic Press.

Chesson, P., Gebauer, R. L. E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M. S. K., Sher, A., Novoplansky, A. & Weltzin, J. F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236-253.

CIA (2009). CIA - the world factbook: Morocco.

Cingolani, A. M., Posse, G. & Collantes, M. B. (2005). Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology*, 42, 50-59.

Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M., Pascual, M., Pielke, R., Jr., Pizer, W., Pringle, C., Reid, W. V., Rose, K. A., Sala, O., Schlesinger, W. H., Wall, D. H. & Wear, D. (2001). Ecological forecasts: An emerging imperative. *Science*, 293, 657-660.

Coley, P. D., Bryant, J. P. & Chapin III, F. S. (1985). Resource availability and plant antiherbivore defense. *Science,* 230, 895-899.

Cooper, S. M. & Owen-Smith, N. (1986). Effects of plant spinescence on large mammalian herbivores. *Oecologia,* 68, 446-455.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Ter, Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G. & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany,* 51, 335-380.

Coughenour, M. B. (1985). Graminoid responses to grazing by large herbivores: Adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden,* 72, 852-863.

Cousins, S. A. O. & Lindborg, R. (2004). Assessing changes in plant distribution patterns - indicator species versus plant functional types. *Ecological Indicators,* 4, 17-27.

Craine, J. M. (2005). Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology,* 93, 1041-1052.

Cunningham, A. B. (1992). The role of ethnobotany and indigenous knowledge in conservation of plant genetic resources. *Dinteria,* 23, 119-131.

Daily, G., Alexander, S., Ehrlich, P. R., Goulder, L., Lubchenco, J., Matson, P. A., Mooney, H. A., Postel, S., Schneider, S. H. & Woodwell, G. M. (1997). Ecosystem services: Benefits supplied to human societies by natural ecosystems. *Issues in Ecology,* 2, 1-18.

Daily, G. C. (1997). *Nature's services: societal dependence on natural ecosystems.* Washington, D.C., USA: Island Press.

Dale, V. H. & Beyeler, S. C. (2001). Challenges in the development and use of ecological indicators. *Ecological Indicators,* 1, 3-10.

Danz, N. P., Regal, R. R., Niemi, G. J., Brady, V. J., Hollenhorst, T., Johnson, L. B., Host, G. E., Hanowski, J. M., Johnston, C. A., Brown, T., Kingston, J. & Kelly, J. R. (2005). Environmentally stratified sampling design for the development of Great Lakes environmental indicators. *Environmental Monitoring and Assessment,* 102, 41-65.

Darkoh, M. B. K. (2003). Regional perspectives on agriculture and biodiversity in the drylands of Africa. *Journal of Arid Environments,* 54, 261-279.

Davies, J. & Hatfield, R. (2007). The economics of mobile pastoralism: A global summary. *Nomadic Peoples,* 11, 91-116.

Davis, D. K. (2005). Indigenous knowledge and the desertification debate: problematising expert knowledge in North Africa. *Geoforum,* 36, 509-524.

De Bello, F., Leps, J. & Sebastia, M. T. (2005). Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology,* 42, 824-833.

de Bruijn, M. E. & van Dijk, H. J. W. M. (1999). Insecurity and pastoral development in the Sahel. *Development and Change,* 30, 115-139.

De la Maza, M., Lima, M., Meserve, P. L., Gutiérrez, J. R. & Jaksic, F. (2009). Primary production dynamics and climate variability: ecological consequences in semiarid Chile. *Global Change Biology,* 15, 1116-1126.

Diaz, S., Cabido, M., Zak, M., Carretero, E. M. & Aranibar, J. (1999). Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science,* 10, 651-660.

Diaz, S., Noy-Meir, I. & Cabido, M. (2001). Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology,* 38, 497-508.

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Marti, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., bbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science,* 15, 295-304.

Diouf, A. & Lambin, E. F. (2001). Monitoring land-cover changes in semi-arid regions: Remote sensing data and field observations in the Ferlo, Senegal. *Journal of Arid Environments,* 48, 129-148.

Díaz, S. & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science,* 8, 463-474.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, L., Clark, A. & Campbell, B. M. (2007). Plant trait responses to grazing - a global synthesis. *Global Change Biology,* 13, 313-341.

Dougill, A. J., Thomas, D. S. G. & Heathwaite, A. L. (1999). Environmental change in the Kalahari: Integrated land degradation studies for nonequilibrium dryland environments. *Annals of the Association of American Geographers,* 89, 420-442.

Drees, R., Kemmerling, B., Baumann, G., Müller, B., Frank, K. & Linstädter, A. Lessons learned from transhumant pastoralism: the role of key resources in a heterogeneous environment. Transformation, Innovation and Adaptation for Sustainability - Integrating Natural and Social Sciences. 2009. 29-6-2009.
Ref Type: Conference Proceeding

Drees, R., Baumann, G. & Linstädter, A. How can pastoralists mitigate drought effects? IMPETUS Africa Conference, Cologne (Germany). 2009.
Ref Type: Conference Proceeding

Dregne, H. E. (2002). Land degradation in the drylands. *Arid Land Research and Management,* 16, 99-132.

Duckworth, J. C., Kent, M. & Ramsay, P. M. (2000). Plant functional types: An alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography,* 24, 515-542.

Dyksterhuis, E. J. (1949). Condition and management of range land based on quantitative ecology. *Journal of Range Management*, 2, 104-115.

Eisold, J., Tönsjost, S. & Linstädter, A. (2009). Towards a synthesis of local and scientific knowledge on ecological items: An interdisciplinary framework. *Human Ecology*.

Ellis, J. E. (1994). Climate variability and complex ecosystem dynamics: Implications for pastoral development. In I. Scoones (Ed) *Living with uncertainty. New directions in pastoral development in Africa* (pp. 37-46). London.

Emberger, L. (1930). Sur une formule applicable en géographie botanique. *Cah.Herb.Seanc.Acad.Sci.*, 191, 389-390.

Emberger, L. (1939). Apercu général sur la végetation du Maroc. *Veröffentlichungen des Geobotanischen Instituts, Eidgenössische Technische Hochschule Rübel in Zürich*, 14, 40-157.

Enfors, E. I. & Gordon, L. J. (2007). Analysing resilience in dryland agro-ecosystems: A case study of the Makanya catchment in Tanzania over the past 50 years. *Land Degradation & Development*, 18, 680-696.

English, N. B., Weltzin, J. F., Fravolini, A., Thomas, L. & Williams, D. G. (2005). The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments*, 63, 324-343.

Ennih, N. & Liégeois, J.-P. (2008). *The boundaries of the West African Craton*. London, UK: Geological Society London.

