Biogeochemistry **46:** 247–293, 1999.

Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation

DAVID U. HOOPER[1] & LORETTA JOHNSON[2]
[1]*Department of Biology, Western Washington University, Bellingham, WA 98225-9160, U.S.A. (e-mail: hooper@biol.wwu.edu);* [2] *Division of Biology, Room 232 Ackert Hall, Kansas State University, Manhattan, KS 66506-4901, U.S.A.*

Received 10 December 1998

Key words: arid, fertilization, nitrogen limitation, net primary productivity, semi-arid, water availability

Abstract. We investigated the relationship between plant nitrogen limitation and water availability in dryland ecosystems. We tested the hypothesis that at lower levels of annual precipitation, aboveground net primary productivity (ANPP) is limited primarily by water whereas at higher levels of precipitation, it is limited primarily by nitrogen. Using a literature survey of fertilization experiments in arid, semi-arid, and subhumid ecosystems, we investigated the response of ANPP to nitrogen addition as a function of variation in precipitation across geographic gradients, as well as across year-to-year variation in precipitation within sites. We used four different indices to assess the degree of N limitation: (1) Absolute Increase of plant production in response to fertilization (the slope of ANPP vs. amount of added N at different levels of annual precipitation); (2) Relative Response (the percent increase in fertilized over control ANPP at different levels of N addition); (3) Fertilizer Use Efficiency (FUE, the absolute gain in productivity per amount of fertilizer N), and (4) Maximum Response (the greatest absolute increase in ANPP at saturating levels of N addition). Relative Response to fertilization did not significantly increase with increasing precipitation either across the geographic gradient or across year-to-year variation within sites. Nor did the Maximum Response to fertilization increase with increasing precipitation across the geographic gradient. On the other hand, there was a significant increase in the Absolute Increase and FUE indices with both geographical and temporal variation in precipitation. Together, these results indicate that there is not necessarily a shift of primary limitation from water to N across the geographic water availability gradient. Instead, our results support the hypothesis of co-limitation. The apparently contradictory results from the four indices of N limitation can best be explained by an integration of plant ecophysiological, community, and ecosystem mechanisms whereby plants are co-limited by multiple resources, species shifts occur in response to changing resource levels, and nitrogen and water availability are tightly linked through biogeochemical feedbacks.

Abbreviations: AAP – actual annual precipitation; AET – actual evapotranspiration; ANPP – aboveground net primary productivity; CPER – Central Plains Experimental Range; FUE – Fertilizer Use Efficiency; IP – ineffective precipitation; LTER – Long-Term Ecological

Research; MAP – mean annual precipitation; MAT – mean annual temperature; N – Nitrogen; PET – potential evapotranspiration; RGR – relative growth rate; WUE – water use efficiency

Introduction

It is well known that plant production responds strongly to water availability in arid and semi-arid ecosystems (Le Houerou et al. 1988; Risser 1988; Lauenroth & Sala 1992; Epstein et al. 1996). However, substantial evidence also suggests limitation or co-limitation by nitrogen (N). Because N and water availability may co-vary across precipitation gradients, it is difficult to separate the effects on plant production of changes in N availability from changes in water availability (Burke et al. 1997; Schimel et al. 1997). To understand how ecosystems may respond to anthropogenic changes, such as increased N deposition, we need to understand how these factors influence ecosystem processes both independently and interactively (Burke et al. 1991; Vitousek et al. 1992; Vitousek et al. 1994).

One of our objectives was to explore questions related to limitation of production by N and water in dryland systems. How do the relative magnitudes of water and N limitation vary along a geographic gradient of water availability? One index of N use efficiency, plant production/available N in soil (Burke et al. 1997), tends to increase, and some estimates of water use efficiency decrease (Risser 1988) with increasing precipitation across geographic gradients. This indicates that N may become relatively more limiting than water as precipitation increases. If this were the case, we would expect a greater relative response of production to N addition (the percent increase above control plots) in more mesic than in drier ecosystems, and perhaps no response to N below some threshold amount of water availability (Hypothesis A in Figure 1). Modeling data from Schimel et al. (1997), however, suggest positive correlations between productivity, N mineralization, and evapotranspiration. They argue that biogeochemical feedbacks (mediated by plant litter quality and decomposition) bring water availability, N availability, and plant production into rough equilibrium across spatial gradients of water availability. Thus, an alternative hypothesis is that the relative response to fertilization should be similar across the precipitation gradient (Hypothesis B in Figure 1). For example, Detling (1979) observed that water is the principal limiting factor in semi-arid blue grama grasslands, but that alleviation of water stress quickly leads to nutrient limitation, suggesting that at least some dry systems are close to co-limitation. In contrast to both of the preceding hypotheses, Seagle and McNaughton (1993) saw evidence for primary limitation by water and only secondary limitation by N in both

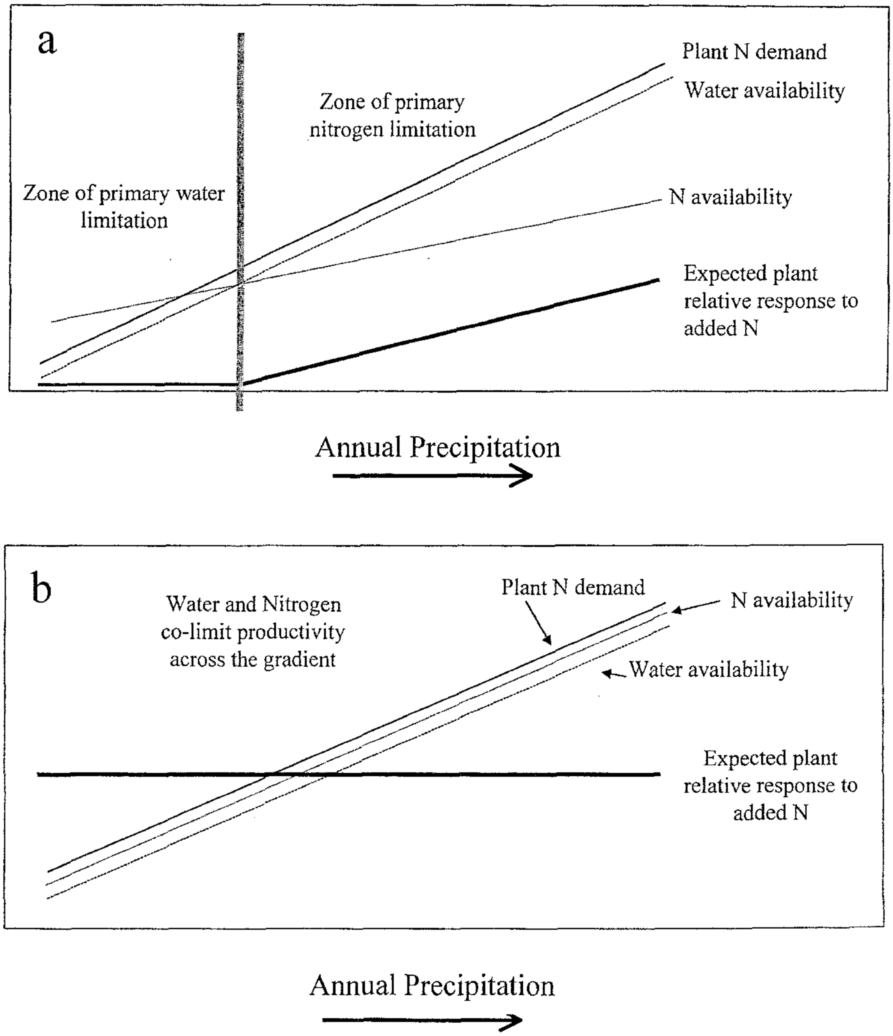

Figure 1. Alternative hypotheses for the relationship between N limitation and variation in water availability: (a) Water is primarily limiting at the dry end of the precipitation gradient and nitrogen is primarily limiting at the wet end; (b) Water and nitrogen co-limit throughout the range of precipitation. The Y-axis is the relative magnitudes of the different parameters identified by the line labels. Relationships among these parameters are simplified for comparison of hypotheses; we recognize that actual shapes of functions might differ.

relatively wet and relatively dry regions of the Serengeti. In both wet and dry sites in that modeling study, changes in N supply influenced productivity only when precipitation was higher than average (>130% of mean annual precipitation).

Interactions between N and water availability may differ for temporal versus geographic gradients of precipitation. Many researchers have seen greater responses to N addition in wet years than in dry years within a given location (Rogler & Lorenz 1957; Kilcher 1958; Smika et al. 1965; Owensby et al. 1970; Lorenz & Rogler 1972). Within a given location, however, plant production response to additional resources may be constrained by limitations of the extant plant community. Chapin et al. (1986) suggest that slow growing species in nutrient limited sites have relatively small responses to increases in resources above what they are accustomed to experiencing. Lauenroth and Sala (1992) and Burke et al. (1997) observed that, in nonfertilized sites, production responded less within a site to a given increase in annual precipitation resulting from yearly variation in rainfall than did production at different sites resulting from geographic variation in precipitation. If growth constraints exist, will there be a greater N response across a geographic precipitation gradient than across temporal variation in precipitation?

