

**Advancing Functional Understanding of Primary
Production in Drylands: Insights from a
Data-Integration Approach**

I n a u g u r a l - D i s s e r t a t i o n

zur

Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Universität zu Köln

vorgelegt von

Jan Christian Ruppert

aus Bad Mergentheim

Berichterstatter:

Prof. Dr. Michael Bonkowski

Prof. Dr. Hartmut Arndt

Prof. Dr. Stefan Porembski (Universität Rostock)

Vorsitz der Prüfung:

Prof. Dr. Frank Schäbitz

Beisitzerin:

Dr. Anja Linstädter

Tag der letzten mündlichen Prüfung: 26. Mai 2014

Table of Contents

1. General Introduction	4
1.1 Dryland Ecosystems of the World	4
1.2 Primary Production in Drylands	8
1.3 General Methodological Approach and Database	16
1.4 Aims of this Dissertation	20
2. Publications of the Dissertation	25
2.1 Meta-Analysis of ANPP and Rain-Use Efficiency confirms indicative value for Degradation and Supports non-linear Response along Precipitation Gradients in Drylands	26
2.2 Convergence between ANPP Estimation Methods in Grasslands – A practical Solution to the Comparability Dilemma.....	51
2.3 Quantifying Dryland Resistance and Resilience to Drought: The Importance of Drought Intensity, Grazing Regime and Vegetation Structure.....	78
3. Additional Publications.....	121
3.1 Response of community-aggregated Plant Functional Traits along Grazing Gradients: Insights from African semi-arid Grasslands	122
3.2 Discrimination and Characterization of Management Systems in semi-arid Rangelands of South Africa using RapidEye Time Series.....	123
3.3 Effect of Tenure System on Biomass and Vegetation Cover in Two Biomes in South Africa	124
3.4 Are there consistent Grazing Indicators in Drylands? Testing Plant Functional Types of various Complexity in South Africa’s Grassland and Savanna Biome	125
4. Discussion	126
5. References	135
6. Summary / Zusammenfassung	143
7. Appendix.....	146
8. Danksagung	149
9. Declaration of Contribution as Author and Co-Author	151
10. Statutory Declaration and Statement (Erklärung).....	152
11. Curriculum Vitae.....	153

1. General Introduction

1.1 Dryland Ecosystems of the World

1.1.1 Definition and Botanical Ecology

Dryland ecosystems – as indicated by their name – are defined and characterized by water deficiency during prolonged periods throughout the year (UNEP, 1997). Based on the UNEP aridity index, drylands are subdivided in four subtypes, in order of decreasing aridity: hyper-arid (desert), arid, semi-arid and dry sub-humid (Figure 1.1; UNEP, 1997).

All dryland-subtypes together cover roughly 41% of terrestrial earth surface spreading across all continents (except Antarctica; Figure 1.1) and are home to circa 35-40 % of Earth's human population (approximately 2.5 billion in 2005; MEA, 2005). Besides the shortage of water availability in these regions – either due to low rainfall and/or high evapotranspiration – they are also characterized by a pronounced spatiotemporal variability in rainfall (Davidowitz, 2002). The combination of a relatively strong water limitation, a high inter- and intra-annual variability of precipitation, and a high spatial heterogeneity in other vegetation-relevant factors (e.g. edaphic parameters), largely limit vegetation growth. This is translated into a pronounced variability in seasonal and annual vegetation dynamics.

Drylands ecosystems comprise four broad biome-types – desert, grassland, shrubland and savanna – which, in this order, represent a gradual increase in architectural complexity of the vegetation, and also in average primary production (see Box 1.1; Hassan et al., 2005).

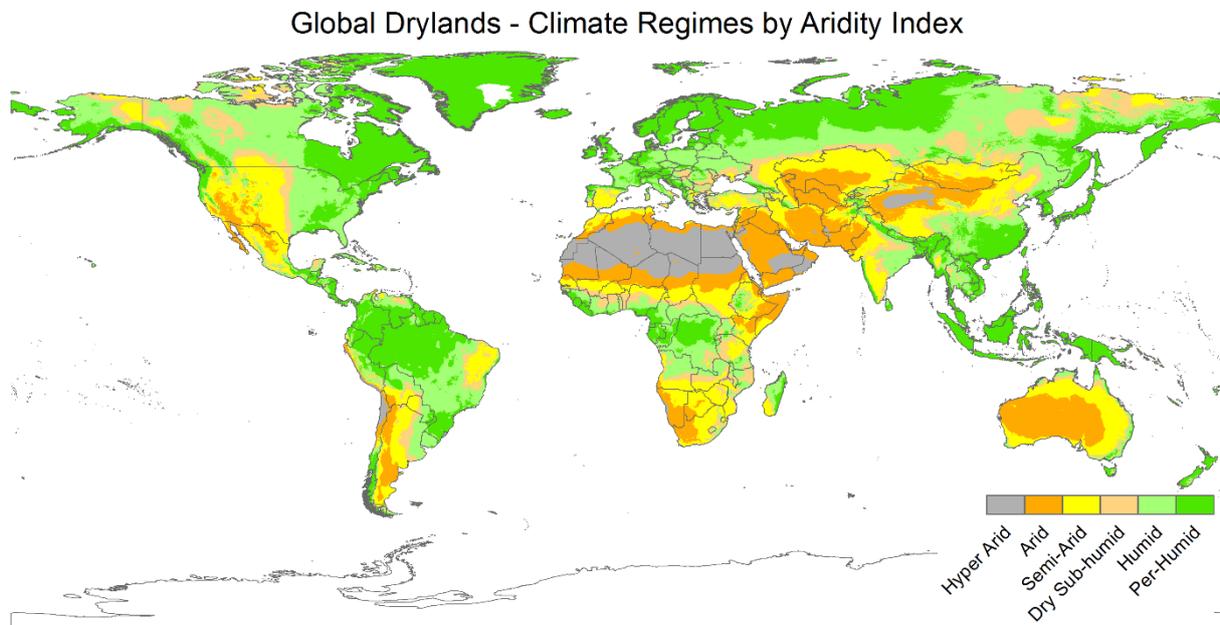


Figure 1.1: Overview on worlds' broad climate regimes as defined by the United Nations Environment Programme (UNEP) aridity index. $Aridity\ Index\ (AI) = MAP / MAE$ where $MAP =$ mean annual precipitation and $MAE =$ mean annual potential evapotranspiration. Drylands, given in grey and yellowish colors, comprise hyper arid ($AI < 0.03$), arid ($0.03 - 0.2$), semi-arid ($0.2 - 0.5$) and dry sub-humid ($0.5 - 0.65$) climates. Map is based on data provided in Trabucco and Zomer (2009).

Box 1.1 – Biome Classification

Throughout this dissertation, and publications presented herein, an adapted version of the WWF biome classification (Olson et al., 2001) was used, following Hassan et al. (2005). This adaptation was applied to account for the differing spatial scales (field vs. landscape). In total, four broad »dryland biomes« are distinguished as compared to the original eight (for drylands). In detail, these biomes are

- (A) Desert: extremely sparse vegetation, mostly woody shrubs or well-adapted herbs, grasses and succulents;
- (B) Grassland: herbaceous layer with relatively dense cover, dominated by annual or perennial grasses; little to no tree and shrub occurrence;
- (C) Shrubland (also called »Mediterranean« or »scrub«): vegetation dominated by relatively dense stands of small or medium-sized shrubs, either with or without an interspersed herbaceous layer;
- (D) Savanna (also called »woodland«): dense and continuous herbaceous layer, co-dominated by intermingled trees or large shrubs but without a closed canopy.

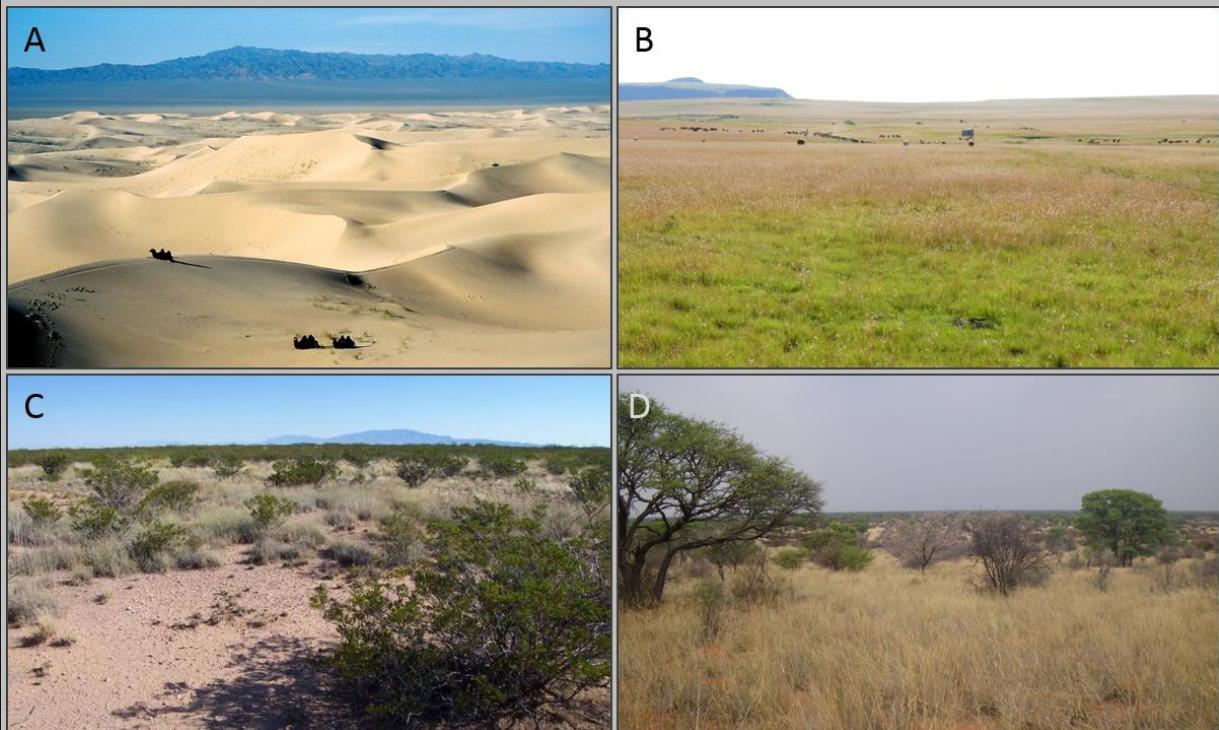


Figure 1.2: Examples of the four dryland biomes. (A) Gobi Desert in Mongolia, (B) *Themeda triandra* grassland in South Africa, (C) Creosote shrubland in New Mexico, USA, and (D) *Acacia* savanna in the Kalahari, South Africa.

Sources: (A) www.worldtopjourneys.com, (C) www.lternet.edu/sites/jrn/. Sources are only given for photographs or graphics that were not produced by me.

Even though these dryland biomes tend to follow a gradient of decreasing aridity (deserts > grassland > shrubland > savanna), their actual distribution can be largely independent from climate and might be more affected by other abiotic and biotic factors (e.g. edaphic factors, topography, current and past land use; Hassan et al., 2005). For example, the hyper-arid dryland subtype nearly exclusively inhabits deserts while the semi-arid subtype shows a mixture of all dryland biomes-types.

The dynamic and unreliable intra- and inter-annual fluctuations in dryland vegetation characteristics described above (e.g. cover, composition and primary production), mostly leave no option for

resource-based human activities other than livestock production and (self-sufficient) crop-farming. In fact, circa one third of drylands' human population directly depends on agriculture for their livelihood. Only 25% of drylands are used as croplands (rain-fed or, in the wealthy dryland regions of North America and Europe, irrigated), while roughly 65% are predominantly used as rain-fed rangelands (MEA, 2005). Thus, livelihood security in these regions mainly relies on provision of basic ecosystem services such as forage and crop yield for animal production and/or self-sufficiency (Gillson and Hoffman, 2007).

1.1.2 Drylands under Threat – Global Change Impacts

Unsurprisingly drylands have been recognized as highly vulnerable and degradation-prone regions, especially in the light of global change (IPCC, 2007, MEA, 2005, Zhao and Running, 2010).

Even though projections in the climate regime of dryland environments exhibit considerable variability and uncertainty across scenarios and regions (Figure 1.3), there is a general trend that most dryland regions are facing unbeneficial changes.

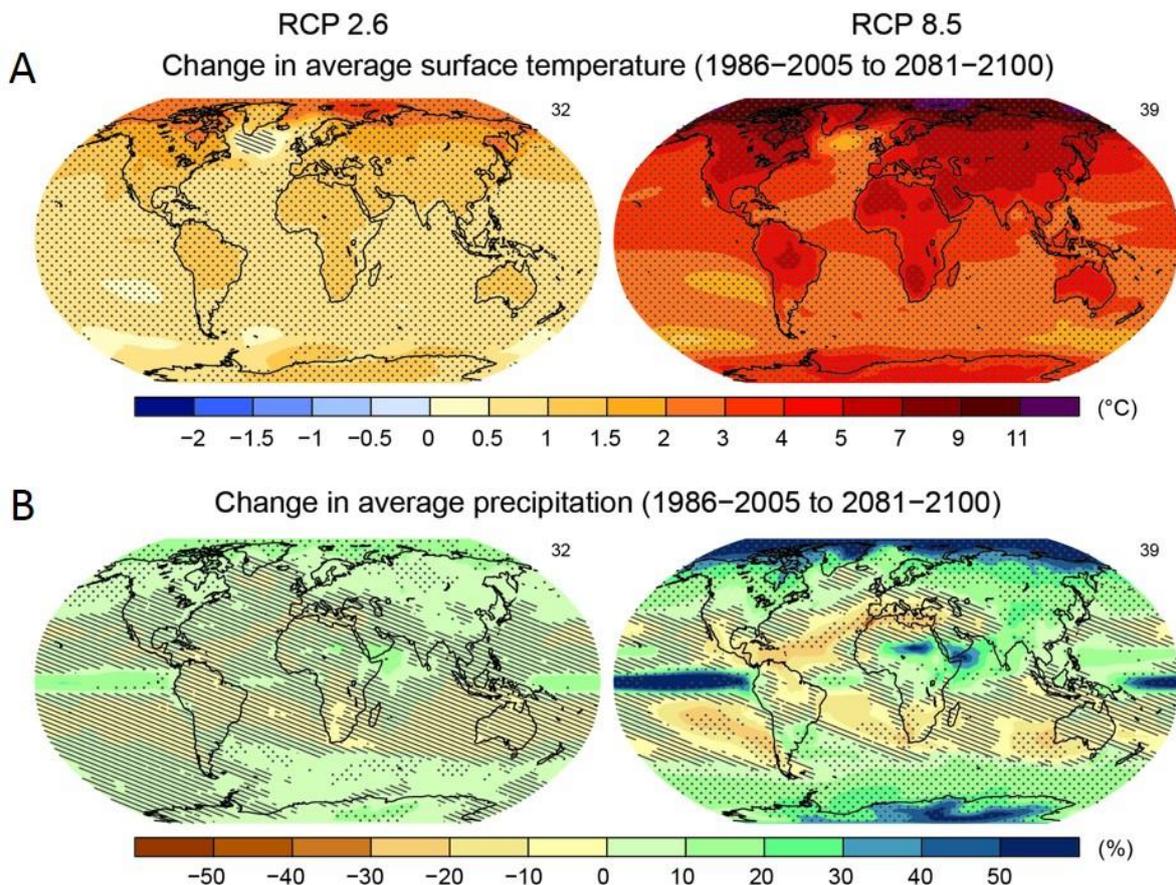


Figure 1.3: Maps of projected late 21st century annual mean surface temperature change (A) and annual mean precipitation change (B). This image is an excerpt from the SPM.8 figure and a courtesy of the IPCC (2013).

Global models for the period of 2081-2100 project a temperature increase in drylands between 1 °C and 5 °C as compared to 1986-2005 across scenarios and regions (Figure 1.3A). For the same period, changes in precipitation are more diverse across scenarios (Figure 1.3B) as projections vary between roughly constant conditions ($\pm 10\%$ in annual precipitation) and large-scale decreases across drylands of up to -20% (but also local increases, e.g. in Tropical and East Africa; IPCC, 2013).

In sum, drylands are facing increased temperatures, while precipitation amounts stagnate or decrease, thus leading to increased evapotranspiration and less plant-available water. Simultaneously, precipitation is becoming more variable and extreme events such as heavy rains and dry spells will occur more frequently (IPCC, 2013), making the overall climate system less reliable.

At the same time large proportions of dryland areas are subject to significant population growth and urbanization (MEA, 2005), both inevitably leading to expansion of agricultural land and intensification of livestock production (i.e. higher stocking rates and densities; Foley et al., 2005).

Please note, that potential effects of elevated CO_2 -concentrations are not regarded throughout this thesis. Most importantly, this is due to a paucity of related monitoring and experimental data. Furthermore, the effects of elevated atmospheric CO_2 on drylands, as well as the role of dryland ecosystems in the global carbon cycle are far from being fully understood (Maestre et al., 2013). However, recent findings suggest that bush encroachment – a common and highly undesirable phenomenon in drylands (Andela et al., 2013) – is partially triggered by elevated CO_2 -concentrations (i.e. »*CO₂-fertilization*«; Buitenwerf et al., 2012, Higgins and Scheiter, 2012).

Altogether, projected changes of the climatic system will – for all we know about drylands – hamper ecosystem functioning and decrease provision with ecosystems services, while land use change will increase the pressure on the systems and act as additional stressor (Zhao and Running, 2010, Zhao et al., 2007). Threats of co-occurrence of these unbeneficial conditions could already be observed during the last decades: severe droughts in densely populated drylands worldwide were responsible for massive reductions in livestock and crop productivity (Zhao and Running, 2010), leading to poverty and famine (UN, 2008). Furthermore, predicted changes in vegetation state and functioning may have the potential to cause rapid ecosystem transitions and/or lead to switches to stable states with undesirable low vegetation cover and biomass: degradation up to desertification (Golodets et al., 2013). In this context, the concept of ecological stability is of major interest and relevance.

1.1.3 Aspects of Ecosystem Stability

In today's ecological research, discerning the mechanisms behind, and the quantification of ecosystem responses to global environmental change is a central theme (Reed et al., 2012) and often related to the concept of ecosystem stability (or resilience; Pimm, 1984, Holling, 1973).

Box 1.2 – Stability and Resilience

Stability and resilience – even though commonly used in ecological literature – both lack a definition that is widely shared among scientists. While some scientists understand resilience as a sub-aspect of stability (Donohue et al., 2013), others understand them as largely unrelated capacities of ecosystems (Holling, 1973). Furthermore, resilience itself has been defined in various ways, emphasizing different aspects of ecosystem behavior, and even leading to competing paradigms of ecosystems understanding (e.g. engineering vs. ecological resilience; Holling, 1996). To avoid confusion or misinterpretation, I follow the approach of Donohue et al. (2013) and use the term »ecosystem stability« in the sense of a »multifaceted and complex concept«, including distinct aspects such as »resilience (recovery), resistance, robustness, persistence and variability« that can be generically defined and estimated.

Throughout this dissertation, I use the term *stability* in favor over *resilience* (see Box 1.2). Unfortunately, little efforts have been made to contribute to a functional understanding of dryland stability. So far results on dryland stability are merely anecdotic as they arrived from single sites or regions and focused on differing estimates of stability (e.g. variability, resistance or recovery; Knapp and Smith, 2001, Bai et al., 2004) that are often based on largely differing ecosystem properties (e.g. species composition, biodiversity or primary production; Peterson et al., 1998, Tilman and Downing, 1994). Due to their vastly varying methodology and their spatiotemporal constraints, these findings lack the potential to be representative across larger scales, nor can they be easily up-scaled. Hence, there is a general demand for an increased functional understanding of dryland ecosystem responses to global change (Reynolds et al., 2007), but no obvious or easy to achieve strategy to satisfy this demand (see Chapter 1.3).

1.2 Primary Production in Drylands

1.2.1 Aboveground Net Primary Production

As stated above, the predominant land use types in drylands are pasture-based livestock production and to a lesser extent crop production. Thus, livelihood and income security in drylands strongly rely on revenues from forage production and crop yield (Gillson and Hoffman, 2007).

Both of these ecosystem services are commonly estimated by aboveground net primary production (ANPP), the sum of produced aboveground plant tissue within one year, usually expressed in $g\ m^{-2}$ or $kg\ ha^{-1}$ (Scurlock et al., 2002). ANPP is very versatile as it can be estimated relatively fast and cheap in all terrestrial ecosystems. More importantly, it is directly connected to essentially all aspects of matter and energy fluxes in terrestrial ecosystems, not only in drylands (Lauenroth et al., 2006). Unsurprisingly, it is one of the best-documented quantitative estimates for several ecosystem services (such as the above mentioned) and a core ecological currency. Hence, ANPP (and derivatives thereof, e.g. rain-use efficiency; Le Houérou, 1984, Yan et al., 2013) are used to assess and represent annual dryland productivity and other key ecosystem characteristics throughout this dissertation.

1.2.2 Drivers of Primary Production in Drylands

As per definition, dryland ecosystems are water-deficient throughout prolonged periods within a year (Figure 1.1). Hence, it is not surprising that water, usually provided by **precipitation** only, acts as the main limiting factor for primary production in these systems (Lauenroth and Sala, 1992, Linstädter and Baumann, 2013); and is also highly important in other terrestrial ecosystems (Huxman et al., 2004). Therefore, ANPP is often interpreted as function of precipitation (Sala et al., 1988) and plotted along precipitation gradients. Even though the generality of water limitation in drylands is widely accepted, there is lack of consensus about the response-pattern of ANPP along these precipitation gradients on different temporal and spatial scales. Most studies report a linear relationship with precipitation (O'Connor et al., 2001, McCulley, 2005, Muldavin et al., 2008, Bai et al., 2008) but differ in intercept and slope. Other studies report a saturation curve, where ANPP increases with precipitation, but levels-off under more humid conditions (Hein, 2006, Yang et al., 2008, and partially Miede et al., 2010, and Huxman et al., 2004).

Given these concurring results in literature, neither of the regression models seems appropriate per se. Hence, continued theoretical and empirical considerations are needed to assess this issue, as the elucidation of general mechanisms in ANPP-precipitation relationships are a useful desideratum not only for functional ecologists but also for ecosystem modelers (see Chapter 2.1).

Not only current but also **previous precipitation conditions** influence ANPP (i.e. those of the last season or year). This aspect of the ANPP-precipitation relationship has been described as the »*memory*«- or legacy effect of grasslands (Wiegand et al., 2004). The relevance of previous precipitation for ANPP can be explained by a carry-over effect of vegetation density (Yahdjian and Sala, 2006, Linstädter and Baumann, 2013), the amount of reserve biomass in perennial species at the beginning of the growth period (Müller et al., 2007, Zimmermann et al., 2010) and by increased seed production and quality in annual plant communities (Harel et al., 2011). This carry-over effect may explain the majority of unexplained variance in grassland production, especially in perennial systems (Wiegand et al., 2004).

Edaphic factors also play a crucial role for biomass production in the context of water limitation. Soil characteristics such as texture, bulk density and depth influence how water infiltrates and penetrates the soil, as well soil's water-holding capacity, thus, these characteristics determine how much intercepted precipitation is available for plants (Archer and Smith, 1972). Furthermore, soil moisture affects nutrient availability and cycles, another prerequisite for plant growth, hence also for primary production (Hooper and Johnson, 1999, Delgado-Baquerizo et al., 2013).

General Introduction

Unlike to humid regions (e.g. central or northern Europe), coarse-texture soils have been recognized as beneficial for plant growth and primary production in drylands as compared to fine-textured soils (Sala et al., 1988). This observation is described as the »*inverse-texture hypothesis*« (Noy-Meir, 1973): in dryland regions, less water evaporates from coarse-textured soils (with a high sand content), as water infiltrates more quickly and deeper in the ground than on fine-textured soils. Furthermore, the top-layer of fine-textured soils dries out more quickly under dryland conditions, hardens and builds a barrier against rise and evaporation from deeper soil levels as well as against infiltration of later precipitation events (Alizai and Hulbert, 1970). This phenomenon leads to the paradox situation that those soils which are described as poor in Middle European contexts (European Soil Bureau, 2005), i.e. deep sands, carry the densest vegetation cover and are often most productive in drylands (Schulte, 2002, Sala et al., 1988, Le Hou  rou, 1984).

As for all vegetation, also deficient provision of **nutrients** (mainly carbon, nitrogen and phosphorus) acts limiting on ANPP in drylands (Hooper and Johnson, 1999, Delgado-Baquerizo et al., 2013). In the context of drylands, this is particularly interesting for two reasons. First, drylands' intense livestock production may deplete soil nutrient pools (Hassan et al., 2005) and second, increased aridity – as projected for most drylands (Figure 1.3) – may decouple soil nutrient cycles (Delgado-Baquerizo et al., 2013). Intense livestock production in drylands leads to a partial decoupling of nutrient in- and output as compared to more natural conditions what may successively deplete soil nutrients pools (Hassan et al., 2005). For once, herbivore density is much higher under livestock production schemes and, given the high metabolic needs of herbivores, leads to a higher proportion of respirational loss of carbon. Furthermore, grazing-/browsing- and roaming-behavior of livestock largely centralizes their excreta and thus nutrients near attraction-loci (boreholes, licks or shade trees) while depleting other parts of the range (Andrew, 1988, Moreno Garc  a et al., 2014). Finally, livestock products (e.g. meat, milk, fur) are extracted from the systems as well, thus preventing in-situ nutrient return.

A recent global assessment of C, N and P cycling in drylands reports that increasing aridity reduces C and N, but increases (inorganic) P concentrations (Delgado-Baquerizo et al., 2013). The study argues that under increased aridity these responses might lead to a progressive decoupling of the mentioned nutrient cycles, with detrimental effects on key ecosystems services such as primary production. The authors assume that lowered plant cover due to increased aridity, which favors physical over biological nutrient cycling processes, is the main mechanism behind this decoupling.

Parallel to the above-mentioned biotic and abiotic factors, also **management-related aspects** affect primary production. In the context of this dissertation, I will mainly highlight the effects of grazing and, however briefly, fire. Even though both aspects are also natural processes in drylands, the

General Introduction

preponderant use of drylands as rangelands and the related anthropogenic management modifies their dynamics in specific ways, which are also highly important in the context of ecosystem functioning and dynamics (Belsky, 1992, Holdo et al., 2007). Hence, both aspects need to be assessed under the premises of (varying) management.

The effect of **grazing** on (herbaceous) primary production has been described as a first-order effect of reduced vegetation cover due to defoliation (Wiegand et al., 2004): mechanic defoliation reduces plants' cover and photosynthetic active tissue, thus the overall carbon-fixation and rate of tissue production. Furthermore, the relative and absolute cover of bare soil might trigger other detrimental effects such as water or wind erosion, run-off and nutrient loss by volatilization which feedback on primary production as well (Figure 1.4; O'Connor et al., 2001, Milchunas and Lauenroth, 1993, Yan et al., 2013). Obviously these effects are directly connected to the intensity, timing and frequency of grazing (Linstädter, 2008), with more extreme regimes (i.e. high stocking densities, cf. Figure 1.4) being more harmful (Milchunas and Lauenroth, 1993, Palmer and Ainslie, 2005). Nevertheless, the actual effect of grazing across different (dryland) environments might fluctuate, which has frequently been related to the evolutionary history of grazing at the given sites (Milchunas et al., 1988, Linstädter, 2008). This explanation stresses the idea that regions, which have been subject to grazing for prolonged evolutionary time scales, will exhibit vegetation that is well adapted to grazing disturbances (e.g. African savanna systems). In fact, prolonged grazing exclusion may lead to completely altered species assemblages in such systems, with the consequence of reduced primary production – however, in other cases the exact opposite might apply (Angassa et al., 2012, Schulte, 2002), underlining variability of dryland ecosystems (Milchunas et al., 1988). Furthermore, the actual impact of grazing is also moderated by the general condition of the rangeland (health or degradation status), with degraded rangelands suffering more strongly (O'Connor et al., 2001).

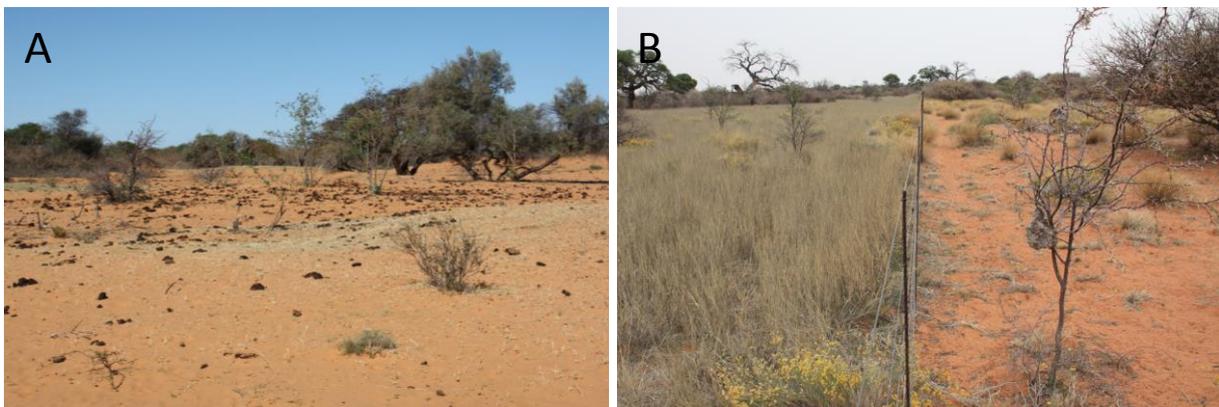


Figure 1.4: Effects of (over-) grazing in drylands. (A) »Piosphere« (i.e. the degraded area around an attraction loci for animals; Andrew, 1988) in a communal grazing land. Clear signs of overutilization are visible: reduced plant cover and a high density of excreta. (B) Marked fence line between two camps of differing land use: the left camp was stocked with game for recreational purposes in low stocking densities. The right camp was used for cattle with a recommended stocking density of ca. 12 ha cow⁻¹. Both photographs derive from the Kalahari, near Hotazel, South Africa, in 2010.

General Introduction

Another aspect related to grazing is compensatory growth – regrowth after tissue loss – that might even lead to »*overcompensation*« (McNaughton, 1983). Compensatory growth is a common and rather fast response of most plants, especially in non-woody tissues. Grasses are particularly well adapted to losses in vegetative organs, as their relatively low-laying and abundant meristems can compensate tissue losses rather rapidly. In grazing-adapted ecosystems, such as most drylands, (perennial) plant mortality after defoliation is virtually non-existent if it is not coincident with unfavorable climate conditions such as severe drought (Zimmermann et al., 2010). Furthermore, under low levels of grazing – or other sources of injuries – regrowth might even exceed the preceding tissue loss, that is »*overcompensation*« (McNaughton, 1983, Belsky et al., 1993; Note: Belsky et al. do not support the term »*overcompensation*« as it is historically connect to grazing, but acknowledge the general phenomenon). Furthermore, severe grazing has also shown to increase seed production and survival in herbs, thus plant fitness, which can be seen as another pathway of overcompensation (Paige and Whitham, 1987).

Altogether, grazing is a complex driver of ecosystem dynamics in drylands and on primary production, as it triggers not only effects on plant individuals but also on communities and their habitats, which again might feedback on primary production (Linstädter and Baumann, 2013). Overall, the most general statement for the influence of grazing on dryland ANPP in this context might be »*Dosis sola facit venenum*« (Paracelsus, 1538 in 1922).

Besides precipitation, edaphic factors, nutrients and grazing, **fire** is one of the most influential effectors of aboveground net primary production in dryland ecosystems and even more on structural aspects of dryland biomes. However, as fire is of less interest for the studies within this dissertation, I will only throw a short spotlight on the most important aspects.

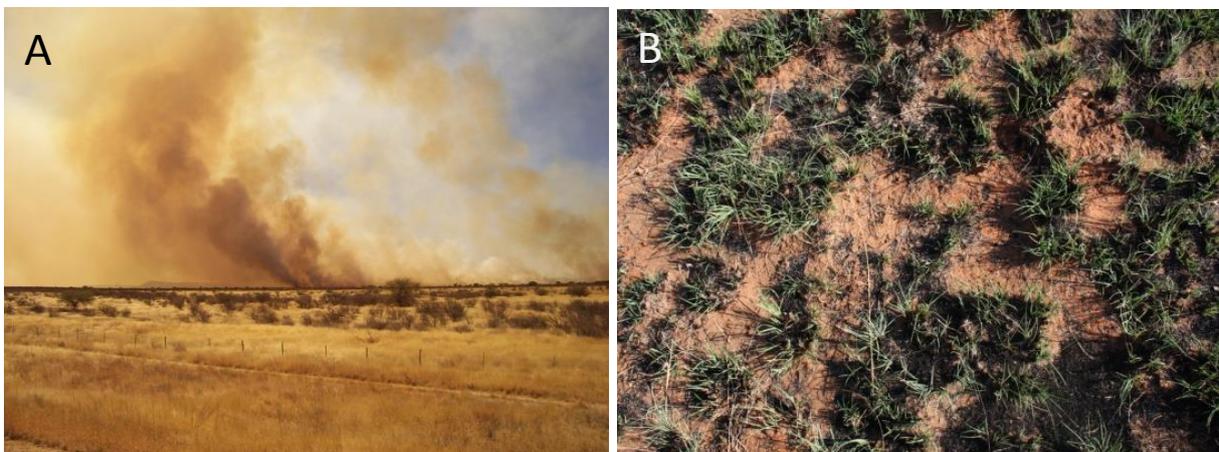


Figure 1.5: Wildfires in drylands. (A) Wildfire at Kamanjab, Namibia, in 2006. (B) Resprouting of a burned bunchgrass community in Bloemfontein, South Africa, in 2010. Photograph (A) is a courtesy of A. Linstädter.

(Wild-) fires are often triggered by lightning, or accidentally by campfires or other anthropogenic sources (Figure 1.5), but might as well be part of land management (*»prescribed burning«*, H.A. Snyman pers. comm.). As fires need a minimum fuel-load to persist and spread (Linstädter and Zielhofer, 2010), they are more frequent and widespread in the semi-arid and dry sub-humid than in the arid or hyper arid dryland-subtypes, as these systems have the tendency to be more productive and thus have the potential to accumulate more flammable dead biomass (Oesterheld et al., 1999, Linstädter and Zielhofer, 2010). Effects of fire on current year's primary production are rather obvious, but highly dependent on the timing of the fire event during the vegetative state of the plant community. For instance fire events at the end of the vegetative cycle might consume all biomass and leave only little opportunity for regrowth in the same season, thus they hardly have an effect on (current year's) ANPP. On the other hand, fire before or in the beginning of a growing season might increase ANPP in various ways. For once, burning of standing (dead) biomass releases nutrients in form of highly fertile ash to the soil, thus boosting nutrient-pools (Buis et al., 2009). Furthermore, fire opens a window of opportunity for increased recruitment and primary production (Zimmermann et al., 2008), as detrimental effects of competition for light and spaces are eased by the re-opening of the woody- and/or grass-canopy (Blair, 1997, Oesterheld et al., 1999, Zimmermann et al., 2010). On the other hand, fires during sensitive vegetative phases (such as shoot growth) might also reduce ANPP, as relative fitness of plant individuals is reduced after the fire, and the soil-fertility boost might not compensate for these losses. Hence, it is not surprising that effects of fire on ANPP have been reported to vary remarkably, reaching from ANPP decreases of -80% up to increases of 300%, depending on frequency and timing of the fire event (Oesterheld et al., 1999).

Despite these first-order effects of fire on ANPP, there are also second-order effects, as fire is also believed to largely affect ecosystems structure. For example, large scale fire-exclusion in grassland and savanna biomes is believed to be one of the driving forces of bush encroachment (cf. Chapter 1.1; Scholes and Archer, 1997, Angassa et al., 2012) what may change ecosystem structure and functioning due to higher bush intensity (Eldridge et al., 2011).

Concisely, aboveground net primary production is one of the most important ecological currencies in dryland ecosystems, reflecting the provision of forage production in these regions. Even though there is a general consensus that ANPP is mainly shaped by precipitation, soil characteristics, nutrient supply as well as grazing and fire (management; Scholes and Archer, 1997), it is unclear if response to these drivers is rectified or even identical across large scales and if there are interactive effects between these factors. Information and data we have thus far are mainly sites-based case studies. This anecdotal data cannot easily be up-scaled. Furthermore, ANPP estimation methods and algorithms vary vastly across studies and sites, what further hampers comparability.

1.2.3 Estimating Aboveground Net Primary Production

Today, ANPP is one of the best-documented estimates for dryland ecosystem services (Scurlock and Olson, 2002). However, representing a concept rather than a precise physical size, ANPP cannot be measured directly, but only be estimated based on surrogate measurements (Lauenroth et al., 2006). Generally, ANPP estimation is a two-step process: first, biomass is estimated or measured (e.g. by volumetric equations or clipping, Figure 1.6); second, the gathered biomass values are translated or recalculated to ANPP estimates depending on the respective method (see Box 1.3). As biomass can be measured and estimated with relatively little error (e.g. clipping or calibrated volumetric equations; Schulte, 2002), I will focus on the second step here.

Given the generality and importance of ANPP as ecosystem variable in terrestrial ecosystems, it is not surprising that many different estimation procedures and methods have been developed, which is particularly true for grass- or herb-dominated ecosystems (Scurlock et al., 2002, Singh et al., 1975, see Box 1.3). However, despite partial consensus about »*best practice methods*« (Scurlock et al., 2002), discussion on various methodological issues is still ongoing, and leads to coexistence of numerous ANPP estimation methods until today (see Box 1.3). Unfortunately, these different ANPP methods differ not only in their general accuracy, or in their tendency to over- or underestimate ANPP, but also with respect to magnitude, variability and uncertainty of ANPP estimates (Scurlock et al., 2002, Lauenroth et al., 2006). For instance, Scurlock et al. (2002) have shown that ANPP estimates at one site and date may vary up to more than 6-fold depending on the used method.

Hence, comparability of ANPP data across studies can be rather poor. Paradoxically, despite the large number of studies presenting ANPP data on field scale, this incomparability of methods de facto leads to a scarcity of ANPP data for data-integration studies. It is an urgent need to overcome these problems of incomparability and to harness the full potential of the globally available ANPP data in future studies.



Figure 1.6: Biomass sampling via cutting for ANPP estimation in a grassland near Bloemfontein, South Africa, in 2010.

Box 1.3 – Common ANPP Estimation Methods

According to Scurlock et al. (2002) as well my as own literature review (Ruppert and Linstädter, 2014), the vast majority of studies presenting ANPP uses a pool of seven common methods. Roughly, these can be classified in (less-elaborated) peak- and (elaborated) incremental methods. As indicated by name, peak-methods use single biomass estimates during peak-season of biomass to estimate ANPP, while incremental-methods use several biomass estimates and (summed) increments thereof. Generally, there is a consensus that incremental-methods are best practice (i.e. Method 5), however, this is in sharp contrast to the actual utilization in literature: only 21% of studies used these elaborated methods (Ruppert and Linstädter, 2014). For illustration, Figure 1.7 visualizes what four selected ANPP methods quantify with respect to in-field biomass.

Table 1.1: The seven most common ANPP estimation methods in terrestrial (mostly herbaceous) ecosystems.

Method for ANPP estimation ^a	Description
Method 1	Peak live biomass
Method 2a ^b	Peak standing crop (live plus recent dead)
Method 2b ^b	Peak standing crop (live plus recent and old dead)
Method 3	Maximum minus minimum live biomass
Method 4	Sum of positive increments in live biomass
Method 5	Sum of positive increments in live and recent dead (Smalley’s Method)
Method 6	Sum of positive increments in live and total dead (recent plus old dead)
Method 7	Sum of positive increments in live and dead biomass with an adjustment for decomposition

^a Nomenclature follows Scurlock et al. (2002).

^b Differing from Scurlock et al. (2002) the »peak standing crop« method was split into two subgroups, to account for actual observed (mis-) use in literature (cf. Chapter 2.2).

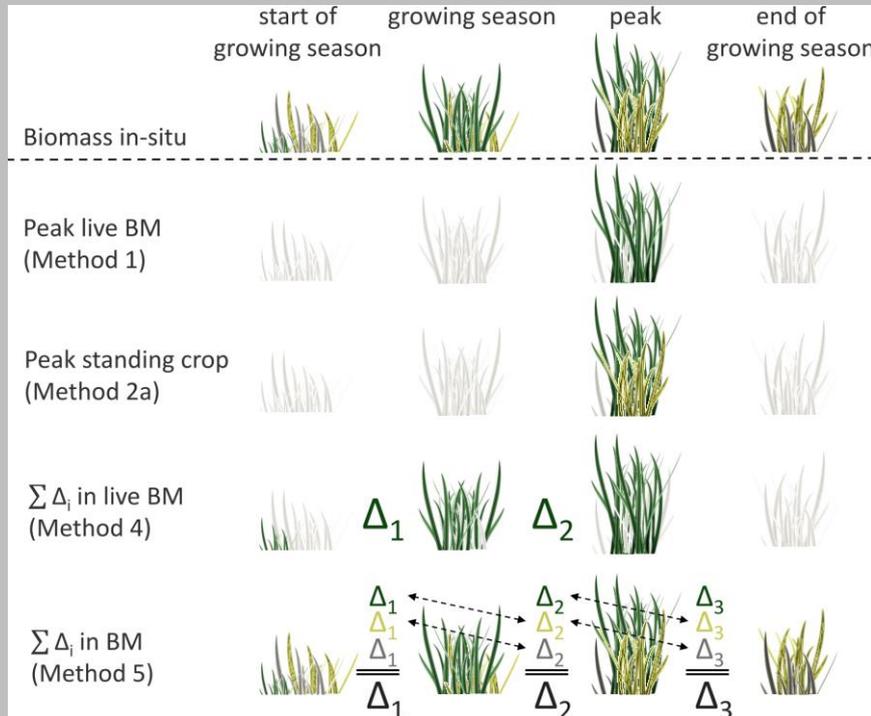


Figure 1.7: Illustrative scheme on four selected ANPP estimation methods, two peak- as well as two incremental methods. The uppermost row represents in-field biomass situation and allocation of biomass age. Green: living plant material; yellow: senescent, recently dead, material; dark-grey: moribund, last year’s dead material; and light-grey: plant biomass that is invisible for the respective method.

1.3 General Methodological Approach and Database

As described above, data on primary production (and related topics, e.g. dryland stability; see Chapter 1.1) in drylands, as well as insights in ecosystems functioning derived thereof, suffer from two general issues: (1) given the high spatiotemporal variability of dryland ecosystems, results from dryland studies are mostly anecdotal and cannot be easily up-scaled, what is hampering synthesis and functional insights. Furthermore, (2) the application of largely varying ANPP estimation methods leads to incomparability of results across studies.

Hence, even though there is an urgent need for an increased functional understanding of dryland ecosystems, especially in the light of global change (Reynolds et al., 2007), there is yet no obvious or easy to achieve strategy to satisfy it.

On a theoretical basis, there are at least two options to tackle the first issue: first, repeated mid- to large-scale long-term experiments, and second, synthesis of available knowledge and data. The first option is increasingly adapted in ecology via coordinated distributed experiments (CDE; Fraser et al., 2013). CDEs usually provide an experimental core protocol that is meant to be applied and repeated by as many scientist and sites as possible. The shared experimental layout assures comparability of results and eases joint analysis as well as spatial and temporal up-scaling of the results. NutNet (<http://www.nutnet.umn.edu/>) and FLUXNET (<http://fluxnet.ornl.gov/>) are among the best-known and most proliferate CDEs of the last decades. However, even though there are currently considerable efforts made in setting up dryland-related CDEs (e.g. Drought-Net; Smith et al., 2014, Smith pers. comm.), it will take at least 5 to 10 years to obtain first reliable results. The second option – to synthesize available knowledge and data – can be performed in various ways. The most prominent and common approach are literature reviews (Baker, 2000). These have repeatedly given proof to be versatile tools for summarization of knowledge or as opportunities to achieve functional insights as well as impetus for new research directions or even research fields. However, at the same time they have the disadvantage of rendering merely qualitative and not quantitative results. During the last decades, a new type of data-synthesis has emerged across natural sciences: meta-analyses (Glass, 1976) or, more broadly speaking, data-fusion or -integration studies (Lenzerini, 2002).

Throughout this dissertation, I will follow the latter option and present results from a meta-analysis (Chapter 2.1: Ruppert et al., 2012), as well as from data-integration studies (Chapter 2.2: Ruppert and Linstädter, 2014, and Chapter 2.3: Ruppert et al., submitted) based on assembled large to global scale data sets of dryland ANPP.

The second issue – the incomparability of ANPP data across estimation methods – is particularly assessed in the second paper underlying this dissertation (see Chapter 2.2). Here, the convertibility

between ANPP estimates derived from differing estimation methods was studied with the ultimate goal to establish reliable conversion models between the most common estimation methods.

The remaining sections of this introduction are meant to give a brief overview on the master database underlying the studies of this dissertation, as well as on data acquisition, handling and processing.

1.3.1 Data Acquisition, Handling and Processing

All studies underlying this dissertation (see Chapter 2) are based on different versions of a global ANPP database assembled between 2008 and late 2013, mostly in 2012. Most data sets derived from dryland ecosystems and only few from humid climate, the latter were added in the context of the second study (see Chapter 2.2) and were only used therein.

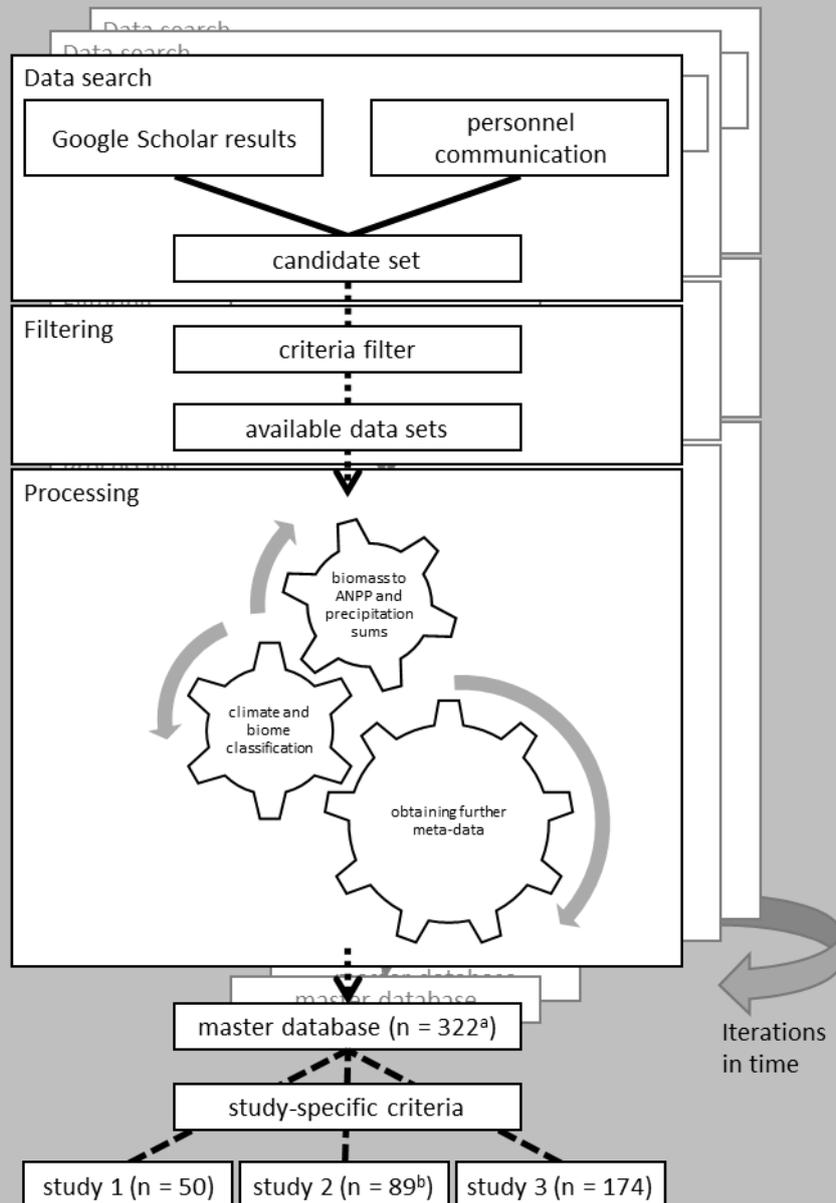
Data acquisition followed an exhaustive literature search using a comprehensive set of keywords (see Box 1.4) in Google Scholar, as this source gives more complete results compared to other systems (e.g. Web of Science; Beckmann and von Wehrden, 2012). Furthermore, especially at a later stage, studies that were received via personnel communication were added. During all stages of data assemblage, the goal was to obtain an as large and unbiased database as possible. For this reason, also data from unpublished studies was added to avoid »*publication bias*« (Rothstein et al., 2006). However, other – ecologically motivated – criteria were used to select upon all potentially available studies. Most importantly, only studies with combined ANPP and precipitation data (or where precipitation data was available from other sources) and which at least presented five years of consecutive observations were further surveyed. The latter aspect was chosen to increase the probability to observe temporal variability in ANPP and precipitation data, which is typical for drylands. This criterion was only set aside for the second study (see Box 1.4).

Studies that were regarded as potential candidates were further screened to assess whether data presented in published sources was sufficient to be incorporated in the database, or if further information was needed. Most often, additional data on soil or management characteristics of the study site, or the biomass sampling technique, and/or used ANPP estimation method were required. Roughly 10% of studies presented sufficient information. Hence, for the vast majority of studies, the original authors were contacted at least once, and were presented with a detailed and mostly study-specific questionnaire. Furthermore, whenever original authors were contacted, original biomass data was requested rather than processed ANPP estimates as well as precipitation data for the longest period available at the respective site. As this effort was surprisingly successful, meta-data for most studies incorporated in the database are more detailed and comprehensive than related published sources.

Box 1.4 – Data Search and Workflow

All data search was performed in Google Scholar. Specifically it was searched for the keywords *biomass*, *standing crop*, *primary production*, *ANPP*, *dryland*, *hyper-arid*, *arid*, *semi-arid*, *dry sub-humid*, *monitoring* and *long-term* in various combinations and spelling alterations. Furthermore, studies where biomass or ANPP derived from modeling or remote sensing were excluded to minimize measurement error, which is intrinsically associated with these techniques.

In those cases, where unpublished data was obtained via personnel communication, the original authors were granted co-authorship in the first publication using their data, if they were willing to contribute to the manuscript as well (see Chapter 2.1 and 2.3). This is common practice in meta-analytical studies (Helmut Hillebrand, pers. comm.).



^a 19.03.2014

^b 59 studies derived from the master database and 30 from the study-specific data search, see Chapter 3.2

Figure 1.8: Workflow for general data search, filtering and processing. Please note, that the literature search was repeated occasionally between 2008 and late 2013, but mostly in 2012. This is also evident in the varying database sizes throughout the three studies.

Once a data set was incorporated into the database, a series of data processing and handling steps followed. If original biomass data was available, ANPP was calculated using as many of the seven common ANPP estimation methods as possible (see Table 1.1; this was a prerequisite for Chapter 2.2). Furthermore, wherever at least daily, weekly or monthly precipitation data was available three common precipitation sums were calculated: annual precipitation, precipitation of the hydrological year, and precipitation of the growing season for the respective site. Based on this data, the standardized precipitation index (SPI, McKee et al., 1993) was calculated. The SPI is an ecological sound and commonly used precipitation index for dryland environments (Vicente-Serrano et al., 2012). All mentioned calculations as well as the data storage was realized in a relational database (MySQL 5.0.95). Besides the mentioned calculations, data processing incorporated classification of all studies, or more precisely: the sites therein, with respect to climate- and vegetation-related systems (see Chapter 1.1). For example, the climate regime of the respective sites was classified using the aridity index based on the CGIAR/UNEP global-aridity map (Trabucco and Zomer, 2009). Furthermore, biome and ecoregions for all sites were classified using the WWF biome classification (Olson et al., 2001). Both classification-steps were realized in GIS (ArcMap 10).

Furthermore, various other meta-variables were obtained from related sources or original authors, such as dominant species in all strata (herb-, bush-, and tree-layer), dominant carbon-metabolism of the community (C3, C4), soil texture (together with sand-, silt-, clay-content), nutrient-status of the soil (C-, P-, N-content, C/N ratio), experimental and management treatment (ungrazed, grazed, prescribed burning, fertilized; if present) and intensity thereof (duration and frequency of treatment; e.g. stocking density or fire-return frequency). The following overview on the database, as well as the excerpts from it, given in Chapter 7, might convey a better impression of the actual database than all description that could have been added.

