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

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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 criticised 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 dataset of 923 years. We used meta-analysis to disentangle the effects of different ecological layers (climate, soil and land use) on ANPP and RUE. Linear piecewise 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 for understanding 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 a precipitation of 200 mm yr^{-1}. Unimodal response was more pronounced for maximum values ($ANPP_{max}$ and 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 as 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 a reconciliation of contradictory findings for ANPP and RUE response along precipitation gradients of varying length.

KEYWORDS

$ANPP_{max}$, Ecosystem functions, Degradation indicator, Grazing, Land use, Linear piecewise quantile regression, Rangeland indicators, RUE_{max}, Water-use efficiency,

ABBREVATIONS

RUE – Rain use efficiency

ANPP – Aboveground net primary production

LPQR – Linear piecewise quantile regression

1. Introduction

In our changing and complex world, there is an urgent need for suitable ecological indicators which 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, the development and application of indicators are not easy tasks, especially in ecosystems where high natural variability has to be parted 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 which 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 years, threatening livelihoods of about 2.5 billion people (MEA 2005, UNDP 2008 a, b).

In drylands two ecological parameters commonly used for assessing ecosystem state are *aboveground 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 is 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 a 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 years - 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 points of criticism 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 interannual variability of precipitation (Milchunas & Lauenroth 1993, Paruelo et al. 1999, Yang et al. 2008, Miehe 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 (Varnamkhasti 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 & Ngairore 2000, O'Connor et al. 2001, McCulley 2005, Muldavin et al. 2008, Bai 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, Miehe 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 1999, O'Connor et al. 2001, Hein 2006, Hein & de Ridder 2006, Miehe 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, to 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 upon that severe overutilization 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 overcompensation of defoliation losses was found in a number of studies from savannas (McNaughton 1979, McNaughton 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 overcompensation 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 on 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 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), though, 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 likewise 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 along 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? And 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, and a quantile regression analysis of ANPP and RUE along precipitation gradients.

Table 1. **Overview on the study-database used for the meta-analysis, and/or for performing the linear piecewise 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/GTZ Project Ferlo (Miehe et al. 2010)	A. Linstädter née Schulte (Schulte 2002)	Wesche & Retzer 2005
Site and study information							
Region	Andes, Argentina	West-Australia	New Mexico, USA	South Africa	Ferlo, Senegal	Namibia	Mongolia
Latitude[1]	32° S to 28° S	24°31' S	34°20' N	28°50' S	15°59' N	17°06' S to 17°11' S	43°36' N
Longitude[1]	67° W to 69° W	113°42' E	106°43' W	26°15' E	15°19' W	13°13' E to 13°24' E	103°46' E
Altitude [m] asl[1]	400 to 600	5	1600	1350	40	740 to 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							
Rain regime	winter rain	winter rain	mixed	summer rain	summer rain	summer rain	summer rain
MAP [mm / a][2]	244 (±54) & 260 (±102)	228 (±90)	259 (±67)	537 (±39)	285 (±93.5)	270 (±93)	130 (±46)
Soil							
Dominant soil class	Silty substrates	Loamy substrates	Loamy substrates	Loamy substrates	Sandy substrates	Sandy substrates	Loamy subtrates
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)

Notes:

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

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

[3] Treatment types: grazing - ca (cattle), ls (largestock), mix (mixed livestock), ss (smallstock); exclosure - l (long), s (short)

[4] TLU 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 landuse 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.

[5] The 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).

2. Materials and methods

2.1. 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* (*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* does not only comprise 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 mm and 537 mm). Since these regions are known for their high interannual variability in precipitation (Davidowitz 2002, Ward 2009) we selected mid- to long-term monitoring studies with at least 5 years 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 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 which is assessed in our meta-analysis. Studies were selected by a structured literature search in well-known literature databases, as well as from personal communication. To keep ANPP proxies comparable, we only included studies which did not use movable cages (see McNaughton et al. 1996) and which measured ANPP either as incremental growth over the whole growing period or – where grazing was excluded or neglectable during the vegetation period – as peak standing biomass.

We searched the literature by using the keywords 'biomass', 'standing crop', 'primary production', 'ANPP', 'rain use efficiency', 'precipitation use efficiency', 'dryland', '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 years 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 latter 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 mm and 540 mm and annual precipitation values between 69 mm and 725 mm (see Table 1).