We wanted to test several hypotheses by using a literature review of fertilization experiments in arid, semi-arid, and subhumid regions:

(1) As ecosystem water availability increases, plant growth becomes more limited by N than by water. Across broad precipitation gradients, we would expect a greater relative response of production to N addition in more mesic locations than in drier locations, even if N availability also increases. A corollary to this would be that in experiments manipulating both water and N availability, NPP response to water addition would be greater than response to N addition at the drier end of the moisture gradient and vice versa at the wetter end.

(2) Water limits production more in dry years, N more in wet years. Therefore, within a given site, we would expect a greater relative response to fertilization in wetter years than in drier years (Figure 1).

(3) Production response to N addition will increase more as precipitation increases across geographical precipitation gradients than it will as precipitation increases within sites. (i.e., response 1 is greater than response 2, above). This is analogous to the response to precipitation for unfertilized conditions seen by others (Lauenroth & Sala 1992; Burke et al. 1997).

The second objective with our literature data set was to assess the utility of different indices of N limitation when comparing a wide variety of sites that differ substantially in a number of ecological characteristics (e.g., water availability, soil type, management regime). We used four indices that reflect different aspects of N limitation across precipitation gradients. First, systems that are more limited by N would be expected to gain more absolute biomass in response to fertilization than systems that are limited or co-limited by other resources. We refer to this absolute gain in biomass in response to fertilization as the *Absolute Increase* index of N limitation. Second, more N limited systems might have greater relative gains in biomass (i.e., the percent increase above control level) than less N limited systems. For example, a system that starts at 50 $g \cdot m^{-2} \cdot yr^{-1}$ of production may not add as much absolute biomass as a system that starts at 400, even if it is more N limited; however, the proportional increase in biomass may be greater. We refer to this relative change in production in response to fertilization as the *Relative Response* index of N limitation. Third, more N limited systems could have greater gains in plant production than less N-limited systems for the same amount of added N. We refer to the biomass gained per unit N added as the *Fertilizer Use Efficiency* (FUE) index of N limitation (to avoid confusion with other definitions of N Use Efficiency). This index is probably most useful at intermediate levels of fertilization: if N addition levels are low, FUE may be influenced by differences in microbial immobilization; if N addition levels are high, FUE will be influenced by saturation of the plant response. Fourth, Chapin et al. (1986) recommended using high levels of fertilization to saturate microbial immobilization to best assess nutrient limitation in plant communities. Therefore, more N limited systems might have a greater absolute response of production than less N limited systems at levels of N addition that are sufficiently high to saturate both microbial and plant demand. We refer to this maximum production response at high levels of added N as the *Maximum Response* index of N limitation. We used these four indices to investigate whether N limitation varies with water availability in dryland ecosystems, and to try to better understand some of the mechanisms underlying such variation.

Methods/data collection

Overview

We did a literature search for experiments on plant production response to N fertilization in arid, semi-arid, and subhumid ecosystems (mean annual precipitation = 200–1100 mm). Our indicator of N limitation was response to fertilization of aboveground plant growth. As independent moisture variables, we used mean annual precipitation (MAP) across the geographic gradient and actual annual precipitation (AAP) for temporal gradients within sites. The advantages of this approach are that we were able to gather large amounts of data from many different ecosystem types. This allowed us to look for broad scale patterns of N limitation using real data. A weakness is that patterns may be obscured by other variables such as differences in climate (e.g., mean annual temperature), topoedaphic features (slope, aspect, soil type and soil depth – which affect water availability to plants), management regime, and plant species composition. Wherever possible, we recorded information about such ecosystem characteristics in an attempt to account for these differences.

While annual precipitation is an imperfect index of plant water availability, it is reported in most experiments and a number of previous studies have found a strong correlation between MAP and plant production in dryland ecosystems (Noy-Meir 1973; Le Houerou & Hoste 1977; Le Houerou et al. 1988; Sala et al. 1988; Epstein et al. 1996). A truer index of plant water availability would incorporate actual evapotranspiration (AET), topography (runon and runoff, slope and aspect), and soil characteristics (e.g., depth and water holding capacity). Similarly, differences in the intensity and distribution of precipitation also influence plant water availability. However, these data are not available for most studies. We therefore used MAP and AAP with the assumption that across sites and across years, they would provide reasonable indices of water availability. Where the data allowed, we investigated effects of differences in site mean annual temperature (MAT) on responses to N because of potentially important temperature effects on plant water availability. For example, 313 mm of precipitation in Manyberries, Alberta (MAT = 4.6 °C) can mean substantially more plant available water than 315 mm of precipitation in Maipu, Chile (MAT = 14.5 °C). Because most of the studies surveyed provided no information on site temperature regime, we obtained MAT normals for 1966–1996 from the National Climate Data Center web site for locations in the United States (http://www.ncdc.noaa.gov) and for 1960–1990 from the Canadian Meteorological Centre (http://www.cmc.ec.gc.ca/climate/) for sites in Canada. Where exact location matches were not available, and for sites outside North America, we used information from the nearest available site or city.

We restricted the scope of our literature search by several criteria. We did not use studies of row crops and we used only fertilization data for N addition alone. A number of studies (e.g., at Cedar Creek LTER in Minnesota; Tilman 1987) also added phosphorus or other nutrients to all plots in a non-factorial manner, so we did not include these in our analyses. Where other nutrients were added in factorial, we used only control and +N data unless there was clearly no effect of the other treatments. We also restricted our analyses to studies in which N additions occurred in the year of production measurements. A number of other studies investigated residual effects of N addition – that is, the plant production response across several years to a single addition of N. In these cases, we only used data for the first year of N addition. We also did separate analyses for a subset of the experiments which included factorial N and water additions.

Data analysis

N limitation across geographic gradients of precipitation

We used data for aboveground plant biomass and aboveground net primary production (ANPP) of the entire ecosystem, not of individual species (except for two studies from desert ecosystems (Ettershank et al. 1978; Stephens & Whitford 1993)). While knowing the response of belowground production would certainly be helpful, these data are exceptionally sparse. Our indices of N limitation were calculated as follows:

Absolute Increase = slope of regression of ANPP vs fertilizer N; regressions were across many sites or experiments, but within levels of precipitation (see below);

Relative Response = (fertilized ANPP – control ANPP)∗100/control ANPP;

Fertilizer Use Efficiency as FUE = (fertilized ANPP – control ANPP)/annual fertilizer N addition, with FUE in g of production/g added N;

Maximum Response to fertilization = (fertilized ANPP – control ANPP) at the highest levels of fertilization encountered in the studies surveyed (20–100 g $N{\cdot}m^{-2}{\cdot}yr^{-1}$).

For analyses involving the geographic precipitation gradient where studies had multiple years of data, we averaged the yearly data to get one overall estimate of response to N addition. We found 40 studies covering 42 different locations ranging in MAP from 211 mm to 1031 mm (control $n = 98$ data points, fertilized $n = 157$ data points). Levels of fertilization ranged from less than 1 to greater than 100 g $N{\cdot}m^{-2}{\cdot}yr^{-1}$.

We analyzed the geographic data set in two different ways. In the first set of analyses (for the Absolute Increase index), we categorized sites into 5 levels of MAP, regressed plant production against level of N fertilization within each of these precipitation levels, then compared the slopes and intercepts of the regressions for sites at different levels of MAP. The MAP levels were 200–300 mm, >300–450 mm, >450–600 mm, and >750–1100 mm. We refer to these as MAP levels 300, 450, 600, and 900, respectively; we had no data in the 600–750 mm level. We restricted the analysis to levels of fertilization < 25 g $N{\cdot}m^{-2}{\cdot}yr^{-1}$ to avoid complications of saturation of production at high levels of fertilization.

To assess the effects of other site variables, we divided plant composition into 3 categories depending on whether natives, exotics or both dominated communities in the experiments. We categorized sites as to whether they were grazed during the experiment, were grazed up until the year before the experiment but not during, were grazed within five years previous to the experiment but not during, or were not grazed within a least five years of the experiment. These categories were chosen in hopes of reflecting potential grazing effects on litter accumulation, plant species composition, and N cycling feedbacks. Where information was available, we divided soil types into six textural classes for analysis: clay, clay loam, loam, silt loam, sandy loam, and sand.

For the Absolute Increase index, we performed the following Analysis of Covariance (ANCOVA) in addition to the simple regressions:

$$ANPP = constant + PPTCAT + Fertilizer\ N + PPTCAT{*}Fertilizer\ N + Graze + Exotics + Soil,$$

where PPTCAT is the precipitation category (300, 450, 600, 900); Fertilizer N is the actual N addition rate (continuous variable), and Graze, Exotics and Soil are all categorical variables as just described.