1.3.2 Database

In March 2014 the assembled database comprised 322 distinct data sets (Figure 1.9) originating from 60 studies or institutions (e.g. experimental farms, see Table 1.2). In total, >4450 years of combined ANPP/precipitation observations were assembled, data on annual precipitation exceed 8550 years. The average data set length was 14.3 years (max. 77 years). Studies came from arid (n = 54), semi-arid (n = 239), dry sub-humid (n = 27) and humid (n = 2) regions and represented all broad dryland biomes as defined in this thesis (see Box 1.1). Data for grasslands (n = 120) and savannas (n = 109) was more abundant than that for shrublands (n = 53), roughly reflecting area-proportions of the respective biomes (MEA, 2005).

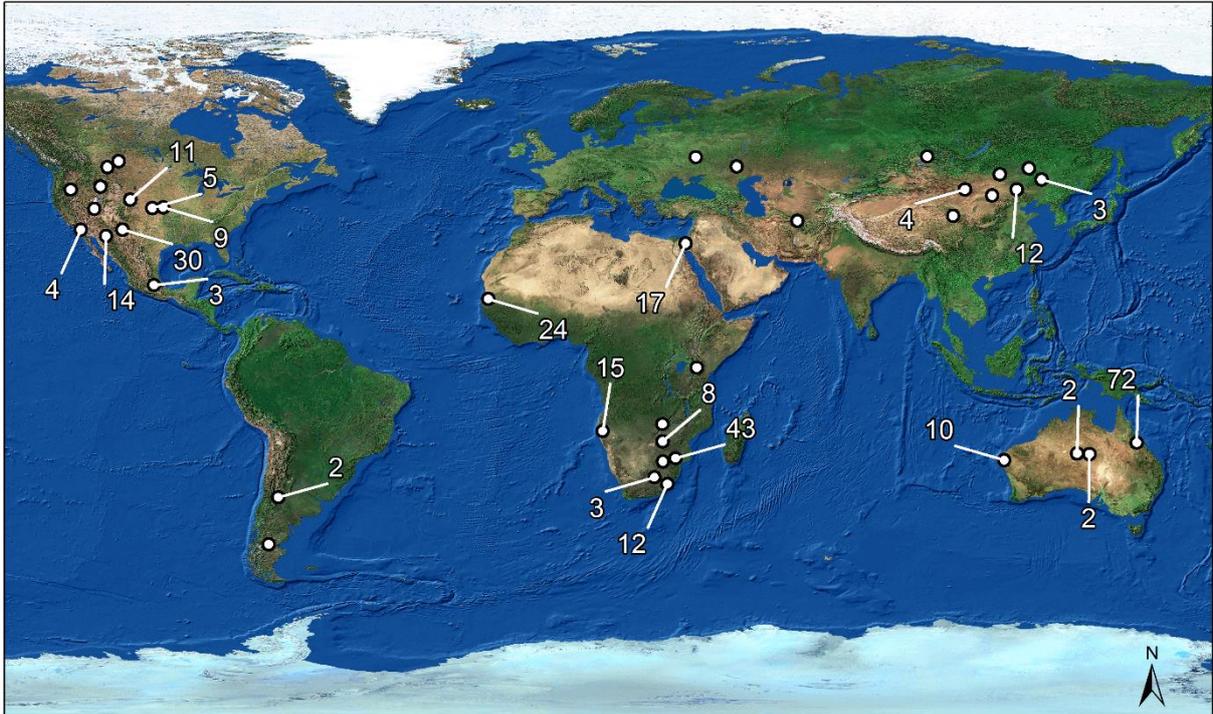


Figure 1.9: Global map of assembled dryland database used in this dissertation. In total, 322 data sets derived from roughly 50 studies were assembled. Points indicate locations, numbers refer to data sets at certain locations if >1.

Some sites (n = 40) could not be classified to either of the broad biome classes, as they were subject to massive experimental impact (i.e. clear-cutting, plowing and/or sowing). If only architectural aspects of vegetation are considered, these sites appeared grassland-like, as they only comprised herbaceous vegetation.

1.4 Aims of this Dissertation

Generally, the aims of this thesis were twofold. One main aim was to improve our understanding of ecological functioning of drylands; the second was to overcome intrinsic difficulties in data-integration approaches.

Assembling a global dryland ANPP database was originally motivated by the necessity to have a basis for a functional and quantitative assessment of the relationships between primary production and its drivers – particularly above the level of case studies. This strategy promised to render more general insights than case studies, as temporal and spatial constraints are eased. Furthermore, sufficient amounts of data, specifically long-term data sets, should allow studying impacts of rare extreme events, such as drought, on ecosystems functioning. In this respect, the functional responses of dryland primary production to climatic shocks (i.e. drought) or changes in land use (i.e. grazing) are of particular interest given the above described global change projections for drylands.

The second aim emerged during an early stage of data assemblage, when it became evident that different studies used largely varying ANPP estimation methods and were thus incomparable: How should one cope with partial incomparability between estimates of primary production?

General Introduction

In Chapter 2.1 an early version of the global ANPP dataset is used to assess global validity of the above-mentioned biotic and abiotic drivers of ANPP and rain-use efficiency. Furthermore, it is tested whether the concurring results on the shape of ANPP-precipitation relationship in literature can be reconciled. Chapter 2.2 studies the recent use of the most common ANPP estimation methods and tries to make a way out of the »*comparability dilemma*« between ANPP estimates derived by different estimation methods. Finally, Chapter 2.3 tests drylands' response to the most common realizations of global change in these regions: i.e. altered drought and grazing regimes. Responses in two aspects connected to ecosystem stability (i.e. ANPP-based resistance and recovery) should allow deduction of general recommendations for land managers as well as insights for ecosystem modelers.

Table 1.2: Overview on all 322 studies and sites in master database.

Site	No.	Country	City & province	Climate	MAP	Biome	Dom. herb. life history	Herb. C3/C4	Treatments	Duration	Source of Data / Reference
Nairobi	1	Kenya	Nairobi	dry sub-humid	680	savanna	perennial	C4	long-term enclosure	10	Kinyamario and Macharia 1992
Kaokoland	15	Namibia	Omuramba, Kunene	arid to semi-arid	340	savanna	annual (13) or perennial (2)	C4	grazed (7) and short- or long-term enclosure (8)	5 to 13	Schulte 2002 (PhD Thesis), A. Linstädter pers. comm.
Widou	24	Senegal	Vendou Barodi, Louga	semi-arid	282	savanna	annual	C4	grazed (19) and long-term enclosure (5)	27	Miehe et al. 2010
Kokstad Agricultural Research Station	12	South Africa	Kokstad, KwaZulu Natal	dry sub-humid	773	grassland	perennial	C4	short- (5) or long-term enclosure (2) or grazed and burnt (5)	5 to 11	Short 2010 (MSc Thesis), Palmer et al. 2010
Kruger National Park	43	South Africa	Kruger National Park	semi-arid	425 to 678	savanna	perennial	C4	grazed	15 to 18	pers. comm. with KNP, VCA data upon request
Sydenham	3	South Africa	Bloemfontein, Free State	semi-arid	553	grassland	perennial	C4	grazed	34	O'Connor et al. 2001
Towoomba	1	South Africa	Bela-Bela (=Warmbaths), Limpopo	semi-arid	629	grassland	perennial	C4	long-term enclosure	32	Donaldson et al. 1984, Swemmer et al. 2007
Lusaka	1	Zambia	Lusaka, Central Zambia	humid	854	grassland	perennial	C4	long-term enclosure	5	Chidumayo 2003
Matapos	4	Zimbabwe	Matapos, Matabeleland South	semi-arid	615	grassland (2) or savanna (2)	perennial	C4	long-term enclosure	16 to 19	Dye and Spear 1982
Nyamandhlovu	2	Zimbabwe	Nyamandhlovu, Matabeleland North	semi-arid	603	grassland (1) or savanna (1)	perennial	C4	long-term enclosure	15	Dye and Spear 1982
Tuli	2	Zimbabwe	Tuli, Matabeleland South	semi-arid	445	grassland (1) or savanna (1)	perennial	C4	long-term enclosure	15	Dye and Spear 1982
El Divisadero	1	Argentina	Mendoza Plains, Mendoza	semi-arid	293	shrubland	perennial	C4	unknown	7	Guevara et al. 1997
Nacunan	1	Argentina	Mendoza Plains, Mendoza	semi-arid	294	shrubland	perennial	C4	unknown	7	Guevara et al. 1997
Rio Mayo	1	Argentina	Rio Mayo, Chubut	semi-arid	163	shrubland	perennial	C3	long-term enclosure	10	Jobbagy and Sala 2000
Agriculture Canada Research Substation	1	Canada	Manyberries, Alberta	semi-arid	335	grassland	perennial	C3	short-term enclosure	77	Smoliak 1986, Thorpe et al. 2008
Matador Field Station	1	Canada	Matador near Swift Current, Saskatchewan	semi-arid	374	grassland	perennial	C3	long-term enclosure	5	DeCouturie and Ripley 1973
Montecillo	3	Mexico	Texcoco City, Texcoco	semi-arid	572	grassland	perennial	C4	annual burnt short-term enclosure	6 to 21	Garcia-Moya pers. comm.
Chihuahuan Desert Rangeland Research Center	1	U.S.A.	Las Cruces, New Mexico	arid to semi-arid	251	grassland	perennial	C4	grazed	34	Khumalo and Holechek 2005
Agricultural Research Center Hays	5	U.S.A.	Hays, Kansas	semi-arid	579	grassland	perennial	C4	short- (2) or long-term enclosure (1), grazed (1) or grazed and burnt (1)	7 to 24	Harmony 2007, Hulett and Tomanek 1969
Desert Experimental Range	1	U.S.A.	near Milford, Utah	arid	143	shrubland	perennial	both	unknown	9	Sneva and Hyder 1962
High Plains Grass Research Station	4	U.S.A.	near Cheyenne, Wyoming	semi-arid	374	grassland	perennial	C4	short- (4) and long-term enclosure (1)	13 to 18	Manley et al. 1997, Andales et al. 2006
LTER Jornada Basin	19	U.S.A.	Las Cruces, New Mexico	arid to semi-arid	216 to 258	grassland (10) or shrubland (9)	annual (1) or perennial (18)	C4	unknown	15 to 20	Herbel et al. 1972
LTER Konza Prairie	9	U.S.A.	Manhattan, Kansas	dry sub-humid	838	grassland	perennial	C4	short- (3) long-term enclosure (6) & prescribed fires (1, 4, 20 yrs)	10 to 28	Heisler and Knapp 2008

Table 1.2 continued.

Site	No.	Country	City & province	Climate	MAP	Biome	Dom. herb. life history	Herb. C3/C4	Treatments	Duration	Source of Data / Reference
LTERR Seviella	10	U.S.A.	Albuquerque, New Mexico	arid	248	grassland (7) or shrubland (3)	perennial	C4	long-term enclosure, some burnt (4) or fertilized (1)	6 to 11	Muldavin et al. 2008
LTERR Shortgrass Steppe	7	U.S.A.	Nunn, Colorado	semi-arid	332 to 342	grassland	perennial	C4 (6) or both (1)	short- (5) or long-term enclosure (2)	17 to 50	Lauenroth and Sala 1992
Santa Margarita Experimental Range	2	U.S.A.	Riverside County, California	semi-arid	329	shrubland	-	-	long-term enclosure (1) or fertilized (1)	8	Vourlitis 2012
Santa Rita Experimental Range	14	U.S.A.	Tucson, Arizona	arid	314 to 434	shrubland	perennial	C4	grazed	10 to 11	Martin and Cable 1974, Cable 1975
Sky Oaks Field Station	2	U.S.A.	San Diego County, California	semi-arid	444	shrubland	-	-	long-term enclosure (1) or fertilized (1)	8	Vourlitis 2012
Squaw Butte Experiment Station	1	U.S.A.	Squaw Butte near Burns, Oregon	arid	267	grassland	perennial	C3	grazed	7	Sneva and Hyder 1962
US Sheep Experimental Station	1	U.S.A.	Upper Snake River Plains near Dubois, Idaho	arid	280	shrubland	perennial	C3	long-term enclosure	13	Blaisdell 1958, Sneva and Hyder 1962
Damao Qi	1	China	Damao Qi, Inner Mongolia	arid	255	grassland	perennial	C3	long-term enclosure	12	Bai et al. 2001
Habai	1	China	Habai Region, Qinghai	semi-arid	589	grassland	perennial	C3	long-term enclosure	14	Qiji et al. 1998, Guo et al. 2006
Inner Mongolia Grassland Ecosystem Research Station	1	China	Xilin River Basin, Inner Mongolia	semi-arid	344	grassland	perennial	C3	long-term enclosure	20	Ma et al. 2010
Inner Mongolia Plateau	3	China	Inner Mongolia	semi-arid	348 to 379	grassland	perennial	C3	long-term enclosure	12	Bai et al. 2001
Tumugi	3	China	Ulan Hot, Inner Mongolia	dry sub-humid	411	grassland	perennial	C3	long-term enclosure	10	Xiao et al. 1996
Xilin Basin	7	China	Xilin River Basin, Inner Mongolia	semi-arid	296	grassland	perennial	C3	short- (6) or long-term enclosure (1)	6	Schönbach et al. 2012
Xilingol	2	China	Xilinhot, Xilingol	semi-arid	361	grassland	perennial	C3	long-term enclosure	10	Xiao et al. 1995
En Ya'aqov	1	Israel	En Ya'aqov, North District	dry sub-humid	727	shrubland	perennial	C3	long-term enclosure	23	Golodets et al. 2013, pers. comm.
Karei Deshe Experimental Farm	7	Israel	Karei Deshe, North District	semi-arid	558	grassland	annual	C3	grazed (6) or long-term enclosure (1)	17	Sternberg et al. 2000, Henkin et al. 2011
Lahav	1	Israel	Lahav, South District	semi-arid	219	shrubland	annual	C3	long-term enclosure	10	Golodets et al. 2013, pers. comm.
Lehavim	2	Israel	Lehavim, South District	semi-arid	298	shrubland	annual	C3	grazed (1) or long-term enclosure (1)	18 to 24	Golodets et al. 2013, pers. comm.
Matta	1	Israel	Mata, Jerusalem	semi-arid	498	shrubland	annual	C3	long-term enclosure	10	Golodets et al. 2013, pers. comm.
Ofer	1	Israel	Ofer, Haifa	semi-arid	580	shrubland	perennial	C3	long-term enclosure	12	Golodets et al. 2013, pers. comm.
Ramat Hanadiv	1	Israel	Ramat Hanadiv, Haifa	semi-arid	610	shrubland	annual	C3	long-term enclosure	11	Golodets et al. 2013, pers. comm.
Sede Boquer	1	Israel	Sede Boker, South District	arid	73	shrubland	perennial	C3	long-term enclosure	10	Golodets et al. 2013, pers. comm.
Shaked Park	1	Israel	Ofakim, South District	semi-arid	165	shrubland	annual	C3	long-term enclosure	12	Golodets et al. 2013, pers. comm.
Yechiam	1	Israel	Yechiam, North District	dry sub-humid	780	shrubland	annual	C3	long-term enclosure	10	Golodets et al. 2013, pers. comm.

Table 1.2 continued.

Site	No.	Country	City & province	Climate	MAP	Biome	Dom. herb. life history	Herb. C3/C4	Treatments	Duration	Source of Data / Reference
Dzhanybek	1	Kazakhstan	Dzhanybek, West Kazakhstan	semi-arid	283	grassland	perennial	C3	long-term enclosure	33	Gilmanov et al. 1997
Gobi Desert	4	Mongolia	Gobi Gurvan Saykhan National Park, Ömnögovī	arid	122	grassland	perennial	C3	grazed (3) or long-term enclosure	6	Wesche and Retzer 2005
Tumentsogt	1	Mongolia	Ondorhaan	semi-arid	271	grassland	perennial	C3	long-term enclosure	9	Togtohyn et al. 1996
Kursk	1	Russia	Kursk, Oblast Kursk	humid	583	grassland	perennial	C3	long-term enclosure	29	Gilmanov et al. 1997
Tuva	1	Russia	Kyzyl, Tuva	semi-arid	285	grassland	perennial	C3	long-term enclosure	6	Gilmanov et al. 1997
Badkhyz	1	Turkmenistan	Kushka	arid	292	grassland	perennial	C3	long-term enclosure	34	Gilmanov et al. 1997
Boothathana Farm	10	Australia	Boothathana Farm, Western Australia	arid	201	shrubland	annual (5) or perennial (5)	C4	grazed	12	Holm et al. 2003
Cardigan	36	Australia	Cardigan, near Charters Towers, Queensland	semi-arid	596	grassland (8), art. grassland (20) or savanna (8)	perennial	C4	grazed + full-factorial comb. of clear-cut, fert., sowing & plowing	8	McIvor et al. 1995, pers. comm.
Central Mount Wedge	2	Australia	Central Mt. Wedge, near Alice Springs, Northern Territory	arid	416	savanna	annual (1) or perennial (1)	C4	long-term enclosure	6	Foran et al. 1982
Hillgrove	36	Australia	Hillgrove, near Charters Towers, Queensland	semi-arid	532	grassland (8), art. grassland (20) or savanna (8)	perennial	C4	grazed + full-factorial comb. of clear-cut, fert., sowing & plowing	11	McIvor et al. 1995, pers. comm.
Mount Riddock	2	Australia	Mt. Riddock, near Hartes Range, Northern Territory	arid	457	savanna	annual	C4	grazed or long-term enclosure	6	Foran et al. 1982

2. Publications of the Dissertation

- 2.1 Meta-Analysis of ANPP and Rain-Use Efficiency confirms indicative value for Degradation and Supports non-linear Response along Precipitation Gradients in Drylands
- 2.2 Convergence between ANPP Estimation Methods in Grasslands – A practical Solution to the Comparability Dilemma
- 2.3 Quantifying Dryland Resistance and Resilience to Drought: The Importance of Drought Intensity, Grazing Regime and Vegetation Structure

2.1 Meta-Analysis of ANPP and Rain-Use Efficiency confirms indicative value for Degradation and Supports non-linear Response along Precipitation Gradients in Drylands

Jan C. Ruppert, Alexander Holm, Sabine Miehe, Esteban Muldavin, Hennie A. Snyman, Karsten Wesche & Anja Linstädter (2012), *Journal of Vegetation Science* 23: 1035-1050, DOI: 10.1111/j.1654-1103.2012.01420.x



Meta-analysis of ANPP and rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands

Jan C. Ruppert, Alexander Holm, Sabine Miehe, Esteban Muldavin, Hennie A. Snyman, Karsten Wesche & Anja Linstädter

Keywords

ANPP_{max}; Degradation indicator; Ecosystem functions; Grazing; Land use; Linear piece-wise quantile regression; Rangeland indicators; RUE_{max}; Water-use efficiency

Abbreviations

RUE = Rain-use efficiency; ANPP = Above-ground net primary production; LPQR = Linear piece-wise quantile regression

Received 31 May 2011

Accepted 3 April 2012

Co-ordinating Editor: David Ward

Ruppert, J.C. (corresponding author, jan.ruppert@uni-koeln.de) & **Linstädter, A.** (anja.linstaedter@uni-koeln.de): Botanical Institute, University of Cologne, D-50674, Cologne, Germany

Holm, A. (aholm@bigpond.net.au): Alexander Holm & Associates, PO Box 1835, Fremantle, WA, 6959, Australia

Miehe, S. (sabine.miehe@gmx.net): Faculty of Geography, University of Marburg, D-35037, Marburg, Germany

Muldavin, E. (muldavin@unm.edu): Biology Department, University of New Mexico, Albuquerque, NM, 87131, USA

Snyman, H.A. (snymanha@ufs.ac.za): Department of Animal, Wildlife & Grassland Sciences, University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa

Wesche, K. (karsten.wesche@senckenberg.de): Department of Botany, Senckenberg Museum for Natural History, PO Box 300 154, D-02806, Görlitz, Germany

Ruppert, J.C.: Current address: Institute for Crop Science and Resource Conservation, University Bonn, D-53115, Bonn, Germany

Abstract

Questions: In drylands *above-ground net primary production* (ANPP) and *rain-use efficiency* (RUE) are common ecological indicators for assessing ecosystem state, including degradation and supply of key ecosystem services. However, both indicators have been criticized as ‘lumped’ parameters, since they aggregate complex information. Their value as ecological parameters in decision-making and their use in ecological modelling therefore have been challenged and their explanatory power remains unclear. Furthermore, there is no consensus about the response of ANPP and RUE along precipitation gradients.

Methods: Taking advantage of several long-term studies in (semi-)arid environments where ANPP and RUE were recorded, we compiled a data set of 923 yr. We used meta-analysis to disentangle the effects of different ecological layers (climate, soil and land use) on ANPP and RUE. Linear piece-wise quantile regression (LPQR) was used to analyse the response of maximum and median ANPP and RUE as functions of precipitation. We assumed that looking at maximum response (instead of ‘average’ response) stratified for land-use intensity was an ecologically more plausible way to understand ANPP constrained by precipitation and land use.

Results: We separated the impact of different environmental factors into distinct, quantitative effect sizes with the aid of meta-analyses. ANPP was affected by recent and previous precipitation, land use, soil and biome. LPQR revealed that both parameters displayed several sequential linear intersects, which together formed a unimodal trend, peaking around precipitation of 200 mm yr⁻¹. Unimodal response was more pronounced for maximum values (ANPP_{max}, RUE_{max}) than for median values. Peak ANPP_{max} and RUE_{max}, as well as post-peak decline (>200 mm yr⁻¹) were affected by land use: higher land-use intensity decreased intercepts and increases post-peak decline.

Conclusions: Our results have important consequences for the use of RUE as an ecosystem indicator and a tool in ecosystem monitoring and decision-making. Most importantly, grasslands, shrublands and savannas significantly differ in their primary production, with a biome-specific importance of precipitation, land use and previous year’s precipitation. We thus propose to establish biome-specific reference values of maximum and average RUE. Our study also contributes to reconcile contradictory findings for ANPP and RUE response along precipitation gradients of varying length.

Introduction

In our changing and complex world, there is an urgent need for suitable ecological indicators that allow a fast and focused access to nature. These should serve as easy-to-use strategies to assess environmental conditions, to detect complex processes or to quantify supply of ecosystem services. Therefore, development and application of indicators are not easy tasks, especially in ecosystems where high natural variability has to be separated from effects of land use and climate change (Niemi & McDonald 2004; Wessels et al. 2007). Examples of ecosystems with high temporal and spatial environmental variability (Sharon 1972; Davidowitz 2002; Ward 2009) and with considerable potential for change are arid and semi-arid environments that are mainly used as rangelands. These drylands have often been considered as nature's 'unappreciated gift' and are expected to undergo tremendous climatic change within the next 100 yr, threatening livelihoods of about 2.5 billion people (MEA 2005; UNDP 2008a,b).

In drylands two ecological parameters commonly used for assessing ecosystem state are *above-ground net primary production* (ANPP) and *rain-use efficiency* (RUE; the quotient of ANPP and the corresponding precipitation; Le Houérou 1984). For these purposes, ANPP and RUE have some major advantages over other ecological indicators such as indicator species or plant functional types. First, ANPP and RUE data are comparatively easy and cheap to collect. Second, the principal ability of ANPP and RUE to assess an ecosystem's state (including degradation and desertification) has been widely confirmed (Sala et al. 1988; Snyman & Fouché 1991; Prince et al. 1998; Diouf & Lambin 2001; Holm et al. 2003; Buis et al. 2009). Lastly, ANPP and RUE allow cross-system and cross-scale comparisons due to their general character and because a large body of data is available. This has made ANPP and RUE common currency for a wide range of environmental studies, not only in drylands (Huxman et al. 2004; McCulley 2005).

Despite their widespread application, both indicators face growing criticism (Prince et al. 1998; Retzer 2006; Linstädter & Baumann 2012). Although RUE has been frequently used in the past 25 yr – particularly as an indicator for land-use effects on ecosystem state – its limitations and opportunities have, since its original publication by Le Houérou (1984), not been studied in a rigorous manner, except for some special applications (e.g. RUE_{max} in Huxman et al. 2004).

One of the strongest criticisms is that ANPP and RUE both aggregate complex information, resulting in a loss of specific information and interpretational power. Consequently, they have been referred to as 'lumped' parameters (Jarvis 1993; Prince et al. 1998). Biotic and abiotic factors known to influence ANPP and/or RUE are precipitation

parameters such as intra- and inter-annual variability of precipitation (Milchunas & Lauenroth 1993; Paruelo et al. 1999; Yang et al. 2008; Miede et al. 2010), soil characteristics (Le Houérou et al. 1988; Sala et al. 1988; Diouf & Lambin 2001; Huxman et al. 2004; Linstädter & Baumann 2012), land use (Snyman & Fouché 1991; Snyman 1998; Paruelo et al. 1999; O'Connor et al. 2001; Holm et al. 2003; Linstädter et al. 2010; Linstädter & Baumann 2012) and biome (Le Houérou 1984; Snyman 1998; O'Connor et al. 2001; Huxman et al. 2004). Even though numerous studies describe the influence of biotic and abiotic factors on ANPP and RUE, none of these were designed to produce standardized quantitative measurements of the complex and interactive factors influencing both indicators. With respect to the large number of factors influencing ANPP and RUE, many authors have come to the conclusion that ANPP or RUE alone are inappropriate to assess ecosystem state or degradation in drylands, and argue that further local information is needed in order to separate degradation from environmental variation (Retzer 2006; Wessels et al. 2007; Bai et al. 2008; Snyman 2009).

The most critical issue in this context is the lack of consensus about trends of ANPP and RUE along precipitation gradients, which makes it difficult to extrapolate these parameters across space and time (Varnamkhandi et al. 1995; Paruelo et al. 1999), or to use them in ecological modelling. While most studies report a linear relationship between precipitation and ANPP (McNaughton et al. 1993; Ward & Ngairorue 2000; O'Connor et al. 2001; McCulley 2005; Bai et al. 2008; Muldavin et al. 2008), others assume a saturation relationship, where ANPP increases with precipitation, but levels off under more humid conditions (Hein 2006; Yang et al. 2008; and partly Huxman et al. 2004; Miede et al. 2010). The same confusion applies to trends between precipitation and RUE: some studies find RUE to be a constant rate across temporal and spatial precipitation gradients (e.g. Paruelo 2000), others describe a linear increase (Bai et al. 2008) or an unimodal response of RUE (Le Houérou 1984; Paruelo et al. 1999; O'Connor et al. 2001; Hein 2006; Hein & Ridder 2006; Miede et al. 2010). If the latter is assumed, conversion of rainfall into primary production is low at the dry and the wet end of a precipitation gradient and peaks at intermediate levels where vegetation-relevant and/or biogeochemical constraints are assumed to be less pronounced. However, due to an inherent autocorrelation between these two parameters, at this point it remains unclear whether it is justified to present such a trend between RUE and annual precipitation at all (Prince et al. 2007). Hence, there is a tremendous gap between the widespread and frequent use of ANPP and RUE in drylands on the one hand, and their theoretical validation as ecological indicators on the other. In particular, their indicative

value for degradation processes along temporal and spatial precipitation gradients remains unclear above the level of case studies.

The usability of ANPP to indicate grazing effects on ecosystem state is further complicated by the fact that grazing effects on plant fitness and growth are highly variable: they can be positive, neutral or negative, depending on the system under consideration (Milchunas & Lauenroth 1993). While it is generally agreed that severe over-utilization will decrease plant growth due to negative effects of frequent defoliation on plant resources (Belsky 1986; Ferraro & Oesterheld 2002), moderate levels of grazing might even promote plant growth. A compensation or over-compensation of defoliation losses was found in a number of studies from savannas (McNaughton 1979, 1983) and other semi-arid ecosystems (McNaughton et al. 1996; Jacobs & Schloeder 2003; Abdel-Magid et al. 2004). While ecologists today agree that plants can, to a certain extent, compensate for the effects of herbivory, a complete compensation or over-compensation is reported to be rare (Belsky et al. 1993; Milchunas & Lauenroth 1993), and a mechanistic understanding of the underlying processes is far from being reached (Bagchi & Ritchie 2011). Compensation at ecosystem level can usually be attributed to the effects of grazing being mitigated by a reduced local competition (Belsky 1987). However, compensation may be limited by available plant resources (Belsky 1986; Leriche et al. 2003). Apparently, compensation depends upon whether, and how, grazing influences the limiting resources for plant growth (Wise & Abrahamson 2005; Bagchi & Ritchie 2011). As we still lack a fundamental understanding of why herbivores have variable effects on plant growth at different sites (Bagchi & Ritchie 2011), different methods to estimate ANPP may over- or underestimate ANPP in different and unpredictable ways (Scurlock et al. 2002). For the time being, the best practical solution is to make cross-system comparisons by using the same or comparable methodology of ANPP estimation. We follow this approach in our study (see Table 1).

The aim of this study is to address conceptual and practical problems with the use of ANPP and RUE as ecological indicators in drylands. It aims to elucidate the response of ANPP and RUE to precipitation, and to other factors known to have an influence, such as biome type, soil conditions and land use (i.e. grazing) in order to achieve a functional understanding to also facilitate a better integration of both ANPP and RUE into ecological models.

The study developed from the following key questions: What is the trend between ANPP and RUE as functions of precipitation? Is it justified to analyse the relationship between RUE and precipitation gradients, despite their inherent autocorrelation? Which factors influence ANPP and RUE, and their response to precipitation? How can

these effects be measured quantitatively and not only qualitatively? To this end we combined conceptual considerations with a meta-analysis on mid- to long-term ecological studies from water-limited environments, with a quantile regression analysis of ANPP and RUE along precipitation gradients.

Methods

Data set

Within the last three decades, effects of different variables on ANPP and RUE have been addressed in numerous studies worldwide. Taking advantage of this body of publications, we aimed to compile field studies covering a broad range of variation to assess the response of ANPP and RUE to various environmental conditions. We identified potentially relevant biotic and abiotic site properties from our literature review, and selected a suite of predictor variables (four climatic and edaphic parameters and two land use parameters; for a detailed description of variables, see Table S1 in Supporting Information). Response variables were ANPP and RUE.

Following the implications of a recent discussion on meta-analysis (Gillman & Wright 2010; Hillebrand & Cardinale 2010; Whittaker 2010), we established a criteria catalogue fitted for our research questions. We only considered studies from rangelands where grazing was experimentally manipulated or excluded and which provided detailed information on land use, or where the original authors could provide such information. We considered two parameters reflecting different aspects of land use. The parameter *stocking density* (as tropical livestock units per hectare) represents recent grazing pressure. Since livestock indices varied between studies, several conversions had to be established (see Appendix S1). The parameter *land-use intensity* not only comprises recent land use by grazing but also considers the environmental history of a site with respect to grazing pressure. It is based on degradation signs of the vegetation, such as changes in plant composition, community structure and/or density (see original studies for more details; Table 1).

As RUE is only useful and valid where precipitation is the main limiting factor for plant growth and productivity (Le Houérou 1984), we only considered studies from arid to semi-arid sites (mean annual precipitation = MAP between 130 and 537 mm). Since these regions are known for their high inter-annual variability in precipitation (Davidowitz 2002; Ward 2009) we selected mid- to long-term monitoring studies with at least 5 yr of consecutive observation in order to cover a wide range of annual variability of rainfall found at the given sites. Hereby, we aimed to capture the full temporal variability in these three parameters, which is

Table 1. Overview on the study database used for the meta-analysis and/or for performing the linear piece-wise quantile regression.

	Guevara et al. 1997	Holm et al. 2003	Muldavin et al. 2008	H. A. Snyman (O'Connor et al. 2001; Snyman 2009)	DEFCCS/GIZ Project Ferlo (Miehe et al. 2010)	A. Linstädler née Schulte (Schulte 2002)	Wesche & Reitzer 2005
Site and study Information							
Region	Andes, Argentina	West Australia	New Mexico, USA	South Africa	Ferlo, Senegal	Namibia	Mongolia
Latitude ¹	32° S–28° S	24°31' S	34°20' N	28°50' S	15°59' N	17°06' S–17°11' S	43°36' N
Longitude ¹	67° W–69° W	113°42' E	106°43' W	26°15' E	15°19' W	13°13' E–13°24' E	103°46' E
Altitude (m) asl ¹	400–600	5	1600	1350	40	740–940	2300
Field study design	Temporal	Temporal	Temporal	Temporal	Temporal	Temporal	Temporal
Duration (years)	7	12	6	30	27	5	5–6
Monitoring sites	2	1	1	1	1	1	1
Treatments	2	10	2	3	24	5	4
Biome	Shrubland	Shrubland	Grass- and shrubland	Grassland	Savanna	Savanna	Grassland
Predominant life form	Perennial	Perennial	Perennial	Perennial	Annual	Annual	Perennial
Precipitation	Winter rain	Winter rain	Mixed	Summer rain	Summer rain	Summer rain	Summer rain
Rain regime	244 (±54) & 260 (±102)	228 (±90)	259 (±67)	537 (±39)	285 (±93.5)	270 (±93)	130 (±46)
MAP (mm/a) ²							
Soil	Silty substrates	Loamy substrates	Loamy substrates	Loamy substrates	Sandy substrates	Sandy substrates	Loamy substrates
Dominant soil class							
Land use							
Treatment type(s) ³	Grazing (mix)	Grazing (ss)	Exclosure (l)	Grazing (ss)	Exclosure (l), grazing (mix)	Grazing (ca)	Exclosure (s), grazing (ls, mix, ss)
Stocking density (TLU) ⁴	0.04–0.08	0–0.1	0	0–0.4	0–0.32	0.1	0–1.6
Land-use intensity ⁴	2	1–3	0	0–3	0–3	2–3	0–4
Method for ANPP estimation ⁵	End-of-season standing crop (2)	End-of-season standing crop (1)	Season's incremental biomass (4)	End-of-season standing crop (2)	End-of-season standing crop (2)	End-of-season standing crop (2)	End-of-season standing crop (2)

¹Where ranges of values are presented (for latitude, longitude, altitude) see original study.

²MAP is mean annual precipitation, the standard deviation (StDev) for the same time period is presented in brackets.

³Treatment types: grazing – ca (cattle), ls (largestock), mix (mixed livestock), ss (smallestock); exclosure – l (long), s (short).

⁴TLU values were partly transformed from other livestock indices (e.g. DSE, LSU). Land use intensity (0 = none, 1 = little, 2 = moderate, 3 = severe, 4 = extreme) subsumes past and recent impacts of land use reflected in rangeland degradation (as indicated in the publication or by the author). It is based on degradation signs of the vegetation, such as changes in composition and structure.

⁵The numbers in brackets refer to the method nomenclature in Scurlock et al. 2002: (1) Peak live biomass, (2) Peak standing crop, (4) Sum of positive increments.

The complete database covers around 30 variables for about 930 single years (duration * treatments).

typical for drylands. Accordingly, we excluded short-term studies. Furthermore, short-term studies are not suitable to measure the impact of previous year's precipitations on plant productivity, an effect that is assessed in our meta-analysis. Studies were selected through a structured literature search in well-known literature databases, as well as from personal communications. To keep ANPP proxies comparable, we only included studies that did not use movable cages (see McNaughton et al. 1996) and that measured ANPP either as incremental growth over the whole growing period or – where grazing was excluded or was negligible during the vegetation period – as peak standing biomass. We searched the literature using the keywords 'biomass', 'standing crop', 'primary production', 'ANPP', 'rain use efficiency', 'precipitation use efficiency', 'dry-

land', 'arid', 'semi-arid', 'grazing', 'pasture', 'rangeland', 'land use', 'soil', 'monitoring' and 'long-term' in various combinations and spelling alterations.

In sum, 50 distinguishable treatment plots from eight monitoring sites published in seven studies were assembled, covering 923 yr of observation (see Table 1 and Table S1). Studies were carried out in Africa, Central and Southern America, Australia and Central Asia. They represent savanna, shrubland and grassland biomes, the last having no tree layer. In the case of savanna vegetation, data refer to the grass layer only due to the positioning and size of harvesting plots. MAP values range between 130 and 540 mm, and annual precipitation values between 69 and 725 mm (Table 1).

Most statistical analyses were performed using the 50 treatments as reference sample ($n = 50$), deviations are

Table 2. Results of weighted meta-analysis of different effect variables on ANPP.

1: Overall Effects on ANPP				
	df	p	Effect size (ϵ^{++})	Bootstrap CI (95%)
Precipitation	49	0.50	0.55	0.4710 to 0.6351
Previous year's precipitation	48	≥ 0.99	0.07	0.0145 to 0.1231
Stocking density ¹	4	0.19	-0.21	-0.4129 to -0.1252
Land-use intensity ¹	4	0.34	-0.30	-0.4985 to -0.1690
2: Categorical models for the effect of precipitation on ANPP				
(a) Biome				
Heterogeneity	df	p ²		
Between groups (QM)	2	≤ 0.001		
Within groups (QE)	47	≥ 0.99		
Total (QT)	49	0.37		
	df	p ²	effect size (ϵ^+)	Bootstrap CI (95%)
Grassland	7	0.84	1.04	0.8884 to 1.2521
Shrubland	12	1.00	0.71	0.6588 to 0.7711
Savanna	28	0.99	0.43	0.3763 to 0.4864
(b) Soil class				
Heterogeneity	df	p ²		
Between groups (QM)	2	≤ 0.001		
Within groups (QE)	43	≥ 0.99		
Total (QT)	45	0.29		
	df	p ²	Effect size (ϵ^+)	Bootstrap CI (95%)
Loamy substrate	18	0.95	0.88	0.7577 to 0.9971
Sandy substrate	19	0.98	0.45 n.s.	0.3849 to 0.5092
Silty substrate	6	0.83	0.37 n.s.	0.2744 to 0.4618

Notes: All randomization calculations were performed with 9999 iterations.

¹Effect sizes were calculated between studies and not between treatments.

²The estimate of the pooled variance was ≤ 0 , therefore the data were analysed using a fixed effects model.

The table gives the effect sizes (ϵ) and the corresponding confidence interval (95%, bootstrapped), the degrees of freedom (df) and the probability levels for heterogeneity (p), which have been calculated through randomization (wherever possible – see above). Effect sizes were calculated on the basis of z-transformed Spearman correlation coefficients (r^2). Table 2-1 reports overall results of effect variables on ANPP. Table 2-2 presents detailed results based on categorical modelled meta-analysis for the effect of precipitation on ANPP, including p-levels for heterogeneity within and between groups; (a) effect of precipitation on ANPP within different biomes and (b) on different soil classes.

indicated (Table 2). For nearly all studies we acquired raw data and additional information from the corresponding authors. Only the data from Guevara et al. (1997) were directly taken from the publication.

Statistical analyses

ANPP data were outlier-adjusted by eliminating values that exceeded the range of twice the standard deviation around the mean of the respective site. Some environmental variables had to undergo standardization (see Appendix S1). To analyse ANPP and RUE along precipitation gradients, we applied a linear piece-wise quantile regression (LPQR; Cade & Noon 2003). Effects of all environmental predictor variables on ANPP and RUE were separated and quantified in a standardized way by calculating weighted meta-analyses (Rosenberg et al. 2000). The LPQR is a non-linear regression method that can be understood as an expansion of linear (least squares) regression (Toms & Lesperance 2003; Ryan & Porth 2007). Not only one, but several sequential, intersecting linear regressions are fitted to user-defined quantiles, respective percentiles, of the data (Koenker & Bassett 1978). Which quantiles are analysed depends on the underlying research questions and hypotheses of the researcher (Cade & Noon 2003). LPQR, or quantile regression in general, can be compared with different measures of central tendency and statistical dispersion.

Thus LPQR provides a flexible and robust analysis of heterogeneous data sets (Cade & Noon 2003; Cottingham et al. 2005). Using high percentiles (95th and higher) instead of the median (i.e. the 50th percentile) also provides a statistical solution to the examination of ecological limiting factors (Cade & Noon 2003; Cox et al. 2006). In our case, (unmeasured) environmental factors may act as limiting constraints on primary production. Analysing the change in the mean (or median) response to precipitation will then not result in an ecologically sound picture (Visser et al. 2006). In contrast, analysing the upper boundary of the distribution will give a better and ecologically more plausible estimation of responses to the variable of interest: along the upper boundary the dependent variable (here: ANPP) is potentially constrained only by the independent variable (here: precipitation; see Cade & Noon 2003; Sankaran et al. 2005). This idea of using the upper boundary in LPQR is highly compatible with the idea of boundary regression (Blackburn et al. 1992; Lessin et al. 2001). Hence, quantile regressions focusing on the upper boundary (≥ 95 th quantile) of a data set have been frequently used in recent ecological studies to analyse limiting factors for plant growth, or to describe a system's production potential (Jauffret & Visser 2003; Sankaran et al. 2004; Cox et al. 2006; Visser et al. 2006; Visser & Sasser 2009; Adler et al. 2011).

To evaluate the response of ANPP and RUE to precipitation as the potential constraint (or limiting factor), we used LPQR along the 99th percentile. For comparison purposes we also calculated the response along the median as a measure of central tendency (see also Table S5). Precipitation values were calculated for local hydrological years, with respect to the corresponding rainfall regime of the sites. Therefore all precipitation values match with primary production of the corresponding growth period. LPQRs were computed with the *quantreg* module (v.4.71) in the statistical software R (R Core Development Team, R Foundation for Statistical Computing, Vienna, Austria).

Meta-analysis

Meta-analysis refers to analysis of analyses and is able to integrate findings of large collections of individual studies into overall results, to reveal new findings and cross-links (Glass 1976). We used this statistical tool to test the effects of biome, climatic and edaphic parameters, and land-use parameters on ANPP and RUE.

We calculated effect sizes as z-transformations of Spearman correlation coefficients (a *Fischer's z-transform*, z or r^z), a standard effect size in meta-analysis (Rosenberg et al. 2000; Cohen 1992). Because all effect sizes were calculated on the same mathematical basis, we were able to compare the magnitude of total effect sizes (ϵ^{++}) and group effect sizes (ϵ^+) in a quantitative manner. Effect sizes were calculated for two different data levels: site level ($n = 8$) and treatment level ($n = 50$), where the number of treatments is the number of distinct experimental settings (e.g. experimental manipulation of grazing pressure or stocking density, see Table 1). Hence, effect sizes were calculated between studies for the variables *stocking density* and *land-use intensity*, as these variables did not vary within treatments but within studies (Table 2 and Table S3). We marked these cases accordingly.

All calculations were performed as weighted meta-analyses using random effects model and 9999 iterations for randomization steps. Average (total) effect sizes (ϵ^{++}) and 95% bootstrapped confidence intervals (CI) were calculated, as well as analyses of heterogeneity (Q). Mixed-model analysis of heterogeneity was used to test variation of effect sizes with important predictor variables, comprising the categorical factors biome (grassland, savanna, shrubland), rain regime (summer and winter rain, mixed regimes) and soil. Using information on soil texture provided in the original publications, soils were assigned to three texture classes (*loamy*, *sandy* and *silty substrates*), reflecting soil characteristics relevant for primary production in drylands, such as infiltration and runoff, water storage capacity and evaporation (Alizai & Hulbert 1970; Noy-Meir 1973). In the case that detailed texture data

were not available, we used medians of the German soil texture triangle to reconvert qualitative texture information into soil classes (see Table S2).

The statistical power and reliability of the meta-analytical results were analysed with fail-safe calculations (Rosenthal's R and Orwin's method; see Supporting Information Table S4). Meta-analyses were computed with MetaWin[®] 2.1 (Statistical Software for Meta-Analysis. 2. Sinauer Associates, Sunderland, MA, US).

Results

Response of maximum ANPP and RUE along a precipitation gradient

The 99th percentile of ANPP and RUE data revealed consistent trends along the annual precipitation gradient (Figs 1, 2). The maximum response of ANPP and RUE to precipitation (hereafter ANPP_{max} and RUE_{max}) had a pronounced unimodal shape, consisting of several adjacent linear intercepts. Both responses differed in slope and peak values between land-use intensities. Due to limitations in LPQR methodology, statistical differences could not be tested for significance and therefore reflect trends (Koenker 2011). Regressions along the median were calculated for illustrational reasons; for regression models see Table S5.

Figure 1a–d gives the development of ANPP_{max} (kg DM ha⁻¹ yr⁻¹) along a gradient of annual precipita-

tion (mm). ANPP_{max} on ungrazed sites (Fig. 1a no grazing, black line) increased up to ca. 200 mm yr⁻¹ ($y = 10.8x - 533.93$). Higher precipitation only led to a slight increase ($y = 0.11x + 1647.6$), and above 300 mm to a decline ($y = -0.58x + 1851.3$) in ANPP_{max}. Results for grazed sites (Fig. 1b–d) are similar: a steep increase in ANPP_{max} was found up to an annual precipitation of ca. 200 mm. For little land-use intensity there was a slight but steady decrease in ANPP_{max} after its peak around ca. 200 mm yr⁻¹ ($y = -0.83x + 1875.2$). Land-use intensity shifted peak ANPP_{max} to more humid conditions: while sites with no and moderate land-use intensity peaked at annual precipitation of about 300 mm, those with severe land use peaked only at 400 mm. Post-peak decline in ANPP_{max} increased with land-use intensity (no grazing $m = -0.58 > 294$ mm; little $m = -0.83 > 217$ mm; moderate $m = -0.96 > 318$ mm; severe $m = -3.78 > 395$ mm land use). In contrast to regressions along 99th quantiles, 50th quantile regressions were only slightly unimodal.

The RUE response along the precipitation gradient (Fig. 2) confirmed trends found for ANPP (Fig. 1). Unimodal response was more pronounced for 99th than for 50th quantiles. If ANPP_{max} (99th quantiles) displayed a disproportionately high increase with precipitation, RUE_{max} was increasing; if ANPP_{max} was increasing to a lesser extent than precipitation, RUE_{max} was decreasing. Therefore RUE_{max} increased for all land-use intensities up to an

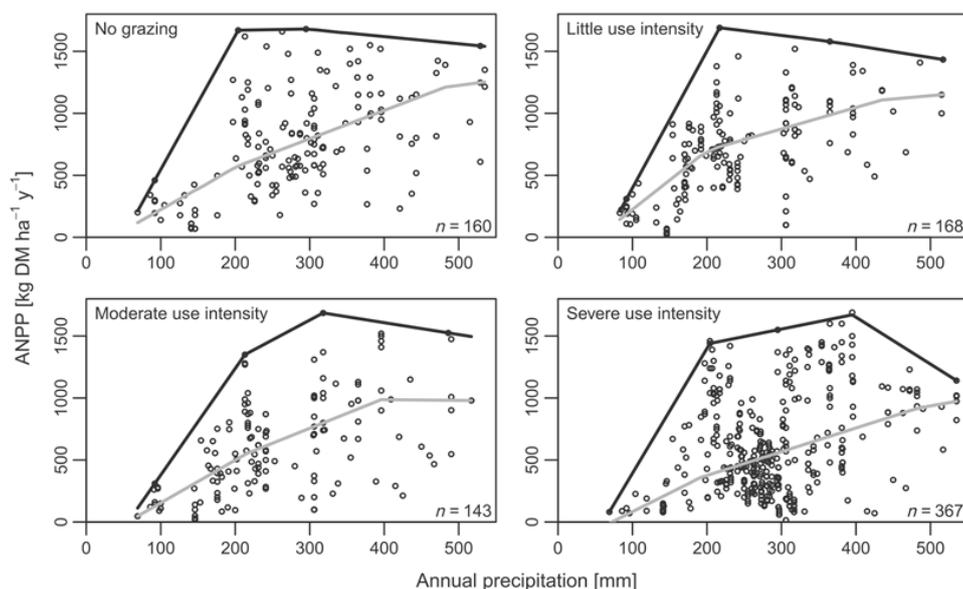


Fig. 1. Maximum and median ANPP as a function of precipitation under different land-use intensities. Black lines represent the 99th quantile of ANPP (ANPP_{max} or production potential) under varying land-use intensities. Grey lines represent the median of ANPP. Regression models at the 99th quantile are based on varying numbers of data points: No grazing $n = 79$, little use intensity $n = 68$, moderate use intensity $n = 64$ and severe land-use intensity $n = 108$. All 99th quantile regressions have a pronounced unimodal shape composed of sequential phases of linearity. 50th quantile regressions are only slightly unimodal. Use intensity influences peak ANPP_{max}, the amount of precipitation needed to reach peak ANPP_{max} as well as the steepness of post-peak decline.

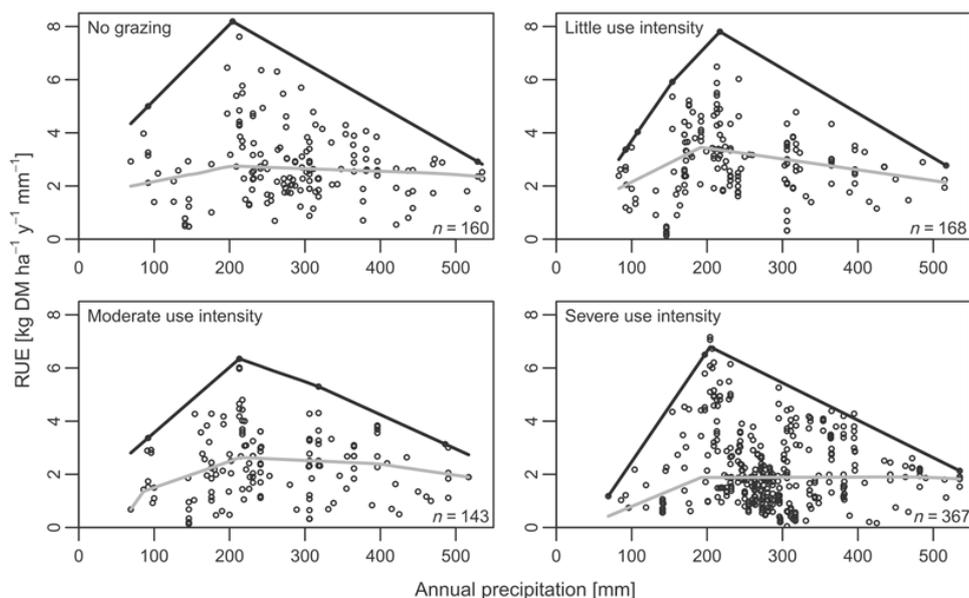


Fig. 2. Maximum and median RUE as function of precipitation under different land-use intensities. Black lines represent the 99th quantile of RUE (RUE_{max} or potential productivity) under varying land-use intensities. Grey lines represent the median of RUE. Regression models at the 99th quantile are based on varying numbers of data points: No grazing $n = 79$, little use intensity $n = 68$, moderate use intensity $n = 64$ and severe land-use intensity $n = 108$. All quantile regressions follow a unimodal shape composed of sequential phases of linearity. Unimodal response is more pronounced for 99th than for 50th quantiles. Use intensity influences peak RUE_{max} as well as the steepness of post-peak decline in RUE_{max} .

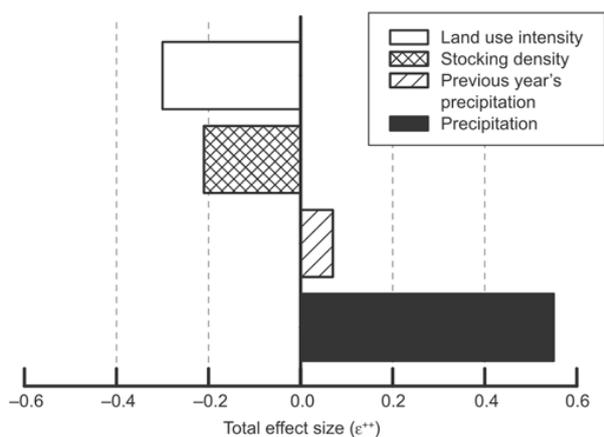


Fig. 3. Bar plot of the effect sizes on (average) ANPP. Bars represent the magnitude of the effects. As indicated by bar length, land use effects can preponderantly hide the effects of precipitation.

annual precipitation of 200–215 mm and decreased with more precipitation. Independent of land-use intensity, RUE_{max} peaked around an annual precipitation of ca. 200 mm (Fig. 2). The highest RUE_{max} value was found under conditions of no grazing (8.2 kg DM ha⁻¹ yr⁻¹ mm⁻¹), followed by little (7.8 kg DM ha⁻¹ yr⁻¹ mm⁻¹), severe (6.8 kg DM ha⁻¹ yr⁻¹ mm⁻¹) and moderate (6.4 kg DM ha⁻¹ yr⁻¹ mm⁻¹) land-use intensities. Sites with severe land use had the steepest increase of RUE_{max} ($y = 0.042x - 1.69$), followed by little land use

($y = 0.036x + 0.16$), no grazing ($y = 0.029x + 2.38$) and moderate land use ($y = 0.025x + 1.11$). The rate of decrease in RUE_{max} was similar for all land-use intensities ($m = -0.017$ to -0.014).