Most statistical analyses where performed using the 50 treatments as reference sample (n=50), deviations are indicated (Table 2). For nearly all studies we inquired raw data and additional information from the corresponding authors. Only the data from Guevara et al. (1997) was directly taken from the publication.

2.2 Statistical analyses

ANPP data were outlier-adjusted by eliminating values which 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 piecewise 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 **linear piecewise quantile regression** is a non-linear regression-method which 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; see Appendix S2.2). 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 datasets (Cade & Noon 2003, Cottingham et al. 2005). Using high percentiles (95^{th} and higher) instead of the median (i.e., the 50^{th} 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. Analyzing 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, analyzing 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 to the idea of boundary regression (Blackburn et al. 1992, Lessin et al. 2001). Hence, quantile regressions focusing on the upper boundary ($\geq 95^{th}$ quantile) of a dataset 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 99^{th} 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 (Version 4.71, Koenker 2011b) in the statistical software *R*.

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 where 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 analyzed by fail-safe calculations (Rosenthal's R and Orwin's method; see Supporting Information Table S4). Meta-analyses were computed with *MetaWin®* 2.1 (Rosenberg et al. 2000). Basic formulas for meta-analytical calculations are provided in Appendix S2.1.

3. Results

3.1 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 (see Figs. 1 and 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 2011a, b). Regressions along the median were calculated for illustrational reasons; for regression models see Table S5.

Figures 1a-d give the development of $ANPP_{max}$ [kg DM ha^{-1} yr^{-1}] along a gradient of annual precipitation [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 (Figs. 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 land use m = -3.78 >395 mm). In contrast to regressions along 99th quantiles, 50th quantile regressions were only slightly unimodal.