In the second kind of analysis for the geographic data (for the other N limitation indices), we categorized the data based on levels of fertilization, and then regressed plant production response to N against MAP within levels of fertilization. We did this with the rationale that if the degree of N limitation increased as water availability increased, we should see a positive slope of our different indices of N limitation with increasing precipitation. We used 7 different levels of fertilization: control, ≤ 3, >3–5 , >5–10, >10–20, >20–50, and >50 g $N{\cdot}m^{-2}{\cdot}yr^{-1}$. These will be referred to as FertN = 0, 3, 5, 10, 20, 50, and 100, respectively, throughout the rest of this paper. Sites in the lowest and highest categories of fertilization (FertN = 3, 50, and 100) were limited to only the dry end of the gradient. Because of this, and because grouping these sites with the other fertilization categories would lead to 10-fold variation in N-addition rates in those groups, we focus on the FertN = 0, 5, 10, and 20 categories for most of the geographical analyses, except for using the high fertilization sites in the Maximum Response analysis.

We used ANCOVA to estimate effects of other site factors on our indices of N limitation. After testing for MAP∗FertN interactions, the ANCOVA design was

$$N\ limitation\ index = constant + MAP + FertN + Graze + Exotics + Soil,$$

with MAP as a covariate, FertN as a categorical variable, and grazing, dominance by exotics, and soil type as categorical variables. Because we did not have factorial combinations for most of the variables, we did not include interaction terms.

As discussed above, mean annual temperature and its effects on water availability could also influence N limitation. For our data set, there was a significant positive correlation between site precipitation and site temperature (solid line, Figure 2(a)), so we could not include MAT directly in the ANCOVA analyses. The positive correlation oversimplifies the relationship, however. From hot, dry sites at the arid end of the gradient, temperature decreases significantly as precipitation increases up to about 600 mm MAP

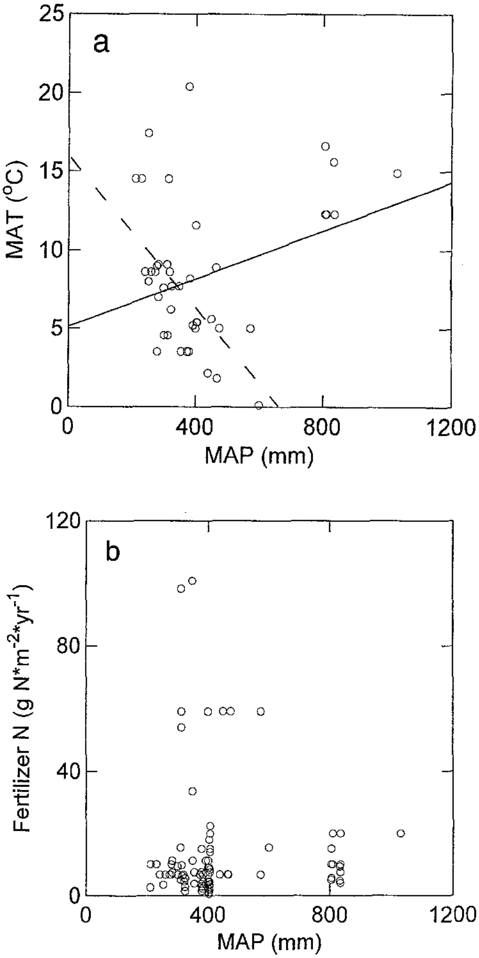

Figure 2. Distribution of sites from the literature survey in terms of (a) MAP and MAT, and (b) MAP and rate of fertilization (g N·m^{-2}·yr^{-1}). For (a), the dashed line is the least squared regression for all points with MAP $\leq$ 600 mm, the solid line is the regression for all points. Both correlations are significant at $P < 0.01$.

(hatched line, Figure 2(a)). Mean annual temperature increases again at the most mesic sites. To avoid the difficulty of correlation between MAP and MAT, we selected a restricted range of MAP (310–410 mm) where the N limitation indices frequently had large variance. We then did an ANCOVA similar to the one above, only using MAT instead of MAP as the covariate.

N limitation across temporal gradients in precipitation

For analyses involving year-to-year variation in precipitation, only studies with at least 4 consecutive years of data were used. We found 9 studies

(n = 129 individual data points) spanning regions of MAP from 311 mm (Lauenroth et al. 1978) to 835 mm (Konza Prairie LTER). Time spans of the studies ranged from 4 to 10 years; fertilization levels ranged from 0.6 to 22.5 g $N \cdot m^{-2} \cdot yr^{-1}$. In these analyses, we used temporal variation in actual annual precipitation (AAP, in mm) as the independent variable against which we regressed either actual ANPP, Relative Response to fertilization, or FUE. Different studies and different levels of N addition within each study were analyzed separately. We did this with the rationale that if the degree of N limitation increases as water availability increases, we should see a positive slope of our indices of N limitation with increasing AAP. We could not analyze the data using the Absolute Increase or Maximum Response indices because of lack of data.

Results

The data set

The data set includes experiments from a precipitation range from 200 to 1100 mm and a fertilization range from <1 to >100 g $N \cdot m^{-2} \cdot yr^{-1}$. However, most of the data are for levels of fertilization at or below 20 g $N \cdot m^{-2} \cdot yr^{-1}$ and within a precipitation range from 200 to 500 mm/yr (Figure 2b). Several studies had exceptionally high rates of N application ($>$ 50 g $N \cdot m^{-2} \cdot yr^{-1}$). A cluster of points around 835 mm/yr is predominantly from studies at the Konza Prairie Long-Term Ecological Research (LTER) site (see Appendix). Many of the following analyses are strongly influenced by the responses at Konza. While there are several studies from this site, we found limited information from other locations at the upper end of the precipitation gradient.

As a first evaluation of the utility of our data set, we regressed plant production in control (nonfertilized) sites against MAP. Several other studies have performed such analyses and our results compare favorably with those (Table 1). There is a large increase in ANPP with increasing precipitation, with a slope and intercept intermediate between values observed by previous studies. We did not see a saturating function as did Risser (1988), who used AET instead of MAP. This comparison gives us confidence in the utility of our data set, despite its limitations. We then compared regressions of ANPP against geographic variation in MAP for each of the fertilization levels (Table 2, Figure 3). (Note that this is not the same as our Absolute Increase index; see below). There is a significant increase in ANPP with precipitation at FertN = 10 and 20, but not FertN = 5. Only the slope for FertN = 10 is significantly greater than the slope for the nonfertilized controls. (This is

Table 1. Response of aboveground net primary productivity (ANPP) to geographic precipitation gradients. ANPP in $g \cdot m^{-2} \cdot yr^{-1}$, mean annual precipitation (MAP) in mm. MAT = Mean annual temperature. Significance < 0.001 in all cases. Equations are presented both in $y = a + bx$ form, as well as ANPP = WUE∗(MAP – IP), where WUE = average community water use efficiency (g/m^2 production per mm increase in precipitation) and IP = "ineffective precipitation", i.e., MAP at which production equals zero (Noy-Meir 1973).

Reference	Geographic range	Regression	r^2	N
This study FertN = 0	World-wide but North America-centric	ANPP = –60 + 0.49∗MAP ANPP = 0.49∗(MAP – 121)	0.66	96
(Epstein et al. 1996)	U.S. Great Plains, MAT 11.5–12 °C	ANPP = –157 + 0.76∗MAP ANPP = 0.76∗(MAP – 207)	0.87	98
(Le Houerou et al. 1988)	World-wide, but U.S.-centric	ANPP = –18.4 + 0.47∗MAP ANPP = 0.47∗(MAP – 39.4)	0.31	77
(Risser 1988)[1]	Western U.S.	ANPP = 496 – $666e^{-0.0025(ET)}$	NA	19
(Sala et al. 1988)	U.S. Great Plains	ANPP = –34 + 0.6∗MAP ANPP = 0.6∗(MAP – 56)	0.90	98
(Le Houerou & Hoste 1977)[2]	Mediterranean Basin – Europe and Africa	FU = –32.7 + 0.73∗MAP FU = 0.73∗(MAP – 45.8)	0.69	45
(Le Houerou & Hoste 1977)[2]	Sudan-Sahel	FU = 20.9 + 0.41∗MAP FU = 0.41∗(MAP + 50.9)	0.67	43
(Noy-Meir 1973)	World-wide, reported from other sources	WUE = 0.5 to 2 g/m^2 per mm IP = 25–75 mm		

[1] For linear regression of live biomass vs. MAP, $r^2 = 0.54$, but no equation is given. ET = evapotranspiration.

[2] Data presented and regressions done using units of production in Scandinavian Feed Units (FU) per ha per year. (1 FU = 1 kg barley = 1650 kcal). However, consistent conversion factors to plant production were not provided. The slope (WUE) is not comparable to the other references, but IP is. Tree and shrub productivity were not included in the Sahel data, but are probably substantial in terms of ANPP (Le Houerou & Hoste 1977).