Effects of environmental variables on ANPP and RUE: results from meta-analysis

Several environmental variables significantly affected average ANPP (Table 2-1 & Fig. 3). *Precipitation* and *previous year's precipitation* had a positive, and *stocking density* and *land-use intensity* a negative effect. Overall *precipitation* ($\epsilon^{++} 0.55$) showed the strongest effect on ANPP, followed by *land-use intensity* ($\epsilon^{++} -0.30$), *stocking density* ($\epsilon^{++} -0.21$) and *previous year's precipitation* ($\epsilon^{++} 0.07$). The effect size for *previous year's precipitation* was homogenous ($P = 0.99$). Values for *precipitation* (0.50), *stocking density* (0.19) and *land-use intensity* (0.34) were heterogeneous, which allowed further analyses through categorical models. However, due to small sample size, *stocking density* and *land-use intensity* ($df = 4$) could not be further analysed (see methods). The effect of precipitation was processed by categorical modelled meta-analyses using biome (Table 2-2a) and soil class (Table 2-2b) as moderating variables. Both models were equally good in explaining heterogeneity ($P(Q_M) \leq 0.001$, $P(Q_E) \geq 0.99$). The effect of precipitation on ANPP varied significantly with biome types (Table 2-2a, Fig. 4a): The strongest effect of precipitation was found in

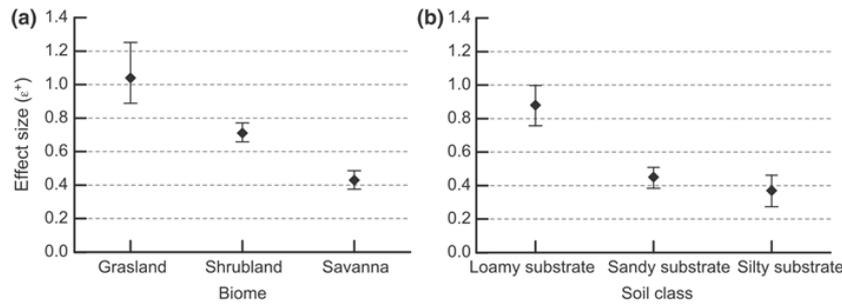


Fig. 4. Results from categorical modelled meta-analyses for the effect of precipitation on ANPP. **(a)** Effect sizes for biomes and their corresponding bootstrapped confidence interval. As indicated by the CIs all effects are significant. **(b)** Effect sizes for soil type and their corresponding bootstrapped confidence interval.

grasslands (ε⁺ 1.04), followed by *shrublands* (ε⁺ 0.71) and *savannas* (ε⁺ 0.43). Effects of precipitation also differed with soil class (Table 2-2b, Fig. 4b). The strongest response was found on *loamy substrates* (ε⁺ 0.88), followed by *sandy substrates* (ε⁺ 0.45) and *silty substrates* (ε⁺ 0.37). The effect on *loamy substrates* significantly differed from that on *sandy substrates* and *silty substrates* (Fig. 4b).

Fail-safe calculations for meta-analysis confirmed the validity of the meta-analytical results: MetaWin[®] 2.1 method predicted that 14.5 up to 3822.7 more studies would have had to be included in the data set to change the significance of meta-analytical results (for details see Table S4). Contrary to the results for ANPP, almost no significant impact of environmental variables on RUE could be identified. Only the effect of stocking density on RUE was significant (ε⁺⁺ -0.30) (Table S3). Categorical modelled meta-analyses for effects of precipitation on RUE in different biomes, respectively on different substrates, found significant effects in *grassland* (ε⁺ 0.40), and on *loamy substrates* (ε⁺ 0.26; Table S3).

Discussion

What is the response of maximum ANPP and RUE along a dryland precipitation gradient?

For the gradient considered in our study, covering sites with MAPs ranging between 130 and 540 mm and annual precipitation between 69 and 725 mm, we found that ANPP_{max} (99th quantile) as a function of precipitation displayed two distinct phases of linear response: (1) a steep linear increase, followed by (2) a shallow increase and/or a decrease. The breakpoint was approximately 200 mm yr⁻¹. Further precipitation only slightly increased ANPP_{max}. Precipitation above 300 mm yr⁻¹ (400 mm yr⁻¹ for sites with strong land use) was generally not translated into more biomass but led to a decline in ANPP_{max}.

This strong unimodal response of ANPP_{max} is accompanied by a slight unimodal response of median ANPP. Hence, both types of quantile regression support the unimodal

shape that has been found in other studies (Diouf & Lambin 2001; Prince et al. 2007; Yang et al. 2008), while other studies report or assume linear relationships (McNaughton et al. 1993; Huxman et al. 2004; McCulley 2005; Bai et al. 2008; Muldavin et al. 2008). However, our results (together with theoretical considerations) enable us to reconcile these contradictory findings on ANPP response (see below).

We interpret the pronounced unimodal response of ANPP_{max} and RUE_{max} with a change in the main limiting factor for plant growth: up to 200 mm yr⁻¹, potential primary production (measured as ANPP_{max}) is mainly constrained by precipitation (see Fig. 1). Above this threshold, potential primary production is increasingly constrained by other limiting factors such as nutrients or soil characteristics (Bremen & De Wit 1983; Paruelo et al. 1999; Linstädter & Baumann 2012).

Although nutrient limitation may constrain primary production even under arid conditions (Wesche & Ronnenberg 2010; Yahdjian et al. 2011), our data suggest that this effect is more pronounced above the threshold of 200 mm rainfall. As land use results in nutrient removal (Penning de Vries & Djitéye 1982), stronger nutrient constraints could also explain the more pronounced post-peak decline in ANPP_{max} on intensively used sites. Another explanation for this phenomenon is that we analysed vegetation data from arid to semi-arid sites only, where vegetation is adapted to low MAP values (130–540 mm). Here, positive precipitation anomalies are commonly associated with events of severe rainfall, which often have a negative impact on primary production, for example by increasing run-off losses and water-induced erosion (Visser et al. 2004; Ridolfi et al. 2008). At the same time, this restriction to relatively arid sites could explain why peak ANPP_{max} found in our study is at a lower annual rainfall (ca. 200 mm) than peaks in studies including more humid sites (e.g. Yang et al. 2008: ca. 380 mm; Diouf & Lambin 2001: ca. 450 mm; Prince et al. 2007: ca. 900 mm). However, as peak position considerably differs between studies, we assume that the position of these thresholds is highly

dependent on the length of the precipitation gradient and on vegetation characteristics, such as biome type.

If not ANPP_{max} but average ANPP (here: its median) is considered, regressions do not show a pronounced unimodal shape (Fig. 1, grey lines). Hence, it is not surprising that studies that used measures of central tendency for regression (instead of upper boundary responses) found simple linear relationships between ANPP and annual precipitation.

As with ANPP_{max}, RUE_{max} monotonically increases for all land-use intensities up to an annual precipitation of ca. 200 mm yr⁻¹. RUE_{max} values in our study (6.4–8.2 kg ha⁻¹ mm⁻¹ depending on land use) correspond well with maximum RUE data reported in literature (e.g. Paruelo et al. 1999: 6.4–7.7 kg ha⁻¹ mm⁻¹; Prince et al. 1998: 8.9 kg ha⁻¹ mm⁻¹; Bai et al. 2008: adjusted RUE_{max} 7.8 kg ha⁻¹ mm⁻¹). Recently, the slope of the regression line between a site's maximum ANPP and precipitation has been interpreted as a common RUE_{max} that is typical for deserts. Huxman et al. (2004) showed this for all biomes in North and South America. In a similar way, Bai et al. (2008) obtained an overall RUE_{max} in the Inner Mongolian steppe of 7.8 kg ha⁻¹ mm⁻¹, which is about twice as high as that for North and South America (4.2 kg ha⁻¹ mm⁻¹).

ANPP_{max} values determined with LPQR can be similarly interpreted as a common RUE_{max}, even though data gained with this method tend to be more extreme than those of Huxman and Bai. RUE_{max} in our data was 8.24 kg ha⁻¹ mm⁻¹ and was found for the more arid part of the gradient (up to 200 mm; see Figs 1, 2) on non-used sites, where it is supposedly independent of environmental constraints such as grazing pressure. RUE_{max} for the more humid part (above 200 mm) displays more variation (6.39 kg ha⁻¹ mm⁻¹ for moderate land use, 6.81 kg ha⁻¹ mm⁻¹ for severe land use and 7.83 kg ha⁻¹ mm⁻¹ for little land-use intensity).

Reconciling contrary findings on the shape of response curves

Our results, together with theoretical considerations, contribute to solve contrary findings in the literature towards the shape of the two response curves.

Gradient length matters

Case studies capturing a relatively short gradient are more likely to detect linear instead of unimodal trends, which might have emerged in a larger-scale analysis. Our results from a gradient of intermediate length show that several linear intersects could be fitted to our data, both for the 50th and 99th quantiles. Shorter gradients could thus be represented by linear relationships. Some case studies failed to detect any statistical relationships at all (Diouf &

Lambin 2001; Holm et al. 2003). This might be a consequence of unfortunate data distribution: if data are scattered around the threshold (peak), a linear trend might become undetectable.

Use efficiencies and linearity

The theoretical background of Verón et al. (2005) strongly implies that studies analysing use efficiencies (UE) along long resource gradients (e.g. Sala et al. 1988; Lauenroth & Sala 1992; Huxman et al. 2004) are also likely to find (quasi-)linear relationships. In general, UEs express the amount of output (y , for RUE: the RUE values) per unit input (x , for RUE: the annual precipitation) and are of the type y/x or $UE = a/x + b$, and therefore non-linear. However, with increasing length of the resource gradient these functions approach (quasi-)linearity and can, however misleadingly, be described by linear regression (for further discussion refer to Verón et al. 2005 or Supporting Information Appendix S2). Therefore studies on very short or very long precipitation gradients are likely to find linear relationships, even though the relationship is actually non-linear.

Space versus time

Another thread of explanation stresses the principal difference between temporal and spatial precipitation gradients: high and low precipitation values on these two scales refer to generally different qualities of precipitation values (Sala et al. 1988; Lauenroth & Sala 1992; Bai et al. 2008). While high and low precipitation values of spatial precipitation gradients refer to 'normal' precipitation near the MAP of the individual sites, values at the edges of a temporal precipitation gradient refer to extreme values (precipitation anomalies) of individual sites, which usually have a negative impact on ANPP (Visser et al. 2004; Ridolfi et al. 2008). For this reason spatial precipitation gradients usually exhibit a steep increase of ANPP, whereas temporal gradients generally show shallower rates of increase, or are unable to detect a clear trend. Our maximum ANPP or RUE values presented here are close to a temporal gradient because values at the edges of the gradient are determined by temporal precipitation anomalies of sites.

RUE along precipitation gradients: the issue of autocorrelation

RUE can be analysed along precipitation gradients in two different ways: first, ANPP could be plotted against precipitation. In this case each point in the scatter plot represents a single RUE value (see Fig. 1). The second option is to plot RUE values themselves along the precipitation gradient (see Fig. 2).

Since RUE is the quotient of ANPP and rainfall, a regression of RUE against precipitation violates the requirement of independence: it plots $1/x$ against x and thus is an autocorrelation (Prince et al. 2007). Nevertheless, we argue that this relationship can be analysed if we explicitly consider an adapted null hypothesis for this regression. This assumes that the ANPP values included in RUE (rather than RUE itself) are unrelated to precipitation. Hence, it corresponds to the null hypothesis of the regression of ANPP against precipitation gradients and results not in a linear but a hyperbolic function $y = 1/x$ (see also Vitousek 1982; Pastor & Bridgman 1999). In our study, this null hypothesis of a hyperbolic response can be rejected (see Fig. 1). The new H0 also implies that standard linear regression is inadequate for analysing the response of RUE as function of precipitation: linear regressions cannot be fitted to hypothetical patterns emerging from that H0. Moreover, as just laid out, it is generally questionable if efficiencies should be explained by linear regressions at all.

How are ANPP and RUE influenced by rainfall, biome, edaphic conditions and land use?

We analysed effects on ANPP and RUE through several weighted meta-analyses, and were able to deduce quantitative effect sizes. Our results show that (average) ANPP was mainly affected by rainfall and land use (Fig. 3). Noteworthy, the effect of annual precipitation on ANPP differed across biomes (*grassland, savanna and shrubland*) and soil types (*loamy, sandy and silty substrates*). In contrast, meta-analysis on average RUE gave almost no significant effects, which can be related to mathematical rather than to ecological issues. As 99th and 50th quantile regressions detected two intersects of contrary linear development, it is not surprising that weighted pooling of effect sizes will result in non-significant effect sizes. In the following we mainly discuss the relevance of predictor variables for ANPP.

Differences across biomes

The highest conversion of precipitation into biomass was found in grasslands ($\epsilon^+ 1.04$), followed by shrublands ($\epsilon^+ 0.71$) and savannas ($\epsilon^+ 0.43$). A higher translational rate of grasslands compared to shrublands has been frequently reported (Milchunas & Lauenroth 1993; Paruelo & Lauenroth 1995). It can be accounted for by physiological differences in growth and life strategies between grasses and shrubs. The comparatively low ANPP in savanna rangelands could be explained by the fact that – as in the studies included – typically only the grass layer is sampled (Fynn & Connor 2000; Retzer 2006). Following the data in Penning de Vries & Djitéye (1982), a proportion of 3–20% should be added to the grass layer ANPP to account for tree

layer production. However, even a 20% increase in primary production leaves the savanna system with the lowest translational rate of the three biomes. Therefore our results confirm that different dryland biomes, even if being equally water-limited, differ in overall RUE.

Differences across soil types

The strongest effect of precipitation on ANPP was observed on loamy substrates ($\epsilon^+ 0.88$), followed by sandy ($\epsilon^+ 0.45$) and silty substrates ($\epsilon^+ 0.37$). Significant differences between loamy textures on the one hand and sandy and silty textures on the other can be explained by the inverse-texture hypothesis, which stresses different soil water retention capacities and differences in nutrient availability (Noy-Meir 1973). In arid environments, coarse (sandy and silty) substrates are predicted to be more favourable for primary production, since relatively more water is available for plant growth due to larger soil pores, and little run-off and evaporation (Alizai & Hulbert 1970; Snyman 1999; English et al. 2005; Li et al. 2007a,b). The crossover point of the inverse texture effect was originally estimated to be at a MAP of 300–500 mm (Noy-Meir 1973). In subsequent studies, crossover points have been found to range between 200 mm (Yang et al. 2009) and 800 mm (Epstein et al. 1997). As the sites included in our study are mostly arid (MAP 130–540 mm), our results imply a crossover point at the more arid side of this range. More generally, our findings support previous studies, showing that soil texture has considerable effects on ANPP (Paruelo et al. 1999; Diouf & Lambin 2001; Huxman et al. 2004; Angassa et al. 2012), which may even mask effects of grazing intensity (Lauenroth et al. 2008; Fensham et al. 2010).

Impact of previous rainfalls

Previous year's precipitation had the smallest effect on ANPP ($\epsilon^+ 0.07$). Its relevance for ANPP can be explained by a carry-over effect of vegetation density (Yahdjian & Sala 2006; Linstädter & Baumann 2012) and by the amount of reserve biomass in perennial species at the beginning of the growth period (Müller et al. 2007; Zimmermann et al. 2010). This carry-over effect may explain the majority of unexplained variance in grasslands (Wiegand et al. 2004). Our study underlines that in arid and semi-arid environments with their high spatio-temporal variability of rainfall (Davidowitz 2002; Ward 2009), environmental history (specifically the history of rainfall events) may considerably influence primary production (Yahdjian & Sala 2006). Since the annual total is a rather coarse measure of past precipitation characteristics, future studies should address how temporal patterns in antecedent rainfall pulses influence vegetation response (Reynolds et al. 2004), and if

there are differences in vegetation response for different functional types (e.g. annuals vs perennials) and in different biomes.

Land use impacts on ANPP

Both stocking density ($\varepsilon^+ -0.21$) and land-use intensity ($\varepsilon^+ -0.30$) had negative effects on ANPP. As land-use intensity had a higher impact on ANPP, our study confirms that parameters comprising both recent and past land use are more able to explain changes in ANPP (Turner 1998; Fynn & Connor 2000). In analogy to the discussion on effects of previous year's rainfall, results can also be related to the 'memory' effect of vegetation (Wiegand et al. 2004; Linstädter & Baumann 2012). Le Houérou (1984) predicted that land use may partly or totally mask effects of precipitation on ANPP and RUE, respectively (Fig. 3). Our findings support this hypothesis. This particularly applies to precipitation effects from certain biomes or soils. Our study allowed us to infer a ranking of predictor variables: primary production was mainly determined by precipitation, followed by land use and previous year's precipitation. However, the relative importance of environmental parameters varied between biomes and soil types.

Conclusions

Our study confirmed that ANPP and RUE in arid and semi-arid environments are significantly affected by precipitation and land use. Meta-analyses revealed that ANPP and RUE response to land use and precipitation were strongly modulated by biome and soil type. We were able to separate the effects of these factors into distinct effect sizes, which allowed us to separate the relative proportion of influence of these factors in a quantitative manner.

While our results support the criticism that ANPP and RUE respond to a complex suite of environmental factors, they also offer an approach to constructively deal with these problems. For example, the diverging magnitude of precipitation effects across biomes (and soils) strongly suggests use of RUE as a biome-specific indicator. We propose to establish reference values of maximum and mean RUE for different biomes, and if possible further stratified for soil types. This would considerably increase the usability of RUE as an ecological indicator for ecosystem state, productivity and degradation.

By analysing the upper boundary of ANPP and RUE along a precipitation gradient, we were more likely to extract effects of the main limiting factor (water) on primary production, than by analysing trends in the mean or median. Future studies should also take the relative position of the sites and the length of the gradient into account as this might influence the linearity (or non-linearity) of

the response. Our study revealed a unimodal response of $ANPP_{max}$ (and RUE_{max}) along a precipitation gradient of medium length. At the arid side of the precipitation gradient, the translation of precipitation into biomass was comparatively uniform across systems with different land-use intensity. In contrast, post-peak declines became more pronounced with increasing land-use intensity. This response pattern should be incorporated into conceptual and mathematical models of $ANPP_{max}$ and RUE_{max} as function of precipitation and land use.

Acknowledgements

We thank the editor and two anonymous referees for their insightful comments on the manuscript. Sincere thanks to Birgit Müller, Henrik von Wehrden and Pierre Fritzsche for stimulating discussions on the concept of rain-use efficiency, as well as to Helmut Hillebrand, Romina Drees and Roger Koenker for their help with statistical issues. We are grateful to Gisela Baumann for comments on earlier drafts of this manuscript, and to Mark Douensnard and Roy Messaros for improving the English. We appreciate the aid of Douglas I. Moore in computing the data of the Seville LTER site. The research of Jan Ruppert was partly funded by the German Science Foundation (Deutsche Forschungsgemeinschaft, DFG) through a grant to a Research Unit (FOR 1501) by the Volkswagen Foundation under grant II/79628 and the Stiftung der Deutschen Wirtschaft. Work of Esteban Muldavin was performed at the Seville Long Term Ecological Research (LTER) Program; the collection of these data was significantly funded by the National Science Foundation Long Term Ecological Research program (NSF Grant numbers BSR 88-11906, DEB 9411976, DEB 0080529 and DEB 0217774). Sabine Miede is grateful to the Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ, former GTZ) for financing data collection in the savanna biome (Senegal). Work of Karsten Wesche was supported by the DFG, the German Academic Exchange Foundation (DAAD) and the GIZ; Vroni Retzer provided invaluable help during the early stages of that experiment. The research of Anja Linstädter was supported by the DFG through FOR 1501 and SFB 586 and by the Volkswagen Foundation (grant II/79041).

References

- Abdel-Magid, A.H., Trlica, M.J. & Hart, R.H. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. *Journal of Range Management* 57: 442–447.
- Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Brown, C.S.,

- Buckley, Y.M., Calabrese, L.B., Chu, C.J., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah, N., Lambers, J.H.R., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P. & Yang, L.H. 2011. Productivity is a poor predictor of plant species richness. *Science* 333: 1750–1753.
- Alizai, H.U. & Hulbert, L.C. 1970. Effects of soil texture on evaporative loss and available water in semi-arid climates. *Soil Science* 110: 328–332.
- Angassa, A., Sheleme, B., Oba, G., Treydte, A.C., Linstädter, A. & Sauerborn, J. 2012. Savanna land use and its effect on soil characteristics in southern Ethiopia. *Journal of Arid Environments* 81: 67–76.
- Bagchi, S. & Ritchie, M.E. 2011. Herbivory and plant tolerance: experimental tests of alternative hypotheses involving non-substitutable resources. *Oikos* 120: 119–127.
- 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.
- Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* 127: 870–892.
- Belsky, A.J. 1987. The effects of grazing: confounding of ecosystem, community, and organism scales. *American Naturalist* 129: 777–781.
- Belsky, A.J., Carson, W.P., Jensen, C.L. & Fox, G.A. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7: 109–121.
- Blackburn, T.M., Lawton, J.H. & Perry, J.N. 1992. A method of estimating the slope of upper-bounds of plots of body size and abundance in natural animal assemblages. *Oikos* 65: 107–112.
- Breman, H. & De Wit, C.T. 1983. Rangeland productivity and exploitation in the Sahel. *Science* 221: 1341–1347.
- Buis, G., Blair, J., Burkepile, D., Burns, C., Chamberlain, A., Chapman, P., Collins, S., Fynn, R., Govender, N., Kirkman, K., Smith, M. & Knapp, A. 2009. Controls of aboveground net primary production in mesic savanna grasslands: an inter-hemispheric comparison. *Ecosystems* 12: 982–995.
- Cade, B.S. & Noon, B.R. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1: 412–420.
- Cohen, J. 1992. A power primer. *Psychological Bulletin* 112: 155–159.
- Cottingham, K.L., Lennon, J.T. & Brown, B.L. 2005. Knowing when to draw the line: designing more informative ecological experiments. *Frontiers in Ecology and the Environment* 3: 145–152.
- Cox, S.B., Bloch, C.P., Stevens, R.D. & Huenneke, L.F. 2006. Productivity and species richness in an arid ecosystem: a long-term perspective. *Plant Ecology* 186: 1–12.
- Davidowitz, G. 2002. Does precipitation variability increase from mesic to xeric biomes? *Global Ecology and Biogeography* 11: 143–154.
- 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.
- 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.
- Epstein, H.E., Lauenroth, W.K. & Burke, I.C. 1997. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology* 78: 2628–2631.
- Fensham, R.J., Fairfax, R.J. & Dwyer, J.M. 2010. Vegetation responses to the first 20 years of cattle grazing in an Australian desert. *Ecology* 91: 681–692.
- Ferraro, D.G. & Oesterheld, M. 2002. Effect of defoliation on grass growth. A quantitative review. *Oikos* 98: 125–133.
- 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.
- Gillman, L.N. & Wright, S.D. 2010. Mega mistakes in meta-analyses: devil in the detail. *Ecology* 91: 2550–2552.
- Glass, G.V. 1976. Primary, secondary, and meta-analysis of research. *Educational Researcher* 5: 3–8.
- 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.
- Hein, L. 2006. The impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland. *Journal of Arid Environments* 64: 488–504.
- Hein, L. & de Ridder, N. 2006. Desertification in the Sahel: a reinterpretation. *Global Change Biology* 12: 751–758.
- Hillebrand, H. & Cardinale, B.J. 2010. A critique for meta-analyses and the productivity–diversity relationship. *Ecology* 91: 2545–2549.
- 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.
- 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.

- Jacobs, M.J. & Schloeder, C.A. 2003. Defoliation effects on basal cover and productivity in perennial grasslands of Ethiopia. *Plant Ecology* 169: 245–257.
- Jarvis, P.G. 1993. Prospects for bottom-up models. In: Ehleringer, J.R. & Field, C.B. (eds.) *Scaling physiological processes leaf to globe*. pp. 115–126. Academic Press, New York, NY, US.
- 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.
- Koenker, R. 2011. Additive models for quantile regression: Model selection and confidence bands. *Brazilian Journal of Probability and Statistics* 25: 239–262.
- Koenker, R. & Bassett, G. 1978. Regression quantiles. *Econometrica* 46: 33–50.
- Lauenroth, W.K. & Sala, O.E. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397–403.
- Lauenroth, W.K., Milchunas, D.G., Sala, O.E., Burke, I.C. & Morgan, J.A. 2008. Net primary production in the shortgrass steppe. In: Lauenroth, W.K. & Burke, I.C. (eds.) *Ecology of the shortgrass steppe: a long-term perspective*. pp. 270–305. Oxford University Press, Oxford, UK.
- 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.
- Leriche, H., Le Roux, X., Desnoyers, F., Benest, D., Simioni, G. & Abbadie, L. 2003. Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecological Applications* 13: 1346–1354.
- Lessin, L.M., Dyer, A.R. & Goldberg, D.E. 2001. Using upper boundary constraints to quantify competitive response of desert annuals. *Oikos* 92: 153–159.
- Li, X.R., He, M.Z., Duan, Z.H., Mao, H.L. & Jia, X.H. 2007a. Recovery of topsoil physicochemical properties in revegetated sites in the sand-burial ecosystems of the Tengger Desert, northern China. *Geomorphology* 88: 254–265.
- Li, X.R., Kong, D.S., Tan, H.J. & Wang, X.P. 2007b. Changes in soil and vegetation following stabilisation of dunes in the southeastern fringe of the Tengger Desert, China. *Plant and Soil* 300: 221–231.
- Linstädter, A. & Baumann, G. 2012. Abiotic and biotic recovery pathways of arid rangelands: lessons from the High Atlas Mountains, Morocco. *CATENA*. doi: 10.1016/j.catena.2012.02.002.
- Linstädter, A., Baumann, G., Born, K., Dieckrüger, B., Fritzsche, P., Kirscht, H. & Klose, A. 2010. Land use and land cover in Southern Morocco: managing unpredictable resources and extreme events. In: Speth, P., Christoph, M. & Dieckrüger, B. (eds.) *Impacts of global change on the hydrological cycle in West and Northwest Africa*. pp. 611–632. Springer, Berlin, DE.
- McCulley, R.L. 2005. Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystems* 8: 106–121.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass–ungulate relationships in the Serengeti. *American Naturalist* 113: 691–703.
- McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40: 329–336.
- McNaughton, S.J., Sala, O.E. & Oesterheld, M. 1993. Comparative ecology of African and South American arid to subhumid ecosystems. In: Goldblatt, P. (ed.) *Biological relationships between Africa and South America*. pp. 548–567. Yale University Press, New Haven, CT, US.
- 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: synthesis*. Island Press, Washington, DC, US.
- Miehe, S., Kluge, J., von Wehrden, H. & Retzer, V. 2010. Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. *Journal of Applied Ecology* 47: 692–700.
- 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.
- 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.
- Niemi, G.J. & McDonald, M.E. 2004. Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics* 35: 89–111.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25–51.
- 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.
- 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. & Lauenroth, W.K. 1995. Regional patterns of normalized difference vegetation index in North American shrublands and grasslands. *Ecology* 76: 1888–1898.
- 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.
- Pastor, J. & Bridgman, S.D. 1999. Nutrient efficiency along nutrient availability gradients. *Oecologia* 118: 50–58.
- Penning de Vries, F.W.T. & Djitéye, M.A. 1982. La productivité des pâturages sahéliens. In: Penning de Vries, F.W.T. & Djitéye, M.A. (eds.) *Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle*. pp. 525f. Centre for

- Agricultural Publishing and Documentation, Wageningen, NL.
- 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.
- 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.
- Ridolfi, L., Laio, F. & D’Odorico, P. 2008. Fertility island formation and evolution in dryland ecosystems. *Ecology and Society* 13: article 5.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J.. 2000. *MetaWin: Statistical Software for Meta-Analysis*. 2. Sinauer Associates, Sunderland, US.
- Ryan, S.E. & Porth, L.S. 2007. *A tutorial on the piecewise regression approach applied to bedload transport data*. United States Department of Agriculture & Forest Service Rocky Mountain Research Station, Fort Collins, CO, US.
- 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.
- Sankaran, M., Ratnam, J. & Hanan, N.P. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7: 480–490.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* 438: 846–849.
- Schulte, A. 2002. *Weideökologie des Kaokolandes: Struktur und Dynamik einer Mopane-Savanne unter pastoralnomadischer Nutzung*. PhD thesis, University of Cologne, Cologne, DE.
- 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.
- Sharon, D. 1972. Spottiness of rainfall in a desert area. *Journal of Hydrology* 17: 161–175.
- 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.
- Snyman, H.A. 1999. Quantification of the soil–water balance under different veld condition classes in a semi-arid climate. *African Journal of Range & Forage Science* 16: 108–117.
- Snyman, H.A. 2009. Root studies on grass species in a semi-arid South Africa along a degradation gradient. *Agriculture Ecosystems and Environment* 130: 100–108.
- Snyman, H.A. & Fouché, 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.
- Toms, J.D. & Lesperance, M.L. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84: 2034–2041.
- Turner, M.D. 1998. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: I. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography* 25: 669–682.
- UNDP 2008b. Human development report country information: Morocco. In: UNDP (ed.) http://hdrstats.undp.org/en/countries/country_fact_sheets/cty_fs_MAR.html. United Nations Development Programme, Nairobi, KE.
- UNDP 2008a. *Generic guidelines for mainstreaming drylands issues into national development frameworks*. United Nations Development Programme, Nairobi, KE.
- 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.
- Verón, S.R., Oesterheld, M. & Paruelo, J.M. 2005. Production as a function of resource availability: slopes and efficiencies are different. *Journal of Vegetation Science* 16: 351–354.
- Visser, J.M. & Sasser, C.E. 2009. The effect of environmental factors on floating fresh marsh end-of-season biomass. *Aquatic Botany* 91: 205–212.
- Visser, S.M., Sterk, G. & Ribolzi, O. 2004. Techniques for simultaneous quantification of wind and water erosion in semi-arid regions. *Journal of Arid Environments* 59: 699–717.
- Visser, J.M., Sasser, C.E. & Cade, B. 2006. The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts* 29: 328–339.
- Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist* 119: 553–572.
- Ward, D. 2009. *The biology of deserts*. Oxford University Press, Oxford, UK.
- Ward, D. & Ngairorue, B.T. 2000. Are Namibia’s grasslands desertifying? *Journal of Range Management* 53: 138–144.
- Wesche, K. & Retzer, V. 2005. Is degradation a major problem in semi-desert environments of the Gobi region in southern Mongolia? In: Stubbe, A. (ed.) *Erforschung biologischer Ressourcen der Mongolei*. pp. 133–146. Martin-Luther-Universität, Halle-Wittenberg, DE.
- Wesche, K. & Ronnenberg, K. 2010. Effects of NPK fertilisation in arid southern Mongolian desert steppes. *Plant Ecology* 207: 93–105.
- 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.

- Whittaker, R.J. 2010. Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. *Ecology* 91: 2522–2533.
- 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.
- Wise, M.J. & Abrahamson, W.G. 2005. Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos* 109: 417–428.
- Yahdjian, L. & Sala, O.E. 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology* 87: 952–962.
- Yahdjian, L., Gherardi, L. & Sala, O.E. 2011. Nitrogen limitation in arid-subhumid ecosystems: a meta-analysis of fertilization studies. *Journal of Arid Environments* 75: 675–680.
- Yang, Y.H., Fang, J.Y., Ma, W. & Wang, W. 2008. Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters* 35: L23710.
- Yang, Y.H., Fang, J.Y., Pan, Y.D. & Ji, C.J. 2009. Aboveground biomass in Tibetan grasslands. *Journal of Arid Environments* 73: 91–95.
- Zimmermann, J., Higgins, S.I., Grimm, V., Hoffmann, J. & Linstädter, A. 2010. Grass mortality in semi-arid savanna: the role of fire, competition and self-shading. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 1–8.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Overview of variables in database used for meta-analysis and LPQR.

Table S2. Classification of soils.

Table S3. Results of weighted meta-analysis of different effect variables on RUE.

Table S4. Results of fail-safe analysis of meta-analytical results.

Table S5. Regression models along the median.

Appendix S1. Established conversions for different livestock indices to TLU.

Appendix S2. Why efficiencies should not be analysed by linear regressions.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Appendix S1: Established conversions for different livestock indices to tropical livestock unit (TLU)

Bodyweight based assignment of tropical livestock units. Reference for 1 TLU is a ruminant with a bodyweight of 250 kg (e.g. cattle).

Bodyweight [kg]	TLU
30	0.20
35	0.23
40	0.25
45	0.28
50	0.30
60	0.34
75	0.41
100	0.50
125	0.59
150	0.68
200	0.85
250	1.00
300	1.15
350	1.29
400	1.42
450	1.55
500	1.68

Conversion of large stock units (LSU) into tropical livestock units (TLU)

LSU is the equivalent of the TLU for moderately tempered climatic zones. Since larger animals can be found in these climatic zones, the units differ only in the weight of the reference animal. While 1 LSU equals one adult cattle with a weight of 500 kg, 1 TLU equals one adult cattle with the weight of 250 kg. Therefore the conversion followed the formula: 1 LSU = 2 TLU.

Applied for O'Connor et al. 2001.

Conversion of dry sheep equivalent (DSE) into tropical livestock units (TLU)

1 DSE accords to the feed consumed by a two year old 45 to 50 kg sheep or the (consumed) energy of 7600 kilojoule per day. Following the allocation of TLU values by body weight (see Table above) one adult sheep with a weight 45 to 50 kg equals a TLU value of 0,28 to 0,30. For the conversion the mean of both values was chosen. Therefore the conversion followed the formula: 1 DSE = 0,29 TLU. Applied for Holm et al. 2003.

Conversion of Mongolian sheep unit (MSU) into tropical livestock units (TLU)

1 MSU accords to the feed consumed by one sheep per day and should therefore be about 1 kg dry matter per day and year [1 kg DM * d⁻¹ * y⁻¹]. Ruminants consume about 3% of their own body-weight per day (Ulgiit & Stewart 2006), therefore 7.5 MSU equal 1 TLU, since 7.5 kg are 3% of 250 kg.

Applied for Wesche & Retzer 2005. The calculated TLU values were checked and accepted by the authors.

References

- Holm,A.M., Watson,I.W., Loneragan,W.A. & Adams,M.A. 2003. Influence of loss of patch-scale heterogeneity on primary productivity and rainfall-use efficiency in the arid shrubland of Western Australia. *Basic and Applied Ecology* 4: 569-578.
- 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.
- Ulgiit,E. & Stewart,T. 2006. *The Mongolian Farm Management Notebook*. 1st ed.
- Wesche,K. & Retzer,V. 2005. Is degradation a major problem in semi-desert environments of the Gobi region in southern Mongolia? In: Retzer, V., Wesche, K., Samiya, R., Stubbe, A., Mieke, G., Stubbe, M. (eds.) *Erforschung Biologischer Ressourcen der Mongolei*, pp. 133-146. Martin-Luther-University, Halle-Wittenberg.

Appendix S2: Why efficiencies should not be analyzed by linear regressions

Verón et al. (2005) point out that utilization efficiencies (UE, e.g. the rain-use efficiency) express the amount of output (y, for RUE: the RUE values) for a given input (x, for RUE: the annual precipitation) and in mathematical terms are of the type y/x or $UE = a/x + b$. Therefore theory predicts non-linear response of RUE along short precipitation gradients. With increasing gradient length, this relationship approaches linearity, as has been found in many studies (e.g. Lauenroth & Sala 1992, Huxman et al. 2005).

References

- 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.
- Lauenroth,W.K. & Sala,O.E. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397-403.
- Verón,S.R., Oesterheld,M., Paruelo,J.M. 2005. Production as a function of resource availability: Slopes and efficiencies are different. *Journal of Vegetation Science* 16: 351-354.

Table S1 Overview of variables in database used for meta-analysis and LPQR

Variable	Explanation	Unit or possible value	level of measurement
RAINREGIME	rainregime of site	WR (winter rain) SR (summer rain) MIX (mixed system)	nominal
PLACE	Place and region of study	e.g. Ferlo, Senegal	nominal
BIOME	Biome at site	shrubland grassland savanna	nominal
RAIN_Y	annual precipitation	[mm yr-1]	interval
RAIN_P	precipitation in hydrological year	[mm yr-1]	interval
RAIN_LAST_Y	previous year's precipitation	[mm yr-1]	interval
BIOMASS_Y	ANPP corresponding to RAIN_Y	[kg DM ha-1 yr-1]	interval
BIOMASS_P	ANPP corresponding to RAIN_P	[kg DM ha-1 yr-1]	interval
RUE	rain-use efficiency	[kg DM ha-1 yr-1 mm-1]	interval
SOIL_TEXTURE	texture of soil	e.g. clay, sand, loam	nominal
SOIL_CLASS	classification of soil	sandy substrates loamy substrates silty substrates	nominal
SOIL_DEPTH	depth of soil	1=shallow(<20 cm) 2=medium (20-100 cm) 3=deep (>100 cm)	ordinal
SOIL_NFK	fieldcapacity of soil	[mm dm-1]	interval
SOIL_FERT	fertilization status of soil	yes/no	nominal
SOIL_LIMIT	limited nutrients	unknown none nitrate	nominal
RAIN_MEAN	mean annual precipitation	[mm yr-1]	interval
RAIN_ST	standard deviation of MAP	[mm yr-1]	interval
RAIN_CV	coefficient of variance	dimensionless	percent
USE_TYPE	recent land use type	e.g. cattle stocking	nominal
USE_INTENSITY	land use intensity	0=none 1=little 2=moderate 3=severe 4=extreme	ordinal / quasi interval
USE_TLU	recent stocking density	[TLU ha-1]	interval
USE_HISTORY	use history	e.g. enclosure, cattle stocking	nominal
USE_HISTORY_Y	years of use history	[yr]	interval

Table S2 Classification of soils

Classification of different soil textures to the variable of soil-class:

sandy substrates	loamy substrates	silty substrates
pure sand	loamy sand	pure silt
clayey sand	sandy loam	sandy silt
		silty sand

All texture assignments were gained from the publications presenting the data or directly from the authors.

Further Information on texture assignment

If detailed original publications were lacking texture information, we used medians of the German soil texture triangle (AG Boden 2005) to reconvert information on soil classes. In this classification, *sandy* substrates comprise pure sands and weakly clayey sands (clay content 5-15%, silt content < 10%); *loamy* substrates comprise loamy sands and sandy loams (clay content 11-21%, silt content 25-32%), and *silty* substrates comprise pure and sandy silts (clay content < 4%, silt content > 65%).

References

Ad-hoc-AG Boden. 2005. *Bodenkundliche Kartieranleitung [Manual of soil mapping]*. Bundesanstalt für Geowissenschaften und Rohstoffe in Zusammenarbeit mit den Staatlichen Geologischen Diensten (eds.), 5th ed. Hannover, Germany.

Table S3 Results of weighted meta-analysis of different effect variables on RUE.

Results of weighted meta-analysis of different effect variables on RUE. The table gives the effect sizes (ϵ) and the corresponding confidence interval (95%, bootstrapped), the degrees of freedom (df) and the probability levels for heterogeneity (p), which have been calculated through randomization (wherever possible - see notes). Effect sizes were calculated on the basis of z-transformed Spearman correlation coefficients (r^2). Tab S3-1 reports overall results of effect-variables on RUE. Tab S3-2 presents detailed results based on categorical modelled meta-analysis for the effect of precipitation on RUE, including p-levels for heterogeneity within and between groups; a. effect of precipitation on RUE within different biomes and b. on different soil classes.

Table S3-1: Overall Effects on RUE

	df	p	effect size (ϵ^{**})	bootstrap CI (95%)		
Precipitation	49	0,45	0,07 n.s.	-0,0013	-	0,1372
Previous year precipitation	48	0,98 ²	0,05 n.s.	-0,0178	-	0,1186
Stocking density ¹	4	0,06	-0,30	-0,6666	-	-0,1097
Land use intensity ¹	4	0,10	-0,10 n.s.	-0,5611	-	0,2518

Table S3-2: Categorical models for the effect of precipitation on RUE

a. Biome

	df	p†				
Heterogeneity						
between groups (Q_M)	2	0,002				
within groups (Q_E)	47	0,70				
total (Q_T)	49	0,31				
	df	p†	effect size (ϵ^*)	bootstrap CI (95%)		
Grassland	7	0,93	0,40	0,2230	-	0,4817
Shrubland	12	0,01	0,05 n.s.	-0,2346	-	0,2876
Savanna	30	1,00	0,01 n.s.	-0,0313	-	0,0562

b. Soil class

	df	p†				
Heterogeneity						
between groups (Q_M)	2	0,01				
within groups (Q_E)	43	0,90				
total (Q_T)	45	0,67				
	df	p†	effect size (ϵ^*)	bootstrap CI (95%)		
Loamy substrate	18	0,25	0,26	0,0426	-	0,3867
Sandy substrate	19	1,00	0,02 n.s.	-0,0197	-	0,0653
Silty substrate	6	0,74	-0,03 n.s.	-0,1326	-	0,0923

Notes: All randomization calculations were performed with 9999 iterations.

* Effect sizes where calculated between studies and not between treatments.

† The estimate of the pooled variance was less than or equal to zero, therefore the data was analyzed using a fixed effects model.

In contrast to the results of weighted meta-analysis for effects on ANPP, the meta-analysis for effects on RUE showed nearly no significant effects, even though some correlations tended to significance (see Table S3). Of course transformed data could have been used to produce significant effect sizes, but this would have resulted in the loss of the direct quantitative measurement which was the intention behind using meta-analysis in the first place. Unfortunately there are currently no suitable correlation-methods which allow a direct analysis of complex non-linear trends, and which provide suitable measures of effect sizes for an application in meta-analyses, and/or which have been validated in the ecology at the same time. In future meta-analytical studies this problem could be overcome by decomposing these relationships into different sequential intersects. These intersects could be obtained from LPQR-analysis, and then effect sizes for each intersect could be computed separately by meta-analysis.

Table S4 Results of fail-safe analysis of meta-analytical results

Table S4-1: Overall Effects on ANPP

	df	p	effect size (ϵ^{++})	Rosenthal's R	Orwin's Method
Precipitation	49	0,50	0,55	3822,7	86,6
Previous year precipitation	48	0,99 ²	0,07	n.a.	n.a.
Stocking density ¹	4	0,19	-0,21	14,5	n.a.
Land use intensity ¹	4	0,34	-0,30	17,8	n.a.

Table S4-2: Overall Effects on RUE

	df	p	effect size (ϵ^{++})	Rosenthal's R	Orwin's Method
Precipitation	49	0,45	0,07 n.s.	2,0	0,0
Previous year precipitation ²	48	0,98 ²	0,05 n.s.	n.a.	n.a.
Stocking density ¹	4	0,06	-0,30	13,8	n.a.
Land use intensity ¹	4	0,10	-0,10 n.s.	0,0	n.a.

Notes: All randomization calculations were performed with 9999 iterations.

¹ Effect sizes where calculated between studies and not between treatments.

² The estimate of the pooled variance was less than or equal to zero, therefore the data was analyzed using a fixed effects model.

Table S5 Regression models for ANPP-precipitation and RUE-precipitation functions along the 50th percentile / median

ANPP		
Use intensity 0	$ANPP_{50th} = \begin{cases} 3.39 * ppt - 115.7 \\ 2.29 * ppt + 109.1 \\ 0.79 * ppt + 830 \end{cases}$	for ppt ≤ 204 mm ≥ 204 mm ≤ 482 mm ≥ 482 mm
Use Intensity 1	$ANPP_{50th} = \begin{cases} 4.73 * ppt - 248.7 \\ 3.02 * ppt + 80.2 \\ 1.73 * ppt + 354.2 \\ 0.53 * ppt + 876.7 \end{cases}$	for ppt ≤ 192 mm ≥ 192 mm ≤ 213 mm ≥ 213 mm ≤ 435 mm ≥ 435 mm
Use Intensity 2	$ANPP_{50th} = \begin{cases} 3.45 * ppt - 191 \\ 2.41 * ppt + 32 \\ -0.06 * ppt + 1010.1 \end{cases}$	for ppt ≤ 215 mm ≥ 215 mm ≤ 396 mm ≥ 396 mm
Use intensity 3	$ANPP_{50th} = \begin{cases} 3.01 * ppt - 217.5 \\ 1.92 * ppt - 8.2 \\ 1.11 * ppt + 382.6 \end{cases}$	for ppt ≤ 192 mm ≥ 192 mm ≤ 482 mm ≥ 482 mm
RUE		
Use intensity 0	$RUE_{50th} = \begin{cases} 0.0056 * ppt + 1.61 \\ -0.0010 * ppt + 2.96 \\ -0.0023 * ppt + 3.6 \end{cases}$	for ppt ≤ 204 mm ≥ 204 mm ≤ 482 mm ≥ 482 mm
Use Intensity 1	$RUE_{50th} = \begin{cases} 0.0142 * ppt + 0.73 \\ -0.0041 * ppt + 4.24 \end{cases}$	for ppt ≤ 192 mm ≥ 192 mm
Use Intensity 2	$RUE_{50th} = \begin{cases} 0.0401 * ppt - 2.09 \\ 0.0099 * ppt + 0.51 \\ -0.0013 * ppt + 2.92 \\ -0.0041 * ppt + 4.04 \end{cases}$	for ppt ≤ 86 mm ≥ 86 mm ≤ 215 mm ≥ 215 mm ≤ 396 mm ≥ 396 mm
Use intensity 3	$RUE_{50h} = \begin{cases} 0.0118 * ppt - 0.39 \\ 7e-05 * ppt + 1.87 \\ -0.0015 * ppt + 2.63 \end{cases}$	for ppt ≤ 192 mm ≥ 192 mm ≤ 482 mm ≥ 482 mm

2.2 Convergence between ANPP Estimation Methods in Grasslands – A practical Solution to the Comparability Dilemma

Jan C. Ruppert & Anja Linstädter (2014), *Ecological Indicators* 36: 524-531, DOI: 10.1016/j.ecolind.2013.09.008

Convergence between ANPP estimation methods in grasslands – A practical solution to the comparability dilemma

Jan C. Ruppert^{a,b}, Anja Linstädter^a

^a Range Ecology and Range Management Group, Botanical Institute, University of Cologne, Zülpicher Straße 47b, D-50674 Cologne, Germany

^b Crop Science Group, INRES, University Bonn, Katzenburgweg 5, D-53115 Bonn, Germany

Corresponding author:

Jan Christian Ruppert

Range Ecology and Management

Botanical Institute, University of Cologne

Cologne Biocenter

Zülpicher Straße 47b

D-50674 Cologne, Germany

Email: jan.ruppert@uni-koeln.de

Tel.: +49 (0) 221 - 470 7906

Keywords: Aboveground net primary production, Grasslands, Global ANPP dataset, ANPP estimation, Ecosystem services

Abbreviations: (A)NPP – (Aboveground) Net Primary Production, ORNL DAAC – Oak Ridge National Laboratory Distributed Active Archive Center

NOTICE: This is the author's version of a work that was accepted for publication in Ecological Indicators. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in:

Ecological Indicators 36: 524-531, <http://dx.doi.org/10.1016/j.ecolind.2013.09.008>

Abstract

Aboveground net primary production (ANPP) is a key ecosystem characteristic and of fundamental importance for essentially all aspects of matter and energy fluxes in terrestrial ecosystems. Various methods for estimating ANPP are available and despite partial consensus on 'best practice methods' important methodological issues remain unresolved: ANPP data obtained with different methods differ in their magnitude, variability and their tendency to over- or underestimate primary production. Paradoxically, despite the large number of published ANPP data, the limited comparability of ANPP estimates across studies leads de facto to a scarcity of ANPP data for assembled large-scale studies. We aimed to overcome these problems by establishing conversion rates between the most commonly used ANPP methods, thus making the large body of published ANPP data more comparable and thus useful for assembled large-scale studies.

Using seasonal biomass dynamics from 89 sites representing various biomes and climata, we established linear conversions for all 21 combinations between the seven most common ANPP estimation algorithms in grass-dominated vegetation. We also checked for confounding effects of environmental factors such as biome, management and climatic aridity. Aridity was the only factor with a clear influence on ANPP conversions, and in six cases we thus calculated separate relationships for dry and humid conditions. In these cases, dryland ANPP was systematically underestimated by the respective methods. As these methods are insensitive to turn-over processes from live to senescent biomass, we assume this underestimation is related to climate-induced differences in biomass turn-over rates, with more arid sites having higher rates.

The majority of the resulting 27 conversions had high (pseudo) R^2 values (≥ 0.65 ; full range: 0.31 - 0.92), indicating clear linear relationships between most ANPP estimation methods. Given the large size of the dataset and the accuracy of statistical models, we assume that most conversion formulae are generally valid. We classified conversions with respect to their R^2 values and their methodological comparability, and concluded that 16 conversions can be fully recommended. For those cases where a recalculation of ANPP on basis of original biomass data is not possible, our conversion formulae offer an easy and practical approach to synchronize ANPP estimates from divergent algorithms and sources.

1. Introduction

Aboveground net primary production (ANPP) is a key ecosystem characteristic and of fundamental importance for essentially all aspects of matter and energy fluxes in terrestrial ecosystems. It is a prominent core ecological currency and one of the best documented quantitative estimate for several ecosystem services such as forage or lumber (Scurlock et al., 2002). However, as it represents a concept

rather than a precise physical quantity or attribute, ANPP can only be estimated by surrogate measurements and not measured directly (Lauenroth et al., 2006).

Many different procedures and methods for estimating ANPP have been developed. Particularly in grass-dominated ecosystems, a wide variety of different estimation protocols have been developed within recent decades. The most common methods to estimate ANPP (hereafter simply 'ANPP methods') have been thoroughly evaluated and compared in literature (Lauenroth et al., 2006; McNaughton et al., 1996; Milner and Hughes, 1968; Sala and Austin, 2000; Scurlock et al., 2002; Singh et al., 1975). However, despite a partial consensus on 'best practice methods', discussion regarding various methodological issues is still ongoing, and as a result, numerous ANPP estimation methods are in use and compete up until today. Generally, ANPP methods can be sub-divided into complex elaborated methods and simple, less elaborated ones. Elaborated methods, which account for dynamics in live, senescent, and moribund tissue simultaneously throughout the growing season, have often been recommended (Singh et al., 1975; Scurlock et al., 2002). However, these methods are far more labor-intensive and costly than other 'simple' estimations (e.g. *Peak standing crop*, or *Peak live biomass*) which have a tendency to underestimate production. Unsurprisingly, less elaborate methods are far more often applied, as they are faster and cheaper. Unfortunately, different ANPP methods differ not only in their general accuracy (i.e. their tendency to over- or underestimate ANPP), but also with respect to magnitude, variability and uncertainty (Scurlock et al., 2002; Lauenroth et al., 2006). These differences render estimates based on different methods more or less incomparable. Scurlock et al. (2002) have shown that ANPP estimates at one site and date may vary up to more than 6-fold depending on the computational method used. Examples from our own dataset show even more extreme differences of up to 10- to 15-fold in certain cases (data not shown).

In the past, simple methods like *Peak standing crop* were sufficient for common questions in vegetation and rangeland ecology. They give robust estimates which are sufficient for determining carrying capacity, assessing the influence of climatic characteristics, or comparing the effects of contrasting management strategies at local scale (e.g. Blaisdell, 1958; Dye and Spear, 1982; Smoliak, 1986). However, in recent years there is a growing demand for both more accurate and better comparable ANPP data across larger scales. In fact the lack of large-scale ANPP data has been stated as one of the most crucial data gaps in ecology in recent times (Ni, 2004; Scurlock et al., 2002; Scurlock and Olson, 2002). Paradoxically, despite the large number of studies presenting ANPP data on field and site scale, the limited comparability of ANPP data across sites, regions and studies de facto leads to a scarcity of ANPP data for supra-regional or large-scale studies.