Enriques-Barroso, A. & Gómez Campo, C. (1991). Les plantes endémiques de l'Afrique du Nord-Ouest: Algérie, Maroc et Tunisie. *Botanika Chronika*, 10, 517-520.

Evans, J. & Geerken, R. (2004). Discrimination between climate and human-induced dryland degradation. *Journal of Arid Environments*, 57, 535-554.

Ewing, M. A. (1999). Annual pasture legumes: A vital component stabilizing and rehabilitating low-rainfall Mediterranean ecosystems. *Arid Soil Research and Rehabilitation*, 13, 327-342.

Faber, M., Frank, K., Klauer, B., Manstetten, R., Schiller, J. & Wissel, C. (2005). On the foundation of a general theory of stocks. *Ecological Economics*, 55, 155-172.

Fazey, I., Proust, K., Johnson, B. & Fazey, J. A. (2006). Eliciting the implicit knowledge and perceptions of on-ground conservation managers of the Macquarie Marshes. *Ecology and Society*, 11, 25-[online] URL: http://www.ecologyandsociety.org/vol11/iss1/art25/.

Fennane, M., Benabid, A., Ibn Tattou, M., Bennig, O., El Alaoui Faris, F. E., El Qualidi, J., Guemmouh, R., Habboury, A., Hormat, K., Jury, S. L., Mathez, J., Navarro, T., Ouyahya, A., Raynaud, Ch., Rejdali, J., Tahiri, H. & Upson, T. Flore pratique du Maroc - manuel de détermination des plantes vasculaires: Pteridophyta, Gymnospermae, Angiospermae (Lauraceae-Neuradaceae). Fennane, M., Ibn Tattou, M., Ouyahya, A., and El Oualidi, J. [1], 1-558. 1999. Agdal, Rabat, Morocco, Institut Scientifique, Université Mohammed V. Travaux de l'Institut Scientifique, Série Botanique, n° 38.
Ref Type: Serial (Book,Monograph)

Fennane, M., Benabid, A., Ibn Tattou, M., Bennig, O., El Alaoui Faris, F. E., El Qualidi, J., Guemmouh, R., Habboury, A., Hormat, K., Jury, S. L., Mathez, J., Navarro, T., Ouyahya,

X

A., Raynaud, Ch., Rejdali, J., Tahiri, H. & Upson, T. Flore pratique du Maroc - manuel de détermination des plantes vasculaires: Angiospermae (Leguminosae-Lentibulariaceae). Fennane, M., Ibn Tattou, M., Ouyahya, A., and El Oualidi, J. [2], 1-636. 2007. Agdal, Rabat, Morocco, Institut Scientifique, Université Mohammed V. Travaux de l'Institut Scientifique, Série Botanique, n° 38.
Ref Type: Serial (Book,Monograph)

Fernandez-Gimenez, M. E. (2000). The role of Mongolian nomadic pastoralists' ecological knowledge in rangeland management. *Ecological Applications,* 10, 1318-1326.

Finckh, M. & Poete, P. (2008). Vegetation map of the Drâa basin. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research results 2000-2007* (pp. 31-32). Bonn, Germany: Department of Geography, University of Bonn.

Firincioglu, H. K., Seefeldt, S. S. & Sahin, B. (2007). The effects of long-term grazing exclosures on range plants in the central Anatolian region of Turkey. *Environmental Management,* 39, 326-337.

Flombaum, P. & Sala, O. E. (2007). A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments. *Journal of Arid Environments,* 69, 352-358.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005). Global consequences of land use. *Science,* 309, 570-574.

Ford, J. & Martinez, D. (2000). Traditional ecological knowledge, ecosystem science, and environmental management. *Ecological Applications,* 10, 1249-1250.

Franklin, D., Petty, A., Williamson, G., Brook, B. & Bowman, D. (2008). Monitoring contrasting land management in the savanna landscapes of northern Australia. *Environmental Management,* 41, 501-515.

Friedel, M. H. (1991). Range condition assessment and the concept of thresholds - a viewpoint. *Journal of Range Management,* 44, 422-426.

Friedel, M. H. (1997). Discontinuous change in arid woodland and grassland vegetation along gradients of cattle grazing in central Australia. *Journal of Arid Environments,* 37, 145-164.

Fritzsche, P. Development of a mesoscale, satellite supported empirical model estimating vegetation dynamics inside Drâa-valley (South Morocco). 2009. Bonn, Germany, Geographisches Institut der Universität Bonn.
Ref Type: Thesis/Dissertation

Fynn, R. W. S. & Connor, T. G. (2000). Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology,* 37, 491-507.

Gabriel, O., Cibils, A., Borelli, P. & Humano, G. (1998). Stable states in relation to grazing Patagonia: a 10-year experimental trial. *Journal of Arid Environments,* 40, 113-131.

Garden, D., Lodge, G., Mitchell, M. & Junor, K. Tips & tools for making change: Grazing management for productive native pastures. 2003. Meat & Livestock Australia. Ref Type: Pamphlet

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R. J., Papadimitriou, M., Papanastasis, V. P., Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J. P., Thebault, A., Vile, D. & Zarovali, M. P. (2006). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99, 967-985.

Genin, D., Fouilleron, B. & Kérautret, L. (2005). Un tempo bien tempéré...Place et rôles des agdals dans les systèmes d'élevage des Ait Bouguemez (Haut-atlas central). In L. Auclair & M. Alifriqui (Eds) *Les Agdals du Haut Atlas marocain: savoir locaux, droits d'accès et gestion de la biodiversité* (pp. 1-18). Rabat: IRD.

Genin, D. (2008). The Adgal system or the art of managing spatio-temporality of forage resources and risks in the High Atlas mountains of Morocco. In Organizing Committee of 2008 IGC/IRC Conference (Ed) *Multifunctional Grasslands in a Changing World - Volume II* (pp. 1092). Guangzhou, China: Guangdong People's Publishing House.

Gertel, J. & Breuer, I. (2007). *Pastoral Morocco: Globalizing scapes of mobility and insecurity*. Wiesbaden, Germany: Reichert.

Getzin, S. (2005). The suitability of the degradation gradient method in arid Namibia. *African Journal of Ecology*, 43, 340-351.

Gitay, H. & Noble, I. R. (1997). What are functional types and how should we seek them? In T. M. Smith, H. H. Shugart & F. I. Woodward (Eds) *Plant Functional Types: Their relevance to ecosystem properties and global change* (pp. 3-19). Cambridge, UK: Cambridge University Press.

Gnanadesikan, R. (1997). *Methods for statistical data analysis of multivariate observations*. New York, USA: John Wiley & Sons.

Greenwood, K. L., MacLeod, D. A. & Hutchinson, K. J. (1997). Long-term stocking rate effects on soil physical properties. *Australian Journal of Experimental Agriculture*, 37, 413-419.