Table 2. Response of aboveground net primary productivity (ANPP) to geographic precipitation gradients at different levels of fertilization (g N·m^{-2}·yr^{-1}). Equations are presented both in $y = a + bx$ form, and as parameters for the equation ANPP = WUE∗(MAP – IP). Abbreviations and units as in Table 1. Standard error of the slope (WUE) in parentheses.

Fert. Rate	$y = a + bx$	WUE (±SE)	P_{slope}	IP	$P_{int.}$	r^2	n
0	ANPP = –59.9 + 0.49∗MAP	0.49 (±0.04)	<0.001	121	0.003	0.66	96
5	ANPP = 139.1 + 0.19∗MAP	0.19 (±0.11)	0.101	–725	0.008	0.08	37
10	ANPP = –61.1 + 0.70∗MAP	0.70 (±0.08)	<0.001	86.9	0.16	0.58	57
20	ANPP = 121 + 0.40∗MAP	0.40 (±0.10)	<0.001	–305.2	0.04	0.30	38

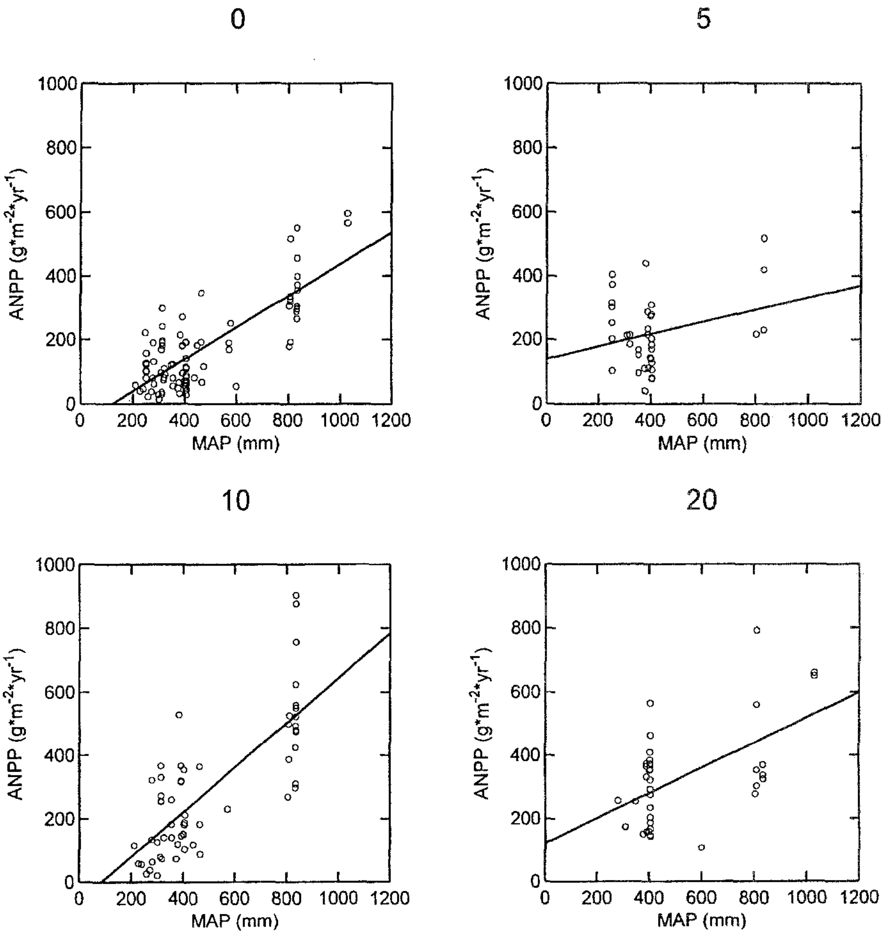

Figure 3. Response of ANPP to precipitation for different levels of FertN (see Methods).

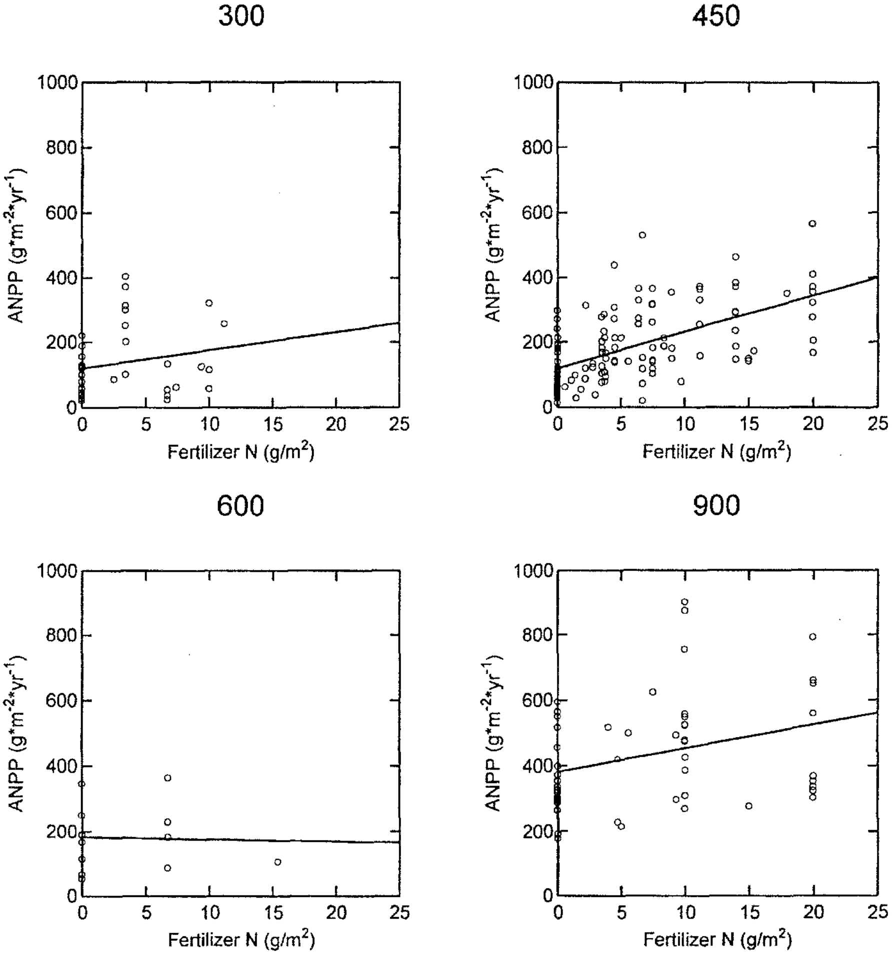

Figure 4. Absolute Increase index of N limitation: the response of ANPP to fertilization at different levels of MAP 300 is MAP $\leq$ 300 mm; 450 is MAP > 300–450 mm; 600 is MAP > 450–600 mm; 900 is MAP > 750–1100 mm. There were no data points between 600 and 750 mm MAP. Lines are least squared regressions; see Table 3 for regression parameters.

in agreement with the significant increase in fertilized ANPP with temporal variation in precipitation described later – see *ANPP response to AAP and fertilization*). Based on this difference in slope and intercept, fertilization with 5–10 g N·m^{-2}·yr^{-1} leads to a 50–60% increase in production all across the geographic gradient in MAP (see results for Relative Response index, below).

While substantial ancillary data exist for plant composition, grazing, soil type, and fire within certain ranges of precipitation, we rarely obtained them across the whole gradient for comparable levels of fertilization, or in factorial combinations. For example, experiments with exotics were common in some

Table 3. Absolute Increase index of N limitation. Response of aboveground net primary productivity (ANPP) to fertilization at different levels of MAP (mm). Equations are ANPP = $a + b*\text{N}$, where N is the yearly N fertilization rate. Standard errors of slope and intercept are in parentheses

MAP level	slope (±SE)	P_{slope}	Intercept	$P_{\text{Int.}}$	r^2	n
300	55 (±47)	0.24	1196 (±225)	<0.001	0.04	36
450	115 (±13)	<0.001	1177 (±109)	<0.001	0.36	135
600	–6.8 (±61)	0.91	1826 (±348)	<0.001	0.0	13
900	71 (±29)	0.016	3817 (±281)	<0.001	0.10	57

drier systems, especially with *Agropyron cristatum* (crested wheatgrass) and *Bromus* spp. (brome), whereas most of the experiments we encountered at higher precipitation were on native grassland (e.g., at Konza Prairie LTER). Similarly, most of the higher precipitation sites were grazed previously but were not grazed concurrently with the fertilization experiment. Finally, fire treatments have been intensively studied at Konza, but we found few fire × fertilization studies elsewhere, especially at lower levels of precipitation, presumably because of insufficient fuel loads to carry fire in drier ecosystems.