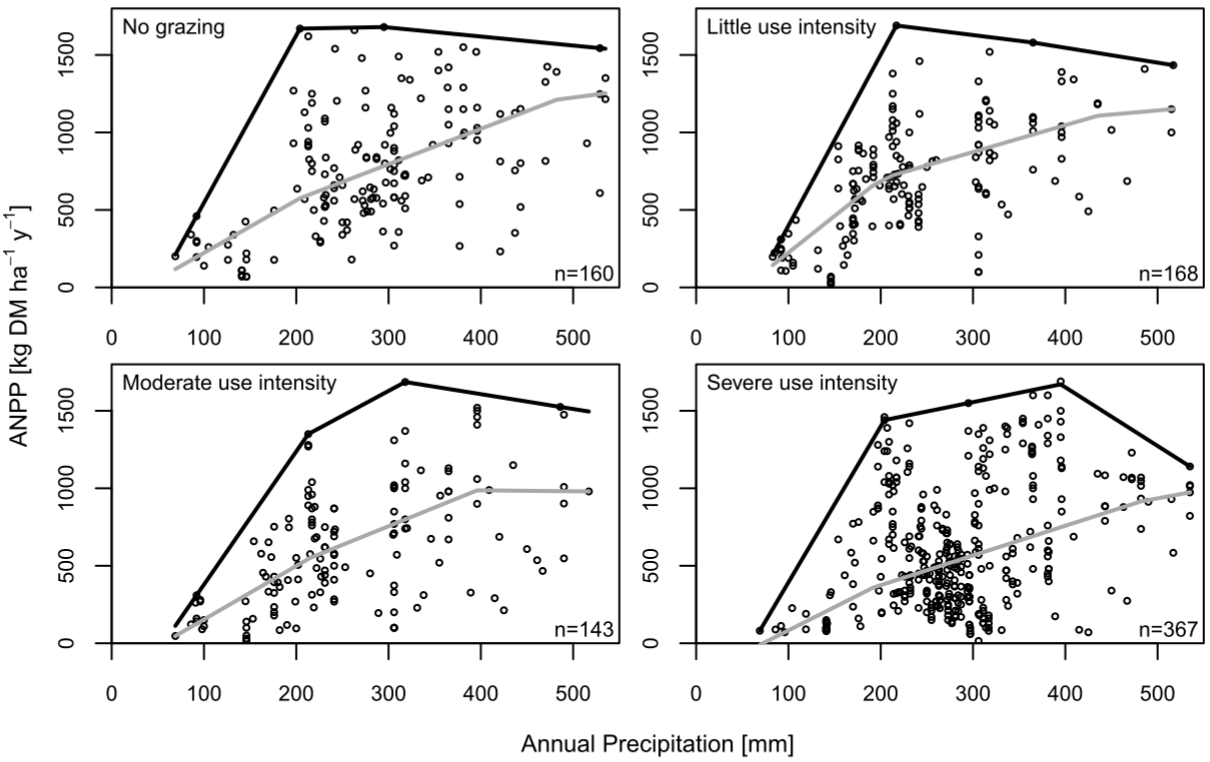

Figure 1. Maximum and median ANPP as function of precipitation under different land use intensities. Black lines represent the 99th quantile of ANPP ($ANPP_{max}$ or production potential) under varying land use intensities. Grey lines represent the median of ANPP. Regression models at the 99th quantile 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 height of peak $ANPP_{max}$, the amount of precipitation needed to reach peak $ANPP_{max}$ as well as the steepness of post-peak decline.

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 disproportionally 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 annual precipitation of 200 to 215 mm and decreased with more precipitation. Independent from land use intensity, RUE_{max} peaked around an annual precipitation of ca. 200 mm. 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 land use intensities (6.4 kg DM ha^{-1} yr^{-1} mm^{-1}). 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).

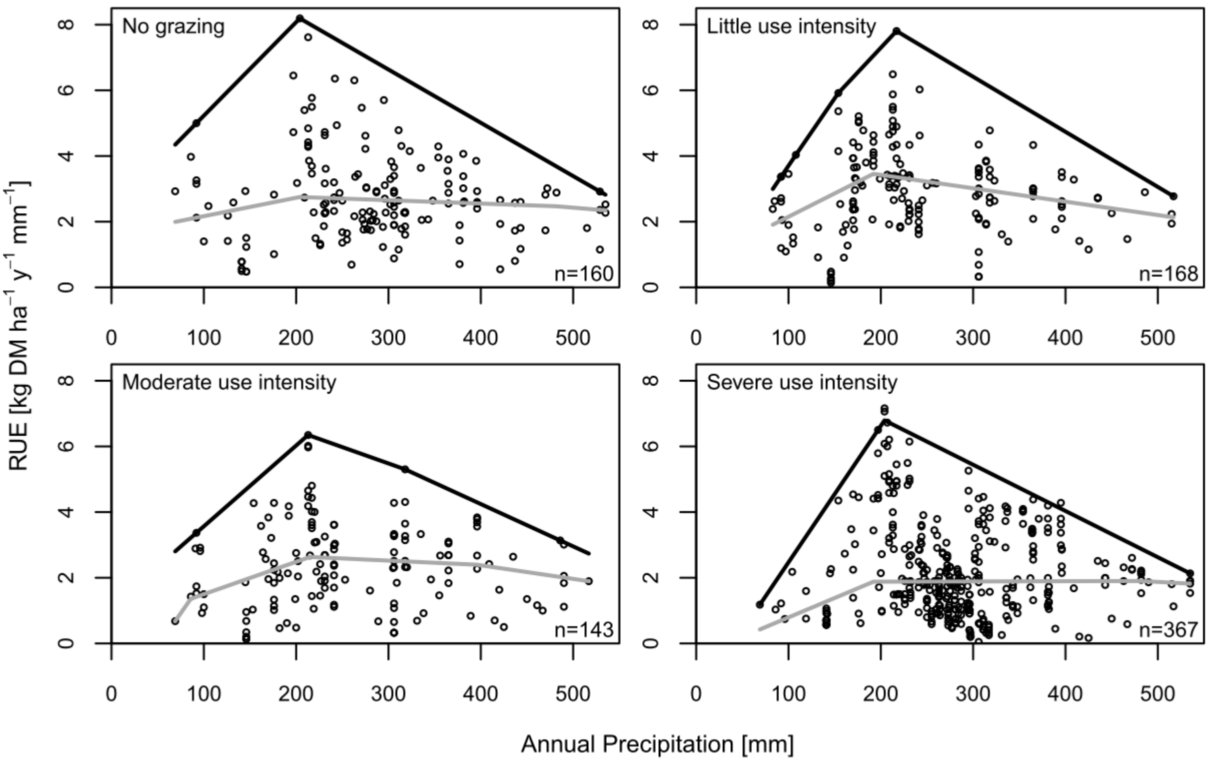

Figure 2. Maximum and median RUE as function of precipitation under different land use intensities. Black lines represent the 99th quantile of RUE (RUE_{max} or potential productivity) under varying land use intensities. Grey lines represent the median of RUE. Regression models at the 99th quantile are 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 height of peak RUE_{max} as well as the steepness of post-peak decline in RUE_{max}.