Grime, J. P. (1979). *Plant strategies and vegetation processes*. Chichester, New York, Brisbane, Toronto: John Wiley & Sons.

Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties*. Chichester, UK: Wiley and sons.

Grubb, P. J. (1998). A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics*, 1, 3-31.

Guevara, J. C., Cavagnaro, J. B., Estevez, O. R., Le Houérou, H. N. & Stasi, C. R. (1997). Productivity, management and development problems in the arid rangelands of the central Mendoza plains (Argentina). *Journal of Arid Environments*, 35, 575-600.

Gurevitch, J., Scheiner, S. M. & Fox, G. A. (2006). *The ecology of plants*. Sunderland, USA: Sinauer.

Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzar, C., Gingrich, S., Lucht, W. & Fischer-Kowalski, M.  (2007). Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences,* 104, 12942-12947.

Hambler, C., Canney, S. M., Coe, M. T., Henderson, P. A. & Illius, A. W.  (2007). Grazing and "degradation". *Science,* 316, 1564-1565.

Hansen, A. J., Rotella, J. J., Kraska, M. P. V. & Brown, D.  (2000). Spatial patterns of primary productivity in the Greater Yellowstone ecosystem. *Landscape Ecology,* 15, 505-522.

Hardy, M. B., Hurt, C. R., Bosch, O. J. H., Vorster, M. & Tainton, N. M. (1999). Veld condition assessment. In N. M. Tainton (Ed) *Veld management in South Africa* (pp. 194-216). Pietermaritzburg, South Africa: University of Natal Press.

Harrison, Y. A. & Shackleton, C.  (1999). Resilience of South African communal grazing lands after the removal of high grazing pressure. *Land Degradation & Development,* 10, 225-239.

Hassani, N., Asghari, H. R., Frid, A. S. & Nurberdief, M.  (2008). Impacts of overgrazing in a long-term traditional grazing ecosystem on vegetation around watering points in a semi-arid rangeland of north-eastern Iran. *Pakistan Journal of Biological Sciences,* 11, 1733-1737.

Hatfield, R. & Davies, J.  Global review of the economics of pastoralism.  2006. Nairobi, Kenya, IUCN. World Initiative for Sustainable Pastoralism.
Ref Type: Report

HCP . Les indicateurs sociaux du Maroc en 2007.  2007. Rabat, Morocco, Haut Commissariat du Plan, Morocco.
Ref Type: Report

Heidecke, C. & Schmidt, T. (2008). Agricultural land use. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research results 2000-2007* (pp. 67-68). Bonn, Germany: Department of Geography, University of Bonn.

Heidecke, C. & Roth, A. (2008). Drought effects on livestock husbandry. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research Results 2000-2007* (pp. 65-66). Bonn, Germany: Department of Geography, University of Bonn.

Hein, L.  (2006). The impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland. *Journal of Arid Environments,* 64, 488-504.

Hely, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M. T. & Guiot, J.  (2006). Sensitivity of African biomes to changes in the precipitation regime. *Global Ecology and Biogeography,* 15, 258-270.

Herms, D. A. & Mattson, W. J.  (1992). The dilemma of plants: To grow or defend. *The Quarterly Review of Biology,* 67, 283.

Herrick, J. E. (2000). Soil quality: An indicator of sustainable land management? *Applied Soil Ecology*, 15, 75-83.

Herrmann, S. M., Anyamba, A. & Tucker, C. J. Exploring relationships between rainfall and vegetation dynamics in the Sahel using coarse resolution satellite data. 2009.
Ref Type: Report

Hillyer, A. E. M., McDonagh, J. F. & Verlinden, A. (2006). Land-use and legumes in northern Namibia - the value of a local classification system. *Agriculture Ecosystems & Environment*, 117, 251-265.

Hirata, M., Koga, N., Shinjo, H., Fujita, H., Gintzburger, G., Ishida, J. & Miyazaki, A. (2005). Measurement of above-ground plant biomass, forage availability and grazing impact by combining satellite image processing and field survey in a dry area of north-eastern Syria. *Grass and Forage Science*, 60, 25-33.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology, Evolution, and Systematics*, 4, 1-23.

Holling, C. S. (2001). Understanding the complexity of economic, ecological, and social systems. *Ecosystems*, 4, 390-405.

Holm, A. M., Watson, I. W., Loneragan, W. A. & Adams, M. A. (2003). Loss of patch-scale heterogeneity on primary productivity and rainfall-use efficiency in Western Australia. *Basic and Applied Ecology*, 4, 569-578.

Homewood, K. M. & Rodgers, W. A. (1984). Pastoralism and conservation. *Human Ecology*, 12, 431-441.

Hooper, D. U. & Dukes, J. S. (2004). Overyielding among plant functional groups in a long-term experiment. *Ecology Letters*, 7, 95-105.

Huenneke, L. F., Clason, D. & Muldavin, E. (2001). Spatial heterogeneity in Chihuahuan Desert vegetation: Implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments*, 47, 257-270.

Huenneke, L. F., Anderson, J. P. E., Remmenga, M. & Schlesinger, W. H. (2002). Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology*, 8, 247-264.

Huntington, H. P. (2000). Using traditional ecological knowledge in science: Methods and applications. *Ecological Applications*, 10, 1270-1274.

Huxman, T., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, R. M., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockmann, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E. & Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429, 651-654.

Huxman, T., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D. R., Potts, D. L. & Schwinning, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141, 254-268.

IAV . Étude relative à l'inventaire participatif de la biodiversité dans le versant sud du Haut Atlas. Institut Agronomique et Vétérinaire Hassan II. 1-78. 2002. Ouarzazate, Morocco, Conservation de la Biodiversité par la Transhumance dans le Versant sud

du Haut Atlas (CBTHA).
Ref Type: Report

IAV . Étude participative des savoirs locaux en matière d'élevage et de transhumance dans le versant sud du Haut Atlas (document de synthese). Institut Agronomique et Vétérinaire Hassan II. 1-50. 2003. Ouarzazate, Morocco, Conservation de la Biodiversité par la Transhumance dans le Versant suddu Haut Atlas (CBTHA).
Ref Type: Report

Ilahiane, H. (1999). The Berber Agdal institution: Indigenous range mangement in the Atlas Mountains. *Ethnology*, 38, 21-45.

Illius, A. W. & O'Connor, T. G. (1999). On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, 9, 798-813.

Illius, A. W. & O'Connor, T. G. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, 89, 283-294.

IMF . World economic outlook. Crises and recovery. 2009. Washington, D.C., USA, International Monetary Fund, Publication Services. World economic and financial surveys.
Ref Type: Report

IRC (2008). *People and policy in rangeland management: A glossary of key concepts*. Beijing, China: Science in China Press.