Indices of N limitation across geographic gradients in precipitation

While production increases with increases in precipitation across the geographic gradient for most levels of N addition, the question we sought to answer was if the *response to N addition* differs across the precipitation gradient. That is, does production increase more in response to added N as precipitation increases, indicating greater N limitation in wetter locations? We evaluate this using our four indices of N limitation.

Absolute Increase Index of N limitation

When comparing all studies within precipitation classes, there was a significant increase in production with rate of fertilization for MAP level 450 and 900 (Table 3, Figure 4). While ANPP is generally higher at all rates of fertilization in MAP level 900 than level 450 (significantly greater intercept in level 900), the change in production per amount of N added is similar for the two levels of precipitation (i.e., the slopes are not significantly different). Slopes are greater for MAP levels 450 and 900 than for level 300 (significant interaction between MAP level and fertilization rate). At MAP level 300, fertilization actually does lead to increased production in most studies, but variation in production rates across sites makes the regression nonsignificant.

Table 4. Influence of precipitation (MAP) on Relative Response (RR) for FertN = 5, 10, and 20, and influence of temperature (MAT) on Relative Response for sites with MAP between 310 and 410 mm. Mean annual precipitation (MAP) in mm. Equations are presented as % change in ANPP = $a + b*$MAP (or MAT), where % change in ANPP is calculated as (fertilized-control)∗100/control

Fert. Rate	slope (±SE)	P_{slope}	intercept (±SE)	$P_{int.}$	r^2	n
RR vs MAP						
5	−0.18 (±0.06)	0.004	157 (±26)	<0.001	0.21	37
10	−0.06 (±0.04)	0.18	101 (±23)	<0.001	0.03	58
20	−0.23 (±0.07)	0.003	268 (±43)	<0.001	0.21	40
RR vs MAT for 310<MAP<410						
5	0.57 (±3.2)	0.86	75 (±23)	0.003	0.00	26
10	−7.0 (±3.2)	0.04	162 (±31)	<0.001	0.17	25
20	−7.6 (±7.8)	0.34	249 (±55)	<0.001	0.04	25

There were too few data points in the 450–600 mm level to adequately assess a general relationship. ANCOVA indicates significant effects of exotics (exotics > natives, $P < 0.001$), grazing (currently grazed > others, $P < 0.004$), and soil type (clay > sandy, $P = 0.031$) on ANPP.

Relative Response Index of N limitation

Contrary to what we initially expected, the Relative Response to N addition did not increase with increasing precipitation. In fact, in multiple regression with annual N fertilization rates as an additional predictor, MAP had a significantly negative effect on relative response to fertilization:

$$\%\ increase\ in\ ANPP = 120 - 0.202*MAP + 7.84*FertN;$$

$$P_{MAP} < 0.001,\ P_{FertN} < 0.001,\ R^2 = 0.26.$$

This regression used only data from FertN = 5, 10, and 20 because of limited data and the potential for saturated responses at higher levels of fertilization. Similarly, when we analyzed the Relative Response index within categories of fertilization, the data do not support the hypothesis that N limitation is greater at higher precipitation (Table 4, Figure 5). For all three levels of N fertilization analyzed, the relative ANPP response to fertilization was either negatively or not significantly related to MAP. In fact, some of the largest relative responses of ANPP to fertilization occurred at MAP between 310 and 410 mm/yr. The Konza data strongly influence the negative slope: most of the relative responses for experiments at Konza Prairie LTER (835 mm)

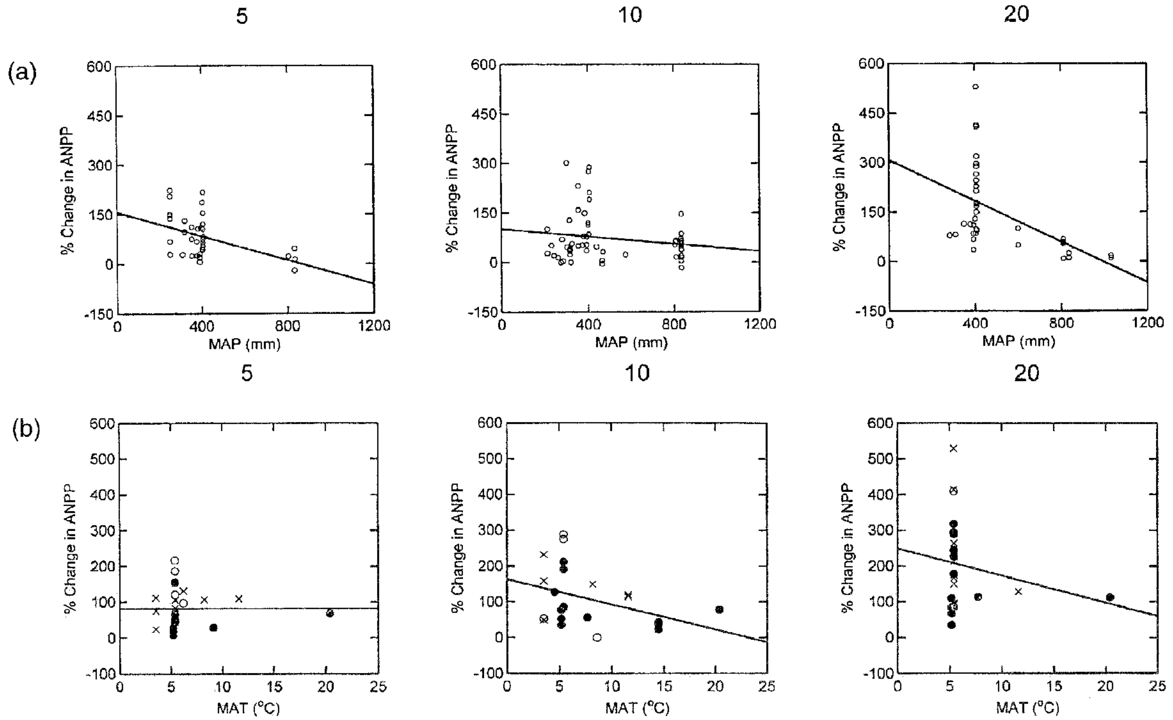

Figure 5. Relative Response of ANPP to N addition for FertN = 5, 10 and 20: (a) Relative Response as a function of MAP (see Table 4 for regression parameters); (b) Relative Response as a function of MAT for sites with MAP between 310 and 410 mm. Symbols: X = exotics, circles = natives. For natives, fill color designates grazing regime: open = ungrazed, shaded = previously grazed, filled = currently grazed.

Table 5. Response of Fertilizer Use Efficiency (FUE) to precipitation at different levels of fertilization (g $N{\cdot}m^{-2}{\cdot}yr^{-1}$). Equations are presented as FUE = a + b*MAP, where FUE is change in ANPP /added N. Mean annual precipitation (MAP) is in mm. The regression for FertN = 10 is also presented for experiments with at least 3 years of data.

Fert. Rate	slope (±SE)	P_{slope}	intercept (±SE)	$P_{int.}$	r^2	n
5	–0.050 (±0.019)	0.012	42.7 (±8.2)	<0.001	0.17	37
10	0.018 (±0.006)	0.004	3.1 (±3.3)	0.35	0.14	57
10 (>3 yrs.)	0.031 (±0.009)	0.002	–0.1 (±4.2)	0.99	0.23	38
20	–0.013 (±0.004)	0.002	16.4 (±2.2)	<0.001	0.24	38

were much more constrained than were those at lower levels of precipitation (Figure 5), though burned sites responded more strongly than unburned sites.

We tested site MAT as a potential explanation for the large amount of variability in Relative Response among the experiments at low precipitation by regressing the data from the precipitation range of 310–410 mm against MAT (Figure 5(b)). There was no significant effect of MAT for FertN = 5 or 20. For FertN = 10, the Relative Response decreased significantly as average site temperature increased, suggesting greater N limitation in the cooler, and therefore relatively moister, sites. However, the Relative Response varied as much among experiments in the northern Great Plains (MAT ≈ 4–6 °C) as it did across the entire 5-fold range in MAT, in part due to differences in grazing regime. Sites with no grazing within the previous 5 years had highest Relative Response (ANCOVA $R^2 = 0.42$, $P_{GRAZE} = 0.017$, $n = 77$).