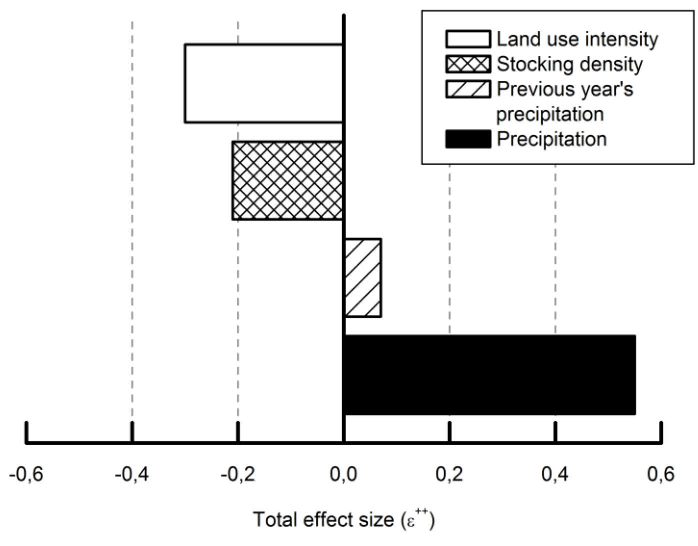

Figure 3. Barplot on the effect sizes on (average) ANPP. Bars represent the magnitude of the effects. As indicated by bar length, land use effects can preponderantly hide the effects of precipitation.

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

Several environmental variables significantly affected average ANPP (Table 2-1). *Precipitation* and *previous year's precipitation* had a positive, *stocking density* and *land use intensity* a negative effect. Overall *precipitation* (ε^{++} 0.55) showed the strongest effect on ANPP, followed by *land use intensity* (ε^{++} -0.30), *stocking density* (ε^{++} -0.21) and *previous year's precipitation* (ε^{++} 0.07). The effect size for *previous year's precipitation* (0.99) was homogenous. Values for *precipitation* (p=0.50), *stocking density* (0.19) and *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 analyzed (see section 2.2). 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 *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).

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

Table 2-1: Overall Effects on ANPP

	df	p	effect size (ε^{++})	bootstrap CI (95%)		
Precipitation	49	0,50	0,55	0,4710	-	0,6351
Previous year's precipitation	48	0,99[2]	0,07	0,0145	-	0,1231
Stocking density[1]	4	0,19	-0,21	-0,4129	-	-0,1252
Land use intensity[1]	4	0,34	-0,30	-0,4985	-	-0,1690

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

a. Biome

Heterogeneity	df	p†
between groups (Q_M)	2	≤0,001
within groups (Q_E)	47	≥0,99
total (Q_T)	49	0,37

	df	p†	effect size (ε^{+})	bootstrap CI (95%)		
Grassland	7	0,84	1,04	0,8884	-	1,2521
Shrubland	12	1,00	0,71	0,6588	-	0,7711
Savanna	28	0,99	0,43	0,3763	-	0,4864

b. Soil class

Heterogeneity	df	p†
between groups (Q_M)	2	≤0,001
within groups (Q_E)	43	≥0,99
total (Q_T)	45	0,29

	df	p†	effect size (ε^{+})	bootstrap CI (95%)		
Loamy substrate	18	0,95	0,88	0,7577	-	0,9971
Sandy substrate	19	0,98	0,45 n.s.	0,3849	-	0,5092
Silty substrate	6	0,83	0,37 n.s.	0,2744	-	0,4618

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.