Jacobs, M. J. & Schloeder, C. A. (2003). Defoliation effects on basal cover and productivity in perennial grasslands of Ethiopia. *Plant Ecology*, 169, 245-257.

Jafari, R., Lewis, M. M. & Ostendorf, B. (2008). An image-based diversity index for assessing land degradation in an arid environment in South Australia. *Journal of Arid Environments*, 72, 1282-1293.

Jauffret, S. & Lavorel, S. (2003). Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes? *Journal of Vegetation Science*, 14, 399-408.

Jauffret, S. & Visser, M. (2003). Assigning life-history traits to plant species to better qualify arid land degradation in Presaharian Tunisia. *Journal of Arid Environments*, 55, 1-28.

Jeltsch, F., Moloney, K., Schurr, F., Köchy, M. & Schwager, M. (2008). The state of plant population modelling in light of environmental change. *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 171-189.

Jenkins, K. D. & Sanders, B. M. (1992). Monitoring with biomarkers: A multi-tiered framework for evaluating the ecological impacts of contaminants. In D. H. McKenzie, D. E. Hyatt & V. J. McDonald (Eds) *Ecological indicators* (pp. 1279-1293). London, New York: Elsevier Applied Science.

Jobággy, E. G., Sala, O. E. & Paruelo, J. M. (2002). Patterns and controls of primary production in the Patagonian steppe: A remote sensing approach. *Ecology*, 83, 307-319.

Johnson, M. Dene traditional knowledge. 1992.
Ref Type: Report

Kaiser, J. (2001). How rain pulses drive biome growth. *Science,* 291, 413a-4414.

Katjiua, M. & Ward, D. (2007). Pastoralists' perceptions and realities of vegetation change and browse consumption in the northern Kalahari, Namibia. *Journal of Arid Environments,* 69, 716-730.

Keith, D. A., Holman, L., Rodoreda, S., Lemmon, J. & Bedward, M. (2007). Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology,* 95, 1324-1337.

Kemmerling, B. Sustainable range management - local strategies of a pastoral-nomadic group in the High Atlas Mountains, Morocco. 2008. Cologne, Germany, Unpublished Diploma Thesis, University of Cologne, Geographical Institute.
Ref Type: Thesis/Dissertation

Kemmerling, B., Linstädter, A., Baumann, G. & Kirscht, H. (2009). Linking local ecological knowledge to mobility decisions - mechanisms of resilience in southern Moroccan rangelands. *Ecology and Society,* resubmitted.

Kessler, W. B. & Thomas, J. W. (2006). Conservation biology from the perspective of natural resource management disciplines. *Conservation Biology,* 20, 670-673.

Kirscht, H. & . (2008). Agricultural strategies: Irrigation management, risk diversion and crop rotation in Tichki. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research results 2000-2007* (pp. 73-74). Bonn, Germany: Department of Geography, University of Bonn.

Kleyer, M. (1999). Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation Science,* 10, 697-708.

Klimesova, J., Latzel, V., De Bello, F. & van Groenendael, J. M. (2008). Plant functional traits in studies of vegetation changes in response to grazing and moving towards a use of more specific traits. *Preslia,* 80, 245-253.

Klose, A. Regionalisation of soil characteristics and modelling of soil erosion risk in a semiarid catchment (Wadi Drâa, South Morocco). 2009.
Ref Type: Thesis/Dissertation

Knapp, A. K. & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. *Science,* 291, 481-484.

Knippertz, P., Christoph, M. & Speth, P. (2003). Long-term precipitation variability in Morocco and the link to the large-scale circulation in recent and future climates. *Meteorology and Atmospheric Physics,* 83, 67-88.

Koricheva, J., Nykänen, H. & Gianoli, E. (2004). Meat-analysis of trade-offs among plant herbivore defenses: Are plant jacks-of-all trades, masters of all? *American Naturalist,* 163, E 64-E 75.

Kraaij, T. & Milton, S. J. (2006). Vegetation changes (1995-2004) in semi-arid Karoo shrubland, South Africa: Effects of rainfall, wild herbivores and change in land use. *Journal of Arid Environments,* 64, 174-192.

Kühner, A. & Kleyer, M. (2008). A parsimonious combination of functional traits predicting plant response to disturbance and soil fertility. *Journal of Vegetation Science,* 19, 681-692.

Ladd, B., Bonser, S. P., Peri, P. L., Larsen, J. R., Laffan, S. W., Pepper, D. A. & Cendón, D. I. (2009). Towards a physical description of habitat: Quantifying environmental adversity (abiotic stress) in temperate forest and woodland ecosystems. *Journal of Ecology,* 97, 964-971.

Lalonde, A. African indigenous knowledge and its relevance to sustainable development. 1993.
Ref Type: Report

Landres, P. B., Verner, J. & Thomas, J. W. (1988). Ecological uses of vertebrate indicator species: A critique. *Conservation Biology,* 2, 316-328.

Landsberg, J., Lavorel, S. & Stol, J. (1999). Grazing response groups among understorey plants in arid rangelands. *Journal of Vegetation Science,* 10, 683-696.

Landsberg, J., James, C. D., Morton, S. R., Muller, W. J. & Stol, J. (2003). Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology,* 40, 1008-1024.

Lanjouw, P. The geography of poverty in Morocco. Micro-level estimates of poverty and inequality from combined census and household survey data. 2004. DECRG.
Ref Type: Report

Lauenroth, W. K., Dodd, J. L. & Sims, P. L. (1978). The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia,* 36, 211-222.

Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology,* 16, 545-556.

Lavorel, S., Diaz, S., Cornelissen, J., Garnier, E., Harrison, S., McIntyre, S., Pausas, J. G., Perez-Harguindeguy, N., Roumet, C. & Urcelay, C. (2007). Plant functional types: Are we getting any closer to the holy grail? In Canadell J.G., D. Pataki & L. Pitelka (Eds) *Terrestrial ecosystems in a changing world* (pp. 149-164). Berlin Heidelberg, Germany: Springer-Verlag.

Le Houérou, H. N., Claudin, J. & Haywood, M. Étude phytoécologique du Hodna. -154. 1974. Rome, Italy, FAO.
Ref Type: Report

Le Houérou, H. N. Browse in northern Africa. Le Houérou, H. N. International Symposium on Browse in Africa Addis Ababa, April 8-12, 1980. Browse in Africa: The current state of knowledge , Chapter 5. 1980. Addis Ababa.
Ref Type: Conference Proceeding

Le Houérou, H. N. (1984). Rain use efficiency: A unifying concept in arid-land ecology. *Journal of Arid Lands,* 7, 213-247.