Fertilizer Use Efficiency Index of N limitation

Support for greater N limitation at locations with higher precipitation was equivocal in terms of Fertilizer Use Efficiency (FUE = g change in ANPP/g of fertilizer N added). In a multiple regression using all data from FertN = 5, 10, and 20, there was no significant effect of precipitation and a significant negative effect of fertilization level:

$$FUE = 22.2 - 0.0015{*}MAP - 0.745{*}\,FertN;$$

$$R^2 = 0.09,\ P_{MAP} = 0.80,\ P_{FertN} = 0.001.$$

An interaction between fertilizer category and effect of precipitation was responsible for the lack of significance of MAP in that analysis: FUE decreased with increasing MAP for FertN = 5 and 20; FUE increased with increasing MAP for FertN = 10 (Table 5, Figure 6). Plant composition, grazing regime, and soil type all had significant effects in ANCOVA but did not change the underlying interaction between MAP and FUE at different levels

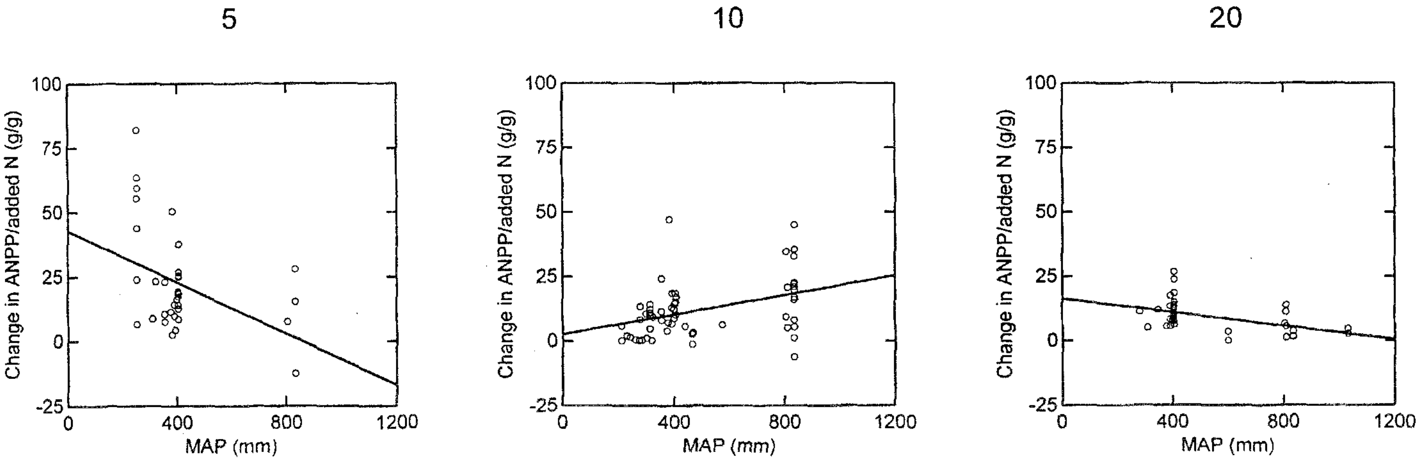

Figure 6. Response of Fertilizer Use Efficiency (change in production per amount of added N) to precipitation for FertN = 5, 10, and 20. See Table 5 for regression parameters.

of N fertilization (ANCOVA $R^2 = 0.48$, $P_{\mathrm{EXOTICS}} = 0.003$, $P_{\mathrm{SOIL}} = 0.005$, $P_{\mathrm{GRAZE}} = 0.024$, $P_{\mathrm{MAP*FERTN}} < 0.001$, $n = 132$). Exotics had greater responses than natives, clay soils had greater responses than sandy or loam soils, and ungrazed and currently grazed sites both had greater responses than one year previously grazed sites. The large spread among points at the lowest level of precipitation (253 mm) for FertN = 5 all came from the same site in eastern Oregon and reflect differences in response among different species of pasture grasses grown under identical conditions (Cooper 1959).

A few cases with negative values of FUE (lower production in fertilized than unfertilized plots) occurred in single year experiments in years of exceptionally low precipitation. If we constrained the analysis to only those experiments with at least three years of data to lower the possibility that the average response was unduly influenced by particularly wet or dry years, there was a stronger significant positive slope for FertN = 10 (the only category with sufficient data for this restriction; Table 5). This is in agreement with the strong production response of FUE to temporal variation in precipitation, described later.

Maximum Response Index of N limitation

The Maximum Response index of N limitation (increase in biomass at high levels of fertilization, > 20 $\mathrm{g\,N{\cdot}m^{-2}{\cdot}yr^{-1}}$) tended to decrease as precipitation increased in a simple regression (Figure 7):

$$\textit{Change in ANPP } (g{\cdot}m^{-2}{\cdot}yr^{-1}) = 249 - 0.17*MAP;\ P_{\mathrm{MAP}} = 0.056,\ r^2 = 0.14$$

In ANCOVA, however, the precipitation effect was attributable to differences in species composition (ANCOVA $R^2 = 0.55$, $P_{\mathrm{MAP}} = 0.66$, $P_{\mathrm{EXOTICS}} = 0.07$, $n = 27$). Most of the highest responses at low precipitation were from sites with exotics (*Agropyron cristatum* and *Bromus* spp.; Power 1980a; Power 1985) (Figure 7). Site MAT did not explain the variation in Maximum Response among experiments at low precipitation (MAP = 310–410 mm; ANCOVA $R^2 = 0.49$, $P_{\mathrm{MAT}} = 0.88$, $n = 15$). At the mesic end of the geographic precipitation gradient, fire regime had a large effect on Maximum Response: burned tallgrass prairie accounted for the higher responses and unburned accounted for the lower responses for two studies at Konza Prairie (Seastedt et al. 1991; Benning & Seastedt 1995).

Factorial experiments with N and water additions

Another way to assess if N limitation changes relative to water limitation across the geographic precipitation gradient is to look at the response of productivity to N and water addition under different rainfall regimes. If water is predominantly limiting at the dry end and N at the wet end, then we would expect that the Relative Response to water addition would be greatest at low

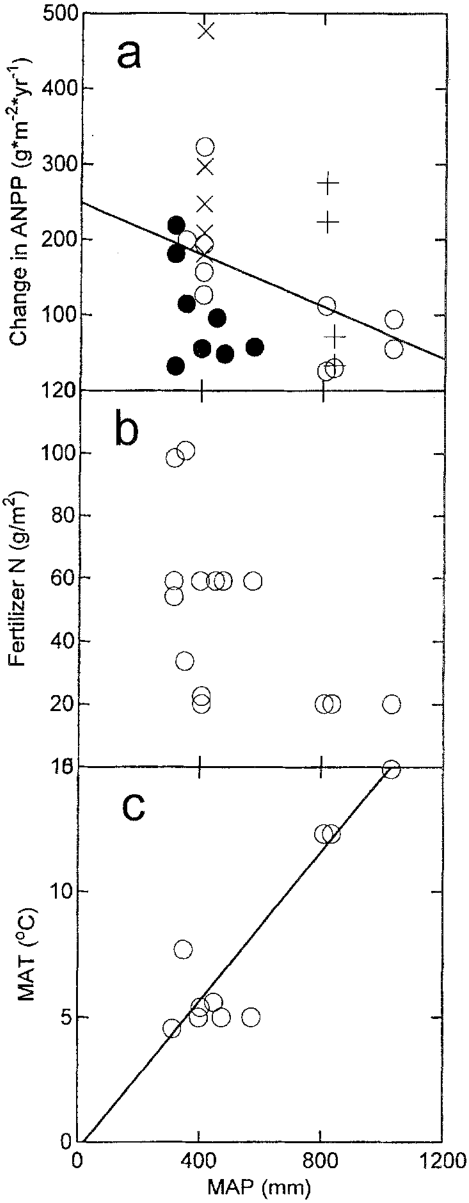

Figure 7. Maximum response of production at high levels of fertilization ($\geq$ 20 g N·m^{-2}·yr^{-1}). (a) Change in ANPP as a function of MAP. Symbols: X = exotics, + = native species, burned, and circles = native species, unburned. Shading in circles represents fertilization level: open = 20–40, gray = 50–60, and black = 90–100 g N·m^{-2}·yr^{-1}; (b) fertilization levels for studies used in the Maximum Response analysis; (c) MAT for studies used in the Maximum Response analysis.

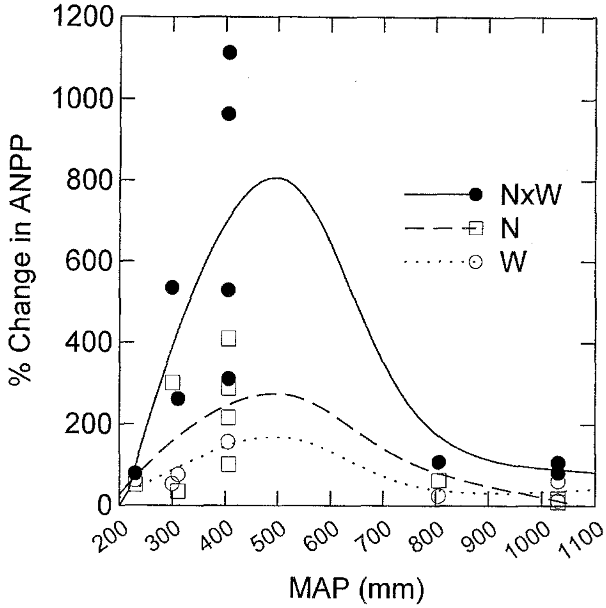

Figure 8. Relative response of ANPP to nitrogen (N), water (W), and nitrogen plus water (N × W) across the precipitation gradient for all levels of fertilization. Multiple points for N and N × W are for different levels of N addition; all studies had only one level of water addition. The curves are fitted by the distance weighted least squares procedure in SYSTAT 7.0 (SPSS 1997), and are intended as a visualization aid, not to imply a statistical relationship of response with MAP. Data are from Stephens & Whitford 1993, MAP = 230 mm; Klages & Ryerson 1965, MAP = 300 mm; Lauenroth et al. 1978, MAP = 311 mm; Smika et al. 1965, MAP = 406 mm; Owensby et al. 1970, MAP = 806 mm; and Parton & Risser 1979, MAP = 1031 mm.

precipitation and Relative Response to N addition would be greatest at high precipitation. With few exceptions, the response to N was equal to or greater than the response to water across the entire gradient (Figure 8). This held whether we looked at the Relative Response or absolute change in ANPP, and whether or not we constrained the analysis to only those cases with 3 or more years of data, or only those cases with fertilizer addition levels from 5–10 g N·m^{-2}·yr^{-1}. The greatest response to both N and water was in the middle of the precipitation gradient. N × water interactions occurred at all levels of precipitation, indicating co-limitation by both of these resources.