In the light of the climate and land-use change debate, the need for reliable and adequately scaled large-scale and global ANPP datasets is urgent, as each of cross-system analyses, meta-analyses, as well as land-use, climate and vegetation models imminently require them. Since adequate biomass

and ANPP monitoring is not only time consuming but also costly, numerous scientists rely on assembling ANPP datasets from published data (Hsu et al., 2012; Lauenroth and Sala, 1992; Ni, 2004; Ruppert et al., 2012). However, due to differences between ANPP estimation methods, this pragmatic solution is not without its pitfalls. Surprisingly, only a small proportion of studies discuss the issue of comparability of ANPP data assembled from various sources, and based on different estimation and/or computation methods (see 3.1 Results). To date, authors of large-scale studies and meta-analyses either had to neglect major proportions of published data for the sake of comparability or accept the limited and unknown comparability, a true '*comparability dilemma*'.

Still, little is known about the incidence and frequency of ANPP comparability issues in assembled datasets.

Being confronted with this comparability dilemma ourselves (Ruppert et al., 2012; Ruppert et al. in prep.), we aimed to overcome these problems by searching for conversions rates between common ANPP methods. We found that Singh et al. (1975) presented conversions for a set of different ANPP method combinations, developed on the basis of ten short-term datasets from North American grasslands. Surprisingly, practically no use was made of these conversions thereafter. A review (see 2.1 Materials and methods) of all 165 studies citing Singh et al. (source: Google Scholar) revealed that only two studies used the conversions, both by authors of the original paper (Lauenroth and Whitman, 1977; Singh et al., 1983). This poor adoption may be explained by various reasons including: (1) the paper was largely a detailed review, and the conversions were not mentioned in the abstract limiting their visibility; (2) the strong interest in large and global scale ANPP datasets was not as virulent in the 1970s as it is today; and (3) perhaps most critically, the study was based on a restricted dataset and did not test whether conversions were applicable to data from other regions or ecosystems.

We believe that the attempt by Singh et al. (1975) was simply ahead of its time and that it offers a starting point to assess the comparability for future assembled studies. However, the problems and shortcomings of Singh's study, as mentioned under point (3) above, can be overcome by using a large global dataset allowing a more systematic assessment of the comparability of the most common ANPP methods. This is the scope of the present study.

We aim to establish simple conversion formulae between the most common ANPP estimation methods for grass-dominated vegetation. Our study is based on data from 89 sites with more than 850 years of biomass data.

2. Materials and methods

2.1 Literature reviews

Two literature reviews were carried out for this study: (1) A review of the 165 studies citing Singh et al. (1975) to determine whether or not they made use of the presented ANPP conversions (see 1. Introduction). (2) We reviewed the 150 most recent studies presenting field measured ANPP data, and noted the ANPP estimation method(s) employed. We only selected papers from peer-reviewed journals, and excluded ANPP data which was derived from modeling or remote sensing indices. In detail, we searched the term 'ANPP' in the years 2012 and 2011 and selected the 150 most recent papers (written in English, French, German or Spanish). ANPP estimation methods were classified into twelve groups (see Table 1), generally based on the nomenclature of Scurlock et al. (2002) but slightly extended (see Table 1 and below). All literature reviews were carried out using Google Scholar in December 2012, as this source gives more complete results compared to other platforms (Beckmann and von Wehrden, 2012).

Table 1. Overview on the most common ANPP estimation algorithms in grass-dominated vegetation and their respective use-frequency in recent literature.

Group / Method for ANPP estimation ^a	Description	%		
Method 1	Peak live biomass	12.7	Peak methods: 50.0%	Incremental + Other incremental methods : 20.7%
Method 2a ^b	Peak standing crop (live plus recent dead)	18.7		
Method 2b ^b	Peak standing crop (live plus recent and old dead)	18.7		
Method 3	Maximum minus minimum live biomass	1.3	Incremental methods: 15.3%	
Method 4	Sum of positive increments in live biomass	12.0		
Method 5	Sum of positive increments in live and recent dead (Smalley's Method)	1.3		
Method 6	Sum of positive increments in live and total dead (recent plus old dead)	0.0		
Method 7 ^c	Sum of positive increments in live and dead biomass with an adjustment for decomposition	0.7		
Other methods	ANPP methods which could not be sorted into the above.	12.6		
	Other – incremental methods	(5.3)		
	Other – sum methods	(4.0)		
	Other – unspecified	(3.3)		
Assembled studies	ANPP Studies which assembled ANPP datasets from more than one source of ANPP data (supposedly) comprising more than one estimation method for ANPP.	5.3		
Misleading (or wrong)	(or Abbreviation ANPP was used in a misleading (or wrong) way. In most cases daily productivity data was presented.	4.0	Wrong or no informatio n: 16.7%	
No information	No information on ANPP estimation methodology was given.	12.7		

^a Nomenclature follows Scurlock et al., 2002.

^b Differing from Scurlock et al. (2002) the 'peak standing crop' method was split into two subgroups.

^c Note that we had to skip Method 7 from analyses due to insufficient data.

2.2 Dataset

Our ANPP dataset combines established datasets with data obtained from complementary literature reviews. It only comprises datasets which allow the calculation of at least two common ANPP estimation methods. All methods considered in this study are given and described in Table 1, their selection and nomenclature follows Scurlock et al. (2002).

One of the two main sources for ANPP data is the *Net Primary Production Dataset* distributed by the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC, <http://daac.ornl.gov>). The second major source is a self-assembled ANPP dataset comprising long-term monitoring data from arid and semi-arid ecosystems. The principal data search and acquisition methods are described in Ruppert et al. (2012), but the current dataset has been considerably updated and extended compared to that presented therein. Furthermore, suitable ANPP datasets which were found during the above described literature reviews (see 2.1) were added. Table S1 in the supplementary material presents a complete overview on sources and references for all 89 datasets included in analyses.

2.3 Data analysis

2.3.1 ANPP estimation methods

Estimating ANPP is a two-step procedure, starting with the measurement (or estimation) of biomass, followed by the computational processing of these measurements. Here we will focus on the latter aspect of calculation algorithms only, and will concentrate on those algorithms most commonly used in recent studies. Generally two groups of estimation methods can be distinguished: (1) '*Peak methods*', using single biomass measurements at peak biomass conditions to estimate ANPP and (2) '*Incremental methods*', which sum the incremental accumulation of biomass on a seasonal or annual basis.

The seven (to eight) most common methods – their calculation, inherent assumptions and possible pitfalls – have been comprehensively described by Scurlock et al. (2002). We generally followed their nomenclature but split Method 2 '*Peak standing crop*' into two sub-methods (Table 1). Method 2a is the original *Peak standing crop* method (as described in Scurlock et al., 2002), which uses the maximum amount of live plus recent (current year's) dead material as estimate of ANPP. We found several studies which also included previous year's dead material (and sometimes even non-standing, de-attached litter), and labeled this approach as Method 2b. We chose to distinguish between these sub-methods for two reasons: Firstly, Method 2b is of limited applicability only, since it can be biased by the previous year's production. Secondly, lumping both methods together would have introduced considerable variability into '*Peak standing crop*' data.

Since only one site reported sufficient data to calculate ANPP via Method 7 (Sum of positive increments in live and dead biomass with an adjustment for decomposition), we excluded this method from our analyses.

2.3.2 Statistical analyses – Regressions and conversion formulae

Data exploration to avoid common statistical problems (e.g. with respect to outliers, normal distribution and homogeneity of variances) was performed visually as proposed by Zuur et al. (2010). Due to several cases of a violation of the homoscedasticity assumption in least squares regression, we used generalized least squares regression (GLS). By implementing flexible variance structures of the covariate, GLS allows to correct for heteroscedasticity (Zuur, 2009). For each conversion model we tested, five (generalized) least squares models were derived, reflecting different common variance structures of the covariate for ecological data (no variance structure, fixed variance structure, power of the covariate variance structure, exponential variance structure, and constant plus power of the variance structure, see Zuur, 2009). We used Akaike's information criterion (AIC) to select the best-fitting model and checked again for homoscedasticity.

For some method combinations we had indications that systematic differences between data from drylands (arid and semi-arid) and humid areas existed, based on either methodological issues or visual observation of the regressions. We thus used ANCOVAs to test the influence of climate regime on the respective regression models. For six method combinations we found a significant influence of the climate regime and therefore split the data accordingly to establish climate-specific conversion formula (see Table 2 and Figure 1).

Established conversion formulae were classified on the basis of their pseudo R^2 values into three groups (highly reliable, reliable, and unreliable), representing their reliability and usability as conversion models. Class borders were set at pseudo $R^2 \leq 0.5$ for unreliable, > 0.5 and < 0.7 for reliable, and ≥ 0.7 for highly reliable, respectively. Pseudo R^2 calculation was based on the generic definition of the coefficient of determination and was calculated as: $1 - \text{residual sum of squares} / \text{total sum of squares}$. If the final selected model was based on standard least squares regression, pseudo R^2 values were thus equivalent to standard R^2 values.

We also assessed the comparability of each method combination. Comparability between *Peak methods* (Method 1, 2a & 2b) was assumed to be moderate (labeled as "+ -" in Table 2): While all methods are based on single observations during peak biomass conditions, they refer to different estimates of biomass. Comparability between *Peak methods* and *Incremental methods* ranged from poor (- -) to moderate (+ -), depending on the type of biomass used for the estimation. If both methods were based on the same type of biomass (live biomass, live plus recent dead, etc.; e.g. Method 1 : Method 3) their comparability was rated as moderate; if not, comparability was rated as poor (e.g. Method 1 : Method 6). The comparability between *Incremental methods* ranged from moderate (+ -) to good (+ +). Comparability was rated as good if both methods were based on the same type of

biomass (e.g. Method 3 : Method 4) and as moderate if not (e.g. Method 3 : Method 5). This assessment of the methodological and ecological comparability adds some information about the applicability of conversions, in addition to the statistical classification based on pseudo R² values. All statistical calculations were performed in R, version 2.15.2 (R Development Core Team, 2012). The *rms* package (version 3.6-3) and the *nlme* package (version 3.1-105) were used to calculate and visualize GLS models.

Table 2. Overview on the established conversion formulae.

	Statistical reliability class & comparability	Conversion formulae	Std. Err. slope	n	Pseudo R ²	
Recommended	Highly reliable	++ Method 3 = 0.89 x Method 4 + 6	0.02	255	0.91	
		++ Method 5 = 0.9 x Method 6	0.04	38	0.78	
		+ - Method 1 = 0.69 x Method 2a	0.02	227	0.82	
		+ - Method 1 = 1.05 x Method 3 + 29	0.02	384	0.92	
		+ - Method 1 = 0.97 x Method 4 + 32	0.02	679	0.89	
		+ - Method 2a = 0.56 x Method 2b + 57	0.06	29	0.71	
		+ - Method 2a = 0.73 x Method 6 + 92	0.06	30	0.71	
		+ - Method 2b = 0.81 x Method 6 + 176	0.10	18	0.80*	
		+ - Method 3 _{arid} = 0.34 x Method 6 _{arid}	0.03	29	0.73	
		+ - Method 4 _{arid} = 0.39 x Method 6 _{arid} + 11	0.03	29	0.71	
		-- Method 1 _{arid} = 0.35 x Method 6 _{arid} + 50	0.03	29	0.81*	
		Reliable	+ - Method 3 _{humid} = 0.49 x Method 5 _{humid} + 85	0.06	47	0.60
		+ - Method 3 _{humid} = 0.44 x Method 6 _{humid} + 103	0.09	24	0.51*	
		+ - Method 4 _{arid} = 0.53 x Method 5 _{arid} + 19	0.05	39	0.65	
		+ - Method 4 _{humid} = 0.64 x Method 5 _{humid}	0.05	44	0.66	
	+ - Method 4 _{humid} = 0.72 x Method 6 _{humid}	0.07	24	0.62		
Not recommended		+ - Method 2a = 0.83 x Method 5 + 96	0.06	70	0.60	
		+ - Method 2b = 0.81 x Method 5 + 188	0.13	39	0.52*	
		-- Method 2a = 1.23 x Method 3 + 87	0.08	79	0.67	
		-- Method 2a = 1.13 x Method 4 + 96	0.08	79	0.63	
	Unreliable	+ - Method 1 = 0.24 x Method 2b + 96	0.05	52	0.33*	
		+ - Method 3 _{arid} = 0.41 x Method 5 _{arid} + 28	0.05	39	0.50	
		-- Method 1 _{arid} = 0.35 x Method 5 _{arid} + 82	0.06	39	0.50*	
		-- Method 1 _{humid} = 0.58 x Method 5 _{humid} + 94	0.06	47	0.50	
		-- Method 1 _{humid} = 0.69 x Method 6 _{humid} + 43	0.04	24	0.31	
		-- Method 2b = 1.27 x Method 3 + 264	0.28	47	0.31*	
	-- Method 2b = 1.25 x Method 4 + 245	0.27	46	0.33*		

All regression parameters were significant on $p \leq 0.001$ (slopes) or on $p \leq 0.05$ (intercepts). Pseudo R² values marked with an asterisk are standard R² values. Here model selection selected non-GLS models (= least squares regression). Statistical reliability class borders were set according to (pseudo) R² values: ≤ 0.5 poor, > 0.5 and < 0.7 moderate, ≥ 0.7 good. Classification of comparability classes (+ +, + -, and - -) is described in 2.3.2 Materials and Methods. For full model descriptions please refer to Table S3.

3. Results

3.1 Literature reviews

The most recent 150 publications presenting ANPP data showed that *Peak biomass* estimates (Methods 1, 2a & 2b) dominated with 50 % of all studies using them. *Incremental methods* (Methods 3-7) followed with 15.3 %. A smaller proportion of 12.7 % of studies used very specific ANPP estimation methods, which could not be assigned to one of the common methods, and therefore were allotted in 'Other ANPP methods'. Within this group, the largest share (representing 5.3% of all studies) were other, 'non-canonical', incremental methods, followed by methods calculating ANPP as the sum of several cuts throughout a season or year (4% of studies). Combining the canonical ANPP methods (Methods 3-7, 15.3 %) and these specific non-canonical methods (5.3 %), increased the total share of incremental methods to 20.7% over all studies.

In total 5.3% of all studies (8 studies of 150) presented *Assembled ANPP datasets* with more than one source of ANPP data. These studies often combined several methods in one dataset. Another 4% of all studies used the term ANPP in a misleading way. In most cases, authors presented aboveground net primary productivity, which is production per time (e.g. $\text{g m}^{-2} \text{d}^{-1}$). The remaining 12.7 % gave no information, on how ANPP was estimated.

The group of *Peak biomass* estimates was dominated by the two varieties of *Peak standing crop*, Method 2a and Method 2b, with 18.7 % each, as compared to *Peak live biomass* (Method 1) with 12.7 %. *Incremental methods* are dominated by Method 4 (Sum of positive increments in live biomass) with 12.0 %. All other methods were rarely used. Method 3 (Maximum minus minimum in live biomass) and Method 5 (Sum of positive increments in live and recent dead, aka Smalley's Method) have been used in 1.3 % of all cases each (2 in 150 each), Method 7 (Sum of positive increments in live and dead biomass with an adjustment for decomposition) were used in 0.7 % of all cases (1 in 150), and Method 6 (Sum of positive increments in live and total dead) was not used in recent publications.

In the group of *Assembled ANPP studies* only three out of eight studies gave information on the respective ANPP estimation method for all datasets and addressed issues of comparability (Adler et al., 2011; Robinson et al., 2012; Ruppert et al., 2012). The other studies either mentioned the most commonly used methodologies only (Hsu et al., 2012; Yahdjian et al., 2011), simply stated that datasets were comparable (Hector et al., 2011), or did not comment on the nature of ANPP data at all (Eldridge et al., 2011; Evans et al., 2011). It should be mentioned that Eldridge et al. (2011) and Yahdjian et al. (2011) only presented ANPP response ratios (treated vs. non-treated), therefore differences in ANPP estimation algorithms should be of minor concern.

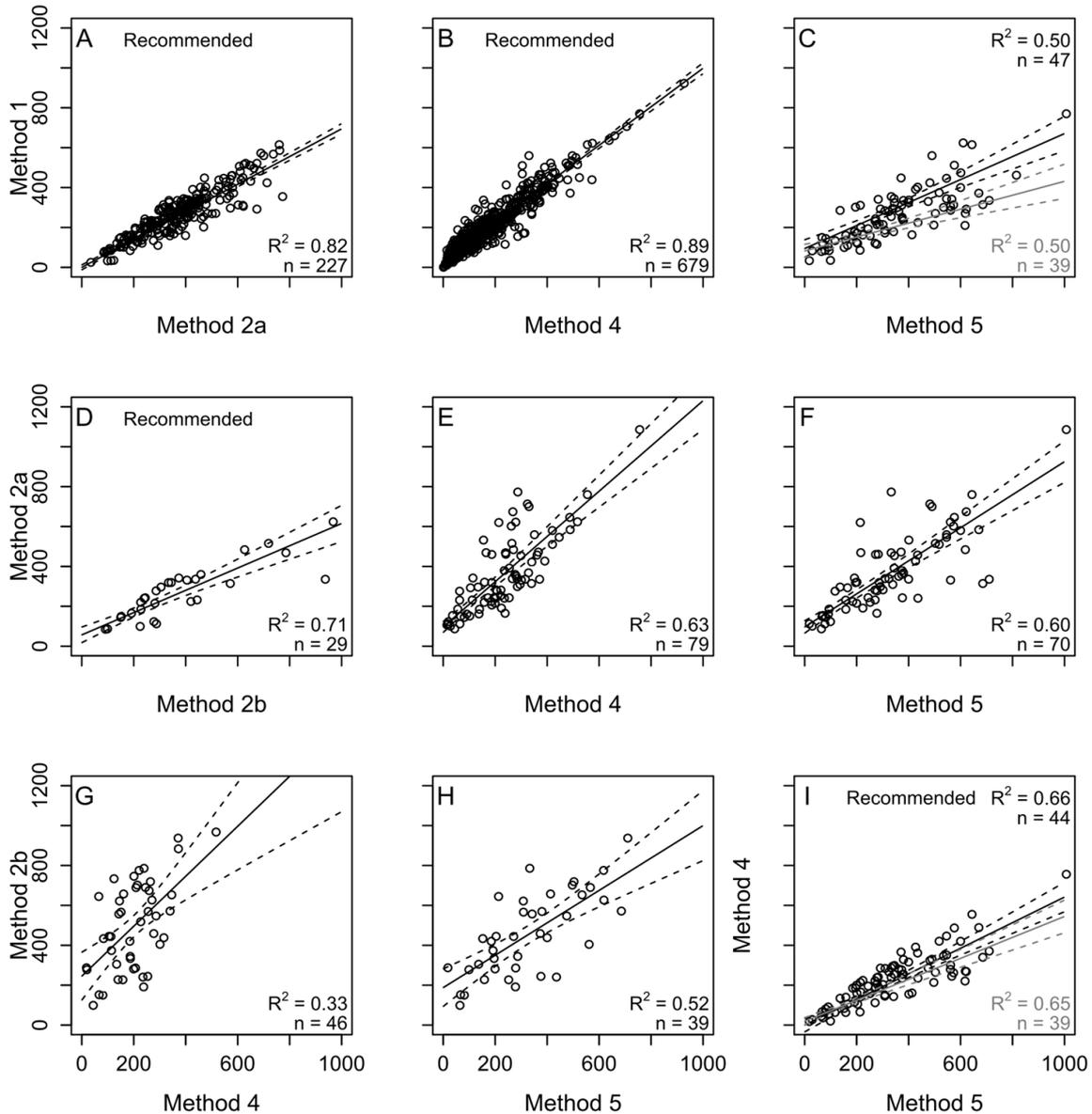


Figure 1. Selection of conversion models (GLS regressions) between common ANPP estimation methods together with corresponding number of observations (n) and (pseudo) R^2 . Linear regressions are given as solid black lines. Where regressions were calculated separately for humid and dry sites (see 2.3.2 Material and Methods), black line represent the humid model. Solid grey lines represent the arid model, where applicable. Broken lines indicate the .95 confidence interval. Note: Selection of models comprises recommended and not recommended conversions models (see 2.3.2 Materials and Methods). Models in A, B, D, and I are recommended. See also Figure S1 for a complete graphical overview on all conversions models.

3.2 Established conversions between ANPP estimations methods

Using the statistical protocol described above (see 2.3.2 Materials and Methods), we analyzed all 21 possible (one-way) combinations between the seven considered ANPP estimation methods (Method 1, 2a, 2b, 3, 4, 5, and 6). Since six of these combinations exhibited systematic influences of climate (dryland vs. humid), we established a total of 27 conversion formulae (Table 2). Based on their coefficients of determination, eleven models were classified as rendering highly reliable conversions, nine as reliable and seven as unreliable. The assessment of method comparability generally mirrored

the statistical classification. The class of *highly reliable models* included the only two method combinations which were rated as highly comparable (Method 3 : Method 4, and Method 5 : Method 6). Furthermore, this class only includes one method combination which has been rated as poorly comparable (Method 1_{arid} : Method 6_{arid}), the remaining eight combinations were rated as moderately comparable. The class of *reliable models* mostly contains combinations which were rated as moderately comparable, and only two poorly comparable combinations. The majority of poorly comparable method combinations are found in the *unreliable class*, which apart from these combinations only includes two moderately comparable combinations.

Table 2 presents all established conversions formulae in a standardized linear model format ($y = mx + b$). Furthermore, the standard error of the slope, the number of observations for the respective model, and the pseudo R^2 is given. Figure 1 gives a graphical representation of selected conversions. It presents nine method combinations and their eleven respective conversion models together with their confidence intervals. These method combinations represent the most frequently used ANPP methods according to our literature review (Methods 1, 2a, 2b and 4; see Table 1). In addition, we have included Method 5 as an example for an often recommended elaborate method (Singh et al., 1975, Scurlock et al., 2002). The selection in Figure 1 also gives examples for all statistical reliability classes: highly reliable (Figure 1A, B, D), reliable (Figure 1E, F, H, I), and unreliable (Figure 1C, G). An overview of all other established conversion formulae can be found in Figure S1 in the supplementary material.

4. Discussion

The aim of this study was to establish conversions between the most common ANPP estimation methods, to improve comparability between ANPP estimates derived from different methods, and thus provide better access to the large body of published ANPP data. This was mainly motivated by the growing demand for large- or global-scale ANPP datasets which has evolved as a direct consequence of the climate and land-use change debate.

We were able to establish linear conversion formulae between the seven most commonly used ANPP estimation methods for grass-dominated biomes, and to assess their reliability and usability with statistical and methodological means.

4.1 Faster, simple methods are more often used than elaborate but labor-intensive methods

The review on the use of ANPP in recent literature revealed that the simple and fast methods of the *Peak biomass* group were most frequently applied. Every second publication in our review used one of these methods. The frequency of use of the three sub-methods in this group was nearly identical. The

more elaborate, but also more time- and labor-intensive, *Incremental methods* were used less often. Only one in five publications used one of these methods; when only the canonical methods are considered, this frequency further drops to one in six to seven. While this general trend is not surprising and consistent with the dataset structure in Scurlock et al. (2002), it is surprising that recommendations to use the more elaborate algorithms, accounting for dynamics of live and dead plant matter (Method 5, 6 and 7), have not been adopted by the scientific community. Indeed, only 3 of 150 publications used one of these methods (Table 1). However, far more concerning is that 12.7 % of the studies did not provide information on which ANPP method was used.

Given this use frequency of common ANPP estimation algorithms, scientists who seek to compile large-scale ANPP datasets from various sources face the '*comparability dilemma*' described above (see 1. Introduction). To make matters worse, the rare data derived from elaborate and supposedly more accurate algorithms would be the first to be dropped for the sake of comparability.

4.2 Using recommended conversion formulae to overcome the '*comparability dilemma*'

Our main impetus for the study was to overcome the above described '*comparability dilemma*' by mitigating the trade-off between the demand for large datasets and data comparability. Motivated by the compilation of a global ANPP dataset for drylands (Ruppert et al., 2012, Ruppert et al., in prep), and inspired by Singh et al. (1975), we found linear conversion formulae to be a simple, versatile, and straight-forward approach to convert between different ANPP estimation algorithms.

Based on seasonal biomass dynamics from 89 sites from various grass-dominated biomes and climate regimes, we deduced conversion formulae for all method combinations representing the most commonly used ANPP estimation algorithms (Scurlock et al., 2002). Six out of all 21 method combinations showed a significant influence of climate regime (dry vs. humid), thus leading to a total of 27 conversions formulae (see 4.3 Influence of climate regime on conversions formulae and ANPP methods). Even though we were able to deduce statistically sound and significant regressions for all model combinations, not all conversions can be fully recommended.

Generally, all models which were rated as *highly reliable* in terms of statistical criteria can be recommended for use without exceptions. In contrast, formulae classified as *unreliable* cannot be recommended and should be avoided. Even though conversion models in the latter group are highly significant, the underlying data exhibit considerable variance, which is also reflected in the pseudo R^2 values. Therefore, products derived from these models would involve considerable uncertainty. The line separating recommendable and non-recommendable conversions runs through the group of statistically *reliable models*. Our decision to classify the conversions between Method 2a and Method 3, 4 and 5, as well as conversions between Method 2b and Method 5 as not recommended is based on

the visual assessment of the respective scatterplots (Figure S1-4, and Figure 1E, F, H respectively). For all combinations, a high spread of relatively equally spaced datapoints can be observed. For most cases, the spread also shows a tendency to increase with higher ANPP values, indicating heteroscedasticity. Therefore, derived conversion products would largely suffer from uncertainty. However, these conversion formulae might still be applicable for ANPP data from less productive sites (e.g. from drylands) with respective input estimates up to circa 200 g m⁻². For this range in ANPP data, the spread in the data is rather small, particularly for the conversions between Method 2a and Method 3, 4 and 5.

4.3 Influence of climate regime on conversions formulae and ANPP methods

The six possible combinations between Methods 1, 3 and 4 on the one hand and Methods 5 and 6 on the other (and only these six) showed a significant influence of climate regime (arid vs. humid) and were split into climate-specific conversion formula (see Figure 1, S1 and Table 2).

Notably, in all six cases, the slope of the dry climate model is less steep as compared to the humid model. If we assume Methods 5 and 6 to be the best proxy to 'real' ANPP (as they are 'best practice' methods), Methods 1, 3 and 4 underestimate ANPP in drylands more strongly than in humid ecosystems.

We assume that this systematic error could be ecologically explained by the higher turn-over rate from live to senescent biomass in drylands due to increased tissue senescence rate in response to water stress (Coughenour and Chen, 1997). While Methods 5 and 6 are sensitive to changes in live, senescent and moribund material and thus account for all biomass turn-over processes, Methods 1, 3 and 4 only assess live biomass. Thus, the latter three methods have specific ways of neglecting turn-over processes. Method 1 registers only live biomass at peak conditions, neglecting all produced live biomass which already turned senescent before peak. Methods 3 and 4 miss all live biomass which has turned over between minimum and maximum live biomass, or between sampling intervals, respectively. Thus these methods are inherently prone to differences in turn-over rates between different climates or ecoregions.

4.4 Applicability and generality of the conversion formulae

Given the clear patterns in the conversion models (Fig. 1 & S1) and considering the large underlying dataset, we expect the conversion formulae to be generally valid. Furthermore, despite the importance of climate regime for some conversions, we found no evidence for systematic influences of other factors (e.g. biome or long-term management). The generality of conversions is also supported by a comparison to those presented in Singh et al. (1975). Although the selection of ANPP estimation

methods differs between the two studies, a subset of six conversions can be compared. The conversions between Method 1 and Method 4 are discussed as an example.

Based on our data we established the conversion formula:

$$\text{Method 1} = 0.97 \times \text{Method 4} + 32 \quad (n = 679)$$

Singh and colleagues (1975) found a very similar conversion formula (the formula has been converted to fit our format, see fourth formula in Table IV, Singh et al., 1975):

$$\text{Method 1} = 1.06 \times \text{Method 4} \quad (n = 33)$$

The slightly higher slope in Singh's formula can be explained by the fact that all linear conversions were forced through the origin. An overview of the remarkable consistency between our results and those of Singh et al. (1975) and other published data (Linthurst and Reimold, 1978) is presented in the Supplementary Material (Table S2 and Figure S2).

Some authors have assumed that differences between ANPP methods might be site-specific (Linthurst and Reimold, 1978; Long et al., 1989; Scurlock et al., 2002). They based this assumption on their observation that ranking sites according to their production, using several ANPP estimation methods, yielded varying outcomes. Interpreted towards the use of the conversion models this means that the respective proportion of under- or overestimating ANPP by applying a respective conversion is site-specific. However, this source of uncertainty is a general feature of predictions based on regression models.

Our analysis clearly shows that there are strong systematic relationships between several ANPP estimation algorithms. This underlines the usability of our conversion models, especially those which have been labeled as recommended on the basis of statistical and methodological criteria.

4.5 Uncertainties in estimating ANPP

Lauenroth et al. (2006) raised the issue of uncertainty in estimating (A)NPP and hypothesized that estimation algorithms differ not only with respect to magnitude and accuracy (over- or underestimation) but also with respect to uncertainty. They analyzed the amount of uncertainty which is mathematically introduced in ANPP estimates based on different estimation algorithms, as compared to the uncertainty in the input data (biomass estimates). Considering their findings we can assume that all estimation methods which we used for conversions should exhibit very low levels of uncertainty (i.e. corresponding to the level found in the biomass input data or even less). *Peak methods* simply transmit the uncertainty of the single biomass measurements on which they are based to the ANPP estimate. Since biomass can be measured or estimated with low uncertainty, these ANPP algorithms will exhibit the same low uncertainty. *Incremental methods* (Methods 3 to 6) are based on sums or differences over sequential biomass data. For these methods, the amount of uncertainty is even lower as compared to the average uncertainty of the input data. Only algorithms which contain

product terms (i.e. Method 7) might increase (or also decrease) uncertainty as compared to the input data (biomass), but these methods have not been used in this study (see 2.3.1 Material and Methods). Hence, we assume that possible interference, caused by divergent uncertainty in the ANPP methods when converting between different methods, can be neglected for the conversion formulae presented here.

4.6 Conclusions and recommendations

The conversions formulae established within this study offer an easy and practical approach to recalculate and compare between ANPP estimates derived by divergent estimation algorithms. Authors who assemble large-scale ANPP datasets, or generally wish to combine ANPP data from various sources, can surely benefit from our approach, since it allows generating comparably scaled ANPP estimates based on published data.

Though we found statistically significant models for all combinations of the most common ANPP estimates in grass-dominated biomes, not all conversions can be recommended. The combined classification via statistical (pseudo R^2) and methodological attributes (comparability of ANPP estimation algorithms) offered a sound basis for recommendations (Table 2). Based on these statistical and methodological criteria, we rated 16 out of 27 conversions formulae as recommendable. The remaining 11 conversions are afflicted with high statistical or methodological uncertainty and should only be used with care, if at all.

In this context another important outcome was that we found an ecological explanation for the phenomenon that certain ANPP methods differ in their tendency to underestimate ANPP across ecoregions (Singh et al., 1975; Scurlock et al., 2002). We assume that this tendency is related to differences in plants' turn-over rates from live to senescent biomass as a function of climatic aridity. We conclude that those methods which are highly sensitive to this turn-over (Methods 1, 3, and 4) should not be used in warm xeric environments where biomass turn-over rates appear to be particularly high.

Note that this study does not advocate relying on conversion options only. Even the best conversion formula is still second best to a recalculation of ANPP which can be done by applying the desired algorithm to the original biomass data. Our approach offers a practical solution for those cases where this option is not possible or feasible, and is superior to previous attempts to solve the comparability dilemma (i.e. combining incomparably scaled ANPP data or skip available published data).

We are confident that a prudent use of conversion formulae, will promote the compilation of assembled ANPP datasets, and that our conversions will greatly facilitate the usability of published ANPP data in assembled regional or global studies.

Acknowledgements

We thank Marcelo Sternberg from Tel Aviv University and Zalmen Henkin from the Agriculture Research Organization for providing unpublished biomass data from the Karei Deshe Experimental Farm, Israel. We thank the editor and two anonymous referees for their insightful comments on the manuscript. Furthermore, we thank Roelof Oomen for fruitful discussions during the development of this study and Heidi Webber for improving the English. The research of Jan C. Ruppert was funded by the Foundation of German Business (Stiftung der Deutschen Wirtschaft, sdw) and by the German Science Foundation (Deutsche Forschungsgemeinschaft, DFG) through a grant to the Research Unit (FOR 1501). Research of Anja Linstädter was supported by the DFG through FOR 1501 and the German Federal Ministry of Education and Research (BMBF) via the WASCAL initiative (West African Science Service Center on Climate Change and Adapted Land Use). Data from Jornada Basin, Konza Prairie, and Sevilleta was provided by the Long Term Ecological Research (LTER) Program which is significantly funded by the U.S. National Science Foundation Long Term Ecological Research program (NSF Grant numbers BSR-8811906, DEB-0080529, DEB-0217774, DEB-0236154, DEB-0618210, DEB-0823341, DEB-0832652, DEB-0936498, DEB-9411976, DEB-9634135). Finally, we thank the many, many – often anonymous – researchers and research assistants who gathered the biomass data underlying our dataset.

References

- Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Brown, C.S., Buckley, Y.M., Calabrese, L.B., Chu, C.J., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah, N., Hille Ris Lambers, J., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P., Yang, L.H., 2011. Productivity is a poor predictor of plant species richness. *Science* 333, 1750-1753.
- Beckmann, M., von Wehrden, H., 2012. Where you search is what you get: literature mining - Google Scholar versus Web of Science using a data set from a literature search in vegetation science. *J Veg Sci* 23, 1197-1199.
- Blaisdell, J.P., 1958. Seasonal development and yield of native plants on the upper Snake River Plains and their relation to certain climatic factors. U.S. Dept. of Agriculture, Washington.
- Coughenour, M.B., Chen, D.-X., 1997. Assessment of grassland ecosystem responses to atmospheric change using linked plant-soil process models. *Ecol Appl* 7, 802-827.
- Dye, P.J., Spear, P.T., 1982. The Effects of Bush Clearing and Rainfall Variability on Grass Yield and Composition in Southwest Zimbabwe. *Zimbabwe J Agr Res* 20, 103-118.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett* 14, 709-722.

- Evans, S.E., Burke, I.C., Lauenroth, W.K., 2011. Controls on soil organic carbon and nitrogen in Inner Mongolia, China: A cross-continental comparison of temperate grasslands. *Global Biogeochem Cycles* 25.
- Hector, A., Bell, T., Hautier, Y., Isbell, F., Kery, M., Reich, P.B., van Ruijven, J., Schmid, B., 2011. BUGS in the Analysis of Biodiversity Experiments: Species Richness and Composition Are of Similar Importance for Grassland Productivity. *Plos One* 6.
- Hsu, J.S., Powell, J., Adler, P.B., 2012. Sensitivity of mean annual primary production to precipitation. *Global Change Biol* 18, 2246-2255.
- Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. *Ecol Appl* 2, 397-403.
- Lauenroth, W.K., Wade, A.A., Williamson, M.A., Ross, B.E., Kumar, S., Cariveau, D.P., 2006. Uncertainty in calculations of net primary production for grasslands. *Ecosystems* 9, 843-851.
- Lauenroth, W.K., Whitman, W.C., 1977. Dynamics of Dry-Matter Production in a Mixed-Grass Prairie in Western North-Dakota. *Oecologia* 27, 339-351.
- Linhurst, R.A., Reimold, R.J., 1978. Evaluation of Methods for Estimating the Net Aerial Primary Productivity of Estuarine Angiosperms. *J Appl Ecol* 15, 919-931.
- Long, S.P., Moya, E.G., Imbamba, S.K., Kamnalrut, A., Piedade, M.T.F., Scurlock, J.M.O., Shen, Y.K., Hall, D.O., 1989. Primary Productivity of Natural Grass Ecosystems of the Tropics - a Reappraisal. *Plant Soil* 115, 155-166.
- McNaughton, S.J., Milchunas, D.G., Frank, D.A., 1996. How can net primary productivity be measured in grazing ecosystems? *Ecology* 77, 974-977.
- Milner, C., Hughes, R.E., 1968. Methods for the measurement of the primary production of grassland, IBP Handbook no. 6. Blackwell, Oxford, UK.
- Ni, J., 2004. Estimating net primary productivity of grasslands from field biomass measurements in temperate northern China. *Plant Ecol* 174, 217-234.
- R Development Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Robinson, T.M.P., La Pierre, K.J., Vadeboncoeur, M.A., Byrne, K.M., Thomey, M.L., Colby, S.E., 2012. Seasonal, not annual precipitation drives community productivity across ecosystems. *Oikos*, 727-738.
- Ruppert, J.C., Holm, A.M., Miehe, S., Muldavin, E., Snyman, H.A., Wesche, K., Linstädter, A., 2012. Meta-analysis of rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands. *J Veg Sci* 23, 1035-1050.
- Sala, O.E., Austin, A.T., 2000. Methods of estimating aboveground net primary production, in: Sala, O.E., Jackson, R.B., Mooney, H.A., Howarth, R.H. (Eds.), *Methods in Ecosystem Science*. Springer, New York, pp. 31-43.
- Scurlock, J.M.O., Johnson, K., Olson, R.J., 2002. Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biol* 8, 736-753.
- Scurlock, J.M.O., Olson, R.J., 2002. Terrestrial net primary productivity - A brief history and a new worldwide database. *Environmental Reviews* 10, 91-109.
- Singh, J.S., Lauenroth, W.K., Heitschmidt, R.K., Dodd, J.L., 1983. Structural and Functional Attributes of the Vegetation of Northern Mixed Prairie of North-America. *Bot Rev* 49, 117-149.
- Singh, J.S., Lauenroth, W.K., Steinhorst, R.K., 1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. *Bot Rev* 41, 181-232.
- Smoliak, S., 1986. Influence of Climatic Conditions on Production of *Stipa-Bouteloua* Prairie over a 50-Year Period. *J Range Manage* 39, 100-103.
- Yahdjian, L., Gherardi, L., Sala, O.E., 2011. Nitrogen limitation in arid-subhumid ecosystems: A meta-analysis of fertilization studies. *J Arid Environ* 75, 675-680.
- Zuur, A.F., 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, NY.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1, 3-14.

Table S1. Overview on study areas and sites in our assembled dataset.

Study area	Sites	Country	City & Region	Climate	Vegetation type	Source of data	References
Badkhyz	1	Turkmenistan	Kushka	arid	grassland	ORNL DAAC	Gilmanov et al. 1997 Nechaeva et al. 1971
Beacon Hill	1	U.K.	Beacon Hill, Sussex	humid	grassland	ORNL DAAC	Williamson 1976
Bhojbasa	2	India	Gangotri, Uttarkashi	humid	grassland	Dhauiakhand et al. 2010	Dhauiakhandi et al. 2010
Burnihat	1	India	Burnihat, Meghalaya	humid	grassland (artificial)	Shankar et al. 1993	Shankar et al. 1993 Sims et al. 1978
Bridger	2	U.S.A.	Bridger near Bozman, Montana	semi-arid	grassland	ORNL DAAC	Sims & Singh 1978a/b
Cañas	1	Costa Rica	Cañas, Guanacaste	semi-arid	savanna	ORNL DAAC	Daubenmire 1972a/b/c Christie 1978
Charleville	2	Australia	Charleville, Queensland	semi-arid	grassland	ORNL DAAC	Christie 1979
Cherrapunji	1	India	Cherrapunji, Meghalaya	humid	grassland (artificial)	Shankar et al. 1993	Shankar et al. 1993 Sims et al. 1978
Dickson	2	U.S.A.	Dickson, North Dakota	arid	grassland	ORNL DAAC	Sims & Singh 1978a/b
Dzhanybek	1	Kazakhstan	Dzhanybek, West Kazakhstan	semi-arid	grassland	ORNL DAAC	Gilmanov et al. 1997
Galveston	2	U.S.A.	Galveston County, Texas	humid	grassland	Harcombe et al. 1993	Harcombe et al. 1993 Sims et al. 1978
Hays	1	U.S.A.	Hays, Kansas	semi-arid	grassland	ORNL DAAC	Sims & Singh 1978a/b
IMGERS	1	China	Xilin River Basin, Inner Mongolia	semi-arid	grassland	Ma et al. 2010	Ma et al. 2010
Karei Deshe	7	Israel	Karei Deshe, Northern Israel	semi-arid	grassland	pers. comm.	Sternberg et al. (2000) Henkin et al. (2011)
Experimental Farm	1	Ukraine	Khomutov, Donezk Region	humid	grassland	ORNL DAAC	Gilmanov et al. 1997 Long et al. 1988
Klong Hoi Kong	1	Thailand	Klong Hoi Khong	humid	grassland	ORNL DAAC	Kamnrat & Evenson 1992 Bazilevich & Gilmanov 1984
Kursk	1	Russia	Kursk, Oblast Kursk	humid	grassland	ORNL DAAC	Gilmanov et al. 1997 Meanut & Cesar 1979
Lamto	1	Ivory Coast	Divo, Sud-Bandama	humid	savanna	ORNL DAAC	Bourliere & Hadley 1970 Sims et al. 1978
LTERR Jornada Basin	15	U.S.A.	Las Cruces, New Mexico	arid to semi-arid	grass-/shrubland	LTER JRN	Sims & Singh 1978a/b Huenneke et al. 2002 Abrams et al. 1986
LTERR Konza Prairie	9	U.S.A.	Manhattan, Kansas	semi-arid to sub-humid	grassland	LTER KNZ	Briggs et al. 1989 Knapp et al. 1998
LTERR Sevilleta	10	U.S.A.	Albuquerque, New Mexico Matador near Swift Current,	arid	grassland	LTER SEV	Heisler & Knapp (2008) Muldavin et al. (2008)
Matador	1	Canada	Saskatchewan Media Luna Ranch, Rio Mayo,	semi-arid	grassland	ORNL DAAC	Couturier & Ripley 1973
Media Luna	1	Argentina	Patagonia	semi-arid	grassland	ORNL DAAC	Defosse et al. 1990

Table S1 continued

Study area	Sites	Country	City & Region	Climate	Vegetation type	Source of data	References
Montecillo	2	Mexico	Texcoco / Mexico City	semi-arid	grassland	ORNL DAAC	Long et al. 1989 Garcia-Moya & Montanez Castro (1992)
Nairobi	1	Kenya	Nairobi	semi-arid	savanna	ORNL DAAC	Long et al. 1989 Kinyamario & Imbamba (1992)
Nyilsvley	1	South Africa	Nyilsvley, Limpopo	semi-arid	savanna	ORNL DAAC	Grunow et al. 1980 Scholes & Walker 1993 Sims et al. 1978
Osage	2	U.S.A.	Osage near Tulsa, Oklahoma	humid	grassland	ORNL DAAC	Sims & Singh 1978a/b Risser et al. 1981
Otradnoe	2	Russia	Otradnoe	humid	grassland	ORNL DAAC	Guricheva et al. 1975 Gilmanov et al. 1997
Pampa de Leman	1	Argentina	Chubut, Patagonia	arid	shrubland	ORNL DAAC	Bertiller 1984
Serengeti	2	Kenya	Western Corridor Serengeti NP	humid	savanna	Hassan 2011	Hassan 2011
Shortandy	1	Kazakhstan	Shortandy near Astana	semi-arid	grassland	ORNL DAAC	Titlyanova et al. 1984 Gilmanov et al. 1997
Sonoita Texas Experimental Ranch	1	U.S.A.	Sonoita, Arizona	semi-arid	grassland	Cox 1984	Cox 1984
Tullgarnsaset	2	U.S.A.	Throckmorton County	semi-arid	grassland	Heitschmidt et al. 1982	Heitschmidt et al. 1982
Tumentsogt	1	Sweden	Tullgarnsaset, near Stockholm	humid	grassland	ORNL DAAC	Wallentius 1973 Dashnyam 1974
Tumugi	1	Mongolia	Ondorhaan	semi-arid	grassland	ORNL DAAC	Chuluun et al. 1995
Tuva	3	China	Ulan Hot, Inner Mongolia	sub-humid	grassland	ORNL DAAC	Xiao et al. (1996) Gorshkova 1986
Upper Shillong	1	Russia	Kyzyi, Tuva	semi-arid	grassland	ORNL DAAC	Gilmanov et al. 1997
	1	India	Shillong, Meghalaya	humid	grassland (artificial)	Shankar et al. 1993	Shankar et al. 1993
Xilingol	2	China	Xilinhot, Xilingol	semi-arid	grassland	Xiao et al. 1995 & 1996	Zhao et al. 1988 Xiao et al. (1995) & (1996)

ORNL DAAC = Oak Ridge National Laboratory Distributed Active Archive Center (<http://daac.ornl.gov>), Net Primary Productivity Grasslands dataset. Datasets from Konza, Jornada, and Xilingol were not used, since more recent data was available from other sources. Other ORNL DAAC NPP dataset sites like Calaboza, CPER, Olokemeji, Rio Mayo, Vindhyan, or Towoomba were omitted, since they did not have enough data to calculate more than one ANPP method or showed inconsistencies. As in Scurlock et al. 2002, we also excluded the Kurukshehra site due to its unusual high (A)NPP estimates (outlier), which might be attributed to undocumented fertilization or similar.

LTER = Long Term Ecological Research Network (<http://www.lternet.edu>).
Climate classification and vegetation type follows the respective references and was cross-checked against the Olson ecoregion classification (Olson et al. 2001) where information was ambiguous.

References

- Abrams, M.D., Knapp, A.K. & Hulbert, L.C. 1986. A 10-Year Record of Aboveground Biomass in a Kansas Tallgrass Prairie - Effects of Fire and Topographic Position. *Am J Bot* 73: 1509-1515.
- Bazilevich, N. I., and T. G. Gilmanov (1984). Conceptual balance models of natural and seminatural ecosystems of the Central Chernozem Biosphere Reserve. In: Conservation, Science and Society (Natural Resources Research XXI, Vol.2) UNESCO-UNEP. pp. 347-350.
- Bertiller, M. 1984. Specific Primary Productivity Dynamics in Arid Ecosystems - a Case-Study in Patagonia, Argentina. *Acta Oecol-Oec Gen* 5: 365-381.
- Bourliere, F., and M. Hadley (1970). The ecology of tropical savannas. *Ann. Rev. Ecology and Systematics* 1: 125-152.
- Briggs, J.M., Seastedt, T.R. & Gibson, D.J. 1989. Comparative-Analysis of Temporal and Spatial Variability in above-Ground Production in a Deciduous Forest and Prairie. *Holarctic Ecol* 12: 130-136.
- Bystrickaya, T. L., and V. V. Osychnyuk (1975). Soils and primary biological productivity of steppes of Pryazovye (as exemplified by the "Khomutovskaya Steppe" reserve). Nauka, Moscow. 112 pp.
- Christie, E. K. (1978). Ecosystem processes in semi-arid grasslands. I. Primary production and water use of two communities possessing different photosynthetic pathways. *Australian J. Agricultural Research* 29: 773-787.
- Christie, E. K. (1979). Ecosystem processes in semi-arid grasslands. II. Litter production, decomposition and nutrient dynamics. *Australian J. Agricultural Research* 30: 29-42.
- Chuluun, Togtohyun, D. S. Ojima, Jargalsaihan Luvsandorjiin, J. Dodd, and S. Williams (1995). Simulation studies of grazing on the Mongolian steppe, pp. 561-562, in: Proceedings of the 5th International Rangeland Congress, Salt Lake City, Utah, U.S.A., July 1995 (N.E. West, ed.). Society of Range Management, Denver, Colorado, U.S.A.
- Couturier, D.E. & Ripley, E.A. 1973. Rainfall Interception in Mixed Grass Prairie. *Can J Plant Sci* 53: 659-663.
- Cox, J.R. 1984. Shoot Production and Biomass Transfer of Big Sacaton [*Sporobolus-Wrightii*]. *J Range Manage* 37: 377-380.
- Dashnyam, B. (1974). Flora and Vegetation of the Eastern Mongolian Steppe. Mongolian Academy of Sciences Publ., Ulaanbaatar (in Mongolian).
- Daubenmire, R. (1972a). Standing crops and primary production in savanna derived from semi-deciduous forest in Costa Rica. *Botanical Gazette* 133: 395-401.
- Daubenmire, R. (1972b). Ecology of *Hyparrhenia rufa* in derived savanna in north-western Costa Rica. *J. Applied Ecology* 9: 11-23.
- Daubenmire, R. (1972c). Some ecological consequences of converting forest to savanna in north-western Costa Rica. *Tropical Ecology* 13: 31-51.
- Defosse, G.E., Bertiller, M.B. & Ares, J.O. 1990. Above-Ground Phytomass Dynamics in a Grassland Steppe of Patagonia, Argentina. *J Range Manage* 43: 157-160.
- Dhaulakhandi, M., Rajwar, G.S. & Kumar, M. 2010. Ecological status and impact of disturbance in an alpine pasture of Garhwal Himalaya, India. *Journal of Plant Development* 17: 127-137.
- Fernandez, R.J., Sala, O.E. & Golluscio, R.A. 1991. Woody and Herbaceous Aboveground Production of a Patagonian Steppe. *J Range Manage* 44: 434-437.
- Garcia-Moya, E., and P. Montanez Castro (1992). Saline grassland near Mexico City. In: Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics. (Long, S.P., M.B. Jones and M.J. Roberts, eds.). Chapman and Hall, London. pp. 70-99.
- Gilmanov, T.G. & Ivaschenko, A.I. 1990. Primary Production of Ecosystems of the Alkali Complex of the Clay Semidesert of the North Transcaspian Area. *Izv an Sssr Biol+* 600-611.
- Gilmanov, T.G., Parton, W.J. & Ojima, D.S. 1997. Testing the 'CENTURY' ecosystem level model on data sets from eight grassland sites in the former USSR representing a wide climatic/soil gradient. *Ecol Model* 96: 191-210.
- Gorshkova, A. A. (1986). In: Titlyanova, A. A. (ed.) Productivity of Haymows and Pastures. Nauka, Novosibirsk. pp. 123-129 (in Russian)
- Grunow, J.O., Groeneveld, H.T. & Dutoit, S.H.C. 1980. Above-Ground Dry-Matter Dynamics of the Grass Layer of a South-African Tree Savanna. *J Ecol* 68: 877-889.
- Guricheva, N. P., O. M. Demina, G. I. Kozlova, et al. (1975). Productivity of meadow communities. In: Resources of the Biosphere (Results of Soviet IBP studies) Vol.1. Nauka, Leningrad. pp. 96-127.
- Harcombe, P.A., Cameron, G.N. & Glumac, E.G. 1993. Aboveground Net Primary Productivity in Adjacent Grassland and Woodland on the Coastal Prairie of Texas, USA. *J Veg Sci* 4: 521-530.
- Hassan, S.N. 2010. Influence of early dry season fires on primary production in western Serengeti grasslands, Tanzania *Open Journal of Ecology* 1: 24-34.