Le Houérou, H. N., Bingham, R. L. & Skerbek, W. (1988). Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments*, 15, 1-18.

Le Houérou, H. N. (2001). Biogeography of the arid steppeland north of the Sahara. *Journal of Arid Environments*, 48, 103-128.

Leishman, M. R. & Westoby, M. (1992). Classifying plants into groups on the basis of associations of individual traits. Evidence from Australian semiarid woodlands. *Journal of Ecology*, 80, 417-424.

Ludwig, J. A., Tongway, D., Bastin, G. N. & James, C. D. (2004). Monitoring ecological indicators of rangeland functional integrity and their relation to biodiversity at local to regional scales. *Austral Ecology*, 29, 108-120.

Maestre, F. T. & Escudero, A. (2009). Is the patch size distribution of vegetation a suitable indicator of desertification processes? *Ecology*, 90, 1729-1735.

Manier, D. & Hobbs, N. (2007). Large herbivores in sagebrush steppe ecosystems: Livestock and wild ungulates influence structure and function. *Oecologia*, 152, 739-750.

McCann, K. S. (2000). The diversity-stability debate. *Nature*, 405, 228-233.

McCulley, R. L. (2005). Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystems*, 8, 106-121.

McIntyre, S., Lavorel, S. & Tremont, R. M. (1995). Plant life-history attributes - their relationship to disturbance responses in herbaceous vegetation. *Journal of Ecology*, 83, 31-44.

McIntyre, 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, 621-630.

McIntyre, S. & Lavorel, S. (2001). Livestock grazing in subtropical pastures: Steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, 89, 209-226.

McKee, T. B., Doesken, N. J. & Kleist, J. The relationship of drought frequency and duration to time scales. 8th Conference on Applied Climatology, January 17-22. Preprints , 179-184. 1993. Anaheim, California.
Ref Type: Conference Proceeding

McNaughton, S. J., Oesterheld, M., Frank, D. A. & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341, 142-144.

McNaughton, S. J., Milchunas, D. G. & Frank, D. A. (1996). How can net primary productivity be measured in grazing ecosystems? *Ecology*, 77, 974-977.

MEA (2005). *Ecosystems and human well-being: Desertification synthesis*. Washington, D.C., USA: World Resources Institute.

Médail, F. & Quézel, P. (1997). Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. *Annals of Missouri Botanical Garden*, 84, 112-127.

MFR, C. (1998). Range monitoring and assessment. *Range manual* British Columbia, Canada: Ministry of Forest and Range, Canada.

Michard, A., Saddiqi, O., Chalouan, A. & Frizon de Lamotte, D. (2008). *Continental evolution: The geology of Morocco. Structure, stratigraphy, and tectonics of the Africa-Atlantic-Mediterranean triple junction*. Springer Verlag.

Middelton, N. J. & Thomas, D. S. G. (1997). *World atlas of desertification*. London, UK: United Nations Environmental Programme (UNEP).

Milchunas, D. G., Sala, O. E. & Lauenroth, W. K.  (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist,* 132, 87.

Milchunas, D. G. & Lauenroth, W. K.  (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs,* 63, 327-366.

Milchunas, D. G. & Noy-Meir, I.  (2002). Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos,* 99, 113-130.

Milner, C. & Hughes, R. E. (1968). Methods for the measurement of the primary production of grassland. *IBP Handbook no. 6* Oxford, UK: Blackwell.

Milton, S. J., Dean, W. R. J., du Plessis, M. A. & Siegfried, W. R.  (1994). A conceptual model of arid rangeland degradation. *BioScience,* 44, 70-76.

Milton, S. J. & Dean, W. R. J.  (2000). Disturbance, drought and dynamics of desert dune grassland, South Africa. *Plant Ecology,* 150, 37-51.

Montés, N., Bertaudiére-Montes, V., Badri, W., Zaoui, E. & Gauquelin, T.  (2002). Biomass and nutrient content of a semi-arid mountain ecosystem: The Juniperus thurifera L. woodland of Azzaden Valley (Morocco). *Forest Ecology and Management,* 166, 35-43.

Moritz, M. & Tarla, F.  Fulani pastoralists' perceptions and perspectives on rangelands and its degradation in northern Cameroon.  1999. Bayreuth.
Ref Type: Report

Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E. M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J. M., Horvitz, C. C., Kalisz, S., Kendall, B. E., Knight, T. M., Lee, C. T. & Menges, E. S.  (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology,* 89, 19-25.

Mouillot, D., Mason, N. W. H. & Wilson, J.  (2007). Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia,* 152, 729-737.

Muldavin, E., Moore, D., Collins, S., Wetherill, K. & Lightfoot, D.  (2008). Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia,* 155, 123-132.

Müller, B., Linstädter, A., Frank, K., Bollig, M. & Wissel, C. (2007). Learning from local knowledge: modeling the pastoral-nomadic range management of the Himba, Namibia. *Ecological Applications,* 17, 1857-1875.

Müller, B., Frank, K. & Wissel, C. (2007). Relevance of rest periods in non-equilibrium rangeland systems - a modelling analysis. *Agricultural Systems,* 92, 295-317.

Navarro, T., Alados, C. L. & Cabezudo, B. (2006). Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. *Journal of Arid Environments,* 64, 298-322.

Nègre, R. (1961). *Petite flore des régions arides du Maroc occidental*. Paris, France: Éditions du Centre de la Recherche Scientifique.

Nègre, R. (1961). *Petite flore des régions arides du Maroc occidental*. Paris, France: Éditions du Centre de la Recherche Scientifique.

Ngugi, M. K. & Conant, R. T. (2008). Ecological and social characterization of key resource areas in Kenyan rangelands. *Journal of Arid Environments,* 72, 820-835.

Niamir-Fuller, M. (1998). The resilience of pastoral herding in sahelian Africa. In C. Fikret Berkes & J. C. Folke (Eds) *Linking social and ecological systems: management practices and social mechanisms for building resilience* (pp. 250-284). Cambridge: Cambridge University Press.

Niemi, G. J., Hanowski, J. M., Lima, A. R., Nicholls, T. & Weiland, N. (1997). A critical analysis on the use of indicator species in management. *The Journal of Wildlife Management,* 61, 1240-1252.

Niemi, G. J., Wardrop, D., Brooks, R., Anderson, S., Brady, V., Paerl, H., Rakocinski, C., Brouwer, M., Levinson, B. & McDonald, M. (2004). Rationale for a new generation of indicators for coastal waters. *Environmental Health Perspectives,* 112, 979-986.

Niemi, G. J. & McDonald, M. E. (2004). Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics,* 35, 89-111.

Noble, I. R. & Gitay, H. (1996). A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science,* 7, 329-336.

Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics,* 4, 25-51.