The only exceptions to these generalizations were at Jornada, New Mexico (230 mm; Stephens & Whitford 1993), the Central Plains Experimental Range (CPER) in Colorado (311 mm; Lauenroth et al. 1978), and in one of the grazing regimes for the modeled data from Osage, Oklahoma (≈1035 mm MAP; Parton & Risser 1979). The differences in responses to N and water for sites with low precipitation could result from differences in MAT between more southerly sites (CPER, MAT = 9.1 °C; Jornada, MAT = 14.5 °C) and more northerly sites (Norris, Montana, MAP = 300 mm, MAT = 7.6 °C; Mandan, North Dakota, MAP = 406 mm, MAT = 5.4 °C). However, MAT at CPER differs from Jornada more than it does from the northern plains sites. On the other hand, annual precipitation during the years of the experiments could have been responsible for differences among sites. For example, added N had a much stronger effect in Norris, MT than did added water, but all three years of the experiment had higher than average precipitation (Klages & Ryerson 1965). On the other hand, added water had a greater effect than did added N at CPER, but the experiment took place in years of average or below average precipitation (Lauenroth et al. 1978). The lack of long-term data spanning wet and dry years for experimental manipulations of N and water hinders our ability to explicitly test these possible explanations.

Indices of N limitation across temporal gradients in precipitation

The question we sought to answer in these analyses was whether or not N limits production more in wet years than in dry years on the same site. Within a given site, we expected a greater response to fertilization in years with higher actual annual precipitation (AAP). We also wanted to compare the magnitude of change in our N limitation indices across temporal versus geographic variation in water availability. We originally had hypothesized that the response of production to N would change more across geographic variation in precipitation than across yearly, within-site variation in precipitation.

ANPP response to AAP and fertilization

In most cases, ANPP in both control and fertilized plots was greater in wetter than drier years on the same site (Figure 9, Appendix 2). In nearly half of the experiments, AAP explains >70% of the variation in the regression with ANPP (slope $p \leq 0.1$). For several studies, AAP explains >90% of the variation in ANPP in both control and fertilized plots (slope $p < 0.05$). There are some notable exceptions, however (Power & Alessi 1971; Lauenroth et al. 1978; Konza LTER unpublished data). For these studies, some other factor besides actual annual precipitation explains variation in ANPP. Light is known to limit primary productivity due to accumulation of detritus in tallgrass prairie and fire typically decreases the degree of this limitation (Knapp & Seastedt 1986; Seastedt & Knapp 1993). Productivity in unburned plots (unburned for 10 years) at Konza Prairie showed no aboveground response to fertilizer even in years of relatively high precipitation (Figure 9, Appendix 2). In contrast, in annually burned plots at Konza, AAP

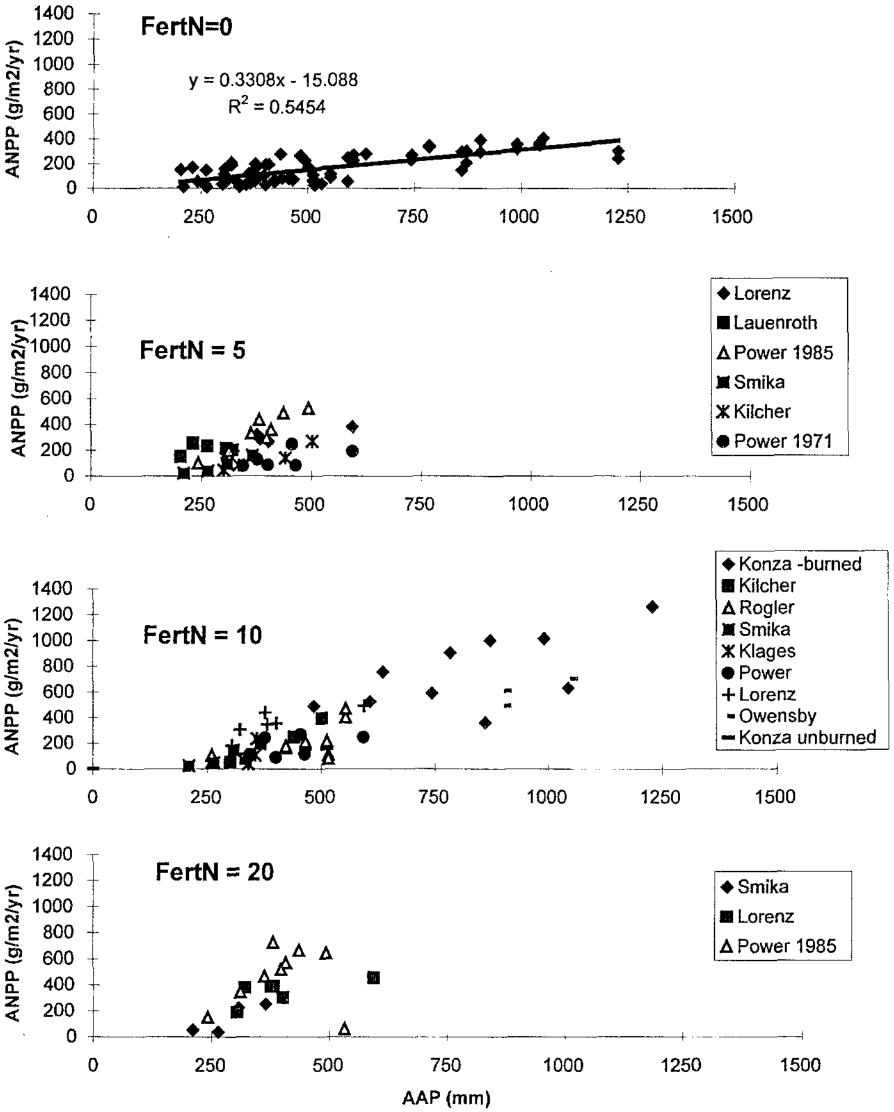

Figure 9. Response of ANPP to AAP at different levels of fertilization. One experiment in the FertN = 20 category had N addition rates of 22.5 g N·m^{-2}·yr^{-1} (Power 1985). Regression shown for control sites only. See Appendix 2 for regression parameters for individual experiments.

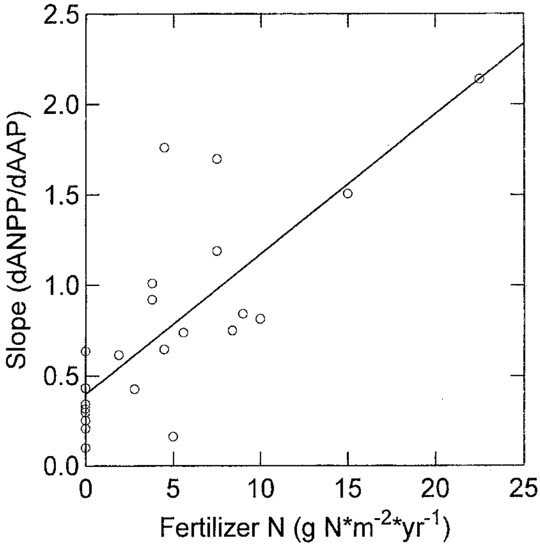

Figure 10. Effects of level of fertilization on the slope of the ANPP vs AAP regressions for within-site variation in rainfall (data from Appendix 2).

explains >40% of the variation in ANPP in fertilized plots (even more, 58%, if one outlier is removed).