- Heisler, J.L. & Knapp, A.K. 2008. Temporal coherence of aboveground net primary productivity in mesic grasslands. *Ecography* 31: 408-416.
- Heitschmidt, R.K., Price, D.L., Gordon, R.A. & Frasure, J.R. 1982. Short Duration Grazing at the Texas-Experimental-Ranch - Effects on above-Ground Net Primary Production and Seasonal Growth Dynamics. *J Range Manage* 35: 367-372.
- Henkin, Z., Ungar, E.D., Dvash, L., Perevolotsky, A., Yehuda, Y., Sternberg, M., Voet, H. & Landau, S.Y. 2011. Effects of cattle grazing on herbage quality in a herbaceous Mediterranean rangeland. *Grass Forage Sci* 66: 516-525.
- Huenneke, L.F., Anderson, J.P., Remmenga, M. & Schlesinger, W.H. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biol* 8: 247-264.
- Kamnalrut, A., and J. P. Evenson (1992). Monsoon grassland in Thailand. In: Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics. (Long, S.P., M.B. Jones and M.J. Roberts, eds.). Chapman and Hall, London. pp. 100-126.
- Kinyamario, J. I., and S. K. Imbamba (1992). Savanna at Nairobi National Park, Nairobi. In: Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics. (Long, S.P., M.B. Jones and M.J. Roberts, eds.). Chapman and Hall, London. pp. 25-69.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, eds. (1998). Grassland Dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York. 386 pp.
- Long, S.P., Moya, E.G., Imbamba, S.K., Kamnalrut, A., Piedade, M.T.F., Scurlock, J.M.O., Shen, Y.K. & Hall, D.O. 1989. Primary Productivity of Natural Grass Ecosystems of the Tropics - a Reappraisal. *Plant Soil* 115: 155-166.
- Ma, W.H., Liu, Z.L., Wang, Z.H., Wang, W., Liang, C.Z., Tang, Y.H., He, J.S. & Fang, J.Y. 2010. Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland. *J Plant Res* 123: 509-517.
- Menaut, J.C. & Cesar, J. 1979. Structure and Primary Productivity of Lamto-Savannas, Ivory-Coast. *Ecology* 60: 1197-1210.
- Muldavin, E.H., Moore, D.I., Collins, S.L., Wetherill, K.R. & Lightfoot, D.C. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155: 123-132.
- Nechaeva, N. T., S. Ya. Prikhod'ko, and K. F. Shuravin (1971). Harvest formation on the Poa-Carex pastures of the foothills of Central Asia in relation to meteorological conditions (as exemplified by Badkhyz, Turkmenian Republic). In: Biokompleksy Pustyn' i Povyshenie ikh Produktivnosti. Ylym, Ashkhabad. pp. 71-113.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Colby, J.L., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience* 51: 933-938.
- Risser, P. G., E. C. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens (1981). The True Prairie Ecosystem. US/IBP Synthesis 16. Hutchinson Ross, Stroudsburg. 557 pp.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K. & Soriano, A. 1989. Resource Partitioning between Shrubs and Grasses in the Patagonian Steppe. *Oecologia* 81: 501-505.
- Scholes, R.J. & Walker, B.H. 1993. An African savanna : synthesis of the Nylsvley study. Cambridge University Press, Cambridge England ; New York.
- Shankar, U., Pandey, H.N. & Tripathi, R.S. 1993. Phytomass Dynamics and Primary Productivity in Humid Grasslands Along Altitudinal and Rainfall Gradients. *Acta Oecol* 14: 197-209.
- Sims, P.L. & Singh, J.S. 1978a. Structure and Function of 10 Western North-American Grasslands .2. Intra-Seasonal Dynamics in Primary Producer Compartments. *J Ecol* 66: 547-572.
- Sims, P.L. & Singh, J.S. 1978b. Structure and Function of 10 Western North-American Grasslands .3. Net Primary Production, Turnover and Efficiencies of Energy Capture and Water-Use. *J Ecol* 66: 573-597.
- Sims, P.L., Singh, J.S. & Lauenroth, W.K. 1978c. Structure and Function of 10 Western North-American Grasslands .1. Abiotic and Vegetational Characteristics. *J Ecol* 66: 251-&.
- Soriano, A. (1983). Deserts and semideserts of Patagonia. In: Temperate Deserts and Semi-deserts (N.E. West, ed.) Elsevier, Amsterdam. pp. 423-460.
- 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. *J Appl Ecol* 37: 224-237.
- Titlyanova, A. A., V. I. Kiryushin, I. P. Okhin'ko, et al. (1984). Agrocoenoses of the Steppe Zone. Nauka, Novosibirsk (in Russian). 247 pp.

- Wallentius, H.-G. 1973. Above-Ground Primary Production of a Juncetum-Gerardi on a Baltic Sea-Shore Meadow. *Oikos* 24: 200-219.
- Williamson, P. 1976. Above-Ground Primary Production of Chalk Grassland Allowing for Leaf Death. *J Ecol* 64: 1059-1075.
- Xiao, X.M., Shu, J., Wang, Y.F., Ojima, D.S. & Bonham, C.D. 1996. Temporal variation in aboveground biomass of *Leymus chinense* steppe from species to community levels in the Xilin River basin, Inner Mongolia, China. *Vegetatio* 123: 1-12.
- Xiao, X.M., Wang, Y.F., Jiang, S., Ojima, D.S. & Bonham, C.D. 1995. Interannual Variation in the Climate and Aboveground Biomass of *Leymus-Chinense* Steppe and *Stipa-Grandis* Steppe in the Xilin River Basin, Inner-Mongolia, China. *J Arid Environ* 31: 283-299.
- Zhao, X., Y. Yao, and R. Yang (1988). Ecological geographical characteristics and outlook of natural grasslands resources in Xilin river basin. In: Inner Mongolia Grassland Ecosystem Research Station (ed.). Research on Grassland Ecosystem 3, 184-226. Science Press, Beijing (Chinese with English abstract).

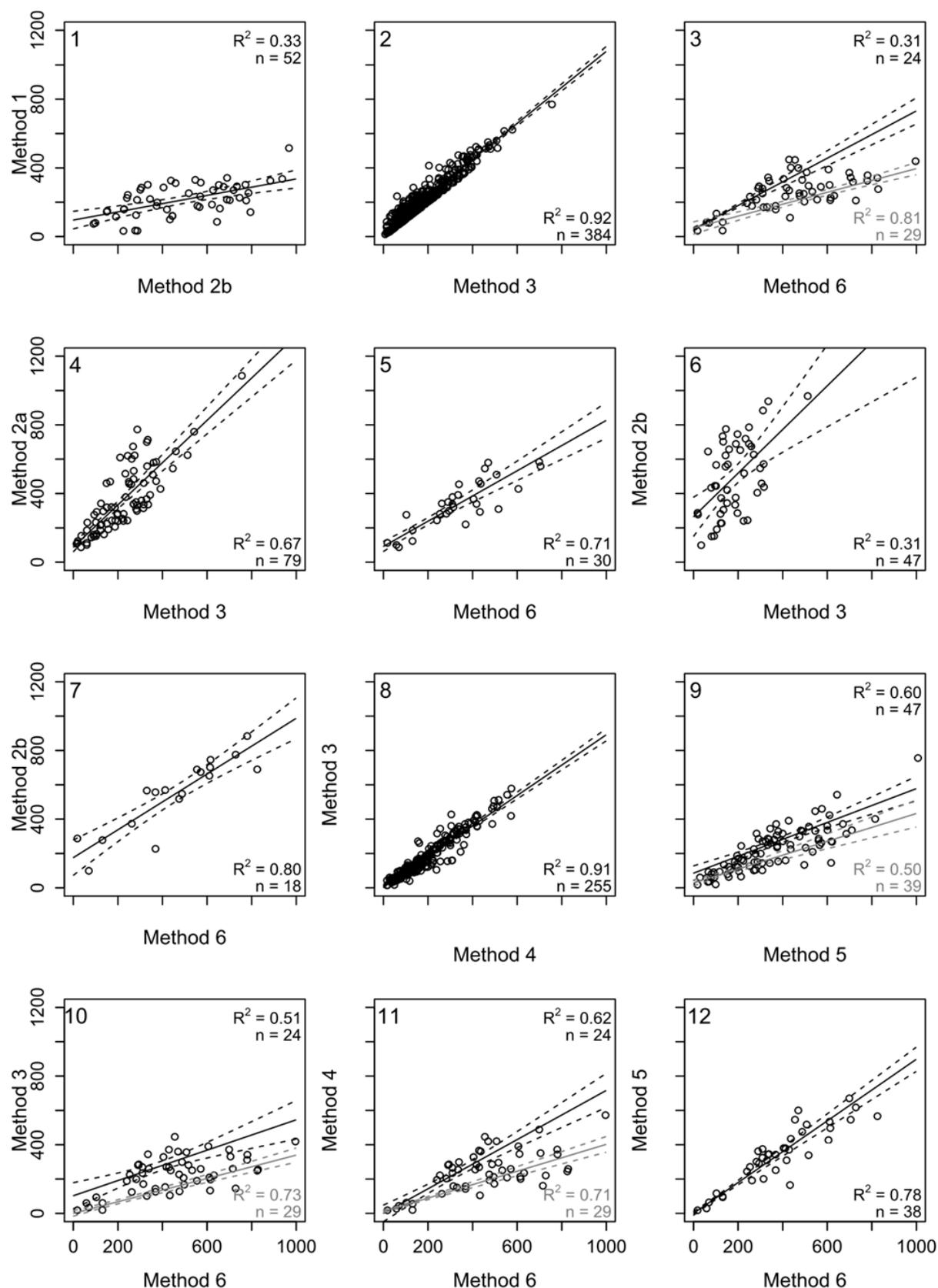


Figure S1. Complementary conversion models (GLS regressions) to Figure 1. Remaining conversion models together with corresponding number of observations (n) and (pseudo) R^2 . Linear regressions are given as solid black lines. Where regressions were calculated separately for humid and dry sites (see 2.3.2 Material and Methods), black line represent the humid model. Solid grey lines represent the arid model, where applicable. Broken lines indicate the .95 confidence interval. Note: Selection of models comprises recommended and not recommended conversions models (see 2.3.2 Materials and Methods). See also Figure 1 for a complete graphical overview on all conversions models.

Consistency of conversions with other published data

We compared our conversion formulae with similar conversions or ratios from literature and generally found them to be highly consistent. Singh et al. (1975) and Linthurst & Reimold (1978) present a set of comparable method combinations. Albeit the selection of ANPP estimation methods differs between the studies, there is a subset of six conversions from Singh et al. 1975 and two ratios from Linthurst & Reimold 1978 which can be compared to a certain extent. Singh and colleagues chose to force their linear regression models through the origin, and in some cases also applied slightly different computational algorithms (i.e. increments between biomass measurements in Method 4 and 5 had to be statistically significant on $p < 0.1$ level, in order to be considered in the calculation). Linthurst &

Reimold (1978) calculated simple ratios between ANPP estimates derived from five different ANPP estimation methods, of which two combinations can be compared to ours (see Table S2).

It should not be concealed, that there is an overlap in data between our and Singh's study. The datasets have five geographical sites in common: Bridger, Dickson, Hays, Osage and Jornada ('Pawnee' in Singh's paper). We share the same data for the first four sites. For the Jornada, we have data from a later (and longer) period. All together, the shared data accumulate to 14 years out of 851 in our dataset. We therefore assume our dataset to be largely independent from the one of Singh and colleagues. Furthermore, our dataset is completely independent from that of Linthurst and Reimold (1978), who worked on data from estuarine systems (three salt marsh sites across the US east coast).

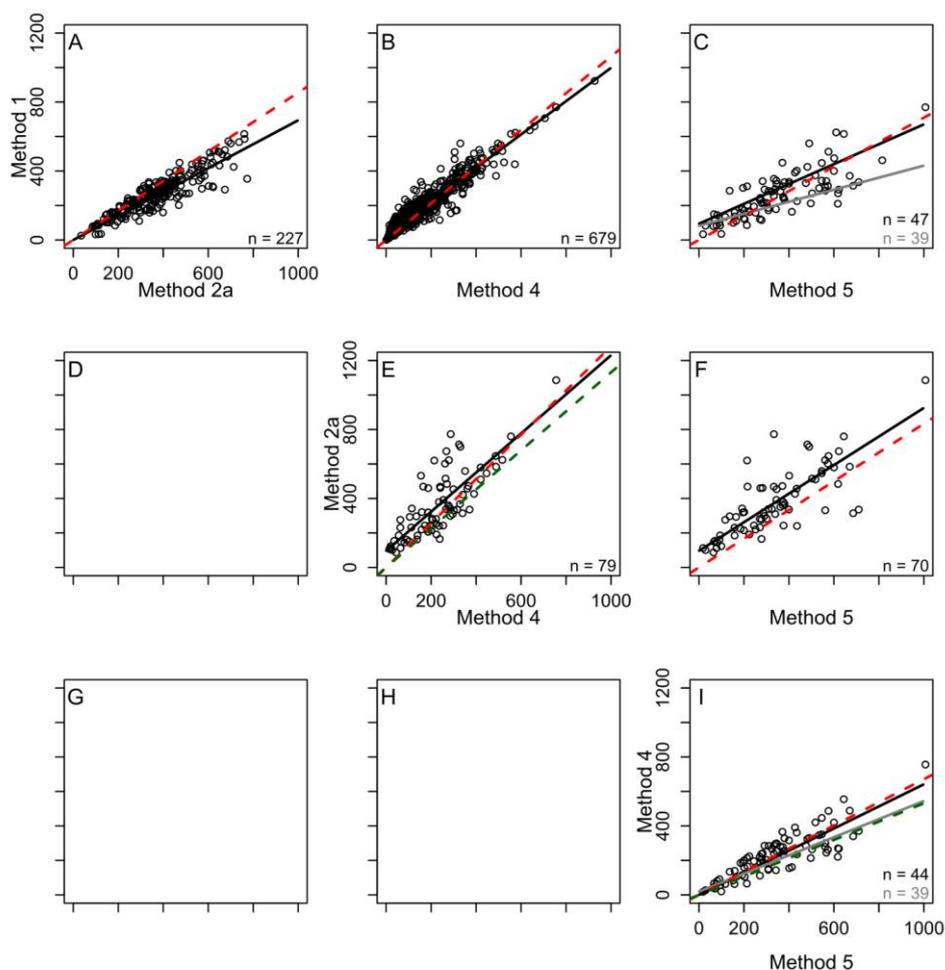


Figure S2: Comparison between derived conversion formulae and published ratios. Figure is based on Fig. 1 - only those conversions are shown, where comparable formulae could be obtained from literature (D, G and H are hidden). Solid black lines: established conversions; overall or humid-model. Solid grey lines: arid model. Dashed red lines: conversion models from Singh et al. 1975. Dashed green lines: ratios from Linthurst & Reimold 1978.

Table S2. Overview on conversion rates and formulae.

Singh et al. 1975 ^a		Linthurst & Reimold 1978 ^b		Ruppert & Linstädter 2013					
Method 1	=	0.85	x	Method 1	=	0.69	x	Method 2a	
Method 1	=	1.06	x	Method 1	=	0.97	x	Method 4	+ 32
Method 1	=	0.71	x	Method 1 _{arid}	=	0.35	x	Method 5 _{arid}	+ 82
Method 2a	=	1.28	x	Method 1 _{humid}	=	0.58	x	Method 5 _{humid}	+ 94
Method 2a	=	0.83	x	Method 2a	=	1.13	x	Method 4	+ 96
Method 4	=	0.67	x	Method 2a	=	0.83	x	Method 5	+ 96
				Method 4 _{arid}	=	0.53	x	Method 5 _{arid}	+ 19
				Method 4 _{humid}	=	0.64	x	Method 5 _{humid}	

^a To ease comparability, we converted the formulae given in Singh et al. 1975 (Table IV, p. 227) to fit our format.

^b Conversion ratios from the three sites presented in Linthurst & Reimold 1978 have been pooled to derive the given formulae (Table 4, p. 929).

Table S3. Full model description.

No.	Conversion formulae	GLS variance structure	Intercept	p	Slope	p	df	Pseudo R ²	Std. Err. slope	In Figure
1	Method 1 ~ Method 2a	Fixed weights	10.564	0.0904	n.s.	<0.001	227	0.82	0.02	1A
2	Method 1 ~ Method 4	Constant plus power of variance covariate	32.39	<0.001		<0.001	679	0.89	0.02	1B
3	Method 1 ~ Method 5 _{humid}	Exponential of variance covariate	94.19	<0.001		<0.001	47	0.50	0.06	1C
4	Method 1 ~ Method 5 _{arid}	-	82.1428	<0.001		<0.001	37	0.50*	0.06	1C
5	Method 2a ~ Method 2b	Fixed weights	56.69	<0.01		<0.001	29	0.71	0.06	1D
6	Method 2a ~ Method 4	Fixed weights	96.41	<0.001		<0.001	79	0.63	0.08	1E
7	Method 2a ~ Method 5	Fixed weights	96.35	<0.001		<0.001	70	0.60	0.06	1F
8	Method 2b ~ Method 4	-	244.87	<0.001		<0.001	44	0.33*	0.27	1G
9	Method 2b ~ Method 5	-	187.536	<0.001		<0.001	37	0.52	0.13	1H
10	Method 4 ~ Method 5 _{humid}	Exponential of variance covariate	33.56	0.0633	n.s.	<0.001	44	0.66	0.05	1I
11	Method 4 ~ Method 5 _{arid}	Fixed weights	19.374	<0.05		<0.001	39	0.65	0.05	1I
12	Method 1 ~ Method 2b	-	95.9644	<0.001		<0.001	50	0.33*	0.05	S1.1
13	Method 1 ~ Method 3	Power of variance covariate	29.23	<0.001		<0.001	384	0.92	0.02	S1.2
14	Method 1 ~ Method 6 _{humid}	Power of variance covariate	42.74	<0.001		<0.001	24	0.31	0.04	S1.3
15	Method 1 ~ Method 6 _{arid}	-	49.956	<0.05		<0.001	27	0.81*	0.03	S1.3
16	Method 2a ~ Method 3	Fixed weights	87.25	<0.001		<0.001	79	0.67	0.08	S1.4
17	Method 2a ~ Method 6	Fixed weights	91.69807	<0.001		<0.001	30	0.71	0.06	S1.5
18	Method 2b ~ Method 3	-	264.253	<0.001		<0.001	45	0.31*	0.28	S1.6
19	Method 2b ~ Method 6	-	175.56	<0.005		<0.001	16	0.80*	0.10	S1.7
20	Method 3 ~ Method 4	Constant plus power of variance covariate	6.446	<0.01		<0.001	253	0.91	0.02	S1.8
21	Method 3 ~ Method 5 _{humid}	Exponential of variance covariate	85.13	<0.001		<0.001	47	0.60	0.06	S1.9
22	Method 3 ~ Method 5 _{arid}	Fixed weights	28.12	<0.01		<0.001	39	0.50	0.05	S1.9
23	Method 3 ~ Method 6 _{humid}	-	102.7866	<0.05		<0.001	24	0.51*	0.09	S1.10
24	Method 3 ~ Method 6 _{arid}	Fixed weights	15.01	0.07	n.s.	<0.001	29	0.73	0.03	S1.10
25	Method 4 ~ Method 6 _{humid}	Fixed weights	7.92	0.7505	n.s.	<0.001	24	0.62	0.07	S1.11
26	Method 4 ~ Method 6 _{arid}	Power of variance covariate	10.925	<0.01		<0.001	29	0.71	0.03	S1.11
27	Method 5 ~ Method 6	Power of variance covariate	0.4303	0.9367	n.s.	<0.001	38	0.78	0.04	S1.12

Pseudo R² values marked with an asterisk are standard R² values. Here model selection selected non-GLS models (= least squares regression).

2.3 Quantifying Dryland Resistance and Resilience to Drought: The Importance of Drought Intensity, Grazing Regime and Vegetation Structure

Jan C. Ruppert, Keith Harmony, Zalmen Henkin, Hennie A. Snyman, Marcelo Sternberg, Walter Willms & Anja Linstädter (in revision), invited for resubmission to *Global Change Biology*

Quantifying dryland resistance and resilience to drought: The importance of drought intensity, grazing regime and vegetation structure

Jan C. Ruppert¹, Keith Harmony², Zalmen Henkin³, Hennie A. Snyman⁴, Marcelo Sternberg⁵, Walter Willms⁶, Anja Linstädter¹

¹ Range Ecology and Management, Botanical Institute, University of Cologne, Germany

² Agricultural Research Center - Hays, Kansas State University, United States

³ Neve-Ya'ar Research Center, Department of Natural Resources, Agricultural Research Organization, Ramat Yishay, Israel

⁴ Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein, South Africa

⁵ Department of Molecular Biology and Ecology of Plants, Faculty of Life Sciences, Tel Aviv University, Israel

⁶ Agriculture and AgriFood Canada, Lethbridge, Alberta, Canada

Corresponding Author:

Jan C. Ruppert

jan.ruppert@uni-koeln.de

AG Linstädter, Biozentrum

Zülpicher Str. 47b

D-50674 Köln

Germany

Tel: +49 221 470 7906

Fax: +49 221 470 7908

Keywords: ANPP, Drought, Stability, Resilience, Recovery, Resistance, Drylands, Climate Change

Abbreviations: (A)NPP – (Aboveground) net primary production, MAP – Mean annual precipitation, CV – Coefficient of variation

Abstract

Climate extremes such as drought can reshape services from dryland ecosystems, including forage production. Still, combined effects of drought and grazing on plant production are poorly understood. We used a large, global dataset on long-term studies from drylands (>3100 observation years) to quantify ecosystem responses to drought and grazing. Resistance to drought, post-drought recovery, and correlations among these key aspects of ecosystem stability were evaluated based on standardized and normalized aboveground net primary production (ANPP) data. Drought events and intensities were classified via the standardized precipitation index (SPI). We tested effects of drought intensity (SPI class), grazing regime (grazed, ungrazed), biome (grassland, shrubland, savanna) or dominant life history of the herbaceous layer (annual, perennial) to assess the relative importance of these factors for ecosystem stability, and to identify predictable relationships between drought severity and ecosystem resistance.

We found that ecosystem stability was better explained by dominant life history of the herbaceous layer than by biome. Increasing drought severity (quasi-)linearly reduced ecosystem resistance; perennial systems lost ~10% of their 'normal' ANPP for each level of drought intensity. For annual systems, slightly dry conditions increased production by 28%, but intense droughts reduced production more strongly than in perennial systems.

Combined effects of drought and grazing were not merely additive. While perennial systems tended to be more resistant to drought, they failed to fully recover in post-drought years. Annual systems showed a contrary response and even increased ANPP in post-drought years. Recovery and resistance were negatively correlated in annual systems, while no correlation was observed in perennial systems. Our study establishes predictable relationships between drought severity and drought-related losses of ANPP and suggests independence of resistance and recovery for perennial systems. This has important implications for dryland management during and after droughts and sheds new light on drought vulnerability across dryland ecosystems.

Introduction

In today's ecological research, discerning the mechanisms behind, and the quantification of ecosystem responses to global environmental change is a central theme (Reed *et al.*, 2012). Nevertheless, although roughly 40% of Earth's terrestrial landmass is covered by drylands (MEA, 2005), our understanding of how the structure and functioning of these ecosystems will respond to changing climate and land use is still surprisingly poor (Maestre *et al.*, 2012, Reynolds *et al.*, 2007).

Drylands are characterized by water-deficiency during prolonged periods throughout the year and comprise arid, semi-arid and dry-subhumid ecosystems (Asner & Heidebrecht, 2005). Here, plant growth is mainly limited by low and highly variable precipitation (Ruppert *et al.*, 2012, Zhao & Running, 2010), which constrains human activities in these regions mainly to livestock production. As a result, only 25% of drylands are used for crop production (rain-fed or more often irrigated), while roughly 65% are used as rain-fed rangelands (MEA, 2005). Thus, livelihood security in drylands relies heavily on the provision of ecosystem services from vegetation (Gillson & Hoffman, 2007). These ecosystem services are often estimated by aboveground net primary production (ANPP) which is a core ecological currency and one of the best documented quantitative estimates for forage provision (Scurlock *et al.*, 2002).

Projected changes for dryland environments predict most of these regions to face an even increased variability in precipitation as well as an increased frequency of extreme events, such as floods or drought (IPCC, 2007). Simultaneously, large dryland areas are facing significant population growth (MEA, 2005), leading to an increased demand for basic ecosystem services from vegetation, which might negatively feedback on vegetation state, and lead to undesirable low plant biomass and production (i.e. degradation; Reynolds *et al.*, 2007). Conceptual and simulation models predict that synergistic interactions between drought and grazing may even accelerate these processes (Lohmann *et al.*, 2012) and reduce the ability of dryland social-ecological systems to buffer climatic variability (Martin *et al.*, 2014). This became particularly evident in past decades, when severe meteorological droughts in densely populated drylands were responsible for massive reductions in livestock and crop productivity (Zhao & Running, 2010), leading to poverty and famine (UN, 2008).

Although, there is ample evidence that terrestrial ecosystems can vary dramatically in their responses to drought (Cherwin & Knapp, 2012, Knapp *et al.*, 2008) and grazing (Díaz *et al.*, 2007), their combined effects on ecosystems' structure and functioning are still poorly understood, as very few studies have considered both effects simultaneously (Zwicke *et al.*, 2013). In this context, an ecosystems' ability to retain a healthy and productive state is of major interest for all agents engaged in the assessment of global change (land owners, decision makers, ecologists, and modelers). This ability is usually called ecosystem stability (Donohue *et al.*, 2013, Pimm, 1984).

Various approaches exist to define and estimate ecosystem stability (Donohue *et al.*, 2013) or its constituents. Here we focus on two aspects of stability: resistance, that is a system's ability to withstand disturbance (Pimm, 1984), and recovery (also: resilience), that is a system's potential to (or rate of) return to a previous state after a disturbance.

For temperate grasslands, results from two experimental studies (Vogel *et al.*, 2012, Zwicke *et al.*, 2013) suggest that the recovery and resistance of these ecosystems to combined drought and management disturbances is non-additive, and apparently idiosyncratic. Drought severity and duration play a crucial role here (Zwicke *et al.*, 2013). Underlying mechanisms of vegetation resistance and recovery seem to be closely related to functional diversity on the one hand (Craine *et al.*, 2013, Vogel *et al.*, 2012), and to species' life history and resource allocation on the other (MacGillivray *et al.*, 1995).

Apart from temperate grassland, information on ecosystems' response to joint effects of drought and grazing is merely anecdotal. For drylands, data are mostly observations from single sites or regions, and were obtained with varying estimates of stability based on various ecosystem properties (e.g. biodiversity, primary production, or indices thereof). To date, these studies have – to the best of our knowledge – never been systematically reviewed, compiled or analyzed in a standardized way. Those scattered results we have for drylands generally support the crucial role of plant diversity and dominant plants' life history (Bai *et al.*, 2004, Frank & McNaughton, 1991, Miede *et al.*, 2010) and also suggest that combined effects of drought and grazing disturbances on ecosystem performance are complex, and (as for temperate grasslands) not merely additive (Carlyle *et al.*, 2014). For example, perennial grasses – which dominate the grass layer of two major dryland biomes, grasslands and savannas – tend to be rather resistant and resilient to drought under conditions of moderate grazing (Boschma *et al.*, 2003, Milton & Dean, 2000), but less resistant if overgrazed (Danckwerts & Stuart-Hill, 1988). With respect to shrubs, which is the dominant life form in the third major dryland biome, shrublands, grazing decreases plants' resistance to drought, but not their recovery (DeMalach *et al.*, 2014).

These results are also in line with general predictions that ecosystems dominated by relatively long-lived, slow-growing plants, such as perennial grasses, would be more resistant but less resilient to disturbances than short-lived but fast-growing plants, such as annual grasses and forbs (Grime, 2001). However, for dryland ecosystems, findings were mostly obtained for populations or individual plants, and we do not know if they also hold for higher levels of aggregation. More importantly, due to vastly varying methodology and spatiotemporal constraints, past findings lack the potential to be easily upscaled and/or to be quantitatively compared across ecosystems or biomes (Reyer *et al.*, 2012).

Generally, there are two options to tackle these problems with the first being '*coordinated distributed experiments*' (CDE; Fraser *et al.*, 2013). CDE initiatives define standardized core protocols using

common metrics, thus making results from all collaborators highly comparable across large spatiotemporal scales. However, while considerable efforts are made in setting up drought-related CDEs (M. Smith pers. comm.) and to combine them with grazing manipulations, it will take some 5-10 years to obtain first reliable results – especially for highly variable dryland ecosystems. The alternative to CDEs are data-fusion or meta-analytical studies, which process and analyze available data.

We will follow the latter approach and quantify how drought and grazing affects ecosystem stability (i.e. resistance and recovery) across dryland sites and biomes while also utilizing fundamental ideas of CDEs (namely the definition of a core protocol, and of common metrics). As we worked with available data, a core protocol and common metrics could not be defined in advance. However, we did not merely compile results qualitatively as done in many meta-analyses (Hillebrand & Cardinale, 2010), but established common metrics for quantifying ecosystem responses to drought and grazing.

With respect to these quantitative comparisons and analyses, our approach is innovative in several aspects. First, we compiled a large, global dataset on long-term studies from drylands to harness the potential of these scattered datasets to understand and quantify ecosystem responses to drought. We only selected long-term datasets as they have the highest probability to enable assessment of ecosystem resistance (*in-drought* vs. *normal* situation) and recovery (*pre-* vs. *post-drought* condition). Given the importance of ANPP as an estimate for ecosystem functioning and services, we focused on this parameter. Due to several competing estimation methods for ANPP (Scurlock *et al.*, 2002), standardization and normalization was a crucial second step to avoid methodological interference (Ruppert & Linstädter, 2014). Thirdly, we used a common and ecologically sound definition of drought and drought severity across all sites and regional climates. Finally, to assess drought response, we selected two key aspects of ecosystem stability (resistance and recovery) and operationalized them with respect to drought severity. To address recent concerns, that stability components may not be independent (Donohue *et al.*, 2013), we analyzed the two components separately and also evaluated potential correlations among them.

With this approach, we aimed to advance the understanding of dryland ecosystem responses to drought and grazing above the level of anecdotal field studies by synthesizing and standardizing available data. Particularly, we addressed the following questions:

- (1) What is the relative importance of drought severity, grazing and vegetation characteristics (biome, life history) for ecosystem resistance and recovery?
- (2) What are response patterns to drought across major dryland biomes (savannas, grasslands, shrublands) or across ecosystems dominated by plants with a different life history (annuals, perennials)?
- (3) Are combined effects of drought and grazing disturbance in drylands additive or interactive?

- (4) Can we identify predictable relationships between the severity of drought events and ecosystem resistance and recovery, including dependencies/correlations between the two stability components?

Materials & Methods

Database

The large spatial extent and the high demand for livelihood security in drylands have led to numerous studies addressing the effects of various abiotic and biotic drivers on primary production. Taking advantage of this large body of literature and databases, we assembled a global dataset of long-term studies (> 5 years consecutive observations), comprising more than 320 datasets derived from about 50 studies and totaling over 4400 years of observations. General methods of data acquisition are described in Ruppert et al. (2012; see also Supporting Information 1).

For this study, we restricted our selection to near-natural and semi-natural vegetation, and excluded sown, fertilized, and annually burned sites, as well as data from years under the influence of unplanned fires. The latter steps were necessary, as fire confounds primary production (Snyman, 2006) in specific ways that can not easily be parted from influences of climate, the main focus of this study. Also sites where precipitation data were not available for all observation years, or inadequate (weather stations located further than 10 km from sites) were rejected. In sum, 174 distinct data sets were included that represent about 35 dryland regions (Figure 1), which yielded >3100 years of observation representing all major dryland biomes: savannas (n = 81), shrublands (n = 22), and grasslands (n = 71) (see Ruppert *et al.*, 2012 for the definition of these major dryland biomes). Mean dataset length was 17.9 years, and mean annual precipitation (MAP) ranged from 183 to 838 mm a⁻¹ across sites (see Supporting Information 1).

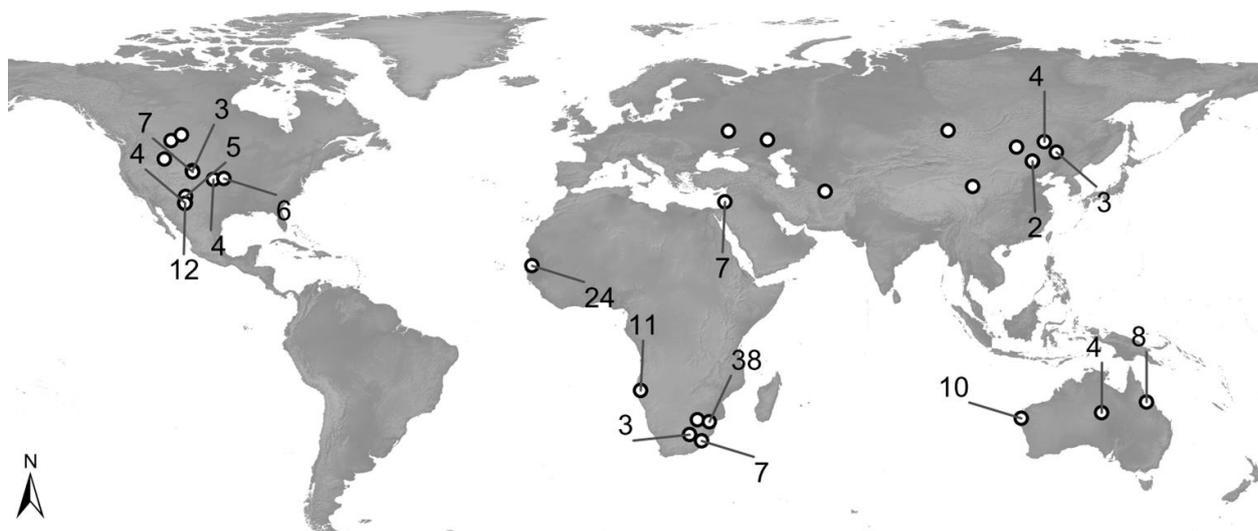


Figure 1: Global distribution of the dryland sites used in the study. In total, 174 datasets derived from 35 studies were available for this study. Points indicate locations, numbers refer to datasets at a certain locations if >1.

To assess relationships between ecosystem properties, drought severity, and ecosystem stability, we assembled data on (i) ANPP, (ii) precipitation of the hydrological year, (iii) dominant life history of the grass layer (annual or perennial), and (iv) grazing regime (ungrazed or grazed). Sites where grazing was excluded or deferred for certain periods of a year were considered as ‘grazed’. Consequently, ‘ungrazed’ refers to prolonged grazing exclusions.

Data standardization procedures

Primary production. We standardized ANPP as ‘peak standing crop’. If ANPP data were not available in this form, we recalculated ANPP either from original biomass data or via conversion rates (Ruppert & Linstädter, 2014). For the savanna biome, all data sets only provided data on the grass layer. Thus total ANPP for this biome is underestimated by ca. 30% (Le Houérou, 1989). For grass- and shrublands, all forage and browse biomass is included in ANPP estimates.

Drought severity. To compare drought responses across dryland sites, we quantified drought severity via the standardized precipitation index (SPI; McKee *et al.*, 1993), which is a well-supported precipitation index in ecology (Vicente-Serrano *et al.*, 2012). We calculated SPI values for the sites’ hydrological years, and assigned drought severity classes (‘SPI classes’) according to the classification of the US National Drought Mitigation Center (<http://droughtmonitor.unl.edu/>), adding the class of ‘normal precipitation’ (SPI class 0, with SPI values $\leq |0.5|$). Above-average rainfall years were excluded from further analyses, reducing the number of observation years to ca. 2000. For further details on SPI, please refer to Supporting Information 1.

Table 1: Classification scheme of drought severity used in this study, adapted from the classification used by the National Drought Mitigation Center of the USA (<http://droughtmonitor.unl.edu/>). In our study, SPI (Standardized Precipitation Index) of hydrological years was calculated to estimate annual drought severity of all observation years. Percentile ranges for drought severity levels refer to general, short- and long-term drought indicator blends given by the Drought Mitigation Center, and to threshold derived from SPI calculations in this study. For illustrative purposes, average deviation from MAP (mean annual precipitation) are also given for our dataset ($n = 1991$).

SPI class	Description	Impacts on rangeland production	SPI range
0	Normal	-	$+0.5 \leq \text{SPI} \leq -0.5$
-1	Abnormally Dry	Slowing growth of vegetation	$-0.5 < \text{SPI} > -0.8$
-2	Moderate Drought	Some damage to vegetation	$-0.8 \leq \text{SPI} > -1.3$
-3	Severe Drought	Production losses likely	$-1.3 \leq \text{SPI} > -1.6$
-4	Extreme Drought	Major production losses	$-1.6 \leq \text{SPI} > -2.0$
-5	Exceptional Drought	Exceptional and widespread production losses	$-2.0 \leq \text{SPI}$

Resistance and recovery. To quantitatively compare ecosystem stability across sites and with respect to drought intensity, a main challenge was to operationalize the generic definitions of resistance and recovery. For recovery, we adopted definitions from field studies (Bai *et al.*, 2004, Tilman & Downing, 1994) and experiments (Vogel *et al.*, 2012), and defined it as the quotient between pre- and post-drought ANPP for a given site and drought event, expressed as percentage. Values above 100%

represent increases in post-drought years as compared to pre-drought; values below 100% represent decreases. To avoid potentially confounding effects of variable pre- and post-drought conditions, we only selected drought events where pre- and post-drought years received normal (=average) precipitation (SPI class 0).

Resistance definitions from the same sources were not suitable for a quantitative comparison, as they usually related in-drought ANPP to pre-drought ANPP, irrespective of the precipitation in pre-drought years. We thus defined resistance as the percentage deviation in ANPP of a certain year from a site's 'normal' (benchmark) ANPP, which is the mean ANPP in the second year of two consecutive years with 'normal' precipitation (SPI class 0). This was done to avoid potentially confounding effects of previous year's rainfall on ANPP (Ruppert *et al.*, 2012, Wiegand *et al.*, 2004). Negative percentages represent reductions in ANPP; positive values represent increases. More extreme values represent relatively low or high resistance respectively.

These definitions lead to selection of the final usable datasets. For resistance, 167 datasets out of 320 allowed the estimation of a benchmark-ANPP leading to roughly 2000 single years of observation. Naturally, in the case of recovery, the strict criteria for the selection of triplets or multiplets of years greatly reduced the dataset for further analyses: recovery estimates could be calculated for 118 drought events (24 two-year, and 94 single-year droughts).

Data analysis

Resistance and recovery were analyzed via Type II ANOVAs. For resistance, we tested the effects of the predictor variables 'drought intensity' (SPI class; 0 to -5; Table 1), 'grazing regime' (grazed, ungrazed), 'biome' (grassland, shrubland, savanna) or 'dominant life history' of the herbaceous layer (annual, perennial). For recovery, we tested the same predictors except drought intensity. Including this variable would have reduced the number of cases in ANOVA subgroups to $n < 5$. Instead, recovery values were lumped across observations for real-drought conditions (SPI class ≤ -2). Note that biome and dominant life history (of the herbaceous layer) were not assessed simultaneously due to their collinearity. Thus, for both analyses, we initially established two competing models with biome or dominant life history included besides other predictors. We used an AIC-based model selection procedure on both models (Johnson & Omland, 2004) and evaluated the competitive final models with respect to explained variance (η^2) and AIC/BIC (critical values: $\Delta\eta^2 > +2\%$; $\Delta\text{AIC} > 2$; $\Delta\text{BIC} > 2$). Finally, following the principle of parsimony (Crawley, 2002), we selected the most parsimonious model as final model and used it for further analyses. In this way, we were able to quantify the relative importance of biome and dominant life history for resistance and recovery.

Interactions in the multifactorial ANOVAs were analyzed by splitting the dataset according to the levels of the interacting variables, and subsequent one-way (split) ANOVAs with adapted p-values to avoid

Type-I-error inflation. Significant effects in split-ANOVAs were analyzed using Tukey's HSD ($p < 0.05$). Additional to η^2 , partial- η^2 and ω^2 were calculated as effect sizes.

Data exploration to avoid common statistical problems (e.g. outliers) and testing of methodological assumptions (such as normal distribution and homogeneity of variances) was performed visually as proposed by Zuur *et al.* (2010). Where necessary, data was transformed (i.e. $\log(x + c)$ -type) to satisfy ANOVA assumptions. All statistical analyses were performed in R 3.0.2 (R Core Team, 2013). Due to the unbalanced design, ANOVAs were calculated using the *car*-package in version 2.0-19 which allows for Type II sums of squares.

Results

Importance of biome and life history for drought effects on ecosystem stability

To quantify the relative importance of biome and dominant life history for ecosystem stability in face of drought, we established contrasting models, together with the same set of other predictor variables. Model selection procedures and effect sizes showed that for both resistance and recovery, dominant life history was a better predictor for ecosystem responses than biome. For resistance, competing final models explained a similar proportion of variance in the dataset ($\Delta\eta^2 +1\%$ for dominant life history), and the final model including dominant life history showed consistently lower AIC and BIC values ($\Delta\text{AIC}_{\text{biome}} = 27$; $\Delta\text{BIC}_{\text{biome}} = 171$). For recovery, the life history model explained a higher proportion of variance ($\Delta\eta^2 +29\%$) in the dataset, and was also selected as the better model via AIC and BIC values ($\Delta\text{AIC}_{\text{biome}} = 46$; $\Delta\text{BIC}_{\text{biome}} = 43$).

Resistance is dependent on drought intensity and varies with dominant life history and grazing ANOVA results for resistance revealed clear connections of this stability mechanism to drought intensity (SPI class), dominant life history, and grazing regime. In total, the model explains 25% (η^2) of variance in ecosystem resistance. Drought intensity, its interaction with dominant life history, as well as the interaction of dominant life history and grazing regime, significantly influenced resistance (Table 2). Nevertheless, corresponding effect sizes illustrate that some of these effects were only marginal (with $\omega^2 = 0.03$ for SPI class x dominant life history and $\omega^2 = 0.01$ for grazing regime x dominant life history). Drought intensity was the most important predictor for ecosystem resistance ($\omega^2 = 0.21$). Figure 2 illustrates how ecosystem resistance was modulated by the interacting effects of drought intensity and dominant life history. It is apparent that drought intensity itself had a strong negative influence on resistance. Moreover, differences in the response across life histories only occurred under certain drought intensities (Figure 2), specifically in abnormally dry years (SPI class -1) and under more intense drought conditions (SPI classes -4 and -5).

Effects of drought intensity on ecosystem resistance were comparable across life histories. Both annual and perennial plants showed a general trend of decreasing resistance with increasing drought intensity, but resistance was reduced more strongly when annuals dominated the herbaceous layer (Figure 2). This trend was particularly strong under true drought conditions (SPI class ≤ -2). In cases of extreme and exceptional drought (SPI class -4 and -5), perennial systems showed a consistently higher resistance (-43% and -48% respectively) than those dominated by annuals (-67% and -73%; Figure 2). However, this general trend of a higher resistance of ecosystems dominated by perennials did not hold true for abnormally dry years (SPI class -1). Surprisingly, ecosystems dominated by annuals even showed a positive response of primary production in these years: ANPP was 28% higher than under average rainfall conditions.

Table 2: Results of final ANOVA for ecosystem resistance in drylands, as affected by drought intensity, dominant life history and grazing regime. Effects of main factors and significant interactions are shown. Significance of estimates is given with * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$. Results of post-hoc test for interactions are given in Supporting Information 2 and are presented in Figures 2 and 3.**

Predictor	Sum Sq	Df	F value	P value	η^2	Partial η^2	ω^2
Drought intensity	5.694	5	111.34	***	0.21	0.22	0.21
Dominant life history	0.001	1	0.06	n.s.	-	-	-
Grazing regime	0.001	1	0.06	n.s.	-	-	-
Drought intensity x Dominant life history	0.893	5	17.45	***	0.03	0.04	0.03
Dominant life history x Grazing regime	0.152	1	14.82	***	0.01	0.01	0.01
Residuals	20.219	1977					
				Total (%)	0.25	0.27	0.25

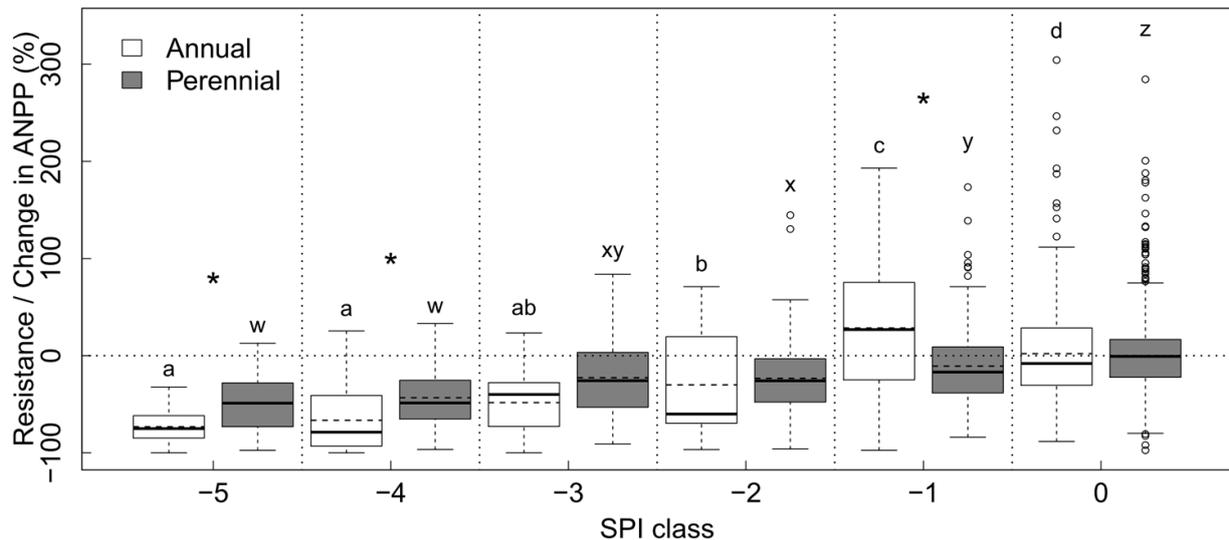


Figure 2: Interacting effects of drought intensity (SPI class) and dominant life history (annual vs. perennial) on ecosystem resistance to drought. Dashed lines in boxplots represent mean values, and solid lines represent medians. Negative percentages represent reductions in ANPP; positive values represent increases. More extreme values represent relatively low or high resistance respectively. Asterisks indicate significant differences between dominant life forms in the respective SPI class (at $p < 0.05$), letter-codes give significant differences ($p < 0.05$) across SPI classes for annual and perennial systems, respectively.

ANOVA results for ecosystem resistance also revealed interacting effects of dominant life history and grazing regime ($\omega^2 = 0.01$). Figure 3 illustrates that this interaction only manifested itself under ungrazed conditions, where annual systems were significantly less resistant (-19%) than perennial systems (-7%).

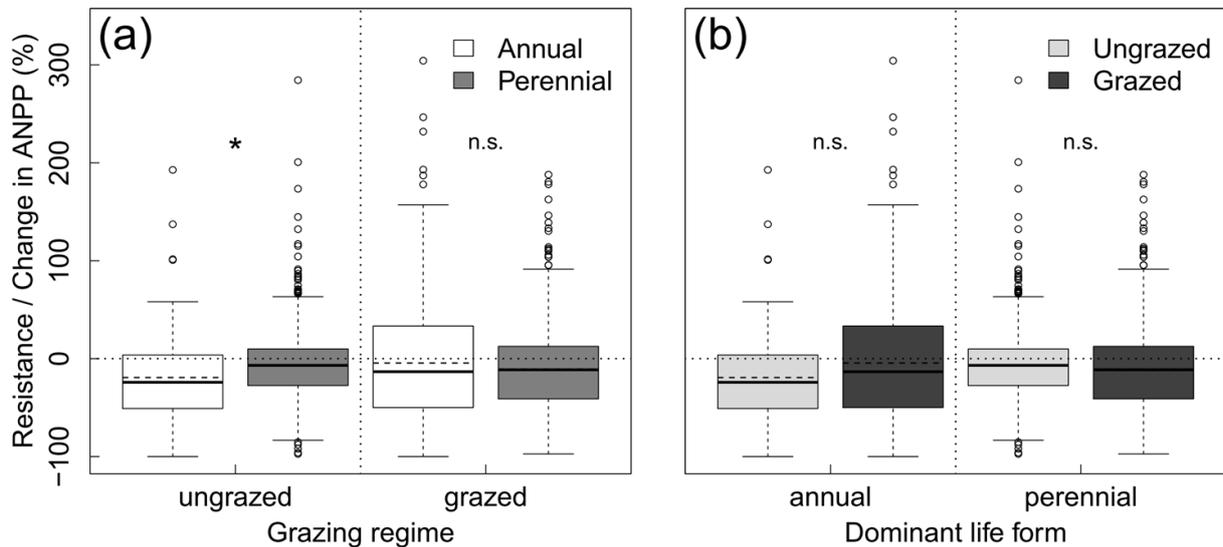


Figure 3: Interactive effect of dominant life history (annual vs. perennial) and grazing regime (ungrazed vs. grazed) on ecosystem resistance to drought. Dashed lines in boxplots represent mean values, and solid lines represent medians. Asterisks indicate significant differences within a panel (at $p < 0.05$). Negative percentages represent reductions in ANPP; positive values represent increases. More extreme values represent relatively low or high resistance respectively.

Recovery depends on dominant life history and its interaction with grazing regime

ANOVA results for ecosystem recovery after drought revealed that this process was significantly influenced by dominant life history, and its interaction with grazing regime (Table 3). These two factors explained about 40% (η^2) of variance in the dataset, with dominant herbaceous life history being more important than the interaction (36% vs. 4%). This finding was also supported by more conservative effect size metrics (see Table 3).

Table 3: Results of final ANOVA for ecosystem recovery in drylands, as affected by dominant life history and grazing regime. Effects of main factors and significant interactions are shown. Significance of estimates is given with * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Results of post-hoc test for the interactions are given in Supporting Information 2 and are presented in Figures 4.

Predictor	Sum Sq	Df	F value	P	η^2	Partial η^2	ω^2
Dominant life history	1.316	1	68.97	***	0.36	0.38	0.35
Grazing regime	0.003	1	0.15	n.s.	-	-	-
Dominant life history x Grazing regime	0.156	1	8.19	**	0.04	0.07	0.04
Residuals	2.176	114					
Total (%)					0.40	0.44	0.39

Effects of dominant life history on recovery were partially mediated by grazing regime or vice versa (Figure 4). Somewhat surprisingly, a drought event could even considerably improve the productivity of the grass layer (increase in ANPP on 189% of pre-drought ANPP), but only for grazed systems

dominated by annual plants. In contrast, grazed systems dominated by perennials only displayed a partial recovery (decrease in ANPP on 81% of pre-drought ANPP; Figure 4B). These differences diminished under ungrazed conditions, where systems dominated by annuals or perennial systems were not significantly different anymore, and annuals systems only scored slightly higher average recovery (post-drought ANPP being 117% of pre-drought ANPP; Figure 4A). Difference in recovery of annual-dominated systems under grazed versus ungrazed conditions was significant ($p < 0.05$), while no differences in recovery of perennial-dominated systems across grazing regimes were present (see Supporting Information 2).

The paucity observations for recovery ($n = 118$) forbade assessing the potential influence of drought severity on recovery due to narrow cell-sizes in ANOVA ($n < 5$; see Supporting Information 4). However, additional analyses suggest, that recovery – especially for sites where perennials dominate the herbaceous layer – is rather constant across drought intensities (see Supporting Information 4).

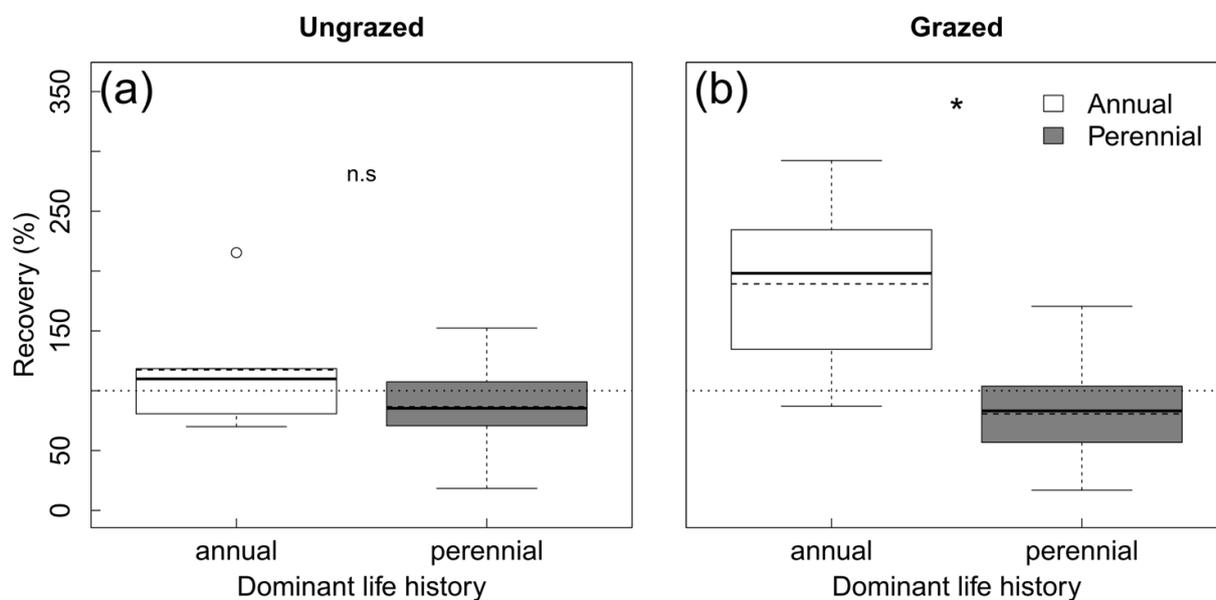


Figure 4: Interactive effect of dominant life history (annual vs. perennial) and grazing regime (ungrazed vs. grazed) on ecosystem recovery from drought. Dashed lines in boxplots represent mean values, and solid lines represent medians. Asterisks indicate significant differences within a panel (at $p < 0.001$). Values above 100% represent increases in post-drought years as compared to pre-drought; values below 100% represent decreases.