Noy-Meir, I. (1982). Stability of plant-herbivore models and possible applications to savanna. In B. J. Huntley & B. H. Walker (Eds) *Ecology of tropical savannas* Springer.

Noy-Meir, I., Gutman, M. & Kaplan, Y. (1989). Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology,* 77, 290-310.

O'Connor, T. G., Haines, L. M. & Snyman, H. A. (2001). Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *Journal of Ecology,* 89, 850-860.

Oba, G. & Lusigi, W. J. An overview of drought strategies and land use in African pastoral systems. Pastoral Network Paper 23a, 1-33. 1987. Overseas Development

Institute.
Ref Type: Report

Oba, G., Stenseth, N. C. & Lusigi, W. J. (2000). New perspectives on substainable grazing management in arid zones of sub-Saharan Africa. *BioScience*, 50, 35-51.

Oba, G., Veetas, O. R. & Stenseth, N. C. (2001). Relationships between biomass and plant species richness in arid-zone grazing lands. *Journal of Applied Ecology*, 38, 836-845.

Oba, G., Weladji, R. B., Lusigi, W. J. & Stenseth, N. C. (2003). Scale-dependent effects of grazing on rangeland degradation in northern Kenya: A test of equilibrium and non-equilibrium hypotheses. *Land Degradation & Development*, 14, 83-94.

Oba, G. & Kaitira, L. M. (2006). Herder knowledge of landscape assessments in arid rangelands in northern Tanzania. *Journal of Arid Environments*, In Press, Corrected Proof.

Ogle, K. & Reynolds, J. F. (2004). Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia*, 141, 282-294.

Oldeland, J. Vegetationsmodellierung am Südrand des Hohen Atlas, Marokko - Habitatmodelle und ihre Anwendung in Trockengebieten. 1-149. 2004. Hamburg, Germany, Institut für Allgemeine Botanik, Universität Hamburg.
Ref Type: Thesis/Dissertation

Oldeland, J., Finckh, M. & Born, K. (2008). A bioclimatic map for southern Morocco. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research Results 2000-2007* (pp. 21-22). Bonn, Germany: Department of Geography, University of Bonn.

Omer, R. M., Hester, A. J., Gordon, I. J., Swaine, M. D. & Raffique, S. M. (2006). Seasonal changes in pasture biomass, production and offtake under the transhumance system in northern Pakistan. *Journal of Arid Environments*, 67, 641-660.

Osman, A. E., Cocks, P. S., Russi, L. & Pagnotta, M. A. (1991). Response of Mediterranean grassland to phosphate and stocking rates: biomass production and botanical composition. *Journal of Agricultural Science*, 116, 37-46.

Owen-Smith, N. (2008). The refuge concept extends to plants as well: storage, buffers and regrowth in variable environments. *Oikos*, 117, 481-483.

Ozenda, P. (2004). *Flore et végétation du Sahara*. Paris, France: CNRS Éditions.

Paeth, H., Born, K., Girmes, R., Podzun, R. & Jacob, D. (2009). Regional climate change in tropical and northern Africa due to greenhouse forcing and land use changes. *Journal of Climate*, 22, 114-132.

Paruelo, J. M., Lauenroth, W. K., Burke, I. C. & Sala, O. E. (1999). Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems*, 2, 64-68.

Paruelo, J. M. (2000). Long-term dynamics of water and carbon in semi-arid ecosystems: A gradient analysis in the Patagonian steppe. *Plant Ecology*, 150, 133-143.

Paruelo, J. M., Pütz, S., Weber, G., Bertiller, M., Golluscio, R. A., Aguiar, M. R. & Wiegand, T. (2008). Long-term dynamics of a semiarid grass steppe under stochastic climate and different grazing regimes: A simulation analysis. *Journal of Arid Environments*, 72, 2211-2231.

Pausas, J. G. & Lavorel, S. (2003). A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science,* 14, 409-416.

Peters, D. & Huenneke, L. F. (2009). Patterns of net primary productivity: Data set documentation form.

Peterson, G. D. (2002). Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems,* 5, 329-338.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J. & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution,* 20, 503-510.

Phinn, S., Franklin, J., Hope, A., Stow, D. & Huenneke, L. F. (1996). Biomass distribution mapping using airborne digital video imagery and spatial statistics in a semi-arid environment. *Journal of Environmental Management,* 47, 139-164.

Pickett, S. T. A., Kolasa, J., Armesto, J. J. & Collins, S. L. (1989). The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos,* 54, 129-136.

Pierotti, R. & Wildcat, D. (2002). Traditional ecological knowledge: the third alternative (commentary). *Ecological Applications,* 10, 1333-1340.

Pillar, V. D. (1999). On the identification of optimal plant functional types. *Journal of Vegetation Science,* 10, 631-640.

Prince, S. D., Brown de Colstoun, E. & Kravitz, L. L. (1998). Evidence from rain-use efficiencies does not indicate extensive Sahelian desertification. *Global Change Biology,* 4, 359-374.

Prince, S. D., Wessels, K. J., Tucker, C. J. & Nicholson, S. E. (2007). Desertification in the Sahel: A reinterpretation of a reinterpretation. *Global Change Biology,* 13, 1308-1313.

Prins, H. H. T., Brunsting, A. M. H. & van Langevelde, F. (2008). Comments on "Relevance of key resource areas for large-scale movements of livestock". In H. H. T. Prins & F. van Langevelde (Eds) *Resource Dynamics: Spatial and Temporal Dynamics of Foraging* (pp. 233-236). Berlin, Germany: Springer.

Puigdefabregas, J. & Mendizabal, T. (1998). Perspectives on desertification: western Mediterranean. *Journal of Arid Environments,* 39, 209-224.

Pykälä, J. (2004). Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. *Plant Ecology,* V175, 217-226.

Quaas, M. F. & Baumgärtner, S. (2008). Natural vs. financial insurance in the management of public-good ecosystems. *Ecological Economics,* 65, 397-406.

Quézel, P. & Santa, S. (1962). *Nouvelle flore de l'Algerie et des régions désertiques méridionales*. Paris, France: Éditions du Centre National de la Recherche Scientifique.

Quézel, P. & Santa, S. (1962). *Nouvelle flore de l'Algerie et des régions désertiques méridionales*. Paris, France: Éditions du Centre National de la Recherche Scientifique.

Quézel, P. & Barbero, M. (1990). Les forêts mediterranéennes: problèmes posés par leur signification historique, écologique et leur conservation. *Acta Botanica Malacitana,* 15, 145-178.

Rachik, H. (2007). Nomads: But how? In J. Gertel & I. Breuer (Eds) *Pastoral Morocco: globalizing scapes of mobility and insecurity* (pp. 211-225). Wiesbaden, Germany: Reichert.

Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography*. Oxford, UK: Oxford University Press.

Reed, E. R., Swanepoel, J. & Bester, F. V. (2003). The influence of stocking rate on the utilization of individual grass species in the sward. *Spotlight on Agriculture*, 76, 1-2.

Reed, M. S. & Dougill, A. J. (2002). Participatory selection process for indicators of rangeland condition in the Kalahari. *The Geographical Journal*, 168, 224-234.

Reed, M. S., Dougill, A. J. & Baker, T. R. (2008). Participatory indicator development: what can ecologists and local communities learn from each other? *Ecological Applications*, 18, 1253-1269.

Reich, P. B., Walters, M. B. & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedingy of the National Academy of Sciences of the United Stated of America*, 94, 13730-13734.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M. & Walters, M. B. (2003). The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, 164, S143-S164.

Retzer, V. (2006). Impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland revisited (Hein, 2006) - new insights from old data. *Journal of Arid Environments*, 67, 157-164.

Reynolds, J. F., Kemp, P. R., Ogle, K. & Fernandez, R. J. (2004). Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, 141, 194-210.

Rolstad, J., Gjerde, I., Gundersen, V. S. & Saetersdal, M. (2002). Use of indicator species to assess forest continuity: A critique. *Conservation Biology*, 16, 253-257.

Rothauge, A., Smit, G. N. & Abate, A. L. (2004). Veld condition is affected by the frame size and stocking rate of free-ranging beef cattle. *Agricola*, 2004, 40-42.

Roughgarden, J., Running, S. W. & Matson, P. A. (1991). What does remote sensing do for ecology? *Ecology*, 72, 1918-1922.

Rusch, G. M., Skarpe, C. & Halley, D. J. (2009). Plant trait link hypothesis about resource-use and response to herbivory. *Basic and Applied Ecology*, 10, 466-474.

Safriel, U. & Adeel, Z. (2005). Dryland systems. In K. Chopra & R. Leemans (Eds) *Ecosystems and human well-being: Current state and trends* (pp. 623-662). Washington DC, USA: Island Press.

Sala, O. E., Parton, W. J., Joyce, L. A. & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology*, 69, 40-45.

Sayre, N. F. & Fernandez-Gimenez, M. E. The genesis of range science, with implications for current development policies. Proceedings of the VIIth International Rangelands Congress , 1976-1985. 2003.
Ref Type: Conference Proceeding

Scanlon, T. M., Albertson, J. D., Caylor, K. K. & Williams, C. A. (2002). Determining land surface fractional cover from NDVI and rainfall time series for a savanna ecosystem. *Remote Sensing of Environment*, 82, 376-388.

Schiller, A., Hunsaker, C. T., Kane, M. A., Wolfe, A. K., Dale, V. H., Suter, G. W., Russell, C. S., Pion, G., Jensen, M. H. & Konar, V. C. (2001). Communicating ecological indicators to decision makers and the public. *Ecology and Society*, 5, -19.

Schimel, D. S., Participants, V. E. M. A. & Braswell, B. H. (1997). Continental scale variability in ecosystem processes: Models, data and the role of disturbance. *Ecological Monographs*, 67, 251-271.

Schlichting, E., Blume, H.-P. & Stahr, K. (1995). *Bodenkundliches Praktikum - Eine Einführung in pedologische Arbeiten für Ökologen, insbesondere Land- und Forstwirte und für Geowissenschaftler*. Berlin; Wien: Blackwell Wissenschafts-Verlag.

Schmidtlein, S. Coarse-scale substrate mapping using plant functional types. Erdkunde 58, 137-156. 2004.
Ref Type: Magazine Article

Scholes, R. J., Dowty, P. R., Caylor, K., Parsons, D. A. B., Frost, P. G. H., Shugart, H. H., Canadell, J. & White, P. S. (2002). Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science*, 13, 419-428.

Scholte, P. & Brouwer, J. (2008). Relevance of key resource areas for large-scale movements of livestock. In H. H. T. Prins & F. van Langevelde (Eds) *Resource Dynamics: Spatial and Temporal Dynamics of Foraging* (pp. 211-232). Berlin, Germany: Springer.

Schulte, A. Weideökologie des Kaokolandes: Struktur und Dynamik einer Mopane-Savanne unter pastoralnomadischer Nutzung. 1-220. 2002. Köln, Germany, Universität zu Köln.
Ref Type: Thesis/Dissertation

Schulz, O. Analyse schneehydrologischer Prozesse und Schneekartierung im Einzugsgebiet des Oued M'Goun, Zentraler Hoher Atlas (Marokko). 2006. Bonn, Germany, Geographisches Institut der Universität Bonn.
Ref Type: Thesis/Dissertation

Schulz, O. & Judex, M. (Eds) (2008). *Impetus Atlas Morocco: Research results 2000-2007*. Bonn, Germany: Department of Geography, University of Bonn.

Schulz, O. (2008). Precipitation in the upper and middle Drâa basin. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research Results 2000-2007* (pp. 19-20). Bonn, Germany: Department of Geography, University of Bonn.

Schulz, O. (2008). The IMPETUS climate monitoring network
517. In O. Schulz & M. Judex (Eds) *IMPETUS Atlas Morocco. Research Results 2000-2007* (pp. 17-18). Bonn, Germany: Department of Geography, University of Bonn.

Schwinning, S., Sala, O. E., Loik, M. E. & Ehleringer, J. R. (2004). Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia*, 141, 191-193.

Scurlock, J. M. O., Johnson, K. & Olson, R. J. (2002). Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology,* 8, 736-753.

Shackleton, C. M., Griffin, N. J., Banks, D. I., Mavrandonis, J. M. & Shackleton, S. E. (1994). Community structure and species composition along a disturbance gradient in a communally managed South African savanna. *Plant Ecology,* 115, 157-167.

Skarpe, C. (1996). Plant functional types and climate in a southern African savanna. *Journal of Vegetation Science,* 7, 397-404.

Smet, M. & Ward, D. (2006). Soil quality gradients around water-points under different management systems in a semi-arid savanna, South Africa. *Journal of Arid Environments,* 64, 251-269.

Snyman, H. A. & Fouche, H. J. (1991). Production and water-use efficiency of semi-arid grasslands of South Africa as affected by veld condition and rainfall. *Water SA,* 17, 263-268.

Snyman, H. A. (1998). Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of southern Africa. *Journal of Arid Environments,* 39, 645-666.

Southwood, T. R. E. (1988). Tactics, strategies and templets. *Oikos,* 52, 3-18.

Sperry, J. S. (2002). Desert shrub water relations with respect to soil characteristics and plant functional types. *Functional Ecology,* 16, 367-378.