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^z). Tab 2-1 reports overall results of effect-variables on ANPP. Tab 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

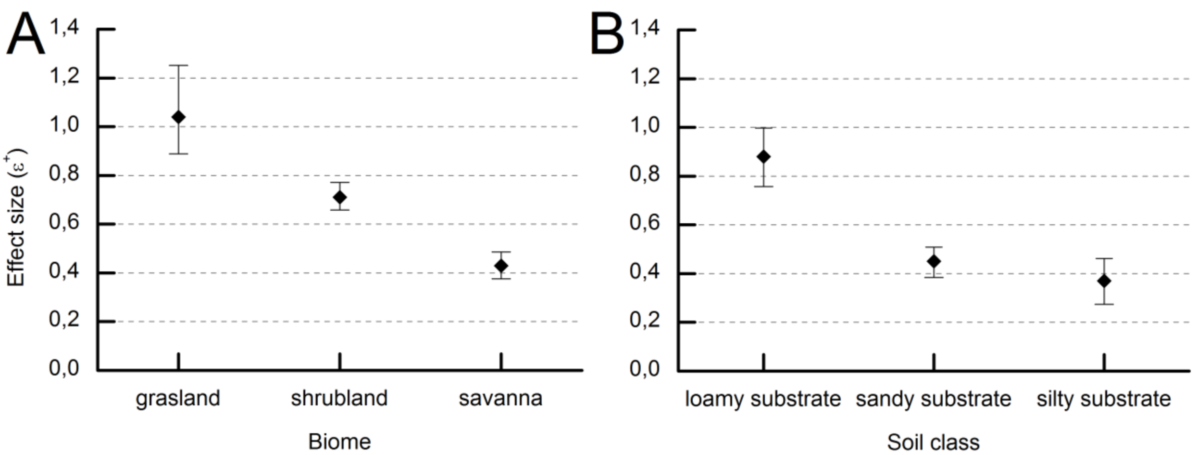

Figure 4. Results from categorical modelled meta-analyses for the effect of precipitation on ANPP. A) Effect sizes for biomes and their corresponding bootstrapped confidence interval. As indicated by the CIs all effects are significant. B) Effect sizes for soil type and their corresponding bootstrapped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

Fail-safe calculations for meta-analysis confirmed the validity of the meta-analytical results: Rosenthal's and Orwin's method predicted that 14.5 up to 3822.7 more studies would have had to be included into 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) (see 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; see Table S3).

4. Discussion

4.1. 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 mm 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 respectively) 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 regressions support the unimodal shape which 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, Muldavin et al. 2008, Bai et al. 2008). However, our results (together with theoretical considerations) enable us to reconcile these contradictory findings on ANPP response (see *section 4.2*).

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 (Breman & 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 analyzed vegetation data from arid to semi-arid sites only, where vegetation is adapted to low MAP values (130 mm to 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 (Ridolfi et al. 2008, Visser et al. 2004). At the same time, this restriction to relatively arid sites could explains 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 which 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 approximately 200 mm yr^{-1}. RUE_{max} values in our study (6.4 to 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 to 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 Fig. 1 and 2) on non-used sites, where it is supposedly independent from 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).

4.2. Reconciling contrary findings on the shape of response curves

Our results together with theoretical considerations contribute to solve contrary findings in 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 50^{th} and 99^{th} quantiles. Shorter gradients could thus be represented by linear relationships. Some case studies failed to detect 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 analyzing use-efficiencies (UE) along long resource gradients (e.g. Sala et al. 1988, Lauenroth & Sala 1992, Huxman et al. 2005) 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 S3). Therefore studies on very short or very long precipitation gradients are likely to find linear relationships, even though the relationship is really 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 (Ridolfi et al. 2008, Visser et al. 2004). 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.

4.3. 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 scatterplot 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 analyzed 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 & Bridgham 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 analyzing 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.

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

We analyzed 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. Noteworthy, the effect of annual precipitation on ANPP differs 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 contraire 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 (ε^{+} 1.04), followed by shrublands (ε^{+} 0.71), and savannas (ε^{+} 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 & Djitèye (1982), a proportion of 3-20 % should be added to 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 (ε+ 0.88), followed by sandy (ε+ 0.45) and silty substrates (ε+ 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, little run-off and evaporation (Alizai 1970, Snyman 1999, English et al. 2005, Li et al. 2007a, 2007b). The crossover point of the inverse texture effect has originally been estimated to be at a MAP of 300 to 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 to 540 mm), our results imply a crossover point at the more arid side of this range. More generally, our findings support previous studies which show 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 (ε^+ 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 (ε^+ -0.21) and land use intensity (ε^+ -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 & O'Connor 2000). In analogy to the discussion on effects of previous years' 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, respectively RUE. 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.

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

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APPENDICES (Supporting Information for Online only)

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 *Statistical methods and formula (meta-analysis and LPQR)*

Appendix S3 *Why efficiencies should not be analyzed by linear regressions*

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