Resistance and recovery are not generally related

Correlation analysis of resistance and recovery estimates from the same sites revealed no clear dependencies between these two stability aspects. However, if analyzed separately, annual systems showed a negative correlation between recovery and resistance ($Resistance = - 3.76 \times recovery - 68$; $R^2=0.32$), while no significant correlation was observed for perennial systems (see Supporting Information 4).

Discussion

What is the relative importance of drought severity, grazing and vegetation characteristics for ecosystem resistance and recovery?

To assess the importance of drought severity, grazing and vegetation characteristics (biome, life history) for ecosystem resistance and recovery, results from model selection and comparison as well as effect size metrics for the respective ANOVAs (Table 2, Table 3, and Supporting Information 3) were used. Comparisons of ecosystem resistance and recovery using either biome or dominant life history as predictors showed that the latter was a slightly better predictor for both aspects of ecosystem stability. Given that life history is closely related to principal plant strategies of resource acquisition and conservation (Grime, 2001), it is of little surprise that it was – as in other studies (MacGillivray *et al.*, 1995) – a good predictor for ecosystem stability in the face of drought. In contrast, differences between biomes are mainly based on structural properties of vegetation (Olson *et al.*, 2001) and not necessarily coupled to functional processes, such as resource acquisition.

Resistance was strongly dependent on drought intensity and dominant life history, followed by their interaction and the interaction between grazing regime and dominant life history (Table 2). For recovery, dominant life history of the herbaceous layer was the best predictor while grazing only slightly moderated its effect (Table 3).

Generally, drought severity was a strong predictor of resistance (but not recovery) across all dryland sites but this relationship was also driven by distinct differences in life histories. Dominant life history of the herbaceous layer was a good predictor for both stability components, while grazing only had a moderating effect. Surprisingly, biome type was of minor importance for both resistance and recovery. Our results are in line with a recent study on ecosystem responses to extreme weather events, which combined satellite-derived ANPP data and climatic records from 11 long-term experimental sites (Zhang *et al.*, 2013). For an increased intra-annual variability in rainfall (including prolonged periods of drought), the study found convergence in overall pattern and control across biomes (including non-dryland biomes). We discuss the underlying ecological mechanisms for these striking differences in ecosystem responses in the following sections.

What are response patterns to drought across ecosystems dominated by plants with a different life history or across dryland biomes?

Resistance. Under true drought conditions we observed that – regardless of life history – resistance decreases linearly with increasing drought intensity (Figure 2). Annual-dominated systems showed a consistently lower resistance under drought conditions than perennial-dominated systems (Figure 2), i.e. the relative loss in aboveground production was more pronounced. We assume that – especially

under high drought intensities – perennial plants benefit from their comparatively better ability to cope with a high intra-seasonal variability of rainfall. For example, the already developed root-systems allow for early and relatively quick emergence after rainfall events and persistence between larger rainfall gaps, which are typical for severe drought years (Zhang *et al.*, 2013). In support of this, Jentsch *et al.* (2011) found no significant influence of extreme in-season drought events on ANPP of a perennial grassland in a greenhouse experiment simulating centennial and millennial extreme drought-events. This advantage of perennials may result in higher ANPP compared to annual plants, which are more prone to intra-seasonal dry spells, especially after the first rainfalls as they might germinate and die off again (Hamilton *et al.*, 1999). Also, during later phenological stages, short-term dry spells, or more general water-deficits, lead to reduced productivity by hampering stem elongation and leaf growth (Shao *et al.*, 2008). Annual plants are particularly prone to these impacts, as they mostly lack morphological traits to counter or sustain short- or long-term in-season water-deficits (i.e. thinner leaves and tillers, less cell-wall components).

However, under only slightly dry conditions (abnormally dry years; SPI class -1), the general trend of less resistance in systems with annuals dominating the herbaceous layers does not hold true. Contrary to those findings from true drought conditions, even beneficial effects (positive resistance values = increase in ANPP) can be observed, while systems with a perennial-dominated herbaceous layer already show significantly reduced ANPP (Figure 2).

This seemingly odd observation can be attributed to a common phenomenon in dryland savannas: savannas with an annual-dominated herbaceous layer show a boost in greening and (herbaceous) production under slightly arid conditions, e.g. in the Sahel region (Le Houérou, 1989, Penning de Vries & Djitéye, 1982). This is commonly attributed to a highly specialized species composition with a high proportion of small annuals, which are well adapted to dry conditions and high inter-annual variability in rainfall ($CV_{MAP} > 30\%$). These plants reach their optimum production already under slightly below-average rainfall, but are outcompeted by other species during normal or above-average conditions. In slightly below average rainfall years, they are released from competition (e.g. shading) and can perform better leading to an overall boost in their productivity. On the community-level, the increased productivity of specialized species leads to a relative increase in total production under low levels of aridity. As a major proportion of data in the abnormally dry year-class originated from such savannas (Miehe *et al.* 2010; see Supporting Information 1), we assume that the above-described effect explains this observation. If resistance is assessed without data from this site (data not shown) or across biomes instead of life history (Supporting Information 3), this effect is diminished or largely centralized, respectively, to the savanna biome.

Our results on the higher resistance of perennial-dominated vegetation to severe drought events seem to contradict numerous observations that perennial plants are prone to considerable drought-induced mortality and loss in production (DeMalach *et al.*, 2014, McAuliffe & Hamerlynck, 2010). However, most of these studies refer to multiple-year droughts, and emphasize the importance of the cumulative effect of successive drought years on perennials' survival and performance. Moreover, the differences in drought resistance across life histories do not preclude the possibility that drought effects on the productivity of perennial-dominated ecosystems are not dramatic; perennial ANPP drops to 52% of average ANPP (Figure 2) in exceptional drought years.

Recovery. We found clear evidence that for the extent of post-drought recovery, vegetation characteristics (i.e. whether the grass layer was dominated by annuals or perennials) were most important. Annual-dominated systems did not only display a full recovery, but post-drought ANPP was increased considerably (173%) as compared to pre-drought ANPP. In contrast, perennial-dominated systems only reached 83% of pre-drought ANPP. As precipitation in pre- and post-drought years was 'normal' in all cases, confounding effects of pre- and post-drought rainfall conditions did not play a role. Results are in line with general predictions from the CSR model: ecosystems dominated by relatively long-lived, slow-growing plants, such as perennial grasses, should be less resilient (here: reduced recovery) to disturbances than short-lived, fast-growing plants, such as annual grasses and forbs (Grime, 2001). Differences in recovery across these groups can thus be attributed to general physiological traits which are functionally related to competitive abilities and stress tolerance (Moreno García *et al.*, 2014). This explanation is also in line with the recent 'fast-slow' plant economics spectrum concept (Reich, 2014), which suggest that traits of all three main plant organs (roots, stem, leaves) can be related to fast or slow strategies of nutrient, light or water acquisition and are largely rectified across organs.

Annual plant communities, as compared to perennial communities, are relatively independent from previous abiotic conditions (as long as the soil seed-bank is not negatively influenced) and thus can respond relatively fast to current beneficial abiotic conditions. Perennials invest more energy and matter in structural elements and storage tissue and are comparably slow-growing and more dependent on their fitness as influenced not only by current but also by previous years' abiotic conditions.

Here, annuals were apparently able to respond more quickly to post-drought favorable conditions and were partially released from competition with perennials due to the reduced fitness and increased mortality of the latter (McAuliffe & Hamerlynck, 2010). These differences in recovery patterns have also been found in species-based field studies (DeMalach *et al.*, 2014, O'Connor, 1995). Despite this

obvious advantage in terms of drought recovery of annuals, there were signs of a moderating effect of grazing regime (Figure 4 and below).

Are combined effects of drought and grazing disturbance additive or interactive?

Grazing moderated the divergent patterns of drought resistance and recovery across dominant life histories in specific ways (Table 2 and 3). Thus simultaneous effects of drought and grazing were not merely additive but highly interactive and closely connected to vegetation characteristics.

Specifically, drought resistance did not differ across ecosystems dominated by different life histories when the systems were grazed, but when ungrazed (Figure 3A), under these conditions perennial systems were more resistant. This effect can be attributed to differences in competitive abilities (Grime, 2001) and to difference in responses to grazing. Here, the long evolutionary history of grazing in dryland systems, especially in African and North American biomes (Sankaran & Anderson, 2009) and its importance for plant productivity have to be considered. Being ungrazed (and unburned, see Materials and Methods - Database) for prolonged periods is a highly artificial state for most dryland systems, under which overall productivity decreases due to increased competition in the herbaceous layer and between strata, e.g. via self-shading (Blair, 1997, Valone & Sauter, 2005). The combination of these effects is the likely reasons for the observed lower resistance of systems with an annual-dominated herbaceous layer, as these species are less competitive in plant-plant-interactions and suffer more from the above-mentioned mechanisms (Fuhlendorf *et al.*, 2001).

However, the interaction between dominant life history and grazing regime was weak and only significant in one out of four cases (Figure 3). The general finding that grazing regime is relatively unimportant for drought resistance in drylands (Table 2) and that drought resistance of dominant herbaceous life histories only slightly differs across grazing regimes (Figure 3), supports the convergence model of aridity and grazing resistance (Milchunas *et al.*, 1988, Quiroga *et al.*, 2010). This hypothesis suggests that aridity (or drought) and grazing act as convergent selective forces upon plants and plant communities, as both lead to partial or total tissue loss and thus select similar plant traits. Thus, finding no general negative effect of grazing on drought resistance in dryland ecosystems, but only a slight impact mediated via the distinct performance of life histories under different grazing regimes, supports this hypothesis. The effect of grazing on dryland ANPP appears to be overridden by the regular impact of drought or aridity that is common and defining for these ecosystems.

A similar but inverse pattern was found for drought-recovery. Under grazed conditions (Figure 4B), the systems with an herbaceous layer dominated by annuals showed roughly twice the rate of recovery as compared to perennial systems (189% vs. 81%). However, under ungrazed conditions, this large difference diminished, and life histories did not significantly differ anymore (117% vs. 87%; Figure 4A). Given the fact, that despite being labeled as annual or perennial systems, life histories coexist and

compete at nearly all sites, this effect can be explained by basic assumptions and hypotheses of the CSR model (Grime, 2001). Under conditions of grazing following a precedent drought, annuals (R or S) are able to outcompete perennials (C) since these cannot make use of their intrinsic advantageous capabilities (i.e. more efficient resource acquisition) as their relative fitness (or vigor) is strongly reduced from the precedent drought, and constantly weakened by ongoing disturbance via grazing (Kirkman, 2002). Under ungrazed conditions however, perennials are not penalized by grazing and can reduce the gap in recovery-potential. However, this finding might as well be an artefact due to the small number of observations (the cell-size of ungrazed annuals was very small, $n = 6$). The relative marginality of this interaction is also underlined by its small effect size (Table 3).

Are there predictable relationships between the severity of drought events and ecosystem response?

Resistance. We found that increasing drought severity (quasi-) linearly reduced ecosystem resistance, and that the strength of response partially differed with dominant life history of the herbaceous layer. As a rule of thumb, perennial systems lost ca. 10% of their 'normal' ANPP for each drought severity level (SPI class). For annual systems, the situation was more complex. Under slightly dry conditions (SPI class -1), we found that production was increased by 28% on average, however, under moderate drought conditions (SPI class -2), production was already reduced by ca. 30% of 'normal' ANPP. From here resistance decreased by ca. 14% for each drought severity level.

Recovery. Based on our findings, perennial-dominated systems were unable to fully restore pre-drought ANPP, but reached only 81% to 87% of pre-drought ANPP for grazed and ungrazed conditions, respectively. Annual-dominated systems had a recovery rate roughly twice as high when grazed (189%) as compared to perennial systems, meaning that they were more productive after the drought than before the drought. When ungrazed, annual systems still produce slightly more biomass (on average) than pre-drought conditions but considerably less (117%) than when grazed.

As the influence of drought severity on recovery could not be assessed systematically, predictions for recovery are rather general. Nevertheless, additive results suggest that drought recovery was remarkably constant across different levels of drought severity. This is particularly true for perennial systems, for which we had more data available. Here we found that average recovery varied only between 79% and 92% across drought intensities (Supporting Information 4). For annual systems, bearing in mind the paucity of data, we saw that – for extreme and exceptional drought conditions (SPI class -4 and -5) – recovery varies between 167% and 243% respectively.

For recovery, drought duration would have been another interesting factor, as theoretical considerations would suggest that annual systems would lose their recovery-potential gradually with

prolonged drought conditions as the soil seed bank depletes. However, we could not assess this response with the currently available data.

Our generalized resistance and recovery estimates for drylands are very similar to those reported in case studies from Cedar Creek (Minnesota, USA; Tilman & Downing, 1994) and the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, Inner Mongolia, China; Bai *et al.*, 2004). Both studies present data from ungrazed perennial grasslands.

In order to compare their findings with our system, we obtained precipitation data for those sites and classified the respective years with our scheme of drought severity (Table 1). The Cedar Creek study presents resistance and recovery data for a severe drought (SPI class -3). For the IMGERS site, resistance and recovery estimates present average values over five distinct drought years (within a 21 year frame) that varied in their respective drought intensities. On average, years can also be classified as 'severe drought' (SPI class -3).

The Cedar Creek grassland showed an overall resistance of -29% and recovery of 112% under severe drought conditions for undisturbed, species-rich plots (≥ 10 species) while on disturbed species-poor plots resistance and recovery dropped to -51% and 104%, respectively. At the IMGERS sites, similar and only slightly higher, resistance and recovery values were reported for two perennial grasslands, scoring a mean resistance of -27% and -22%, respectively, as well as a mean recovery of 119% and 122%.

In comparison, we found an average resistance (for SPI class -3) and recovery in perennial-dominated systems of -23% and 83%, respectively. For grasslands, resistance and recovery estimates were -25% and 80%, respectively. Thus, resistance estimates are similar with respect to total magnitude, while recovery values are somewhat higher than our average values but score well within the variability of the respective resilience estimates (Figure 2 & 4A; Figure S3-2A).

Donohue *et al.* (2013) suggested that resistance and recovery may correlate either positively or negatively depending on the natural growth rates and the sensitivity of the respective environment. We found no general correlation between these two stability components within our dataset. Only if dominant life histories were analyzed separately, annual systems showed a negative correlation between recovery and resistance, while no correlation was observed for perennial systems. This might suggest a higher sensitivity of annual-dominated systems as compared to perennial systems.

Strengths and weaknesses of our data-fusion approach

Generally, our data-fusion approach was well-suited for ascertaining the relative importance of drought intensity and ecosystem properties in explaining variation in dryland systems' stability to

drought. It synthesized and standardized available data in order to identify general patterns of ecosystem stability to drought, and is the first large-scale assessment of ecosystem stability across a large number of ecosystems. As for all studies focusing on ecological stability, our approach highlights specific components while neglecting others. Here, the large number of drought events in our dataset allowed us to quantify two key aspects of ecosystem stability (resistance and recovery), and to evaluate potential correlations among them. This approach followed recent recommendations with respect to the multidimensionality of ecosystem stability (Donohue *et al.*, 2013).

However, our data-fusion approach also had some limitations with respect to the selection of variables. The focus on ANPP was mostly motivated by data availability, and obviously imposes restrictions with respect to interpretability. Most importantly, we could not complement ANPP dynamics with related changes in species composition or diversity, which have been shown to be functionally connected to ecosystem stability (Bai *et al.*, 2004, Pfisterer & Schmid, 2002, Tilman & Downing, 1994, Vogel *et al.*, 2012). Nevertheless, our approach of standardizing and normalizing ANPP data across assembled studies (Ruppert & Linstädter, 2014) should ensure the comparability of ANPP data and related stability estimates. Furthermore, using dominant life history as a proxy for vegetation characteristics might represent an adequate level of aggregation of plant communities, as it has been suggested that a sites' dominance hierarchies, rather than biodiversity, may drive ecosystem functioning (Sasaki & Lauenroth, 2011).

Similar to the selection of ANPP, the selection of explanatory variables was also partly restricted by data availability. Despite having already >4400 years of observational data from >320 separate datasets at hand, data were still insufficient to analyze and/or detect the effects of some potentially interfering parameters. For example, although previous studies and preliminary analyses (Supporting Information 4) suggested that rainfall legacy may affect dryland ANPP (Ruppert *et al.*, 2012, Wiegand *et al.*, 2004), we were not able to quantify these effects with respect to ecosystem stability. Furthermore, data on soil conditions (e.g. soil texture, depth or nutrient availability) had a low frequency in the dataset, and existing data were often inadequate with respect to their quality or spatiotemporal resolution and thus could not be considered in our analyses.

Another crucial step in our data analysis was the selection of a drought index and classification applicable to all sites. Here, we chose the SPI, which can be calculated solely from precipitation data (McKee *et al.*, 1993). Although other drought indices exist (e.g. SPIE; Vicente-Serrano *et al.*, 2012), these are based on additional variables, such as temperature, which were not consistently available in our dataset. Nevertheless, we are confident that the SPI-based classification of drought intensity is straightforward, ecologically sound (Guttman, 1998), and superior to approaches used in other studies, such as the percentage deviation from mean annual precipitation. It overcomes the spatiotemporal limits of site-based studies and allows regional and global assessments of ecosystem functioning.

Our methodological toolbox – a combination of a large global dataset, normalization of ANPP and precipitation data, and selection of two key estimates for ecosystem stability – enabled us to assess timely questions on global change-related ecosystem functioning in drylands, which thus far could only be answered on a theoretical or anecdotal basis, if at all. Ideally our study should in future be combined with experimental and modeling studies to overcome caveats of the respective individual approaches (Reyer *et al.*, 2012). For experimental approaches, coordinated distributed experiments (Fraser *et al.*, 2013) are promising. In this context, a coincidence of drought and other environmental stressors such as fire might also be of interest.

Implications for rangeland management

Generally, our results showed that the relative importance of resistance to, and recovery from, drought in dryland systems is largely dependent on the dominant life history of the herbaceous layer. This has major implications for dryland management during and after drought events and sheds new light on why dryland biomes differ in their drought vulnerability. We conclude that systems with a dominant annual herbaceous layer (e.g. arid shrubland and savannas) are more prone to the combined effects of drought and human (mis-)management for two reasons: (1) they suffer more during drought events; (2) their fast post-drought recovery might encourage overutilization, which may lead to long-term degradation under conditions of increased drought intensities and frequencies. *Vice versa*, perennial systems have shown to be more resistant during drought-situations, what might prevent managers from destocking herds and thus promote in-drought overutilization, what might detrimentally affect already low post-drought recovery and increase risk of degradation under multiyear drought-regimes. In conclusion, our results promote an improved understanding of ecosystem functioning in drylands that could enhance dryland vegetation models and improve decision-making.

Acknowledgements

We thank Roelof Oomen and Kristijan Canak for fruitful discussions during the development of this study. Furthermore, we thank Andreas Tewes for his assistance and help in GIS. The research of Jan C. Ruppert was funded by the Foundation of German Business (Stiftung der Deutschen Wirtschaft, sdw) and by the German Federal Ministry of Education and Research (BMBF) through a grant to the SPACES initiative (Science Partnerships for the Assessment of Complex Earth System Processes; grant number 01LL1304D). Research of Anja Linstädter was supported by the German Federal Ministry of Education and Research (BMBF) via the WASCAL (West African Science Service Center on Climate Change and Adapted Land Use) and SPACES initiatives. John McIvor generously provided data from Cardigan, Australia. Data from Jornada Basin, Konza Prairie, Sevilleta, and Short Grass Steppe was provided by

the Long Term Ecological Research Program (LTER) which is significantly funded by the U.S. National Science Foundation Long Term Ecological Research program (NSF grant numbers BSR-8811906, DEB-0080529, DEB-0217774, DEB-0236154, DEB-0618210, DEB-0823341, DEB-0823405, DEB-0832652, DEB-0936498, DEB-9411976, DEB-9634135). The manuscript-review by Alan Short (Short Ecological Consulting) prior to submission is very much appreciated, as well as his provision of data from Kokstad, South Africa. His work there as well as data were funded and managed by the KwaZulu-Natal Department of Agriculture and Environmental Affairs. Finally, we thank the many, often anonymous, researchers and research assistants who gathered the biomass data underlying our database.

References

- Asner GP, Heidebrecht KB (2005) Desertification alters regional ecosystem–climate interactions. *Global Change Biology*, **11**, 182-194.
- Bai Y, Han X, Wu J, Chen Z, Li L (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181-184.
- Blair JM (1997) Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology*, **78**, 2359-2368.
- Boschma SP, Hill MJ, Scott JM, Rapp GG (2003) The response to moisture and defoliation stresses, and traits for resilience of perennial grasses on the Northern Tablelands of New South Wales, Australia. *Australian Journal of Agricultural Research*, **54**, 903-916.
- Carlyle C, Fraser L, Turkington R (2014) Response of grassland biomass production to simulated climate change and clipping along an elevation gradient. *Oecologia*, **174**, 1065-1073.
- Cherwin K, Knapp A (2012) Unexpected patterns of sensitivity to drought in three semi-arid grasslands. *Oecologia*, **169**, 845-852.
- Craine JM, Ocheltree TW, Nippert JB, Towne EG, Skibbe AM, Kembel SW, Fargione JE (2013) Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change*, **3**, 63-67.
- Crawley MJ (2002) *Statistical computing, an introduction to data analysis using S-Plus*, New York, John Wiley and Sons.
- Danckwerts JE, Stuart-Hill GC (1988) The effect of severe drought and management after drought on the mortality and recovery of semi-arid grassveld. *Journal of the Grassland Society of Southern Africa*, **5**, 218-222.
- DeMalach N, Kigel J, Voet H, Ungar ED (2014) Are semiarid shrubs resilient to drought and grazing? Differences and similarities among species and habitats in a long-term study. *Journal of Arid Environments*, **102**, 1-8.
- Díaz S, Lavorel S, McIntyre S *et al.* (2007) Plant trait responses to grazing - a global synthesis. *Global Change Biology*, **13**, 313-341.
- Donohue I, Petchey OL, Montoya JM *et al.* (2013) On the dimensionality of ecological stability. *Ecology Letters*, **16**, 421-429.
- Frank DA, McNaughton SJ (1991) Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos*, **62**, 360-362.
- Fraser LH, Henry HAL, Carlyle CN *et al.* (2013) Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment*, **11**, 147-155.
- Fuhlendorf SD, Briske DD, Smeins FE (2001) Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. *Applied Vegetation Science*, **4**, 177-188.
- Gillson L, Hoffman MT (2007) Rangeland ecology in a changing world. *Science*, **315**, 53-54.

- Grime JP (2001) *Plant strategies, vegetation processes, and ecosystem properties*, Chichester, UK, John Wiley and Sons.
- Guttman NB (1998) Comparing the Palmer drought index and the standardized precipitation index. *Journal of the American Water Resources Association*, **34**, 113-121.
- Hamilton JG, Claus H, Bruce EM (1999) Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia*, **V121**, 518-526.
- Hillebrand H, Cardinale BJ (2010) A critique for meta-analyses and the productivity-diversity relationship. *Ecology*, **91**, 2545-2549.
- IPCC (2007) *Climate Change 2007: Synthesis Report. Summary for Policymakers*. In: *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Parry ML, Canziani OF, Palutikof JP, Van der Linden PJ, CE H) pp 81-82, Cambridge, Cambridge University Press.
- Jentsch A, Kreyling J, Elmer M *et al.* (2011) Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *Journal of Ecology*, **99**, 689-702.
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101-108.
- Kirkman K (2002) The influence of various types and frequencies of rest on the production and condition of sourveld grazed by sheep or cattle. 2. Vigour. *African Journal of Range and Forage Science*, **19**, 93-105.
- Knapp AK, Beier C, Briske DD *et al.* (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, **58**, 811-821.
- Le Houérou HN (1989) *The grazing land ecosystems of the African Sahel*. Berlin, Springer.
- Lohmann D, Tietjen B, Blaum N, Joubert DF, Jeltsch F (2012) Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing. *Journal of Applied Ecology*, **49**, 814-823.
- MacGillivray CW, Grime JP, Team TISP (1995) Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Functional Ecology*, **9**, 640-649.
- Maestre FT, Salguero-Gómez R, Quero JL (2012) It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3062-3075.
- Martin R, Müller B, Linstädter A, Frank K (2014) How much climate change can pastoral livelihoods tolerate? Modelling rangeland use and evaluating risk. *Global Environmental Change*, **24**, 183-192.
- McAuliffe JR, Hamerlynck EP (2010) Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought. *Journal of Arid Environments*, **74**, 885-896.
- McKee TB, Doesken NJ, Kleist J (1993) The relationship of drought frequency and duration to time scales. In: *8th Conference on Applied Climatology, January 17-22, 1993*. pp 179-184, Anaheim, California.
- MEA (2005) *Ecosystems and human well-being: Desertification synthesis*, Washington, D.C., USA, World Resources Institute.
- Miehe S, Kluge J, von Wehrden H, Retzer V (2010) Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. *Journal of Applied Ecology*, **47**, 692-700.
- Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, **132**, 87.
- Milton SJ, Dean WRJ (2000) Disturbance, drought and dynamics of desert dune grassland, South Africa. *Plant Ecology*, **150**, 37-51.
- Moreno García CA, Schellberg J, Ewert F *et al.* (2014) Response of community-aggregated plant functional traits along grazing gradients: insights from African semi-arid grasslands. *Applied Vegetation Science*.
- O'Connor TG (1995) Transformation of a savanna grassland by drought and grazing. *African Journal of Range & Forage Science*, **12**, 53-60.

- Olson DM, Dinerstein E, Wikramanayake ED *et al.* (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, **51**, 933-938.
- Penning de Vries FWT, Djitéye MA (1982) La productivité des pâturages sahéliens. In: *Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle*. (eds Penning de Vries FWT, Djitéye MA) pp 525f. Wageningen, The Netherlands, Centre for Agricultural Publishing and Documentation.
- Pfisterer AB, Schmid B (2002) Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, **416**, 84-86.
- Pimm SL (1984) The complexity and stability of ecosystems. *Nature*, **307**.
- Quiroga RE, Golluscio RA, Blanco LJ, Fernández RJ (2010) Aridity and grazing as convergent selective forces: an experiment with an arid Chaco bunchgrass. *Ecological Applications*, **20**, 1876-1889.
- R Core Team (2013) R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.
- Reed SC, Coe KK, Sparks JP, Housman DC, Zelikova TJ, Belnap J (2012) Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change*, **2**, 752-755.
- Reich PB (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275-301.
- Reyer C, Leuzinger S, Rammig A *et al.* (2012) A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. *Global Change Biology*, **19**, 75-89.
- Reynolds JF, Smith DMS, Lambin EF *et al.* (2007) Global desertification: building a science for dryland development. *Science*, **316**, 847-851.
- Ruppert JC, Holm AM, Miede S, Muldavin E, Snyman HA, Wesche K, Linstädter A (2012) Meta-analysis of rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands. *Journal of Vegetation Science*, **23**, 1035-1050.
- Ruppert JC, Linstädter A (2014) Convergence between ANPP estimation methods in grasslands — A practical solution to the comparability dilemma. *Ecological Indicators*, **36**, 524-531.
- Sankaran M, Anderson TM (2009) Management and restoration in African savannas: interactions and feedbacks. In: *New models for ecosystem dynamics and restoration*. (eds Hobbs RJ, Suding KN) pp 136-155. Washington, Island Press.
- Sasaki T, Lauenroth W (2011) Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, **166**, 761-768.
- Scurlock JMO, Johnson K, Olson RJ (2002) Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology*, **8**, 736-753.
- Shao HB, Chu LY, Jaleel CA, Zhao CX (2008) Water-deficit stress-induced anatomical changes in higher plants. *Comptes Rendus Biologies*, **331**, 215-225.
- Snyman H (2006) Short-term response of burnt grassland to defoliation in a semi-arid climate of South Africa. *African Journal of Range and Forage Science*, **23**, 1-11.
- Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363-365.
- UN (2008) *Trends in sustainable development. Agriculture, rural development, land, desertification and drought*, New York, United Nations, Department of Economic and Social Affairs.
- Valone TJ, Sauter P (2005) Effects of long-term cattle exclosure on vegetation and rodents at a desertified arid grassland site. *Journal of Arid Environments*, **61**, 161-170.
- Vicente-Serrano SM, Beguería S, Lorenzo-Lacruz J *et al.* (2012) Performance of drought indices for ecological, agricultural, and hydrological applications. *Earth Interactions*, **16**, 1-27.
- Vogel A, Scherer-Lorenzen M, Weigelt A (2012) Grassland resistance and resilience after drought depends on management intensity and species richness. *Plos One*, **7**, e36992.
- Wiegand T, Snyman HA, Kellner K, Paruelo JM (2004) Do grasslands have a memory: modeling phytomass production of a semiarid South African grassland. *Ecosystems*, **7**, 243-258.
- Zhang Y, Susan Moran M, Nearing MA *et al.* (2013) Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes. *Journal of Geophysical Research: Biogeosciences*, **118**, 148-157.

- Zhao MS, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, **329**, 940-943.
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3-14.
- Zwicke M, Alessio GA, Thiery L *et al.* (2013) Lasting effects of climate disturbance on perennial grassland above-ground biomass production under two cutting frequencies. *Global Change Biology*, **19**, 3435-3448.

S1-1: Overview on datasets

Data research, acquisition, and processing

In detail, we searched the literature using the keywords 'biomass', 'standing crop', 'primary production', 'ANPP', 'dryland', '(semi-)arid' in various combinations and spelling alterations. All literature research was carried out using Google Scholar, as this source gives more complete results compared to other platforms (Beckmann and von Wehrden, 2012). Furthermore, especially during a later stage of the data-collection, we obtained additional (mostly historic) datasets via personal communication.

Wherever possible, we tried to obtain raw biomass and precipitation data at the highest spatial and temporal resolution available. Precipitation data were aggregated to monthly as well as 12-month sums representing the hydrological year at the respective site. Where raw biomass data were available, these raw biomass data were translated to ANPP using the peak standing crop method (Scurlock et al., 2002). Where only readily estimated ANPP estimates were available and not of the *peak standing crop*-type, we used established conversions to recalculate between these ANPP-methods (Ruppert and Linstädter, 2014). Furthermore, ANPP data were aggregated at a level representative for the respective (sub-) site and – where applicable – treatment (e.g. grazing), i.e. we averaged estimates across replicates as indicated by the original authors. All data storage, handling, and processing was done in MySQL and R.

Table S1-1: Overview of all 174 datasets used in one of the analyses. The table gives site or dataset name, number of distinct datasets at that site, location, grazing regime, biome, dominant life history of the herbaceous layer, mean annual precipitation, climate and source of data and/or most representative reference for the dataset.

Site	No.	Country	City & Province	Grazing regime	Biome	Dom. herb. life history	MAP	Climate	Source of data / Reference
Agriculture Canada Research Substation	1	Canada	Manyberries, Alberta	grazed	grassland	perennial	335	semi-arid	Smoliak 1986; Thorpe et al. 2004; Walter Wilms pers. comm.
Badkhyz	1	Turkmenistan	Kushka	ungrazed	grassland	perennial	292	arid	ORNL DAAC; Gilmanov et al. 1997
Bloemfontein	3	South Africa	Bloemfontein, Free State	grazed	grassland	perennial	553	semi-arid	O'Connor et al. 2001
Cardigan	8	Australia	Cardigan, near Charters Towers, Queensland	grazed	grassland (4) & savanna (4)	perennial	596	semi-arid	Mclvor et al. 1991; pers. comm.
Chihuahuan Desert Rangeland Research Center	1	U.S.A.	Las Cruces, New Mexico	grazed	grassland	perennial	251	arid to semi-arid	Khumalo & Holechek 2005
Dzhanybek	1	Kazakhstan	Dzhanybek, West Kazakhstan	ungrazed	grassland	perennial	283	semi-arid	ORNL DAAC; Gilmanov et al. 1997
Habai	1	China	Habai Region, Qinghai	ungrazed	grassland	perennial	589	Mediterranean	Guo et al. 2006
High Plains Grasslands Research Station	3	U.S.A.	near Cheyenne, Wyoming	grazed	grassland	perennial	374	semi-arid	Andales et al. 2006; Manley et al. 1997
Inner Mongolia (Bai et al. 2001)	4	China	Damao Qi, Inner Mongolia	ungrazed	grassland	perennial	255 to 379	arid to semi-arid	Bai et al. 2001
Kaokoland	11	Namibia	Omuramba, Kunene	grazed (9) & ungrazed (2)	savanna	annual (10) & perennial (1)	340	arid to semi-arid	Schulte 2002 (PhD Thesis); pers. comm.
Karei Deshe Experimental Farm	7	Israel	Karei Deshe, Northern Israel	grazed (6) & ungrazed (1)	grassland	annual	558	Mediterranean	Sternberg et al. 2000; Henkin et al. 2011
Kokstad	7	South Africa	Kokstad, KwaZulu Natal	grazed (5) & ungrazed (2)	grassland	perennial	773	sub-humid	Palmer et al. 2010; Alan Short pers. comm.
Kruger National Park	38	South Africa	Kruger National Park, Limpopo	grazed	savanna	perennial	426 to 678	semi-arid	KNP
KSU Agricultural Research Center	4	U.S.A.	Hays, Kansas	grazed (3) & ungrazed (1)	grassland	perennial	579	semi-arid	Harmony 2007; Hulett & Tomanek 1969
Kursk	1	Russia	Kursk, Oblast Kursk	ungrazed	grassland	perennial	583	sub-humid	ORNL DAAC; Gilmanov et al. 1997
LTERR Jornada Basin	12	U.S.A.	Las Cruces, New Mexico	ungrazed	grassland (3) & shrubland (9)	annual (1) & perennial (11)	225 to 260	arid to semi-arid	LTERR; Peters et al. 2012
LTERR Jornada Basin (historic)	4	U.S.A.	Las Cruces, New Mexico	ungrazed	grassland	perennial	183	arid	Herbel et al. 1972
LTERR Konza	6	U.S.A.	Manhattan, Kansas	grazed (2) & ungrazed (4)	grassland	perennial	838	sub-humid	LTERR; Heisler & Knapp 2008
LTERR Sevilleta	5	U.S.A.	Albuquerque, New Mexico	ungrazed	grassland (3) & shrubland (2)	perennial	242 to 257	arid	LTERR; Muldavin et al. 2008
LTERR Short Grass Steppe	7	U.S.A.	Nunn, Colorado	grazed (5) & ungrazed (2)	grassland	perennial	332 to 342	semi-arid	LTERR; Lauenroth & Sala 1992
Matador	1	Canada	Matador near Swift Current, Saskatchewan	ungrazed	grassland	perennial	374	semi-arid	ORNL DAAC; Couturier & Ripley 1973
Northern Territory (Foran et al. 1982)	4	Australia	Central Mt. Wedge & Mt. Riddock, Northern Territory	grazed (1) & ungrazed (3)	savanna	annual (3) & perennial (1)	416 to 457	arid	Foran et al. 1982
Towoomba	1	South Africa	Bela-Bela (=Warmbaths), Limpopo	ungrazed	grassland	perennial	629	semi-arid	ORNL DAAC; Donaldson et al. 1984; Swemmer et al. 2007
Turmentsogt	1	Mongolia	Ondorhaan	ungrazed	grassland	perennial	272	semi-arid	ORNL DAAC
Turnugi	3	China	Ulan Hot, Inner Mongolia	ungrazed	grassland	perennial	411	semi-arid	ORNL DAAC; Xiao et al. 1996
Tuva	1	Russia	Kyzyl, Tuva	ungrazed	grassland	perennial	285	semi-arid	ORNL DAAC; Gilmanov et al. 1997
US Sheep Experimental Station	1	U.S.A.	Upper Snake River Plains near Dubois, Idaho	ungrazed	shrubland	perennial	280	arid	Blaisdell 1958; Sneva & Hyder 1962

Site	No.	Country	City & Province	Grazing regime	Biome	Dom. herb. life history	MAP	Climate	Source of data / Reference
Western Australia (Holm et al. 2003)	10	Australia	Boothathana near Camarvon Shire, Western Australia	grazed grazed (19) & ungrazed (5)	shrubland	annual (5) & perennial (5)	201 to 216	arid	Holm et al. 2003
Widou	24	Senegal	Vendou Barodi, Louga	ungrazed (5)	savanna	annual	281	semi-arid	Miehe et al. 2010
Xilin River (Ma et al. 2010)	1	China	Xilin River Basin, Inner Mongolia	ungrazed	grassland	perennial	344	semi-arid	Ma et al. 2010
Xilingol	2	China	Xilinhot, Xilingol	ungrazed	grassland	perennial	361	semi-arid	ORNL DAAC; Xiao et al. 1995; 1996

Abbreviations:

KNP = Kruger National Park – Scientific Service (<http://www.sanparks.org/parks/kruger/conservation/scientific/>)

LTER = Long Term Ecological Research Network (<http://www.lternet.edu>)

ORNL DAAC = Oak Ridge National Laboratory Distributed Active Archive Center (<http://daac.ornl.gov>), Net Primary Productivity Grasslands dataset. Datasets from Konza, Jornada, and Xilingol were not used, since more recent data was available from other sources.

S1-2: Methodological background

Formal description of stability estimates

Formally, resistance was calculated as:

$$Resistance = (ANPP_{drought} - \bar{ANPP}) / \bar{ANPP}$$

where $ANPP_{drought}$ is the ANPP at a certain site and year (SPI class 0 to -5), and \bar{ANPP} is the average ANPP of that specific site under non-drought conditions. Non-drought conditions are defined as the mean ANPP in the second year of two consecutive years with normal, average rainfall (SPI class 0). Negative deviations represent reductions in ANPP; positive values represent increases. More extreme values represent relatively low or high resistance respectively. Similar to the calculation of resistance, we defined recovery as:

$$Recovery = ANPP_{post-drought} / ANPP_{pre-drought}$$

with $ANPP_{pre-drought}$ being ANPP in the year previous to a specific drought year at a certain site and $ANPP_{post-drought}$ being the ANPP in the year after this drought. Here drought is defined as a one-year or multi-year period of moderate drought conditions or worse (SPI class ≤ -2). Values above 100% represent increases in post-drought years as compared to pre-drought; values below 100% represent decreases. Pre- and post-drought years had to receive normal or average precipitation (SPI class 0).

Some background on the standardized precipitation index

To compare drought responses across dryland sites, regions and biomes, we quantified drought severity via the standardized precipitation index (SPI; McKee et al., 1993), which is a common and well-supported precipitation index in ecology (Vicente-Serrano et al., 2012, Guttman, 1998). The SPI is a standardized and normalized index, based on the conversion of precipitation data to probabilities. Based on (long-term) precipitation data at a given site, a gamma-distribution for the observed probabilities is estimated, and then projected to a standardized distribution with a mean of zero and a standard deviation of unity. Thus, SPI values near zero represent 'normal' and average rainfall conditions at the respective site, while positive and negative values represent rectified anomalies, where stronger deviations indicating stronger anomalies. Theoretically, the SPI can be calculated for precipitation sums on various time scales (3 to 48 month sums are recommended). We calculated SPI values for sites' hydrological years (or 'crop years'), and assigned drought severity classes ('SPI classes') according to the classification of the US National Drought Mitigation Center (<http://droughtmonitor.unl.edu/>), adding the class of 'normal precipitation' (SPI class 0, with SPI values $\leq |0.5|$).

References

- Andales, A.A., Derner, J.D., Ahuja, L.R., Hart, R.H., 2006. Strategic and Tactial prediction of forage production in northern mixed-grass prairie. *Rangeland Ecol Manag* 59, 576-584.
- Bai, Y.F., Li, L.H., Huang, J.H., Chen, Z.Z., 2001. The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia Plateau. *Acta Bot Sin* 43, 280-287.
- Beckmann, M. & von Wehrden, H. (2012) Where you search is what you get: literature mining - Google Scholar versus Web of Science using a data set from a literature search in vegetation science. *Journal of Vegetation Science*, 23, 1197-1199.
- Blaisdell, J.P., 1958. Seasonal development and yield of native plants on the upper Snake River Plains and their relation to certain climatic factors. U.S. Dept. of Agriculture, Washington.
- Couturier, D.E. & Ripley, E.A. 1973. Rainfall Interception in Mixed Grass Prairie. *Can J Plant Sci* 53: 659-663.
- Donaldson, C.H., G. Rootman, and D. Grossman. 1984. Long-term nitrogen and phosphorus application to veld. *Journal of the Grassland Society of Southern Africa* 1: 27-32.
- Foran, B.D., Bastin, G., Remenga, E., Hyde, K.W., 1982. The response to season, enclosure, and distance from water of three central australian pasture types grazed by cattle. *Australian Rangeland Journal* 4, 5-15.
- Gilmanov, T.G., Parton, W.J. & Ojima, D.S. 1997. Testing the 'CENTURY' ecosystem level model on data sets from eight grassland sites in the former USSR representing a wide climatic/soil gradient. *Ecol Model* 96: 191-210.
- Guo, R., Wang, X.K., Ouyang, Z.Y., Li, Y.N., 2006. Spatial and temporal relationships between precipitation and ANPP of four types of grasslands in northern China. *J Environ Sci (China)* 18, 1024-1030.
- Guttman, N. B. (1998) Comparing the Palmer drought index and the standardized precipitation index. *Journal of the American Water Resources Association*, 34, 113-121.
- Harmoney, K.R., 2007. Grazing and burning Japanese brome (*Bromus japonicus*) on mixed grass rangelands. *Rangeland Ecol Manag* 60, 479-486.
- Heisler, J.L. & Knapp, A.K. 2008. Temporal coherence of aboveground net primary productivity in mesic grasslands. *Ecography* 31: 408-416.
- Henkin, Z., Ungar, E.D., Dvash, L., Perevolotsky, A., Yehuda, Y., Sternberg, M., Voet, H. & Landau, S.Y. 2011. Effects of cattle grazing on herbage quality in a herbaceous Mediterranean rangeland. *Grass Forage Sci* 66: 516-525.
- Herbel, C.H., Ares, F.N., Wright, R.A., 1972. Drought effects on a semidesert grassland range. *Ecology* 53, 1084-1093.
- 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.
- Hulett, G.K., Tomanek, G.W., 1969. Forage Production on a Clay Upland Range Site in Western Kansas. *J Range Manage* 22, 270-&.
- Khumalo, G., Holechek, J., 2005. Relationships between Chihuahuan desert perennial grass production and precipitation. *Rangeland Ecol Manag* 58, 239-246.
- Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. *Ecol Appl* 2, 397-403.
- Ma, W.H., Liu, Z.L., Wang, Z.H., Wang, W., Liang, C.Z., Tang, Y.H., He, J.S. & Fang, J.Y. 2010. Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland. *J Plant Res* 123: 509-517.
- Manley, W.A., Hart, R.H., Samuel, M.J., Smith, M.A., Waggoner, J.W., Manley, J.T., 1997. Vegetation, cattle, and economic responses to grazing strategies and pressures. *J Range Manage* 50, 638-646.

- McKee, T. B., Doesken, N. J. & Kleist, J. (1993) The relationship of drought frequency and duration to time scales. *8th Conference on Applied Climatology, January 17-22, 1993*, pp. 179-184. Anaheim, California.
- McIvor, J. G., Gardener, C. J., and Spain, A. V. (1991). A description of the ECOSSAT experimental site at Hillgrove near Charters Towers, north Queensland. CSIRO Australia Tropical Agronomy Technical Memorandum No. 70.
- Miehe, S., Kluge, J., von Wehrden, H., Retzer, V., 2010. Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. *J Appl Ecol* 47, 692-700.
- Muldavin, E.H., Moore, D.I., Collins, S.L., Wetherill, K.R. & Lightfoot, D.C. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155: 123-132.
- 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. *J Ecol* 89, 850-860.
- Palmer, A.R., Short, A., Yunusa, I.A., 2010. Biomass production and water use efficiency of grassland in KwaZulu-Natal, South Africa. *African Journal of Range & Forage Science* 27, 163-169.
- Peters, D.P.C., Yao, J., Sala, O.E., Anderson, J.P., 2012. Directional climate change and potential reversal of desertification in arid and semiarid ecosystems. *Global Change Biol* 18, 151-163.
- Ruppert, J. C. & Linstädter, A. (2014) Convergence between ANPP estimation methods in grasslands — A practical solution to the comparability dilemma. *Ecological Indicators*, 36, 524-531.
- Schulte, A., 2002. PhD Thesis. Weideökologie des Kaokolandes: Struktur und Dynamik einer Mopane-Savanne unter pastoralnomadischer Nutzung. Universität zu Köln, Köln, Germany, pp. 1-220.
- 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.
- Smoliak, S., 1986. Influence of Climatic Conditions on Production of Stipa-Bouteloua Prairie over a 50-Year Period. *J Range Manage* 39, 100-103.
- Sneva, F.A., Hyder, D.N., 1962. Estimating Herbage Production on Semiarid Ranges in The Intermountain Region. *J Range Manage* 15, 88-93.
- 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. *J Appl Ecol* 37: 224-237.
- Swemmer, A.M., Knapp, A.K., Snyman, H.A., 2007. Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *J Ecol* 95, 780-788.
- Thorpe, J., Wolfe, S. A., Houston, B. 2008. Potential impacts of climate change on grazing capacity of native grasslands in the Canadian prairies. *Can J of Soil Sci* 88: 595-609.
- Vicente-Serrano, S. M., Beguería, S., Lorenzo-Lacruz, J., Camarero, J. J., López-Moreno, J. I., Azorin-Molina, C., Revuelto, J., Morán-Tejeda, E. & Sanchez-Lorenzo, A. (2012) Performance of Drought Indices for Ecological, Agricultural, and Hydrological Applications. *Earth Interactions*, 16, 1-27.
- Xiao, X.M., Shu, J., Wang, Y.F., Ojima, D.S. & Bonham, C.D. 1996. Temporal variation in aboveground biomass of *Leymus chinense* steppe from species to community levels in the Xilin River basin, Inner Mongolia, China. *Vegetatio* 123: 1-12.
- Xiao, X.M., Wang, Y.F., Jiang, S., Ojima, D.S. & Bonham, C.D. 1995. Interannual Variation in the Climate and Aboveground Biomass of *Leymus-Chinense* Steppe and *Stipa-Grandis* Steppe in the Xilin River Basin, Inner-Mongolia, China. *J Arid Environ* 31: 283-299.

S2: Post-hoc analyses for ANOVAs on resistance and recovery

Resistance ANOVA

The resistance ANOVA showed two significant interaction terms (Dominant life history x SPI class & Grazing regime x Dominant life history). In order to assess those interactions, we used the split ANOVA approach: given an interaction between variable A and B this means splitting the data within each level of A and testing for the effect of B and vice versa. In order to avoid type-I-error inflation, the significance levels for the ANOVAs were adapted.

Table S2-1: Results for split-ANOVAs of the resistance analyses. All split ANOVAs for the two interactions are given together with adapted probability levels to avoid type I error inflation. Significant results highlight details of the interactions and are subject to subsequent Tukey HSD analyses where variables have more than two levels.

Interaction	Subset		Sum Sq	Df	F value	p
Dominant life history : SPI class	SPI class = 0	Dominant life history	5E-05	1	0,005	n.s.
		Residuals	11.46	1214		
	SPI class = -1	Dominant life history	0.413	1	29.67	***
		Residuals	3.761	270		
	SPI class = -2	Dominant life history	0.022	1	2.085	n.s.
		Residuals	2.106	200		
	SPI class = -3	Dominant life history	0.078	1	7.129	n.s.
		Residuals	1.118	102		
	SPI class = -4	Dominant life history	0.228	1	19.74	***
		Residuals	1.371	119		
	SPI class = -5	Dominant life history	0.137	1	18.39	***
		Residuals	0.552	74		
	Dominant life history = Annuals	SPI class	4.689	5	65.7	***
		Residuals	8.535	598		
Dominant life history = Perennials	SPI class	1.873	5	43.72	***	
	Residuals	11.84	1381			
Dominant life history : Grazing regime	Grazing regime = Ungrazed	Dominant life history	0.154	1	15.44	***
		Residuals	7.151	716		
	Grazing regime = Grazed	Dominant life history	6E-04	1	0.041	n.s.
		Residuals	19.65	1271		
	Dominant life history = Annuals	Grazing regime	0.086	1	3.919	n.s.
		Residuals	13.14	602		
	Dominant life history = Perennials	Grazing regime	0.043	1	4.344	n.s.
		Residuals	16.37	1385		

Significant results for Dominant life history x SPI class interaction are subject to subsequent Tukey HSD test.

Table S2-2: Results for Tukey HSD on significant split ANOVAs. These results are shown as letter-code in the respective figures (Fig. 2, 3) of the main paper.

Interaction	Subset	Assumption			Estimate	Std Err	t value	p	
Dominant life									
history : SPI class	Annual	-2: moderately dry	-	-1: abnormally dry	==	0	-0.14880	0.03040	-4.895 ***
		-3: severely dry	-	-1: abnormally dry	==	0	-0.19455	0.03506	-5.550 ***
		-4: extremely dry	-	-1: abnormally dry	==	0	-0.25855	0.01807	-14.310 ***
		-5: exceptionally dry	-	-1: abnormally dry	==	0	-0.27412	0.02463	-11.129 ***
		±0: near normal	-	-1: abnormally dry	==	0	-0.05169	0.01306	-3.959 **
		-3: severely dry	-	-2: moderately dry	==	0	-0.04576	0.04348	-1.052
		-4: extremely dry	-	-2: moderately dry	==	0	-0.10975	0.03144	-3.491 **
		-5: exceptionally dry	-	-2: moderately dry	==	0	-0.12532	0.03562	-3.518 **
		±0: near normal	-	-2: moderately dry	==	0	0.09711	0.02885	3.366 **
		-4: extremely dry	-	-3: severely dry	==	0	-0.06400	0.03596	-1.779
		-5: exceptionally dry	-	-3: severely dry	==	0	-0.07956	0.03967	-2.006
		±0: near normal	-	-3: severely dry	==	0	0.14286	0.03373	4.236 ***
		-5: exceptionally dry	-	-4: extremely dry	==	0	-0.01557	0.02591	-0.601
		±0: near normal	-	-4: extremely dry	==	0	0.20686	0.01533	13.493 ***
	±0: near normal	-	-5: exceptionally dry	==	0	0.22243	0.02270	9.798 ***	
	Perennial	-2: moderately dry	-	-1: abnormally dry	==	0	-0.0326662	0.0099577	-3.281 *
		-3: severely dry	-	-1: abnormally dry	==	0	-0.0321435	0.0121143	-2.653 .
		-4: extremely dry	-	-1: abnormally dry	==	0	-0.0903752	0.0152028	-5.945 ***
		-5: exceptionally dry	-	-1: abnormally dry	==	0	-0.1076392	0.0154560	-6.964 ***
		±0: near normal	-	-1: abnormally dry	==	0	0.0282749	0.0079121	3.574 **
		-3: severely dry	-	-2: moderately dry	==	0	0.0005228	0.0118641	0.044
		-4: extremely dry	-	-2: moderately dry	==	0	-0.0577089	0.0150041	-3.846 **
		-5: exceptionally dry	-	-2: moderately dry	==	0	-0.0749730	0.0152606	-4.913 ***
		±0: near normal	-	-2: moderately dry	==	0	0.0609412	0.0075234	8.100 ***
		-4: extremely dry	-	-3: severely dry	==	0	-0.0582317	0.0165144	-3.526 **
		-5: exceptionally dry	-	-3: severely dry	==	0	-0.0754958	0.0167478	-4.508 ***
±0: near normal		-	-3: severely dry	==	0	0.0604184	0.0102079	5.919 ***	
-5: exceptionally dry	-	-4: extremely dry	==	0	-0.0172641	0.0191012	-0.904		
±0: near normal	-	-4: extremely dry	==	0	0.1186501	0.0137321	8.640 ***		
±0: near normal	-	-5: exceptionally dry	==	0	0.1359142	0.0140119	9.700 ***		

Recovery ANOVA

The Recovery ANOVA showed one significant interaction term (Dominant life history x Grazing regime).

In order to assess this interaction, we used the split ANOVA approach (see above).

Table S2-3: Results for split-ANOVAs of the resistance analyses. All split ANOVAs for the two interactions are given together with adapted probability levels to avoid type I error inflation. Significant results highlight details of the interactions. Here no subsequent Tukey HSD analyses were necessary, since both variables had only two levels. Results are partially shown as letter-code in the respective figure (Fig.4) of the main paper.