Steiner, C. F., Long, Z. T., Krumins, J. A. & Morin, P. J. (2006). Population and community resilience in multitrophic communities. *Ecology,* 87, 996-1007.

Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E. D. & Kigel, J. (2000). Vegetation response to grazing management in a Mediterranean herbaceous community: A functional group approach. *Journal of Applied Ecology,* 37, 224-237.

Strauss, S. Y. & Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution,* 14, 179-185.

Su, Y., Li, Y., Cui, J. & Zhao, W. (2005). Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *CATENA,* 59, 267-278.

Sutrop, U. (2001). List task and a cognitive salience index. *Field Methods,* 13, 263-276.

Suzuki, J. I. & Stuefer, J. (1999). On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biology,* 14, 11-17.

Swemmer, A. M., Knapp, A. K. & Snyman, H. A. (2007). Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *Journal of Ecology,* 95, 780-788.

Swinton, S. M., Lupi, F., Robertson, G. P. & Hamilton, S. K. (2007). Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. *Ecological Economics,* 64, 245-252.

Tengoe, M. & Belfrage, K. (2004). Local management practices for dealing with change and uncertainty: A cross-scale comparison of cases in Sweden and Tanzania. *Ecology and Society,* 9(3), 4-[online] URL: http://www.ecologyandsociety.org/vol9/iss3/art4/.

Ter Braak, C. J. F. & Smilauer, P. (2002). *Canoco 4.5 Reference manual and CanoDraw for Windows user's guide*.

Tews, J., Esther, A., Milton, S. J. & Jeltsch, F. (2006). Linking a population model with an ecosystem model: Assessing the impact of land use and climate change of savanna shrub cover dynamics. *Ecological Modelling*, 195, 219-228.

Thuiller, W., Lavorel, S., Midgley, G. F., Lavergne, S. & Rebelo, T. (2004). Relating plant traits and species distributions along bioclimatic gradients for 88 Leucadendron taxa. *Ecology*, 85, 1688-1699.

Todd, S. W. & Hoffman, M. T. (2000). Correlates of stocking rate and overgrazing in the Leliefontein Communal Reserve, central Namaqualand. *African Journal of Range and Forage Science*, 17, 36-45.

Trabut, L. (2006). *Noms indigènes des plantes d'Afrique du Nord*. Paris, France: Ibis Press.

Tremlova, K. & Münzbergova, Z. (2007). Importance of species traits for species distribution in fragmented landscapes. *Ecology*, 88, 965-977.

Turner, I. M. (1994). Sclerophylly: Primarily protective? *Functional Ecology*, 8, 669-675.

Turner, M. D. (1998). Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 2. Effects of a phosphorus gradient on spatial patterns of annual grassland production. *Journal of Biogeography*, 25, 683-694.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. & Steininger, M. (2003). Remote sensing for biodiversity science and conservation. *Trends in Ecology & Evolution*, 18, 306-314.

UNDP . Generic guidelines for mainstreaming drylands issues into national development frameworks. 1. 2008. Nairobi, Kenya, United Nations Development Programme.
Ref Type: Report

UNDP (2008). Human Development Report country information: Morocco. Available via http://hdrstats.undp.org/en/countries/country_fact_sheets/cty_fs_MAR.html

Valone, T. J., Meyer, M., Brown, J. H. & Chew, R. M. (2002). Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. *Conservation Biology*, 16, 995-1002.

van de Koppel, J., Rietkerk, M., van Langevelde, F., Kumar, L., Klausmeier, C. A., Fryxell, J. M., Hearne, J., van Andel, J., de Ridder, N., Skidmore, A. K., Stroosnijder, L. & Prins, H. H. T. (2002). Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *The American Naturalist*, 159, 209-218.

van der Merwe, J. P. A. & Kellner, K. (1999). Soil disturbance and increase in species diversity during rehabilitation of degraded arid rangelands. *Journal of Arid Environments*, 41, 323-333.

Van Lynden, G. W. J. & Kuhlmann, T. LADA - Land degradation assessment in dryland areas. 2002.
Ref Type: Report

Varnamkhasti, A. S., Milchunas, D. G., Lauenroth, W. K. & Goetz, H. (1995). Production and rain use efficiency in short-grass steppe: Grazing history, defoliation and water resource. *Journal of Vegetation Science*, 6, 787-796.

Vesk, P. A. & Westoby, M. (2001). Predicting plant species' responses to grazing. *Journal of Applied Ecology*, 38, 897-909.

Vitousek, P. M. & Howarth, R. W. (1991). Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, 13, 87-115.

Vlek, P. L. G., Bao Le, Q. & Tamene, L. Land decline in land-rich Africa: A creeping disaster in the making. 1-55. 2008. Bonn, Center for Development Research (ZEF).
Ref Type: Report

Wainwright, J. & Mulligan, M. (2004). *Environmental modelling - finding simplicity in complexity*. Chichester, UK: John Wiley & Sons.

Wang, G. & Ni, J. (2005). Responses of plant functional types to an environmental gradient on the northeast China transect. *Ecological Research*, 20, 563-572.

Weiher, E., van der Werf, 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.

Weltz, M. A., Dunn, G., Reeder, J. & Frasier G. (2003). Ecological sustainability of rangelands. *Arid Land Research and Management,* 17, 369-388.

Wesche, K. & Retzer, V. Is degradation a major problem in semi-desert environments of the Gobi region in southern Mongolia? Erforschung biologischer Ressourcen der Mongolei 9, 133-146. 2005.
Ref Type: Abstract

Wessels, K. J., Prince, S. D., Malherbe, J., Small, J., Frost, P. E. & VanZyl, D. (2007). Can human-induced land degradation be distinguished from the effects of rainfall variability? A case study in South Africa. *Journal of Arid Environments,* 68, 271-297.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil,* 199, 213-227.

Westoby, M. & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution,* 21, 261-268.

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews,* 42, 207-264.

Wiegand, T., Milton, S. J., Esler, K. J. & Midgley, G. F. (2000). Live fast, die young: estimating size-age relations and mortality pattern of shrubs species in the semi-arid Karoo, South Africa. *Plant Ecology formerly Vegetatio,* 150, 115-131.

Wiegand, T., Snyman, H. A., Kellner, K. & Paruelo, J. M. (2004). Do grasslands have a memory: Modeling phytomass production of a semiarid South African grassland. *Ecosystems,* 7, 243-258.

Yahdjian, L. & Sala, O. E. (2006). Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology,* 87, 952-962.

Zimmermann, I., Graz, F. P., Berry, M. H., Imasiku, N. N. T., Muroua, N. D., Sibalantani, M. M. & Sikopo, C. S. (2001). Quantified range condition assessment of open Camelthorn savanna along a degradation gradient. *African Journal of Range & Forage Science*, 18, 111-116.

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