Interaction	Subset		Sum Sq	Df	F value	p
Dominant life history : Grazing regime	Dominant life history = Annual	Grazing regime	0.1451	1	8.444	*
		Residuals	0.4297	25		
	Dominant life history = Perennial	Grazing regime	0.01398	1	0.4008	n.s.
		Residuals	1.746	89		
	Grazing regime = Ungrazed	Dominant life history	0.05422	1	2.924	n.s.
		Residuals	0.7233	39		
Grazing regime = Grazed	Dominant life history	1.418	1	73.24	***	
	Residuals	1.452	75			

S3-1: Resistance model using biome, including post-hoc analyses

Table S3-1: ANOVA on resistance. ANOVA model on the influence of SPI class and Biome on drought resistance in drylands. The ANOVA found two significant main effects (SPI class, Biome) and two significant interactions (SPI class x Biome & Biome x Grazing regime). Based on η^2 estimates, the main effect of SPI class (= drought intensity) and its interaction with biome explain relatively large proportions of variance in resistance, 21% and 2% respectively. The other significant terms, biome and its interaction with grazing regime, only explain <1% each. The other effect size estimates (Partial η^2 and ω^2) support these findings. Significance of estimates is given with * = $p < 0.05$. ** = $p < 0.01$. *** = $p < 0.001$. Results of the post-hoc test for the interactions are given below (Tables S3-2, S3-3) and are presented in Figures S3-1, S3-2 and S3-3.

Response: Resistance							
	Sum Sq	Df	F value	p	η^2	Partial η^2	ω^2
SPI class	5.6135	5	108.6798	***	0.21	0.22	0.21
Biome	0.0674	2	3.2610	*	0.00	0.00	0.00
Grazing regime	0.0014	1	0.1369		-	-	-
SPI class x Biome	0.6105	10	5.9095	***	0.02	0.03	0.02
Biome x Grazing regime	0.2379	2	11.5158	***	0.01	0.01	0.01
Residuals	20.3507	1970					
				Total (%)	0.24	0.26	0.24

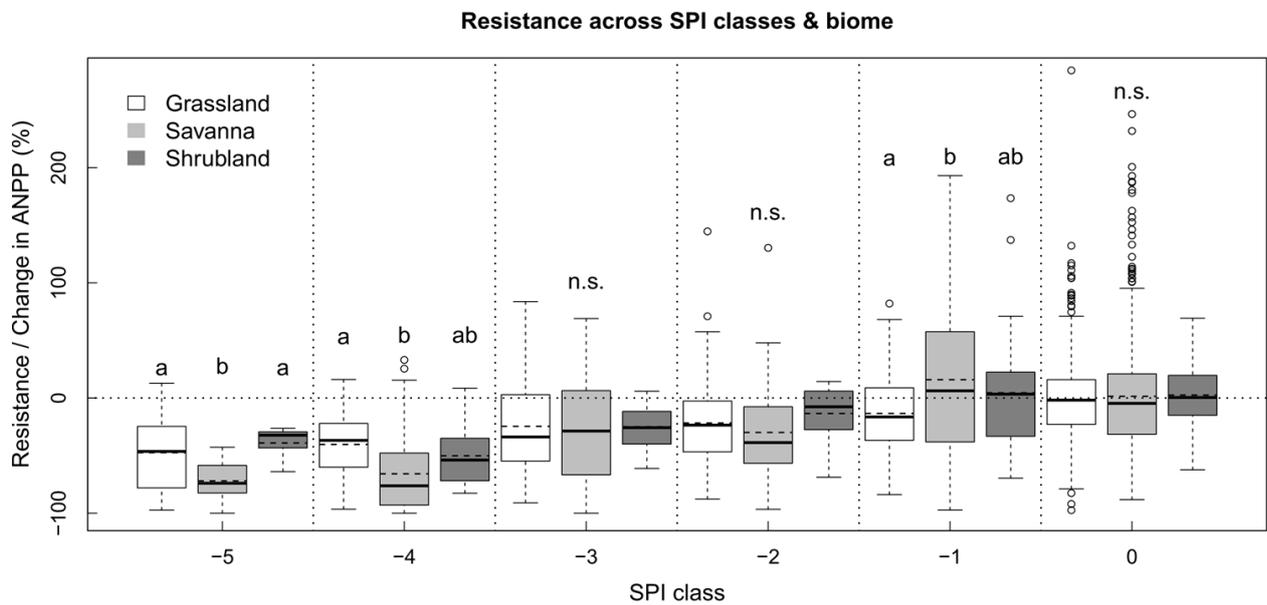


Figure S3-1: Graphical representation of the interaction between SPI class x Biome on resistance. The boxplots illustrate the resistance of grassland (white), savanna (light grey), and shrubland (dark grey) across the SPI classes as estimate for drought intensity. Dashed lines in boxplots represent mean values, and solid lines represent medians. Letter-codes give the significant differences between biomes within a specific SPI class ($p < 0.05$).

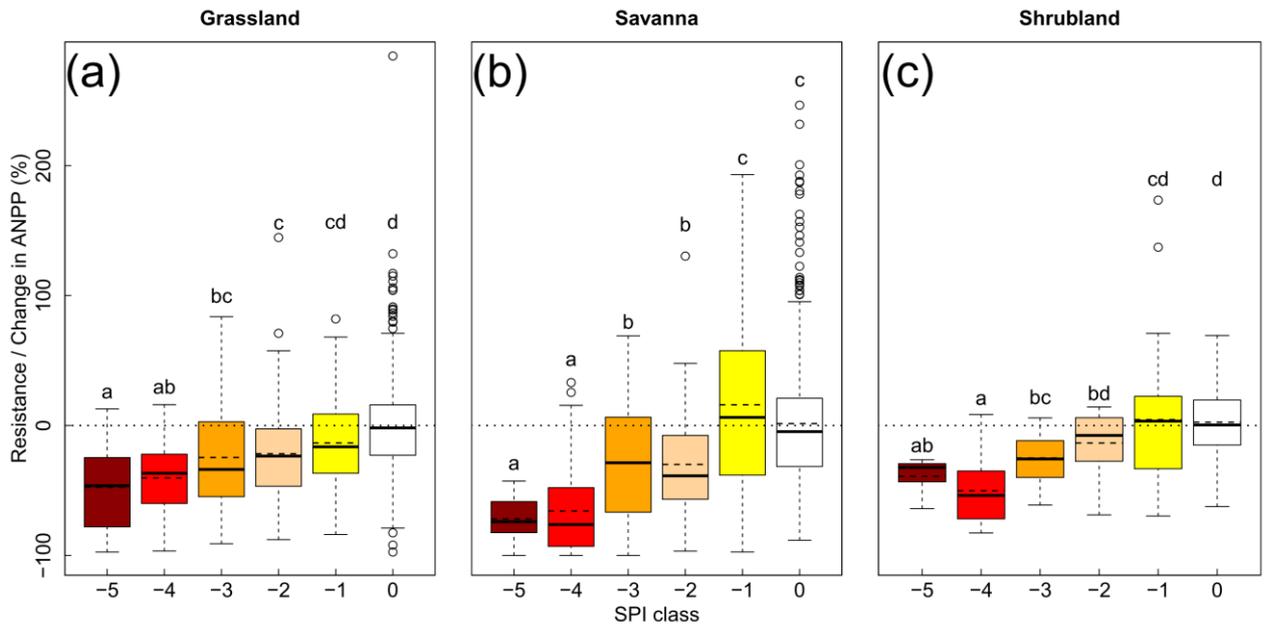


Figure S3-2: Graphical representation of the interaction between SPI class x Biome on resistance. The boxplots illustrate the distinct resistance of the three biomes (grassland, savanna, and shrubland) across SPI classes as estimates for drought intensity. Dashed lines in boxplots represent mean values, and solid lines represent medians. Letter-codes give the significant differences across SPI class within a specific biome ($p < 0.05$).

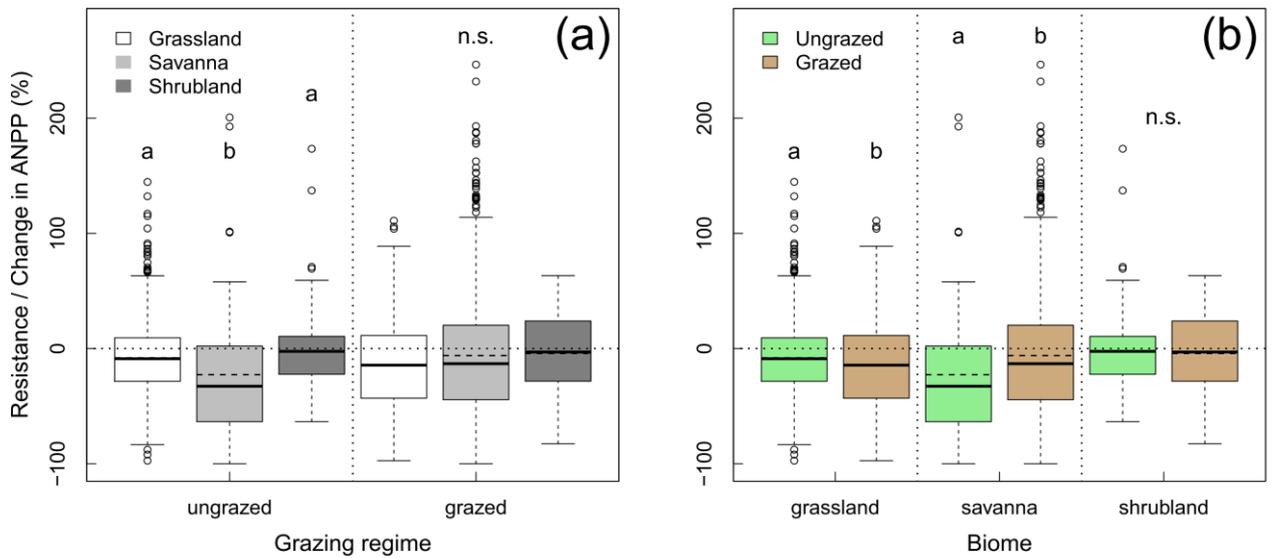


Figure S3-3: Graphical representation of the interaction between Biome x Grazing regime. The boxplots illustrate A) the resistance of grassland (white), savanna (light grey), and shrubland (dark grey) across ungrazed vs. grazed conditions and B) the resistance of vegetation under ungrazed (green) or grazed (brown) conditions within biomes. Dashed lines in boxplots represent mean values, and solid lines represent medians. Letter-codes give the significant differences between biomes in a respective grazing regime ($p < 0.05$).

Table S3-2: Results for split-ANOVAs of the resistance analyses. All split ANOVAs for the two interactions are given together with adapted probability levels to avoid type I error inflation. Significant results highlight details of the interactions and are subject to subsequent Tukey HSD analyses where variables have more than two levels.

Interaction	Subset		Sum Sq	Df	F value	p
Biome : SPI class	SPI class = 0	Biome	0.0281	2	1.488	n.s.
		Residuals	11.4300	1213		
	SPI class = -1	Biome	0.1903	2	6.425	*
		Residuals	3.9840	269		
	SPI class = -2	Biome	0.0593	2	2.851	n.s.
		Residuals	2.0680	199		
	SPI class = -3	Biome	0.0091	2	0.387	n.s.
		Residuals	1.1870	101		
	SPI class = -4	Biome	0.2239	2	9.608	***
		Residuals	1.3750	118		
	SPI class = -5	Biome	0.1482	2	9.993	***
		Residuals	0.5414	73		
	Biome = Grassland	SPI class	1.1220	5	26.300	***
		Residuals	6.9430	814		
	Biome = Savanna	SPI class	4.757	5	70.33	***
		Residuals	12.35			
	Biome = Shrubland	SPI class	0.3617	5	13.73	***
		Residuals	1.296	246		
Biome : Grazing regime	Grazing regime = Ungrazed	Biome	0.3158	2	16.150	***
		Residuals	6.9890	715		
	Grazing regime = Grazed	Biome	0.0690	2	2.238	n.s.
		Residuals	19.5900	1270		
	Biome = Grassland	Grazing regime	0.0616	1	6.299	*
		Residuals	8.0030	818		
	Biome = Savanna	Grazing regime	0.1887	1	10.230	**
		Residuals	16.9200	917		
	Biome = Shrubland	Grazing regime	0.0055	1	0.839	n.s.
		Residuals	1.6520	250		

Significant results for Biome x SPI class interaction are subject to subsequent Tukey HSD test.

Table S3-3: Results for Tukey HSD on significant split ANOVAs. These results are show as letter-code in the respective figures (Fig. S3-1, S3-2 and S3-3).

Interaction	Subset	Assumption	Estimate	Std Err	t value	p			
Biome x SPI class	SPI class = -1	savanna	- grassland	== 0	0.05802	0.01619	3.585	**	
		shrubland	- grassland	== 0	0.03694	0.02566	1.440		
		shrubland	- savanna	== 0	-0.02108	0.02431	-0.867		
	SPI class = -4	savanna	- grassland	== 0	-0.09569	0.02250	-4.252	***	
		shrubland	- grassland	== 0	-0.03175	0.03639	-0.872		
		shrubland	- savanna	== 0	0.06394	0.03353	1.907		
	SPI class = -5	savanna	- grassland	== 0	-0.08248	0.02044	-4.035	***	
		shrubland	- grassland	== 0	0.03605	0.04110	0.877		
		shrubland	- savanna	== 0	0.11853	0.04117	2.879	*	
	Biome = Grassland	-2: moderately dry	- -1: abnormally dry	== 0	-0.02381	0.01307	-1.821		
		-3: severely dry	- -1: abnormally dry	== 0	-0.03360	0.01532	-2.194		
		-4: extremely dry	- -1: abnormally dry	== 0	-0.07598	0.01880	-4.042	***	
		-5: exceptionally dry	- -1: abnormally dry	== 0	-0.10172	0.01821	-5.585	***	
		±0: near normal	- -1: abnormally dry	== 0	0.03018	0.01060	2.848	*	
		-3: severely dry	- -2: moderately dry	== 0	-0.00979	0.01470	-0.666		
		-4: extremely dry	- -2: moderately dry	== 0	-0.05217	0.01829	-2.852	*	
		-5: exceptionally dry	- -2: moderately dry	== 0	-0.07791	0.01769	-4.403	***	
		±0: near normal	- -2: moderately dry	== 0	0.05399	0.00968	5.579	***	
		-4: extremely dry	- -3: severely dry	== 0	-0.04238	0.01996	-2.123		
		-5: exceptionally dry	- -3: severely dry	== 0	-0.06812	0.01941	-3.510	**	
		±0: near normal	- -3: severely dry	== 0	0.06378	0.01254	5.085	***	
		-5: exceptionally dry	- -4: extremely dry	== 0	-0.02575	0.02226	-1.157		
		±0: near normal	- -4: extremely dry	== 0	0.10615	0.01661	6.390	***	
		±0: near normal	- -5: exceptionally dry	== 0	0.13190	0.01595	8.269	***	
		Biome = Savanna	-2: moderately dry	- -1: abnormally dry	== 0	-0.10985	0.01664	-6.602	***
			-3: severely dry	- -1: abnormally dry	== 0	-0.11000	0.02324	-4.734	***
			-4: extremely dry	- -1: abnormally dry	== 0	-0.22969	0.01634	-14.057	***
			-5: exceptionally dry	- -1: abnormally dry	== 0	-0.24222	0.02181	-11.108	***
			±0: near normal	- -1: abnormally dry	== 0	-0.02663	0.01065	-2.500	
			-3: severely dry	- -2: moderately dry	== 0	-0.00015	0.02527	-0.006	
			-4: extremely dry	- -2: moderately dry	== 0	-0.11984	0.01913	-6.265	***
			-5: exceptionally dry	- -2: moderately dry	== 0	-0.13238	0.02397	-5.523	***
			±0: near normal	- -2: moderately dry	== 0	0.08322	0.01457	5.711	***
-4: extremely dry			- -3: severely dry	== 0	-0.11969	0.02508	-4.773	***	
-5: exceptionally dry			- -3: severely dry	== 0	-0.13222	0.02894	-4.569	***	
±0: near normal			- -3: severely dry	== 0	0.08337	0.02180	3.824	**	
-5: exceptionally dry	- -4: extremely dry		== 0	-0.01254	0.02376	-0.528			
±0: near normal	- -4: extremely dry		== 0	0.20306	0.01423	14.273	***		
±0: near normal	- -5: exceptionally dry		== 0	0.21559	0.02027	10.636	***		
Biome = Shrubland	-2: moderately dry	- -1: abnormally dry	== 0	-0.03278	0.02164	-1.515			
	-3: severely dry	- -1: abnormally dry	== 0	-0.06236	0.02410	-2.587			
	-4: extremely dry	- -1: abnormally dry	== 0	-0.14467	0.02480	-5.835	***		
	-5: exceptionally dry	- -1: abnormally dry	== 0	-0.10262	0.03507	-2.926	*		
	±0: near normal	- -1: abnormally dry	== 0	0.00750	0.01435	0.523			
	-3: severely dry	- -2: moderately dry	== 0	-0.02958	0.02642	-1.119			
	-4: extremely dry	- -2: moderately dry	== 0	-0.11189	0.02705	-4.136	***		
	-5: exceptionally dry	- -2: moderately dry	== 0	-0.06984	0.03670	-1.903			
	±0: near normal	- -2: moderately dry	== 0	0.04028	0.01797	2.241			
	-4: extremely dry	- -3: severely dry	== 0	-0.08231	0.02906	-2.832	*		
	-5: exceptionally dry	- -3: severely dry	== 0	-0.04026	0.03820	-1.054			
	±0: near normal	- -3: severely dry	== 0	0.06986	0.02087	3.347	*		
	-5: exceptionally dry	- -4: extremely dry	== 0	0.04205	0.03864	1.088			
	±0: near normal	- -4: extremely dry	== 0	0.15217	0.02167	7.023	***		
	±0: near normal	- -5: exceptionally dry	== 0	0.11012	0.03293	3.344	*		
Grazing regime x Biome	Grazing regime = Ungrazed	savanna	- grassland	== 0	-0.05103	0.01077	-4.740	***	
		shrubland	- grassland	== 0	0.01930	0.00931	2.074		
		shrubland	- savanna	== 0	0.07024	0.01267	5.551	***	

S3-2: Recovery model using biome, including post-hoc analyses

Table S3-4: ANOVA on recovery index. ANOVA model on the influence of biome on post-drought ANPP-recovery in drylands. The ANOVA found one significant main effect (biome). Based on η^2 estimates, biome explains 12% of variance in post-drought recovery. ω^2 generally supports this finding (Partial η^2 is mathematically identical to η^2 in single-term models). Significance of estimates is given with * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Results of the post-hoc test for the main effect are given below and in Figure S3-4.

Response: Recovery							
	Sum Sq	Df	F value	p	η^2	Partial η^2	ω^2
Biome	0.4306	2	7.5825	***	0.12	0.12	0.10
Residuals	3.2657	115					
Total (%)					0.12	0.12	0.10

Table S3-5: Results for Tukey HSD on Biome. These results are shown as letter-code in Figure S3-4.

Term	Assumption	Estimate	Std Err	t value	p	
Biome	savanna - grassland ==	0	-0.08707	0.03491	2.494	*
	shrubland - grassland ==	0	-0.16660	0.04390	3.795	***
	shrubland - savanna ==	0	-0.07953	0.04196	1.895	n.s.

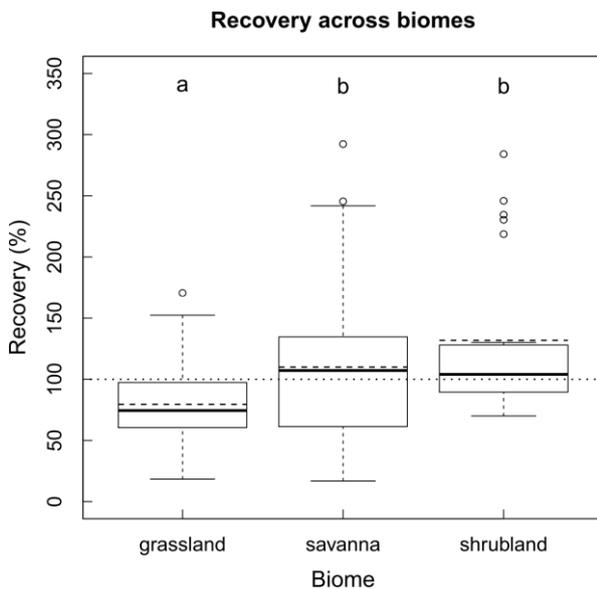


Figure S3-4: ANPP-based recovery as influenced by biome. The boxplots illustrate the distinct recovery values in grassland, savanna and shrubland. Dashed lines in boxplots represent mean values, and solid lines represent medians. Letter-codes give the significant differences across dominant life histories ($p < 0.05$).

S4-1: Alternative resistance analyses illustrating the effect(-size) of rainfall legacy

Table S4-1: ANOVA on resistance including previous SPI class (negative, normal, positive) as explanatory variable. Please note that as for the model in Table S4-1, the explained variance increased by ca. 11%. Significance of estimates is given with * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Response: Resistance							
	Sum Sq	Df	F value	p	η^2	Partial η^2	ω^2
SPI class	5.2926	5	124.5650	***	0.23	0.26	0.23
Dominant life form	0.0255	1	3.0044	n.s.			
Grazing regime	0.0024	1	0.2781	n.s.			
Previous SPI class	0.4578	2	26.9357	***	0.02	0.03	0.02
SPI class x Dominant life form	0.5782	5	13.6085	***	0.02	0.04	0.02
SPI class x Grazing regime	0.1308	5	3.0773	**	0.01	0.01	0.00
Dominant life form x Grazing regime	0.1155	1	13.5897	***	0.00	0.01	0.00
SPI class x Previous SPI class	0.5314	10	6.2535	***	0.02	0.03	0.02
Previous SPI class x Dominant life form	0.5543	2	32.6153	***	0.02	0.04	0.02
Previous SPI class x Grazing regime	0.0080	2	0.4717	n.s.			
SPI class x Dominant life form x Previous SPI class	0.5669	7	9.5306	***	0.02	0.04	0.02
Dominant life form x Grazing regime x Previous SPI class	0.0645	2	3.7955	*	0.00	0.00	0.00
Residuals	14.8879	1752					
Total (%)					0.36	0.46	0.34

Table S4-2: ANOVA on resistance based on filtered data. Only resistance values of drought years following a normal precipitation year (SPI class 0) are included in analysis. Results resemble those of the original model (Table 2 in Ruppert et al. 2014). The only differences are the significant effect of dominant life form and the insignificance of the last interaction (Dominant life form x Grazing regime) due to missing data. Please note that the explained variance of the filtered model increased by ca. 13% as compared to the original model without data filtering. Significance of estimates is given with * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Response: Resistance							
	Sum Sq	Df	F value	p	η^2	Partial η^2	ω^2
SPI class	2.6821	5	85.2144	***	0.35	0.36	0.34
Dominant life form	0.0895	1	14.2192	***	0.01	0.02	0.01
Grazing regime	0.0053	1	0.8497	n.s.	-	-	-
SPI class x Dominant life form	0.1873	5	5.9517	***	0.02	0.04	0.02
Dominant life form x Grazing regime	0	1	0.0039	n.s.	-	-	-
Residuals	4.7841	760					
Total (%)					0.38	0.42	0.37

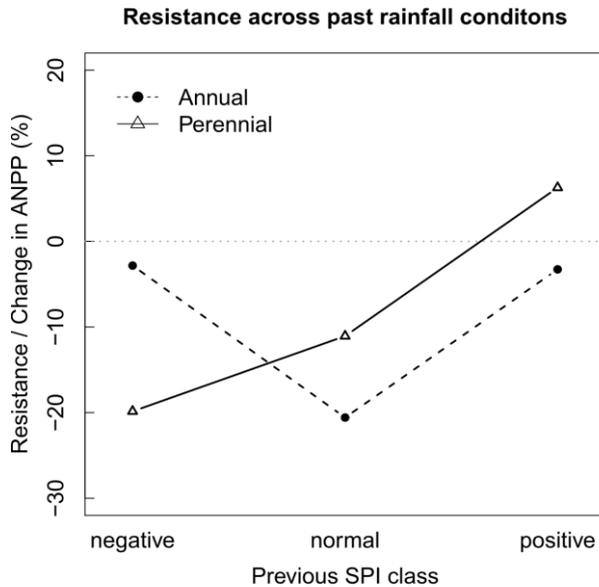


Figure S4-1: Interaction between resistance and dominant life form of the herbaceous layer as effected by previous precipitation conditions. Points connected by a dashed-line represent mean resistance from sites with a dominating annual herb-layer, triangles connected by a solid-line represent those of perennials. As can be seen, perennials on average have higher resistance under conditions of preceding normal rainfall or positive rainfall anomalies. Under conditions of preceding negative rainfall anomalies (i.e. drought), annuals have higher resistance.

The final model (Table 2 in main document) explained 25% of variance in ANPP resistance to drought. Here, the proportion of explained variance could be increased to ca. 36-38% by either including the effect of previous year's precipitation in the model (Table S4-1), or by filtering out resistance estimates from drought years not following an average precipitation year (Table S4-2). However, since both options led to loss of considerable amounts of data and/or to untraceable interactions (due to empty cells), we opted for the simpler, yet more parsimonious, model.

The most important effect was an interaction of previous year's precipitation status (below, average, or above) and dominant herbaceous life history (see Figure S4-1). While resistance for perennial-dominated systems was higher in years following average or above-average precipitation years, annual-dominated systems outperformed those in years following below-average precipitation years. This can be explained by a legacy effect (also 'memory-effect') of previous rainfalls on vegetation (Wiegand et al. 2004, Ruppert et al. 2012, Linstädter and Baumann 2013). Below-average precipitation years reduce the relative fitness of perennial vegetation in subsequent years, as root-stocks and -system are less developed, as well as competitive ability. Annual vegetation is not influenced as much by previous year's precipitation, as species grow *de novo* every year. However, the latter is only true as long as the seed bank is not depleted by prolonged drought conditions (several years).

S4-2: Effect of drought severity on recovery

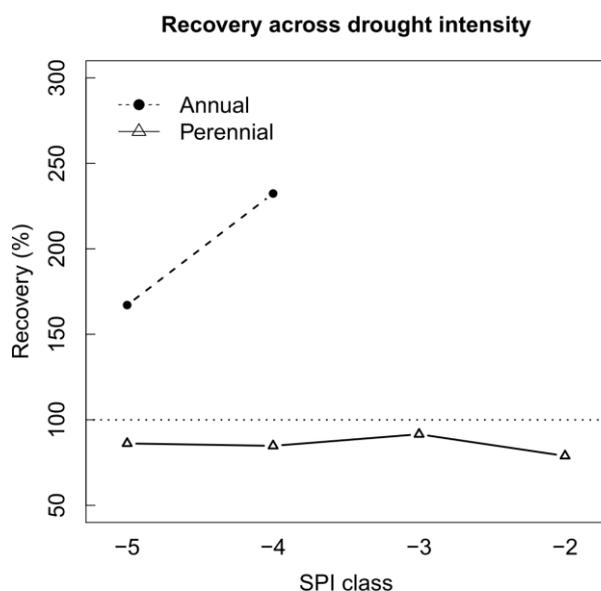


Figure S4-2: Recovery split by dominant life history across drought intensity. Recovery of systems where the herbaceous layer is dominated by perennials is largely unaffected by drought intensity; recovery varies around ca. 89% irrespective of increasing drought intensity. For annuals, few data were available, concentrated in severe drought years. These data suggest that recovery drops with drought intensity, however, this is highly speculative.

S4-3: Relationship between resistance and recovery

Table S4-3: ANCOVA on the relationship between resistance and recovery. Results from ANCOVA (type II) suggest that there is no overall linear relationship between resistance and recovery, but only within each dominant life form. This significant interaction is analyzed in Figure S4-3.

Response: Recovery								
	Sum Sq	Df	F value	p	η^2	Partial η^2	ω^2	
Resistance	1	1	0.0005	n.s.	-	-	-	
Dominant life form	76610	1	55.1277	***	0.37	0.40	0.36	
Resistance x Dominant life form	18508	1	13.3184	***	0.09	0.14	0.08	
Residuals	113955	82						
					Total (%)	0.45	0.54	0.44

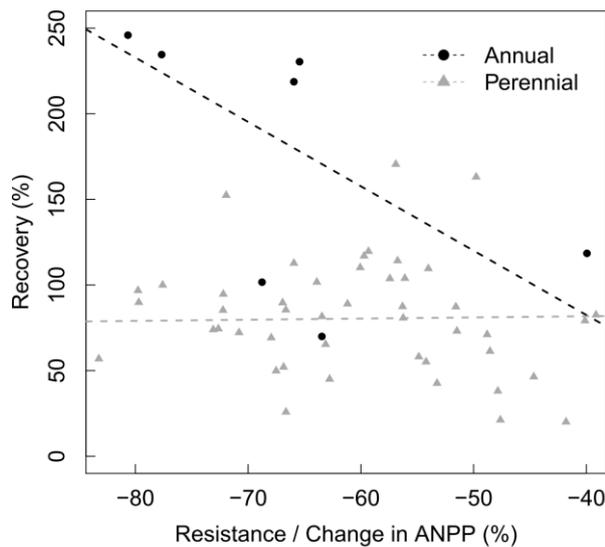


Figure S4-3: Relationship between resistance and recovery across dominant life histories. For systems with a perennial herbaceous layer, no signs for a connection between resistance and recovery could be observed (dashed grey line, linear model not significant). In contrast, recovery and resistance are reciprocally connected in annual systems – high recovery seems to be correlated with low resistance and vice versa ($Recovery = -3.76 \times resistance - 68$; $R^2=0.32$).

References

- Linstädter, A. and G. Baumann. 2013. Abiotic and biotic recovery pathways of arid rangelands: Lessons from the High Atlas Mountains, Morocco. *CATENA* **103**:3-15.
- Ruppert, J. C., A. M. Holm, S. Miehe, E. Muldavin, H. A. Snyman, K. Wesche, and A. Linstädter. 2012. Meta-analysis of rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands. *Journal of Vegetation Science* **23**:1035-1050.
- Wiegand, T., H. A. Snyman, K. Kellner, and J. M. Paruelo. 2004. Do grasslands have a memory: Modeling phytomass production of a semiarid South African grassland. *Ecosystems* **7**:243-258.

3. Additional Publications (Appendix)

- 3.1 Response of community-aggregated Plant Functional Traits along Grazing Gradients: Insights from African semi-arid Grasslands
- 3.2 Discrimination and Characterization of Management Systems in semi-arid Rangelands of South Africa using RapidEye Time Series
- 3.3 Effect of Tenure System on Biomass and Vegetation Cover in Two Biomes in South Africa
- 3.4 Are there consistent Grazing Indicators in Drylands? Testing Plant Functional Types of various Complexity in South Africa's Grassland and Savanna Biome

Note to the referees: Publications in this Chapter are not a formal part of the dissertation, as I am only co-author and not first- or corresponding-author.

3.1 Response of community-aggregated Plant Functional Traits along Grazing Gradients: Insights from African semi-arid Grasslands

Cristian A. Moreno García, Jürgen Schellberg, Frank Ewert, Katharina Brüser, Pablo Canales-Prati, Anja Linstädter, Roelof J. Oomen, Jan C. Ruppert, Susana B. Perelman (2014), *Applied Vegetation Science*, in press, DOI: 10.1111/avsc.12092

3.2 Discrimination and Characterization of Management Systems in semi-arid Rangelands of South Africa using RapidEye Time Series

Katharina Brüser, Hannes Feilhauer, Anja Linstädter, Jürgen Schellberg, Roelof J. Oomen, Jan C. Ruppert, Frank Ewert (2014), *International Journal of Remote Sensing* 35: 1653-1673, DOI: 10.1080/01431161.2014.882028

3.3 Effect of Tenure System on Biomass and Vegetation Cover in Two Biomes in South Africa

Roelof J. Oomen, Anja Linstädter, Jan C. Ruppert, Katharina Brüser, Jürgen Schellberg, Frank Ewert (submitted), *Journal of Arid Environments*

3.4 Are there consistent Grazing Indicators in Drylands? Testing Plant Functional Types of various Complexity in South Africa's Grassland and Savanna Biome

Anja Linstädter, Jürgen Schellberg, Katharina Brüser, Cristian A. Moreno García, Roelof J. Oomen, Chris C. du Preez, Jan C. Ruppert, Frank Ewert (submitted),
PLOS ONE

4. Discussion

4.1 Drivers of Primary Production Revisited

In my thesis, I could demonstrate that drivers of dryland ANPP are not only important on a local scale, but are of general (global) importance (Ruppert et al., 2012, Chapter 2.1). Using quantitative meta-analysis as data-integration method, I found that dryland ANPP was influenced by recent and past precipitation, as well as by land use (i.e. grazing) intensity. Throughout drylands, the relative importance of these drivers varied across biomes and soils. Furthermore, as quantitative effects size metrics were used, effect magnitudes could be compared and an average impact ranking was deduced. ANPP was most strongly influenced by precipitation, followed by land use (i.e. grazing) intensity and last year's precipitation. Hence, these results support the significance of water limitation in dryland ecosystems. Furthermore, this ranking also supports an hypothesis of Le Houérou (1984), who claimed that the two most important drivers of dryland productivity (i.e. grazing and rainfall) may mask each other's effect. For instance, detrimental effects of high grazing pressure may completely mask the positive effects of previous year's precipitation, or partially those of recent precipitation.

Given the relatively small sample size of the study (50 data sets derived from 8 studies), reviewers questioned the reliability and generality of meta-analysis results at the time the study was submitted. During the peer-review process, these doubts were dispelled by fail-safe calculations (see Supporting Information, Table S4 in Chapter 2.1). At the end of 2012, validity of results could also be ensured in a repeated meta-analysis based on a much larger database (150 data sets, Figure 4.1).

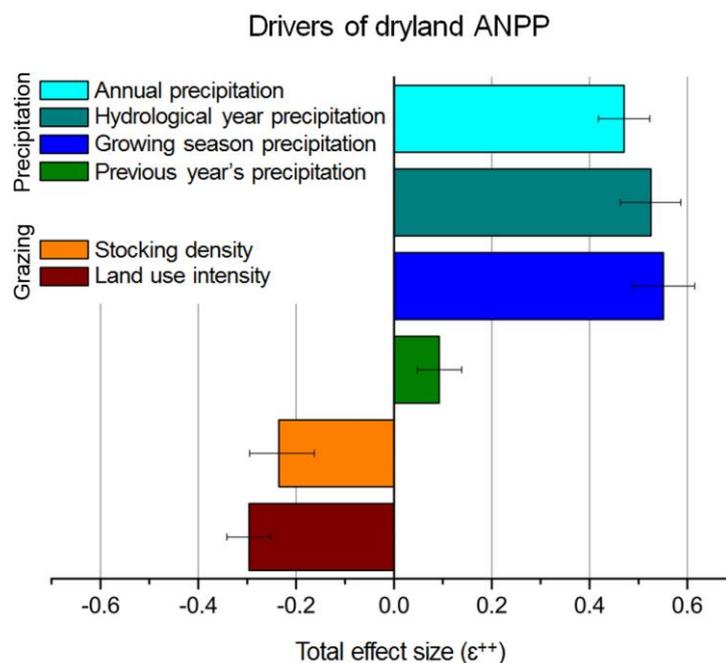


Figure 4.1: Total effect sizes quantifying the two most important drivers of dryland ANPP (precipitation and grazing). Bars represent magnitude of the respective effects. Comparison to Ruppert et al. (2012, Figure 3) shows virtually identical results. Effect sizes (ϵ^{++}): annual (0.47 ± 0.05), hydrological year (0.53 ± 0.06), growing season (0.55 ± 0.06), previous year's precipitation (0.09 ± 0.05), stocking density (-0.24 ± 0.07) and land use intensity (-0.30 ± 0.05).

Comparison of results given in Figure 4.1 and those from Ruppert et al. (2012, Chapter 2.1, Figure 3) shows that these are virtually identical. Effect sizes of differing precipitation sums (ϵ^{**} 0.47 to 0.55, Figure 4.1) fall well within the range reported in Chapter 2.1 (ϵ^{**} 0.55 ± 0.08), the same is true for all other factors (previous precipitation: ϵ^{**} 0.07 ± 0.05 vs. 0.09 ± 0.05 ; stocking density: ϵ^{**} -0.21 ± 0.14 vs. -0.24 ± 0.07 ; land use intensity: ϵ^{**} -0.30 ± 0.17 vs. -0.30 ± 0.05 for original and repeated meta-analysis, respectively). Hence, drivers of primary production in drylands appear to be valid across large spatial scales. This also implies that studies reporting dryland biomass or primary production, as well as other related variables, should measure or estimate the strength of the described drivers in order to make their findings interpretable and comparable.

4.2 Primary Production and Rain-Use Efficiency as Functions of Precipitation

The universal importance of precipitation for dryland ANPP underlines the necessity to understand the shape and dynamics of this relationship. As described above (see Chapter 1 and 2.1), there is no consensus about the shape of ANPP development across precipitation gradients. Convenient, yet potentially oversimplified, linear models (e.g. O'Connor et al., 2001) are challenged by more complex unimodal or saturation curves (e.g. Yang et al., 2008).

Generally, there is no reason why ANPP, within certain boundaries, should not be linearly coupled to precipitation. However, the idea of general positive linearity is misleading. Production of individual plants and plant communities is subject to physiological and ecological constraints, which limit their growth. For each plant species, or vegetation type, a specific optimal range of water for plant growth can be assumed (Tilman, 1982, Ellenberg et al., 1991). Below that, production is limited by water availability; above that range, other factors are increasingly limiting (e.g. nutrients, light and/or space). Hence, the relationship between ANPP and precipitation will certainly change at low and high precipitation values, dividing the response along the precipitation gradient in a number of sequential relationships (cf. Figure 1, Chapter 2.1). Therefore, linear relationships between ANPP and precipitation can only be assumed for clearly defined relatively narrow sections of moisture gradients and are thus scale dependent (i.e. gradient length and type).

Especially differences between temporal and spatial gradients have been reported and comprehensively assessed by Lauenroth and Sala (1992), who found the relationship between ANPP and precipitation to be steeper in spatial than in temporal models (see Box 4.1).

Box 4.1 – Temporal vs. Spatial Models of ANPP-Precipitation Relationships

Figure 4.2 illustrates the scale dependency of ANPP-precipitation relationships, comparing temporal (A; several sequential observations at a single location) and spatial gradients (B; several sequential observations, or averages thereof, from various sites). Generally, extreme values on the precipitation axis are of fundamentally different quality for the two distinct scales. For the temporal gradient, the dry and wet end represent anomalies in (annual or seasonal) precipitation, which would be considered extreme events (i.e. drought or heavy rains, respectively). Values in the mid-part of the gradient correspond to ‘normal’ (average) precipitation amounts, near to the mean annual precipitation (MAP) of the respective site. For the spatial gradient, extremes of the precipitation axis do not correspond to precipitation anomalies, but also to relatively ‘normal’ (average) precipitation amounts for sites found at that part of the gradient, e.g. hyper-arid sites at the drier end and dry sub-humid sites at the wetter end for precipitation gradients across drylands.

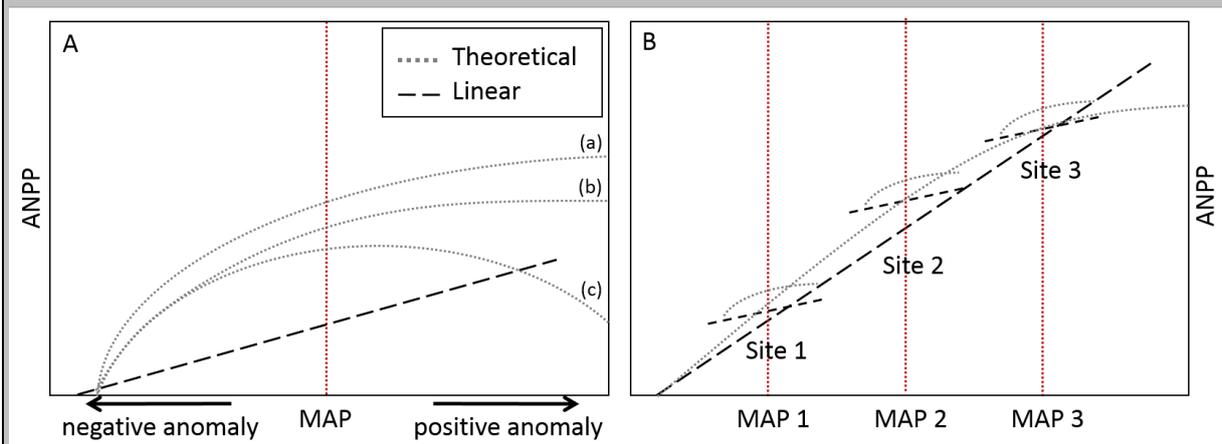


Figure 4.2: Schematic difference between temporal (A) and (spatio-) temporal (B) precipitation gradients. Note that the slope of ANPP across precipitation is steeper for spatiotemporal gradients than for temporal gradients.

At the dry end of a temporal gradient (Figure 4.2A), negative rainfall anomalies (drought) will largely limit ANPP. At the wetter end production could increase slowly (a), stagnate (b) or even drop again (c). A drop in ANPP may be due to the fact that high annual or seasonal precipitation is usually coupled to extreme events like heavy rain, hail- or thunderstorms, which negatively influence plant production (Rosenzweig et al., 2002, Ludwig et al., 2005). These response patterns will result in a relatively shallow slope in linear regression analysis. This does not apply for spatial gradients (Figure 4.2B): as peripheral values along the spatial gradient do not reflect anomalies but ‘normal’ (average) precipitation values for relatively dry, intermediate or humid sites, production should consistently increase along the gradient, resulting in a relatively steep slope in linear regressions.

These theoretical considerations on the different outcome of linear regressions of ANPP along spatial and temporal precipitation gradients are consistent with empirical findings (cf. Chapter 2.1, Ruppert et al. 2012). For instance, Lauenroth and Sala (1992) found that a spatial model developed by Sala et al. (1988) for the Central Grasslands of the U.S. predicts a much steeper slope between ANPP and precipitation than a temporal model (52 years) for data from the Central Plains Experimental Range.

Given these theoretical considerations and concurring results in literature, the use of linear regression for ANPP as function of precipitation, although frequently applied (see Chapter 1.2), is problematic, as it may oversimplify ecological complexity. If the precipitation gradient (or more general: gradient of plant-available moisture) is narrow, e.g. if only data from one site is considered, chances are high that linear regression is adequate. This is also evident in the meta-analysis results, which are based on correlation coefficients from linear regressions (see Chapter 2.1). The high total effect size for the

impact of precipitation on ANPP shows that correlation coefficients across sites are high on average, what in turn shows that site-specific ANPP-precipitation relationships can be well described by linear models. However, with increasing gradient length, e.g. if data from various sites along a precipitation gradient are combined, other regression models should be considered. This became evident in the results of linear piece-wise quantile regression (LPQR; see Chapter 2.1, Figure 1). Irrespective whether results from high values (99th percentile) or average values (median) were considered, the ANPP-precipitation curve progressively leveled-off with increasing humidity.

Unfortunately, only few scientists (including modelers) consider these assumptions when formulating general ANPP-precipitation relationships. Often, they merely rely on statistical convenience and/or significance while neglecting ecological adequateness. However, first signs of adaptations are observable (e.g. Jakoby et al., 2014, Yan et al., 2013). For instance, Jakoby et al. (2014) adapted findings from Ruppert et al. (2012) for a rangeland model and defined that accumulation of annual green biomass with increased precipitation was only valid within predefined boundaries. Precisely, their model defined a frame for »*plausible biomass accumulation*« and assumed an upper limit of production. Thus, they considered production to level-off with high precipitation (cf. Figure 3 in Jakoby et al., 2014).

Compared to the mentioned debate around the ANPP-precipitation relationships, the shape of the rain-use efficiency (RUE) response to precipitation is even more disputed: some studies found that rain-use efficiency is a constant rate across temporal and spatial precipitation gradients (e.g. Paruelo, 2000), others report a linear increase with precipitation (Bai et al., 2008) or a hump-shaped, unimodal response (e.g. O'Connor et al., 2001, Hein and de Ridder, 2006, Miede et al., 2010). However, due to the inherent autocorrelation between RUE and precipitation, there is doubt whether it is even reasonable to present this relationship at all (Prince et al., 2007).

Since RUE is the quotient of ANPP and rainfall, a regression of RUE against precipitation violates the assumption of independence. As it is a y/x over x relationship, it represents an autocorrelation. Nevertheless, I argue that this relationship can be analyzed if an adapted null hypothesis is considered for this regression. This assumes that the ANPP included in RUE (rather than RUE itself) is unrelated to precipitation. Hence, it corresponds to the null hypothesis of the regression of ANPP against precipitation gradients and results not in a linear constant, but in a hyperbolic function (Figure 4.3, cf. considerations on »*nutrient use-efficiency*« in Pastor and Bridgman, 1999, and Vitousek, 1982). This adapted null hypothesis implies that linear regression is inadequate for analyzing the response of RUE as function of precipitation: linear regressions cannot be fitted adequately to hypothetical patterns emerging from that null hypothesis. Instead, regression methods that do not anticipate a fixed shape should be used (e.g. linear piece-wise quantile regression, LPQR). Furthermore, established regressions should be thoroughly checked, whether they correspond to the adapted null hypothesis or not.

Discussion

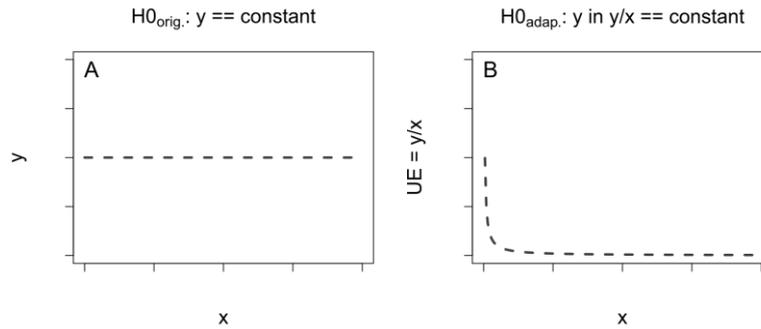


Figure 4.3: Graphical representation of original and adapted null hypothesis (H0) for analysis of rain-use efficiency along precipitation gradients. (A) Original H0 for linear regressions that assumes that y (e.g. ANPP) is independent from x (e.g. precipitation) and thus constant. (B) Adapted H0 for use-efficiencies (UE) which assumes that the y-term in the UE is constant, rather than the UE itself. Hence, it predicts a hyperbolic relationship (cf. considerations on »nutrient use-efficiency« in Pastor and Bridgham, 1999, and Vitousek, 1982).

Results on the RUE-precipitation relationship reported in Chapter 2.1 (based on LPQR) suggest an unimodal, hump-shaped RUE development across dryland precipitation gradients, peaking around 200 mm of annual precipitation. It is obvious, that the found response of RUE across the precipitation gradient is different from the adapted null hypothesis (Figure 4.3). Furthermore, these findings are in line with other reports from literature, even though position of peak in RUE may differ (Hein and de Ridder, 2006, Miehe et al., 2010, Yan et al., 2013). Generally, a hump-shaped response of RUE across precipitation gradients is support for non-linearity of ANPP-precipitation relationships (cf. Verón et al., 2005).

4.3 Overcoming the »Comparability Dilemma«

As reported in Ruppert and Linstädter (2014, Chapter 2.2), ANPP estimates drawn from different estimation methods can be largely incomparable. Despite the large amount of published ANPP data this de facto leads to a scarcity of ANPP data for data-integration studies: a »comparability dilemma«. Thus far, authors of data-fusion studies and meta-analyses based on ANPP had only limited options. For once, incomparable data could be omitted; consequently, major proportions of published data would be neglected. Another option was to accept the limited comparability or even incomparability between input data with unpredictable outcome for results – a common issue in meta-analyses (»comparing apples and oranges«; Rosenberg et al., 2000, Borenstein, 2009). Somewhat surprising, the latter option has frequently been chosen (e.g. Evans et al., 2011) – if authors were aware of these problems at all.

Confronted with this issue, I followed the first option during the data analysis for my first paper (Ruppert et al., 2012, see Chapter 2.1) and only included ANPP data that was derived by comparable methods (see Box 4.2). However, as data acquisition for the database proceeded a third option was studied: Are ANPP estimates deriving from the most common estimation algorithms convertible?

Box 4.2 – Conversion formulae and meta-analysis

The fact that ANPP conversion formulae were not used for the meta-analysis presented in Chapter 2.1 (Ruppert et al., 2012) is unproblematic. As effect sizes in the conducted meta-analysis were based on correlation coefficients, linear conversions of ANPP data would not have changed the results in any way: correlation coefficients of linear regressions are not influenced by any linear recalculation of one of the variables. Similar applies if study- or site-specific ratios of ANPP (e.g. treated vs. non-treated) are compared across varying ANPP estimation methods (cf. comment in Ruppert and Linstädter, 2014, concerning Eldridge et al., 2011, Yahdjian et al., 2011). Here, linear recalculations will only have an effect if the intercept is not zero.

As previously shown in Ruppert and Linstädter (2014, Chapter 2.2), I was able to derive conversion formulae between the seven most common ANPP estimation methods. As some conversions were sensitive for climate regime (due to differing turnover rates from live to senescent biomass as a function of aridity), altogether 27 conversions for the 21 method combinations were established. Based on statistical and methodological aspects 16 of those could be fully recommended.

Nevertheless, the study was not meant to advocate an imprudent use of the established conversions, as even the best conversion formula is still second best to de-novo calculations of ANPP using the desired estimation method. However, the presented approach offers a practical solution in those cases where de-novo calculation is no option, and it is certainly superior to previous attempts to cope with the »comparability dilemma«, i.e. combining incomparably ANPP data or skip available published data.

The master database was updated with recalculated ANPP data prior to the third study (Ruppert et al., submitted, Chapter 2.3). First, ANPP was calculated using as many estimation methods as possible for each data set. The set of possible methods was determined by the type and temporal resolution of biomass data available. Only thereafter, conversion formulae were used to recalculate ANPP, to further increase the amount of available data. Here, peak standing crop (Method 2a) was chosen as main ANPP estimate, as (1) it has given proof to be an ecologically meaningful estimate of ANPP across various ecosystems (Ruppert and Linstädter, 2014, Chapter 2.2), and as (2) it was the most abundant estimate available in the database, thus minimizing the proportion of recalculated estimates. To this end, two recommended conversion formulae were used to increase ANPP data for subsequent analyses. Namely, the conversions from the second peak standing crop method (Method 2b, Table 1.1) as well as that from peak live biomass (Method 1) were used; both of these conversions are recommended in Ruppert and Linstädter (2014, Chapter 2.2).

4.4 Drylands in Times of Global Change – Impacts of Drought and Grazing

Chapter 2.3 (Ruppert et al., submitted) studied dryland ecosystems' response to combined effects of drought and grazing regime (grazed vs. ungrazed). In particular, responses in ANPP-based estimates for resistance, i.e. a system's ability to withstand disturbance, and recovery, i.e. a system's potential

to (or rate of) return to a previous state after a disturbance, have been studied (Tilman and Downing, 1994, Bai et al., 2004). Both parameters represent constitutional aspects of ecosystem stability (Pimm, 1984, Holling, 1973, Donohue et al., 2013). Studying these responses is of high relevance, as altered rainfall (e.g. more extreme events) and land use regimes (e.g. increased grazing intensity) are the most likely projections for global change in drylands (see Chapter 1.1, cf. Hartmann, 2011). The importance of understanding plants' response to drought is further underlined by an ongoing debate about the actual physiological response of plants to drought (Reyer et al., 2012). The opposing positions in the debate can be summarized metaphorically as plants either starving to death (stomata closed with chance of CO₂-starvation) or dying from thirst (stomata open with chances of hydraulic failure; cf. Reyser et al., 2012). Even though my approach cannot add to the closure of this debate, it can describe quantitative responses of dryland ecosystems to drought and grazing, and assess whether differences exist across biomes or systems whose life histories of dominant plants differ.

One of the general results was that ecosystem stability was better explained by dominant life history of the herbaceous layer than by biome. This is particularly interesting, as many ecological studies and models use biome-definitions as main classification tool (e.g. Hely et al., 2006, Heubes et al., 2011, Huxman et al., 2004, Knapp and Smith, 2001), including myself (Chapter 2.1, Ruppert et al., 2012). Even though biome classifications have given proof to explain differences across spatial scales (see above), my recent results suggest that classifications connected to plant strategies (e.g. life history) are particularly good in explaining process-based responses. Hence, they should be considered more frequently, especially in modelling approaches (as concluded by Martin et al., 2014, Lohmann et al., 2012), and will certainly be given further consideration in my work (e.g. in repeated meta-analyses).

Considering the main results of the study, I found that increasing drought severity (quasi-)linearly reduced ecosystem resistance. Resistance of perennial systems was less strongly affected by drought, especially for higher intensities, as compared to that of annual systems. Besides a production increase in slightly dry years, the latter were less resistant, i.e. ANPP in drought years was reduced more strongly. For recovery, an opposing trend was found. While perennial systems failed to fully recover to pre-drought conditions in the first year after a drought, annual systems had the potential to even exceed pre-drought ANPP – but only when being grazed. Even though this opposing trend in annual and perennial systems looks like a textbook trade-off, resistance and recovery were only inversely correlated in annual systems (and sample size for this analysis was very low, $n = 8$).

Altogether and for the first time, this study established predictable relationships between drought severity and related losses in dryland primary production. This is particularly valuable for impact projections of global change and dryland modelling-approaches. Furthermore, it has important implications for dryland management during and after droughts. In particular, results show that

systems with a dominant annual herbaceous layer (e.g. arid savannas) are more prone to the combined effects of drought and human (mis-)management for two reasons: (1) they suffer more during drought events; (2) their fast post-drought recovery might encourage overutilization, which may lead to long-term degradation under conditions of increased drought intensities and frequencies.

4.5 Major Findings and Future Prospects

Within my dissertation, I could show that dryland primary production is driven by precipitation and grazing, not only locally but also on a global scale (Chapter 2.1). Another important outcome of my dissertation was that effects of grazing and rainfall are not merely additive, but can mask each other (Chapter 2.1) or interact in complex ways (Chapter 2.3). Similarly, drought severity may influence primary production either linearly or non-linearly, depending on vegetation characteristics (Chapter 2.3). These findings underline the complex dynamics of dryland ecosystems.

My quantitative projections for the influence of drought severity on primary production also showed that ecosystems whose herbaceous layer is dominated by perennial plants are more resistant to drought than annual systems. On the other hand, annual systems have displayed a higher post-drought recovery potential.

Progress could also be made concerning the highly disputed relationships between ANPP and rain-use efficiency (RUE) along precipitation gradients (Chapter 2.1). In particular, I could show – on empirical and theoretical basis – that ANPP levels-off with high precipitation amounts (along large precipitation gradients). In line with this, RUE exhibits a unimodal, hump-shaped development across precipitation gradients. Nevertheless, if precipitation gradients are narrow (e.g. if only data from one site is assessed), linear models appear adequate to formulate ANPP-precipitation relationships. These findings already drew some attention (e.g. Fensholt et al., 2013, Yan et al., 2013, Jakoby et al., 2014). I will conclude my thesis with suggestions for future research. Although I could further advance scientific understanding on the relative importance of grazing as a driver of ANPP dynamics (as compared to other drivers), effects of grazing intensity on primary production are still not well understood, specifically in interaction with precipitation (e.g. drought, cf. Chapter 2.3).

Also edaphic effects should be analyzed in more detail, as they moderate the translation of precipitation into plant-available water, and also play an important role with respect to other limiting factors for plant growth. Hence, soil texture and potential influences of co-limitation by nutrients should be assessed in subsequent studies. Considering the effects of climatic extreme events (i.e. drought and heavy rains), only effects of negative anomalies have been studied and quantified thus far (see Chapter 2.3), even though effects of positive anomalies are of similar relevance and may be even more diverse. For instance, not only response magnitude, but also direction might change with

increasing positive rainfall anomalies (e.g. positive effects of good rainfall years vs. detrimental effects of heavy rains).

Altogether and besides the gained findings, my novel methodological toolbox as well as the assembled global database of dryland primary production are among the main merits of this dissertation. The combination of a large global database, the normalization of ANPP and precipitation data (cf. Chapter 2.2), and the collection of additional site- or study-based information (cf. Chapter 1.3) enabled me to assess aspects of ecosystem functioning and stability on a global scale, which thus far could only be answered on a theoretical or anecdotal basis.

4.6 Personal Outlook

The completion of my PhD thesis will be an important milestone in my scientific career. In the next years I will take part – under the lead of Anja Linstädter – in a BMBF-funded research project in the Limpopo Province, South Africa, in which we will study coincidental effects of drought and grazing with the aid of a field experiment. Furthermore, as this project participates in a newly formed coordinated distributed experiment, namely the International Drought Experiment (IDE, Melinda Smith, pers. comm.), it has the potential to harness joint research efforts across large geographical scales. Hence, in future I will be a bit more on the experimental part of dryland ecology. This also offers me the opportunity to engage in some questions that could not have been answered by my data-integration approaches. In particular, the experiment in South Africa is meant to give insights in effects of management interventions (such as grazing exclusion) within and after severe drought events, and to better understand the role of drought duration for ecosystem resistance and recovery – two questions that I could not answer satisfactorily on the basis of existing data (see Chapter 2.3).

I will also continue searching for long-term observation studies on ANPP. Here, I will particularly concentrate on dryland regions (such as South America) and biomes (such as shrublands, or annual dominated grasslands) which are up to now under-represented in my database, and also include non-dryland sites. I will successively combine these data-integration approaches with my own experimental data, with data from coordinated distributed experiments, and with modelling approaches to overcome caveats of the respective individual approaches (Reyer et al., 2012).

5. References

- Alizai, H. U. & Hulbert, L. C. (1970) Effects of soil texture on evaporative loss and available water in semi-arid climates. *Soil Science*, **110**, 328-332.
- Andales, A. A., Derner, J. D., Ahuja, L. R. & Hart, R. H. (2006) Strategic and Tactial prediction of forage production in northern mixed-grass prairie. *Rangeland Ecology & Management*, **59**, 576-584.
- Andela, N., Liu, Y. Y., van Dijk, A. I. J. M., de Jeu, R. A. M. & McVicar, T. R. (2013) Global changes in dryland vegetation dynamics (1988-2008) assessed by satellite remote sensing: comparing a new passive microwave vegetation density record with reflective greenness data. *Biogeosciences*, **10**, 6657-6676.
- Andrew, M. H. (1988) Grazing impact in relation to livestock watering points. *Trends in Ecology & Evolution*, **3**, 336-339.
- Angassa, A., Sheleme, B., Oba, G., Treydte, A., Linstädter, A. & Sauerborn, J. (2012) Savanna land use and its effect on soil characteristics in southern Ethiopia. *Journal of Arid Environments*, **81**, 67-76.
- Archer, J. R. & Smith, P. D. (1972) The relationship between bulk density, available water capacity, and air capacity of soils. *Journal of Soil Science*, **23**, 475-480.
- Bai, Y., Han, X., Wu, J., Chen, Z. & Li, L. (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181-184.
- 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, Y. F., Li, L. H., Huang, J. H. & Chen, Z. Z. (2001) The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia Plateau. *Acta Botanica Sinica*, **43**, 280-287.
- Baker, M. J. (2000) Writing a literature review. *The Marketing Review*, **1**, 219-247.
- Beckmann, M. & von Wehrden, H. (2012) Where you search is what you get: literature mining - Google Scholar versus Web of Science using a data set from a literature search in vegetation science. *Journal of Vegetation Science*, **23**, 1197-1199.
- 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.
- Belsky, A. J., Carson, W. P., Jensen, C. L. & Fox, G. A. (1993) Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology*, **7**, 109-121.
- Blair, J. M. (1997) Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology*, **78**, 2359-2368.
- Blaisdell, J. P. (1958) Seasonal development and yield of native plants on the upper Snake River Plains and their relation to certain climatic factors. U.S. Dept. of Agriculture, Washington.
- Borenstein, M. (2009) Introduction to meta-analysis. John Wiley & Sons, Chichester, U.K.
- Brüser, K., Feilhauer, H., Linstädter, A., Schellberg, J., Oomen, R. J., Ruppert, J. C. & Ewert, F. (2014) Discrimination and characterization of management systems in semi-arid rangelands of South Africa using RapidEye time series. *International Journal of Remote Sensing*, **35**, 1653-1673.
- Buis, G., Blair, J., Burkepile, D., Burns, C., Chamberlain, A., Chapman, P., Collins, S., Fynn, R., Govender, N., Kirkman, K., Smith, M. & Knapp, A. (2009) Controls of aboveground net primary production in mesic savanna grasslands: an inter-hemispheric comparison. *Ecosystems*, **12**, 982-995.
- Buitenwerf, R., Bond, W. J., Stevens, N. & Trollope, W. S. W. (2012) Increased tree densities in South African savannas: > 50 years of data suggests CO₂ as a driver. *Global Change Biology*, **18**, 675-684.
- Cable, D. R. (1975) Influence of Precipitation on Perennial Grass Production in Semidesert Southwest. *Ecology*, **56**, 981-986.
- Chidumayo, E. N. (2003) Effect of tillage, clipping and climate on grass phytomass in a Zambian savanna. *Journal of Tropical Ecology*, **19**, 407-415.

- Davidowitz, G. (2002) Does precipitation variability increase from mesic to xeric biomes? *Global Ecology and Biogeography*, **11**, 143-154.
- DeCouturie & Ripley, E. A. (1973) Rainfall Interception in Mixed Grass Prairie. *Canadian Journal of Plant Science*, **53**, 659-663.
- Delgado-Baquerizo, M., Maestre, F. T., Gallardo, A., Bowker, M. A., Wallenstein, M. D., Quero, J. L., Ochoa, V., Gozalo, B., Garcia-Gomez, M., Soliveres, S., Garcia-Palacios, P., Berdugo, M., Valencia, E., Escolar, C., Arredondo, T., Barraza-Zepeda, C., Bran, D., Carreira, J. A., Chaieb, M., Conceicao, A. A., Derak, M., Eldridge, D. J., Escudero, A., Espinosa, C. I., Gaitan, J., Gatica, M. G., Gomez-Gonzalez, S., Guzman, E., Gutierrez, J. R., Florentino, A., Hepper, E., Hernandez, R. M., Huber-Sannwald, E., Jankju, M., Liu, J., Mau, R. L., Miriti, M., Monerri, J., Naseri, K., Noumi, Z., Polo, V., Prina, A., Pucheta, E., Ramirez, E., Ramirez-Collantes, D. A., Romao, R., Tighe, M., Torres, D., Torres-Diaz, C., Ungar, E. D., Val, J., Wamiti, W., Wang, D. & Zaady, E. (2013) Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature*, **502**, 672-676.
- Donaldson, C. H., Rootman, G. & Grossman, D. (1984) Long term nitrogen and phosphorus application to veld. *Journal of the Grassland Society of Southern Africa*, **1**, 27-32.
- Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E. & Emmerson, M. C. (2013) On the dimensionality of ecological stability. *Ecology Letters*, **16**, 421-429.
- Dye, P. J. & Spear, P. T. (1982) The Effects of Bush Clearing and Rainfall Variability on Grass Yield and Composition in Southwest Zimbabwe. *Zimbabwe Journal of Agricultural Research*, **20**, 103-118.
- Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F. & Whitford, W. G. (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709-722.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Erich Goltze KG, Göttingen.
- European Soil Bureau (2005) Soil atlas of Europe. (eds European Commission, Joint Research Centre & E. S. Bureau). European Communities, Luxembourg.
- Evans, S. E., Burke, I. C. & Lauenroth, W. K. (2011) Controls on soil organic carbon and nitrogen in Inner Mongolia, China: A cross-continental comparison of temperate grasslands. *Global Biogeochemical Cycles*, **25**.
- Fensholt, R., Rasmussen, K., Kaspersen, P., Huber, S., Horion, S. & Swinnen, E. (2013) Assessing Land Degradation/Recovery in the African Sahel from Long-Term Earth Observation Based Primary Productivity and Precipitation Relationships. *Remote Sensing*, **5**, 664-686.
- 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.
- Foran, B. D., Bastin, G., Remenga, E. & Hyde, K. W. (1982) The response to season, enclosure, and distance from water of three central Australian pasture types grazed by cattle. *Australian Rangeland Journal*, **4**, 5-15.
- Fraser, L. H., Henry, H. A. L., Carlyle, C. N., White, S. R., Beierkuhnlein, C., Cahill, J. F., Casper, B. B., Cleland, E., Collins, S. L., Dukes, J. S., Knapp, A. K., Lind, E., Long, R. J., Luo, Y. Q., Reich, P. B., Smith, M. D., Sternberg, M. & Turkington, R. (2013) Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment*, **11**, 147-155.
- Gillson, L. & Hoffman, M. T. (2007) Rangeland ecology in a changing world. *Science*, **315**, 53-54.
- Gilmanov, T. G., Parton, W. J. & Ojima, D. S. (1997) Testing the 'CENTURY' ecosystem level model on data sets from eight grassland sites in the former USSR representing a wide climatic/soil gradient. *Ecological Modelling*, **96**, 191-210.
- Glass, G. V. (1976) Primary, secondary, and meta-analysis of research. *Educational Researcher*, **5**, 3-8.

- Golodets, C., Sternberg, M., Kigel, J., Boeken, B., Henkin, Z., Seligman, N. G. & Ungar, E. D. (2013) From desert to Mediterranean rangelands: will increasing drought and inter-annual rainfall variability affect herbaceous annual primary productivity? *Climatic Change*, **119**, 785-798.
- 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.
- Guo, R., Wang, X. K., Ouyang, Z. Y. & Li, Y. N. (2006) Spatial and temporal relationships between precipitation and ANPP of four types of grasslands in northern China. *Journal of environmental sciences*, **18**, 1024-30.
- Harel, D., Holzapfel, C. & Sternberg, M. (2011) Seed mass and dormancy of annual plant populations and communities decreases with aridity and rainfall predictability. *Basic and Applied Ecology*, **12**, 674-684.
- Harmoney, K. R. (2007) Grazing and burning Japanese brome (*Bromus japonicus*) on mixed grass rangelands. *Rangeland Ecology & Management*, **60**, 479-486.
- Hartmann, H. (2011) Will a 385 million year-struggle for light become a struggle for water and for carbon? - How trees may cope with more frequent climate change-type drought events. *Global Change Biology*, **17**, 642-655.
- Hassan, R. M., Scholes, R. & Ash, N. (2005) Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group. Island Press.
- Hein, L. (2006) The impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland. *Journal of Arid Environments*, **64**, 488-504.
- Hein, L. & de Ridder, N. (2006) Desertification in the Sahel: a reinterpretation. *Global Change Biology*, **12**, 751-758.
- Heisler, J. L. & Knapp, A. K. (2008) Temporal coherence of aboveground net primary productivity in mesic grasslands. *Ecography*, **31**, 408-416.
- 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.
- Henkin, Z., Ungar, E. D., Dvash, L., Perevolotsky, A., Yehuda, Y., Sternberg, M., Voet, H. & Landau, S. Y. (2011) Effects of cattle grazing on herbage quality in a herbaceous Mediterranean rangeland. *Grass and Forage Science*, **66**, 516-525.
- Herbel, C. H., Ares, F. N. & Wright, R. A. (1972) Drought effects on a semidesert grassland range. *Ecology*, **53**, 1084-1093.
- Heubes, J., Kühn, I., König, K., Wittig, R., Zizka, G. & Hahn, K. (2011) Modelling biome shifts and tree cover change for 2050 in West Africa. *Journal of Biogeography*, 2248-2258.
- Higgins, S. I. & Scheiter, S. (2012) Atmospheric CO₂ forces abrupt vegetation shifts locally, but not globally. *Nature*, **488**, 209-212.
- Holdo, R. M., Holt, R. D., Coughenour, M. B. & Ritchie, M. E. (2007) Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. *Journal of Ecology*, **95**, 115-128.
- Holling, C. S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology, Evolution, and Systematics*, **4**, 1-23.
- Holling, C. S. (1996) Engineering resilience versus ecological resilience. *Perspective on Ecology and Engineering* (ed P. C. Schulze), pp. 31-44. National Academy of Engineering.
- 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.
- Hooper, D. U. & Johnson, L. (1999) Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. *Biogeochemistry*, **46**, 247-293.
- Hulett, G. K. & Tomanek, G. W. (1969) Forage Production on a Clay Upland Range Site in Western Kansas. *Journal of Range Management*, **22**, 270-276.
- Huxman, T. E., 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.
- IPCC (2007) Climate Change 2007: Synthesis Report. Summary for Policymakers. Intergovernmental Panel on Climate Change.
- Jakoby, O., Grimm, V. & Frank, K. (2014) Pattern-oriented parameterization of general models for ecological application: Towards realistic evaluations of management approaches. *Ecological Modelling*, **275**, 78-88.
- Jobbagy, E. G. & Sala, O. E. (2000) Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications*, **10**, 541-549.
- Khumalo, G. & Holechek, J. (2005) Relationships between Chihuahuan desert perennial grass production and precipitation. *Rangeland Ecology & Management*, **58**, 239-246.
- Kinyamario, J. I. & Macharia, J. N. M. (1992) Aboveground Standing Crop, Protein-Content and Dry-Matter Digestibility of a Tropical Grassland Range in the Nairobi-National-Park, Kenya. *African Journal of Ecology*, **30**, 33-41.
- Knapp, A. K. & Smith, M. D. (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481-484.
- Lauenroth, W. K. & Sala, O. E. (1992) Long-term forage production of North American shortgrass steppe. *Ecological Applications*, **2**, 397-403.
- Lauenroth, W. K., Wade, A. A., Williamson, M. A., Ross, B. E., Kumar, S. & Cariveau, D. P. (2006) Uncertainty in calculations of net primary production for grasslands. *Ecosystems*, **9**, 843-851.
- Le Houérou, H. N. (1984) Rain use efficiency: A unifying concept in arid-land ecology. *Journal of Arid Lands*, **7**, 213-247.
- Lenzerini, M. (2002) Data integration: A theoretical perspective. *Proceedings of the twenty-first ACM SIGMOD-SIGACT-SIGART symposium on Principles of database systems*, pp. 233-246. ACM.
- Linstädter, A. (2008) Landscape ecology of savannas - from disturbance regime to management strategies. *African Landscapes: Interdisciplinary Approaches* (eds M. Bollig & O. Bubenzer), pp. 79-103. Springer, New York; London.
- Linstädter, A. & Baumann, G. (2013) Abiotic and biotic recovery pathways of arid rangelands: Lessons from the High Atlas Mountains, Morocco. *CATENA*, **103**, 3-15.
- Linstädter, A. & Zielhofer, C. (2010) Regional fire history shows abrupt responses of Mediterranean ecosystems to centennial-scale climate change (Olea-Pistacia woodlands, NE Morocco). *Journal of Arid Environments*, **74**, 101-110.
- Lohmann, D., Tietjen, B., Blaum, N., Joubert, D. F. & Jeltsch, F. (2012) Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing. *Journal of Applied Ecology*, **49**, 814-823.
- Ludwig, J. A., Wilcox, B. P., Breshears, D. D., Tongway, D. J. & Imeson, A. C. (2005) Vegetation patches and runoff: Erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology*, **86**, 288-297.
- Ma, W. H., Liu, Z. L., Wang, Z. H., Wang, W., Liang, C. Z., Tang, Y. H., He, J. S. & Fang, J. Y. (2010) Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland. *Journal of Plant Research*, **123**, 509-517.
- Maestre, F. T., Escolar, C., de Guevara, M. L., Quero, J. L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B. & Gallardo, A. (2013) Changes in biocrust cover drive carbon cycle responses to climate change in drylands. *Global Change Biology*, **19**, 3835-3847.
- Manley, W. A., Hart, R. H., Samuel, M. J., Smith, M. A., Waggoner, J. W. & Manley, J. T. (1997) Vegetation, cattle, and economic responses to grazing strategies and pressures. *Journal of Range Management*, **50**, 638-646.
- Martin, R., Müller, B., Linstädter, A. & Frank, K. (2014) How much climate change can pastoral livelihoods tolerate? Modelling rangeland use and evaluating risk. *Global Environmental Change*, **24**, 183-192.

- Martin, S. C. & Cable, D. R. (1974) Managing semidesert grass-shrub ranges - Vegetation responses to precipitation, grazing, soil texture, and mesquite control. U.S. Department of Agriculture - Forest Service, Washington.
- McCulley, R. L. (2005) Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystems*, **8**, 106-121.
- McIvor, J. G. & Gardener, C. J. (1995) Pasture Management in Semiarid Tropical Woodlands - Effects on Herbage Yields and Botanical Composition. *Australian Journal of Experimental Agriculture*, **35**, 705-715.
- McKee, T. B., Doesken, N. J. & Kleist, J. (1993) The relationship of drought frequency and duration to time scales. *8th Conference on Applied Climatology, January 17-22, 1993*, pp. 179-184. Anaheim, California.
- McNaughton, S. J. (1983) Compensatory plant growth as a response to herbivory. *Oikos*, **40**, 329-336.
- MEA (2005) Ecosystems and human well-being: Desertification synthesis. World Resources Institute, Washington, D.C., USA.
- Miehe, S., Kluge, J., von Wehrden, H. & Retzer, V. (2010) Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. *Journal of Applied Ecology*, **47**, 692-700.
- 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., Sala, O. E. & Lauenroth, W. K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, **132**, 87-106.
- Moreno García, C. A., Schellberg, J., Ewert, F., Brüser, K., Canales-Prati, P., Linstädter, A., Oomen, R. J., Ruppert, J. C. & Perelman, S. B. (2014) Response of community-aggregated plant functional traits along grazing gradients: insights from African semi-arid grasslands. *Rangeland Ecology and Management*, in press.
- 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., Frank, K. & Wissel, C. (2007) Relevance of rest periods in non-equilibrium rangeland systems - a modelling analysis. *Agricultural Systems*, **92**, 295-317.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25-51.
- 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.
- Oesterheld, M., Loreti, J., Semmartin, M. & Paruelo, J. M. (1999) Grazing, fire, and climate effects on primary productivity of grasslands and savannas. *Ecosystems of disturbed ground* (ed L. Walker), pp. 287-306. Elsevier Science, Oxford.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Colby, J. L., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience*, **51**, 933-938.
- Paige, K. N. & Whitham, T. G. (1987) Overcompensation in Response to Mammalian Herbivory: The Advantage of Being Eaten. *The American Naturalist*, **129**, 407-416.
- Palmer, A. R. & Ainslie, A. M. (2005) Grasslands of South Africa. *Grasslands of the World* (eds J. M. Suttie, S. G. Reynolds & C. Batello), pp. 77-120. FAO, Rome.
- Palmer, A. R., Short, A. & Yunusa, I. A. (2010) Biomass production and water use efficiency of grassland in KwaZulu-Natal, South Africa. *African Journal of Range & Forage Science*, **27**, 163-169.
- Paracelsus (1922) *Sämtliche Werke*. R. Oldenbourg, München,.
- 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.
- Pastor, J. & Bridgman, S. D. (1999) Nutrient efficiency along nutrient availability gradients. *Oecologia*, **118**, 50-58.
- Peterson, G., Allen, C. R. & Holling, C. S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6-18.

- Pimm, S. L. (1984) The complexity and stability of ecosystems. *Nature*, **307**, 321-326.
- 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.
- Qiji, W., Wenying, W. & Zifa, D. (1998) The dynamics of biomass and the allocation of energy in alpine Kobresia meadow communities, Habei region of Qinghai Province. *Acta Phytocologica Sinica*, **22**, 222-230.
- Reed, S. C., Coe, K. K., Sparks, J. P., Housman, D. C., Zelikova, T. J. & Belnap, J. (2012) Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change*, **2**, 752-755.
- Reyer, C., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R. P., Bonfante, A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoudé, R., Klein, T., Kuster, T. M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., François, L., Menzel, A. & Pereira, M. (2012) A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Global Change Biology*, **19**, 75-89.
- Reynolds, J. F., Smith, D. M. S., Lambin, E. F., Turner, B. L., II, Mortimore, M., Batterbury, S. P. J., Downing, T. E., Dowlatabadi, H., Fernandez, R. J., Herrick, J. E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F. T., Ayarza, M. & Walker, B. (2007) Global desertification: building a science for dryland development. *Science*, **316**, 847-851.
- Rosenberg, M. S., Adams, D. C. & Gurevitch, J. (2000) MetaWin: Statistical Software for Meta-Analysis. Sinauer Associates, Sunderland, Massachusetts.
- Rosenzweig, C., Tubiello, F. N., Goldberg, R., Mills, E. & Bloomfield, J. (2002) Increased crop damage in the US from excess precipitation under climate change. *Global Environmental Change*, **12**, 197-202.
- Rothstein, H. R., Sutton, A. J. & Borenstein, M. (2006) Publication bias in meta-analysis: Prevention, assessment and adjustments. John Wiley & Sons, New York.
- Ruppert, J. C., Harmony, K. R., Henkin, Z., Snyman, H. A., Sternberg, M., Willms, W. D. & Linstädter, A. (submitted) Quantifying dryland resistance and resilience to drought: The importance of drought intensity, grazing regime and vegetation structure. *Global Change Biology*.
- Ruppert, J. C., Holm, A. M., Miede, S., Muldavin, E., Snyman, H. A., Wesche, K. & Linstädter, A. (2012) Meta-analysis of rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands. *Journal of Vegetation Science*, **23**, 1035-1050.
- Ruppert, J. C. & Linstädter, A. (2014) Convergence between ANPP estimation methods in grasslands — A practical solution to the comparability dilemma. *Ecological Indicators*, **36**, 524-531.
- 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.
- Scholes, R. J. & Archer, S. R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517-544.
- Schönbach, P., Wan, H., Gierus, M., Loges, R., Müller, K., Lin, L., Susenbeth, A. & Taube, F. (2012) Effects of grazing and precipitation on herbage production, herbage nutritive value and performance of sheep in continental steppe. *Grass and Forage Science*, **67**, 535-545.
- Schulte, A. (2002) Weideökologie des Kaokolandes: Struktur und Dynamik einer Mopane-Savanne unter pastoralnomadischer Nutzung. Universität zu Köln, Köln, Germany.
- 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.
- Scurlock, J. M. O. & Olson, R. J. (2002) Terrestrial net primary productivity - A brief history and a new worldwide database. *Environmental Reviews*, **10**, 91-109.
- Short, A. D. (2010) Rangeland and Animal Performance Trends in Highland Sourveld. MSc, University of KwaZulu-Natal, Pietermaritzburg.
- Singh, J. S., Lauenroth, W. K. & Steinhorst, R. K. (1975) Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. *The Botanical Review*, **41**, 181-232.

- Smith, M., Sala, O. E. & Phillips, R. (2014) Drought-Net RCN: A global network to assess terrestrial ecosystem sensitivity to drought Project Summary. *European Geosciences Union (EGU) General Assembly 2014*. Geophysical Research Abstracts, Vienna, Austria.
- Smoliak, S. (1986) Influence of Climatic Conditions on Production of Stipa-Bouteloua Prairie over a 50-Year Period. *Journal of Range Management*, **39**, 100-103.
- Sneva, F. A. & Hyder, D. N. (1962) Estimating Herbage Production on Semiarid Ranges in The Intermountain Region. *Journal of Range Management*, **15**, 88-93.
- 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.
- 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.
- Thorpe, J., Wolfe, S. A. & Houston, B. (2008) Potential impacts of climate change on grazing capacity of native grasslands in the Canadian prairies. *Canadian Journal of Soil Science*, **88**, 595-609.
- Tilman, D. (1982) Resource competition and community structure. Princeton University Press, Princeton, USA.
- Tilman, D. & Downing, J. A. (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363-365.
- Togtohyn, C. & Ojima, D. S. (1996) NPP Grassland: Tumentsogt, Mongolia, 1982 - 1990. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Trabucco, A. & Zomer, R. J. (2009) Global Aridity Index (Global-Aridity) and Global Potential Evapo-Transpiration (Global-PET) Geospatial Database. CGIAR Consortium for Spatial Information via CGIAR-CSI GeoPortal (<http://www.csi.cgiar.org>).
- UN (2008) Trends in sustainable development. Agriculture, rural development, land, desertification and drought. United Nations, Department of Economic and Social Affairs, New York.
- UNEP (1997) World atlas of desertification. United Nations Environmental Programme (UNEP), London, UK.
- Verón, S. R., Oesterheld, M. & Paruelo, J. M. (2005) Production as a function of resource availability: Slopes and efficiencies are different. *Journal of Vegetation Science*, **16**, 351-354.
- Vicente-Serrano, S. M., Beguería, S., Lorenzo-Lacruz, J., Camarero, J. J., López-Moreno, J. I., Azorin-Molina, C., Revuelto, J., Morán-Tejeda, E. & Sanchez-Lorenzo, A. (2012) Performance of Drought Indices for Ecological, Agricultural, and Hydrological Applications. *Earth Interactions*, **16**, 1-27.
- Vitousek, P. M. (1982) Nutrient Cycling and Nutrient Use Efficiency. *American Naturalist*, **119**, 553-572.
- Vourlitis, G. L. (2012) Aboveground net primary production response of semi-arid shrublands to chronic experimental dry-season N input. *Ecosphere*, **3**, 1-9.
- Wesche, K. & Retzer, V. (2005) Is degradation a major problem in semi-desert environments of the Gobi region in southern Mongolia? *Erforschung biologischer Ressourcen der Mongolei* pp. 133-146. Martin-Luther-Universität, Halle-Wittenberg, Halle, Germany.
- 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.
- Xiao, X. M., Shu, J., Wang, Y. F., Ojima, D. S. & Bonham, C. D. (1996) Temporal variation in aboveground biomass of *Leymus chinense* steppe from species to community levels in the Xilin River basin, Inner Mongolia, China. *Vegetatio*, **123**, 1-12.
- Xiao, X. M., Wang, Y. F., Jiang, S., Ojima, D. S. & Bonham, C. D. (1995) Interannual Variation in the Climate and Aboveground Biomass of *Leymus-Chinense* Steppe and *Stipa-Grandis* Steppe in the Xilin River Basin, Inner-Mongolia, China. *Journal of Arid Environments*, **31**, 283-299.
- Yahdjian, L., Gherardi, L. & Sala, O. E. (2011) Nitrogen limitation in arid-subhumid ecosystems: A meta-analysis of fertilization studies. *Journal of Arid Environments*, **75**, 675-680.
- Yahdjian, L. & Sala, O. E. (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, **87**, 952-962.
- Yan, L., Luo, Y., Sherry, R. A., Bell, J. E., Zhou, X. & Xia, J. (2013) Rain use efficiency as affected by climate warming and biofuel harvest: results from a 12-year field experiment. *GCB Bioenergy*.

References of Introduction and Discussion

- Yang, Y., Fang, J., Ma, W. & Wang, W. (2008) Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters*, **35**.
- Zhao, M. & Running, S. W. (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, **329**, 940-943.
- Zhao, W. Y., Li, J. L. & Qi, J. G. (2007) Changes in vegetation diversity and structure in response to heavy grazing pressure in the northern Tianshan Mountains, China. *Journal of Arid Environments*, **68**, 465-479.
- Zimmermann, J., Higgins, S. I., Grimm, V., Hoffmann, J. & Linstädter, A. (2010) Grass mortality in semi-arid savanna: the role of fire, competition and self-shading. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 1-8.
- Zimmermann, J., Higgins, S. I., Grimm, V., Hoffmann, J., Münkemüller, T. & Linstädter, A. (2008) Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. *Journal of Ecology*, **96**, 1033-1044.

6. Summary / Zusammenfassung

Summary

Dryland ecosystems are highly vulnerable and degradation-prone regions, especially under the premises of global change. Since drylands are preponderantly used as rangelands for livestock production, reliable provision of natural resources and basic ecosystem services, such as forage, are indispensable for local livelihoods. Even though climate projections for drylands still exhibit considerable variation and uncertainty across scenarios and regions, there is a general trend that most dryland regions are facing unbeneficial changes. In particular, climatic aridity and variability are projected to increase even above the already high level of today. Simultaneously, population growth will further increase the demand for ecosystem services from drylands, with negative feedbacks on ecosystem functioning.

Given the high natural variability in drylands, as well as future projections, the assessment of drylands' current and future provision of ecosystem services is challenging, yet essential. The most common estimate for a major ecosystem service of dryland ecosystems (i.e. forage) is aboveground net primary production (ANPP).

This cumulative dissertation aimed at advancing our understanding of dryland ecosystems' functioning and ecosystem service provision, taking a global perspective. Particularly, data integration and standardization techniques were used to derive new insights from available data on drylands' primary production. With this innovative approach, it could be shown that dryland primary production is mainly driven by precipitation and grazing, not only locally but also on a global scale (Chapter 2.1). Another important outcome was that effects of grazing and rainfall are not merely additive, but could mask each other (Chapter 2.1) or interact in complex ways (Chapter 2.3). Similarly, drought severity may influence primary production either linearly or non-linearly, depending on vegetation characteristics (Chapter 2.3). These findings underline the complex dynamics of dryland ecosystems.

Besides these general findings, the established methodological toolbox as well as the assembled global database of dryland primary production are among the main merits of this dissertation. The combination of a large global database, the normalization of ANPP and precipitation data (Chapter 2.2), and the collection of additional site- or study-based information allowed the assessment of ecosystem functioning and stability on a global scale, which thus far could only be done on a theoretical or anecdotal basis.

Zusammenfassung

Trockengebiete gelten als hochgradig variabel und Degradations-anfällig, vor allem unter den Vorzeichen Globalen Wandels. Da Trockengebiete überwiegend als Weideland für Viehproduktion genutzt werden, ist die ausreichende Versorgung mit natürlichen Ressourcen und Ökosystemdienstleistungen, wie z.B. Futterpflanzen, unverzichtbar für die Existenzgrundlage der örtlichen Bevölkerung.

Obleich die verfügbaren Vorhersagen bezüglich des Klimawandels in Trockengebieten noch mit nennenswerter Variabilität und Unsicherheit behaftet sind, kann ein genereller Trend von nachteiligen Veränderungen festgemacht werden. Insbesondere werden in den meisten Regionen die Aridität sowie Variabilität des Klimas zunehmen, obgleich diese bereits als hoch angesehen werden müssen.

Zudem wird der prognostizierte und bereits heute beobachtbare Bevölkerungszuwachs negativ auf das natürliche System in Trockengebieten rückkoppeln. Die erhöhte Nachfrage und die damit einhergehende Intensivierung der Landnutzung werden sich negativ auf die Funktionalität der betroffenen Ökosysteme auswirken. Berücksichtigt man die hohe natürliche Variabilität in Trockengebieten, sowie die Prognosen im Rahmen des Globalen Wandels, dann ist die adäquate Abschätzung von Ökosystemdienstleistungen schwierig, jedoch zugleich unabdingbar. Das geläufigste und am besten dokumentierte Schätzmaß für die wichtigste Ökosystemdienstleistung in weidewirtschaftlich genutzten Trockengebieten (Menge an verfügbaren Futterpflanzen) ist oberirdische Nettoprimärproduktion (engl. »*aboveground net primary production*«, ANPP).

Ziel dieser kumulativen Dissertation war es, das funktionelle Verständnis von Trockengebieten auf globaler Skala zu verbessern und zu bereichern. Hierzu wurden Methoden eingesetzt, welche Daten- und Wissens-Integration ermöglichen, vor allem mit dem Zweck, verfügbare Daten zu neuem Wissen zu integrieren. Hierbei wurden insbesondere verfügbare Datensätze zu Primärproduktion in Trockengebieten und deren Einflussgrößen zusammengetragen.

Mit diesem innovativen Ansatz, konnte im Rahmen meiner Dissertation gezeigt werden, dass ANPP in Trockengebieten (lokal wie global) vor allem von Niederschlag und Beweidung gesteuert wird. Zudem konnte gezeigt werden, dass Effekte der beiden Einflussgrößen nicht additiv wirken, sondern sich gegenseitig maskieren können (s. Kapitel 2.1) oder komplex interagieren (s. Kapitel 2.3). Darüber hinaus konnte beobachtet werden, dass Dürre-Intensität in linearer als auch nicht-linearer Weise auf ANPP wirken kann, dies ist jeweils abhängig von wesentlichen Merkmalen der Vegetationsgesellschaft (s. Kapitel 2.3). Insgesamt unterstreichen meine Befunde die vorherrschende Meinung, dass Trockengebiete von hoher natürlicher Variabilität und komplexer Dynamik gekennzeichnet sind.

Neben den beschriebenen Ergebnissen, stellen auch die etablierte Toolbox sowie die zusammengetragene globale Datenbank von ANPP-Daten aus Trockengebieten einen wesentlichen Mehrwert der Arbeit dar. Die Kombination einer großen globalen Datenbank, die Normalisierung und

Summary / Zusammenfassung

Standardisierung von ANPP und Niederschlagsdaten (s. Kapitel 2.2), sowie das Zusammentragen von weiteren standortbezogenen Daten hat es ermöglicht, funktionelle Zusammenhänge in Trockengebieten und deren Stabilität besser zu verstehen, als dies auf rein theoretischer oder auf Basis von Fallbeispielen möglich gewesen wäre.

7. Appendix

Table 7.1: Excerpt from header data of the master database.

Table 7.2: Excerpt from ANPP-precipitation master database.

Appendix

Table 7.1: Excerpt from header data of the master database. Given are 14 of 73 variables in the server version, which describe each data set. Annual data is saved in an additional database, see Table 7.2.

site_id	site_name	climate	vegetation_type	map	cvmap	grow_seas	crop_year	elevation	dominant_under	dominant_over	sand	silt	clay
001.01	Badkhyz	arid	grassland	291.9	27.8	(nov-apr)	jun-mai	700	Poa bulbosa		0.68	0.23	0.09
002.01	Holm_non-degraded_075	arid	shrubland	201.3	39.4		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.02	Holm_non-degraded_112	arid	shrubland	202.4	39		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.03	Holm_non-degraded_168	arid	shrubland	204	39.1		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.04	Holm_non-degraded_252	arid	shrubland	209.8	37.1		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.05	Holm_non-degraded_380	arid	shrubland	216	35.6		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.06	Holm_degraded_075	arid	shrubland	208.6	44.1		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.07	Holm_degraded_112	arid	shrubland	211.4	43.1		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.08	Holm_degraded_168	arid	shrubland	213.3	42.9		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.09	Holm_degraded_252	arid	shrubland	208.4	44.4		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
002.10	Holm_degraded_380	arid	shrubland	201.5	46.7		oct-sept	5	Eremophila spp.	Acacia sclerosperma	0.78	0.15	0.07
003.01	Dzhanybek	semi-arid	grassland	283.3	26.1	(apr-aug)	sept-aug	20	Agropyron desertorum		0.28	0.28	0.44
006.01	Kursk	humid	grassland	582.7	16.8	(apr-oct)	nov-oct	250	Bromus riparius		0.32	0.31	0.37
008.01	Montecillo	semi-arid	grassland	572.1	18.9	year round	nov-oct	2241	Distichlis spicata		0.47	0.35	0.18
009.01	Nairobi	sub-humid	savanna			(may-dec)	jan-dec	1600	Themeda triandra		0.13	0.17	0.7
010.01	Rio Mayo	semi-arid	shrubland	162.5	34.3	(oct-jan)	oct-sept	500	Stipa speciosa	Senecio laginoides	0.92	0.04	0.04
011.01	Tumugi	sub-humid	grassland	411	24.6	(apr-sept)	oct-sept	190	Filifolium sibiricum		0.35	0.32	0.33
011.02	Tumugi	sub-humid	grassland	411	24.6	(apr-sept)	oct-sept	190	Stipa baicalensis		0.42	0.21	0.37
011.03	Tumugi	sub-humid	grassland	411	24.6	(apr-sept)	oct-sept	190	Leymus chinense		0.43	0.22	0.35
012.01	Tumentsogt	semi-arid	grassland	271.5	33.6	(jun-sept)	oct-sept	1100	Stipa grandis		0.6	0.2	0.2
013.01	Tuva	semi-arid	grassland	285.3	30.8	(may-aug)	sept-aug	800	Agropyron crystatum		0.74	0.17	0.09
014.01	Towoomba	semi-arid	grassland	629.4	21.1	(oct-mar)	jul-june	1130	Cymbopogon plurinodis		0.5	0.14	0.36
015.01	Xilingol. L. chinense Site	semi-arid	grassland	360.6	33.3	(apr-sept)	nov-oct	1200	Leymus chinense		0.6	0.19	0.21
015.02	Xilingol. S. grandis Site	semi-arid	grassland	360.6	33.3	(apr-sept)	nov-oct	1130	Stipa grandis		0.49	0.3	0.21
017.01	ACRS	semi-arid	grassland	335	26.8	(apr-july)	oct-sept	930	Stipa comata	Artemisia frigida	0.66	0.17	0.17

Appendix

Table 7.2: Excerpt from ANPP-precipitation master database (shortened Kursk, Russia, data set). Table / database gives annual-based information on year, annual precipitation (ppt_yr), precipitation of the hydrological year (ppt_hyr) and growing season (ppt_grs) ending in the respective calendar year, corresponding standardized precipitation index (spi), ANPP estimates for all applicable methods (here methods 1, 2a, 3, 4, 5), rain-use efficiency (rue, based on anpp2a) and tropical livestock units (tlu, measure of stocking density).

site_id	site	treatment	year	ppt_yr	ppt_hyr	ppt_grs	ppt_uni	ppt_prv	spi_yr	spi_hyr	spi_grs	spi_uni	anpp1	anpp2a	anpp3	anpp4	anpp5	rue	tlu
006.01	krs	lte	1947	547.4		344.9	547.4		-0.312		-0.484	-0.312							
006.01	krs	lte	1948	568.0	658.8	418.2	658.8	547.4	-0.095	0.813	0.320	0.813							
006.01	krs	lte	1949	503.2	456.9	339.5	456.9	658.8	-0.796	-1.461	-0.548	-1.461							
006.01	krs	lte	1950	583.4	631.3	455.1	631.3	456.9	0.063	0.534	0.691	0.534							
006.01	krs	lte	1951	649.2	658.7	519.8	658.7	631.3	0.711	0.812	1.295	0.812							
006.01	krs	lte	1952	734.6	659.1	507.3	659.1	658.7	1.491	0.816	1.182	0.816							
006.01	krs	lte	1953	403.6	497.8	325.9	497.8	659.1	-2.005	-0.952	-0.711	-0.952							
006.01	krs	lte	1954	419.5	380.8	300.0	380.8	497.8	-1.799	-2.497	-1.037	-2.497	403	581	383	383		1.52	0
006.01	krs	lte	1955	769.2	748.4	575.0	748.4	380.8	1.79	1.674	1.773	1.674	390	562	383	383		0.75	0
006.01	krs	lte	1956	431.8	473.9	351.9	473.9	748.4	-1.644	-1.246	-0.402	-1.246	244	460	149	187	273	0.97	0
006.01	krs	lte	1957	566.8	565.7	419.2	565.7	473.9	-0.108	-0.167	0.331	-0.167	337	532	271	155	401	0.94	0
006.01	krs	lte	1958	575.2	555.7	411.0	555.7	565.7	-0.021	-0.278	0.246	-0.278	313	602	262	262	573	1.08	0
006.01	krs	lte	1959	703.9	640.8	469.5	640.8	555.7	1.218	0.631	0.830	0.631	292	674	268	268	622	1.05	0
006.01	krs	lte	1960	435.9	479.4	236.6	479.4	640.8	-1.593	-1.178	-1.922	-1.178	306	622	275	279	561	1.30	0
006.01	krs	lte	1961	609.8	634.1	456.0	634.1	479.4	0.328	0.563	0.699	0.563	510	735	480	480		1.16	0
006.01	krs	lte	1962	503.6	463.0	264.0	463.0	634.1	-0.792	-1.383	-1.522	-1.383	311	620	244	214	214	1.34	0
006.01	krs	lte	1963	725.7	690.5	512.0	690.5	463.0	1.412	1.126	1.225	1.126	202	469	165	165	216	0.68	0
006.01	krs	lte	1964	650.9	645.9	399.8	645.9	690.5	0.727	0.683	0.128	0.683	270	389	262	262		0.60	0
006.01	krs	lte	1965	538.8	543.4	310.2	543.4	645.9	-0.404	-0.417	-0.906	-0.417	240	346	220	220		0.64	0
006.01	krs	lte	1966	443.0	483.0	184.0	483.0	543.4	-1.505	-1.133	-2.793	-1.133	403	581	395	395		1.20	0
006.01	krs	lte	1967	565.4	595.8	407.8	595.8	483.0	-0.122	0.161	0.212	0.161	351	506	343	343		0.85	0
006.01	krs	lte	1968	523.4	464.6	242.7	464.6	595.8	-0.571	-1.363	-1.831	-1.363	227	327	220	220		0.70	0
006.01	krs	lte	1969	597.4	652.9	455.2	652.9	464.6	0.204	0.754	0.692	0.754	363	523	358	358		0.80	0
006.01	krs	lte	1970	651.1	622.1	336.1	622.1	652.9	0.729	0.438	-0.588	0.438	249	359	242	242		0.58	0
006.01	krs	lte	1971	487.9	511.0	334.6	511.0	622.1	-0.971	-0.794	-0.606	-0.794	369	532	364	364		1.04	0
006.01	krs	lte	1972	569.8	538.1	432.0	538.1	511.0	-0.077	-0.478	0.461	-0.478	341	461	316	241	283	0.86	0

8. Danksagung

Zuallererst möchte ich mich bei Dr. Anja Linstädter bedanken, die mir unter exzellenter Betreuung und Anleitung die Möglichkeit gegeben hat, in ihrer Arbeitsgruppe meine Doktorarbeit anzufertigen. Darüber hinaus vielen Dank für die zahlreichen Anregungen und interessanten Diskussionen rund um das Thema Wissenschaft, Forschung und auch Privates, sowie die Möglichkeit, eigene Ideen in dieser Doktorarbeit umzusetzen und letztendlich für das Korrekturlesen dieser Arbeit.

Außerdem danke ich meinem Doktorvater Prof. Dr. Michael Bonkowski für die Übernahme der Erstkorrektur und Begutachtung, sowie Prof. Dr. Hartmut Arndt für die Übernahme der Zweitkorrektur und Begutachtung dieser Arbeit.

Prof. Dr. Frank Schäbitz danke ich für die Übernahme des Vorsitzes in meiner mündlichen Prüfung.

Bei Prof. Dr. Frank Ewert möchte ich mich für die Unterstützung vor allem in der Anfangsphase meiner Dissertation bedanken sowie für die bis heute andauernde, gute Zusammenarbeit.

Ferner gilt mein Dank der ganzen AG Linstädter und AG Ewert. Vor allem Roelof, Kristijan, Andreas T., Gunther, Andreas E., Heidi, Anja S., Jürgen und Hubert sowie den ehemaligen Kollegen Jenny, Gisi und Nico möchte ich für zahlreiche Anregungen und Hilfestellungen in den letzten Jahren danken. In besonderer Erinnerung sind mir die schönen – wenn auch anstrengenden – Forschungsaufenthalte in Südafrika. Vielen Dank für das angenehme Arbeitsklima, die Unterstützung und Hilfsbereitschaft.

Ein besonderer Dank gilt auch der Stiftung der deutschen Wirtschaft, welche meine Promotion durch ihre Förderung finanziell abgesichert hat und die Promotionszeit durch zahlreiche Kurse und Mittel für Auslandsreisen bereichert hat. Insbesondere möchte ich auch der Kölner Regionalgruppe für die tolle Zeit in ihrer Mitte danken.

In besonderer Weise möchte ich auch allen Kollegen danken, die mir ihre, teilweise unpublizierten, Daten zur Verfügung gestellt haben und so erst meine Dissertation möglich gemacht haben. Auch wenn der begrenzte Platz hier nicht ausreicht um allen zu danken, so möchte ich doch insbesondere Karsten, Sabine, Hennie, Alec, Marcelo und Alan danken, die mir nicht nur ihre Daten zur Verfügung gestellt haben, sondern mich auch in allen anderen Belangen meiner Studien mit Rat und Tat unterstützt haben.

Danksagung

Nicht zuletzt möchte ich mich bei meinen Eltern bedanken. Bei meiner Mutter Annerose dafür, dass sie mich immer vorbehaltlos unterstützt hat und mir immer das Gefühl gegeben hat, dass da jemand ist – ich vermisse dich. Auch bei meinem Vater Martin möchte ich mich bedanken, dass er mich immer unterstützt, gefördert und gefordert hat und mir nicht zuletzt die Möglichkeit gegeben hat, mein Studium sorgenfrei und konzentriert durchführen zu können.

Abschließend möchte ich mich in ganz besonderer Weise bei meiner Frau Ann-Kathrin bedanken, die mir die beste Partnerin ist, die man sich vorstellen kann. Mein Dank gilt weiterhin meinen Freunden, die mir auch in stressigen Zeiten immer wieder eine willkommene Ablenkung geboten haben, sowie explizit Andi und Philipp für das Korrekturlesen dieser Arbeit.

9. Declaration of Contribution as Author and Co-Author

I am first author in all studies underlying this dissertation (Chapter 2). I contributed majorly in the following processes in the studies listed in Chapter 2:

- Study design
- Data acquisition
- Data handling and processing
- Statistical analyses
- Interpretation of data and results
- Manuscript writing
- Submission process and correspondence with editors and/or reviewers

Furthermore, I am co-author in all studies included in Chapter 3. Here, I contributed in the following processes:

- Data acquisition and handling
- Data interpretation
- Manuscript writing

10. Statutory Declaration and Statement (Erklärung)

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen –, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie – abgesehen von unten angegebenen Teilpublikationen – noch nicht veröffentlicht worden ist, sowie, dass ich eine solche Veröffentlichung vor Abschluss des Prüfungsverfahrens nicht vornehmen werde.

Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Dr. Anja Linstädter sowie Prof. Dr. Michael Bonkowski betreut worden.

Teilpublikationen:

Ruppert, J. C., Holm, A. M., Miehe, S., Muldavin, E., Snyman, H. A., Wesche, K. & Linstädter, A. (2012) Meta-analysis of rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands. *Journal of Vegetation Science*, **23**, 1035-1050.

Ruppert, J. C. & Linstädter, A. (2014) Convergence between ANPP estimation methods in grasslands — A practical solution to the comparability dilemma. *Ecological Indicators*, **36**, 524-531.

Sowie die als Appendix anzusehenden Publikationen in Kapitel 3:

Brüser, K., Feilhauer, H., Linstädter, A., Schellberg, J., Oomen, R. J., Ruppert, J. C. & Ewert, F. (2014) Discrimination and characterization of management systems in semi-arid rangelands of South Africa using RapidEye time series. *International Journal of Remote Sensing*, **35**, 1653-1673.

Moreno García, C. A., Schellberg, J., Ewert, F., Brüser, K., Canales-Prati, P., Linstädter, A., Oomen, R. J., Ruppert, J. C. & Perelman, S. B. (2014) Response of community-aggregated plant functional traits along grazing gradients: insights from African semi-arid grasslands. *Rangeland Ecology and Management*, in press.

Köln, den 31.03.2014

(Jan Christian Ruppert)

11. Curriculum Vitae

Personal Data

Name: Jan Christian Ruppert
Date of birth: 03.03.1984
Place of birth: Bad Mergentheim
Nationality: German
Marital status: Married
Address: Mayener Str. 8, D-50935 Köln
Email: jan.ruppert@uni-koeln.de, janruppert@gmail.com

Education & Training

04/2010 – 06/2014 PhD Thesis in Biology, University of Cologne
06/2010 – 06/2014 Fellow of the Theodor-Brinkmann-Graduate School, University of Bonn
10/2004 – 12/2009 First state-exam in Biology and German Linguistic & Literature, University of Cologne
08/1994 – 06/2003 Gymnasium zum Altenforst, Troisdorf (Abitur)

Professional Experience (scientific only)

Since 11/2013 Researcher in the BMBF-project “Limpopo Living Landscapes” (SPACES-LLL), Range Ecology and Management Group – AG Linstädter, University of Cologne
01/2013 – 06/2014 Associated Researcher in Crop Science and Resource Conservation Group – AG Ewert, University of Bonn
06/2010 – 12/2012 Research Assistant in the DFG-Research-Unit 1501 “Resilience, Collapse and Reorganisation in Social-Ecological Systems of African Savannas”, Crop Science and Resource Conservation Group – AG Ewert, University of Bonn
04/2010 – 06/2010 Research-Assistant at Ecological Systems-Analysis Group – AG Frank, Helmholtz Center for Environmental Research Leipzig
Since 04/2010 PhD Researcher at the Range Ecology and Management Group – AG Linstädter, Botanical Institute, University of Cologne

Honors and Grants

01/2011 – 12/2013 Full, merit-based PhD-scholarship assigned by Stiftung der Deutschen Wirtschaft and funded by BMBF
Since 06/2010 Several travel-grants assigned by the Theodor-Brinkmann-Graduate School, University of Bonn