Slopes in control plots (FertN = 0) range from 0.10 (Konza) to 0.64 (Kilcher 1958), with most in the range of 0.2 to 0.43. Pooling all studies, control plots had a production/precipitation slope of 0.33 ± 0.04 (Appendix 2). This regression included effects of both within- and across-site variation (since sites differ in their MAP and range of AAP). Despite this mixture of influences, the slope of this temporal relationship in control plots (FertN = 0) was still significantly less than the value for the average response of ANPP with MAP across the geographic gradient for FertN = 0 (compare Table 2). This indicates that, for control plots, geographic gradients in MAP had a larger effect on plant response to precipitation than did temporal variation in AAP, in agreement with other studies (Lauenroth & Sala 1992; Burke et al. 1997).

In fertilized plots, however, we saw the opposite. For ANPP response to precipitation at different levels of N addition, slopes of the regression lines are steeper and often more significant in the temporal (Appendix 2) than in the geographic analysis (Table 2). Furthermore, the more N added, the greater the responsiveness to increased precipitation across years on the same site (Figure 10). For all locations pooled, slopes increase from 0.33 (FertN = 0) to 0.63 (FertN = 5), to 0.74 (FertN = 10), and reach a maximum at 1.56 (FertN = 10–22.5) (Figure 9, Appendix 2). These results indicate that year to year variation in precipitation had a larger effect on plant response to N than did geographic variation in precipitation. We tested this further using the Relative Response and FUE indices of N limitation.

Relative Response Index of N limitation versus AAP

We hypothesized that the Relative Response of production to N in years of higher precipitation would be greater than in years of lower precipitation. We also predicted that the within-site slope would be lower than the between-site slope over the broad geographic gradient. Similar to the pattern across the geographic gradient with MAP, however, there was no significant effect of AAP on the Relative Response to N within any of the sites (Appendix 3). Some sites had large variations in Relative Response that was not explained by the variation in AAP (Rogler & Lorenz 1957 – with a 7-fold variation in Relative Response over a 20–25% variation in AAP; Smika et al. 1965; Power 1971). Other sites (Owensby et al. 1970; Lorenz & Rogler 1972) have a very wide range in AAP, but the same Relative Response to N across that range. We could not compare the within-site slopes to the between-sites slopes because in neither case were the regressions significant. These results suggest that the relative degree of N limitation is not related to yearly precipitation.

Fertilizer Use Efficiency Index of N limitation versus AAP

We hypothesized that FUE in fertilized plots would be greater in wetter than in drier years on the same site. This hypothesis was generally supported by the data. In approximately three-quarters of the studies, there was a significant increase in FUE with increasing AAP, indicating that plants were able to grow more per amount of added N in wetter years than in drier years (Figure 11, Appendix 4). For several studies, AAP explains >90% of the variation in FUE. Again, there are some notable exceptions (Power & Alessi 1971; Lauenroth et al. 1978).

At a given level of fertilization, slopes of FUE vs AAP within sites are greater than slopes of FUE vs MAP across sites (where slopes are negative at FertN = 5 and 20 and positive only at FertN = 10; compare Appendix 4 with Table 5). In sites with more than one level of fertilization, slopes decrease with increasing fertilization except for one study (Kilcher et al. 1965). The pattern of response to AAP within sites changes when the data are pooled across sites but within levels of fertilization (Figure 11, Appendix 4). In the latter case, the highest slopes are seen at intermediate levels of fertilization, which may occur because pooling mixes effects within sites with effects across sites. In summary, these results support our hypothesis that within a site, plants are able to use N fertilizer more efficiently (i.e. have greater gains in biomass per amount of added N) in wetter years than drier years.

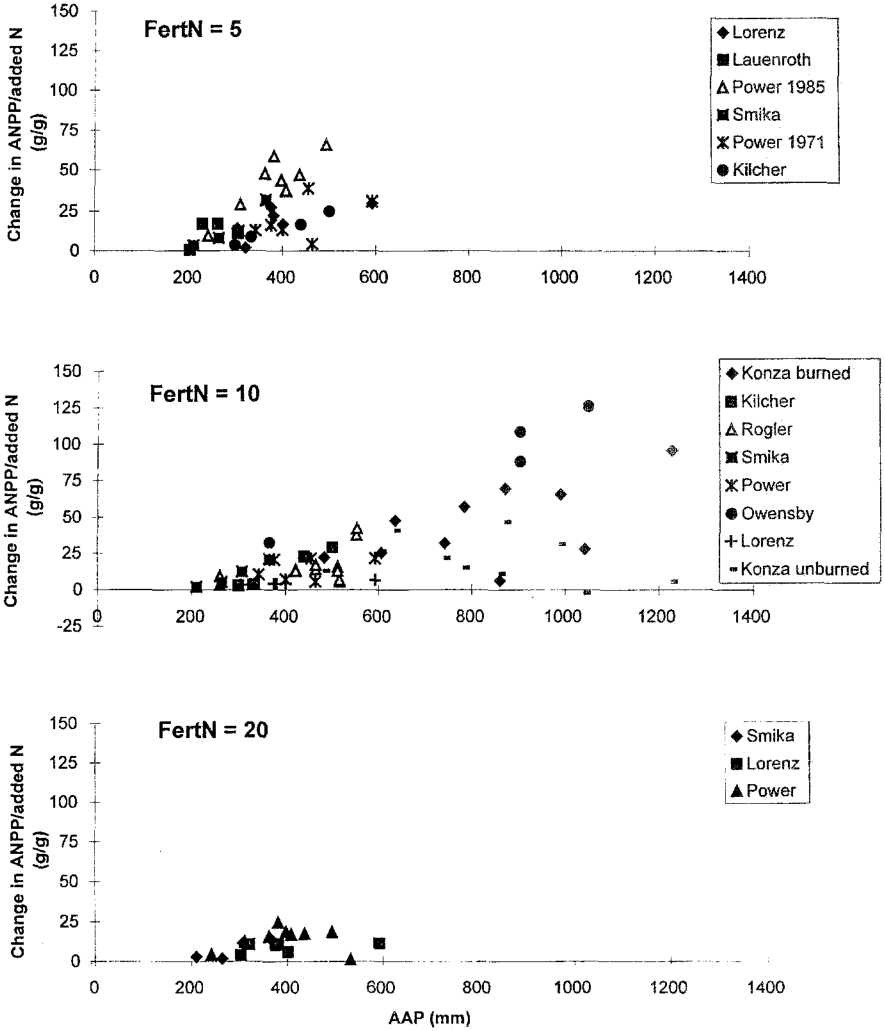

Figure 11. Response of FUE to AAP at different levels of fertilization. One experiment in the FertN = 20 category had N addition rates of 22.5 g N· m^{-2}·yr^{-1} (Power 1985). See Appendix 4 for regression parameters for individual experiments.

Disscussion

Our data set shows a response of ANPP to precipitation for control sites that is similar to several other studies (Noy-Meir 1973; Le Houerou & Hoste 1977; Le Houerou et al. 1988; Risser 1988; Sala et al. 1988; Epstein et al. 1996). In general, WUE ranges from 0.46 to 0.76 g ANPP/mm MAP, and ineffective precipitation (IP) from 0 to 200 mm. We were near the lower end of the WUE range and in the middle of the IP range (Table 1). This gives us

Table 6. Summary of results of N limitation in response to variation in precipitation. Symbols are based on significant slopes: + represents positive slope, – represents negative slope, 0 = not significantly different from zero. The number of symbols indicates the strength of response (relative comparison of slopes) for those relationships with significant effects of either MAP or AAP. NA = not applicable, ND = no data.

	Geographic variation in MAP				Temporal variation in AAP			
Index	FertN 0	FertN 3–5	FertN 5–10	FertN 10–20	FertN 0	FertN 3–5	FertN 5–10	FertN 10–22.5
1. ANPP	++	++	+++	+	++	+++	+++	+++
2. Relative Response	NA	–	0	–	NA	0	0	0
3. Fertilizer Use Efficiency	NA	–	+	–	NA	+	+++	++
4. Maximum Response	NA	NA	NA	0	NA	NA	NA	ND
	MAP 300	MAP 450	MAP 600	MAP 900	MAP 300	MAP 450	MAP 600	MAP 900
5. Absolute Increase	0	++	0	+	NA	NA	NA	NA

confidence that our regression functions for control conditions are reasonably close to other studies. To our knowledge, however, this is the first attempt to look at fertilization responses across the precipitation gradient in a similar way.

The variety of responses we saw using our different indices of N limitation emphasize that the mechanisms underlying production response to fertilization need close inspection before we can infer how N limitation changes across gradients of water availability. In general, indices of N limitation based on absolute changes in plant production in response to fertilization increased with increased precipitation both temporally and geographically (Table 6). FUE increased with actual annual precipitation within sites (Appendix 4, Figure 11) and, for the intermediate level of N fertilization, FUE increased with MAP across sites (Table 5, Figure 6). Similarly, slopes of ANPP vs AAP within sites increased with fertilization, indicating alleviation of N limitation in wetter years (Appendix 2, Figure 9). Finally, Absolute Increase to fertilization was greater for MAP levels 450 and 900 mm than for 300 mm. These indices indicate that absolute production responds more to added N when water availability increases. On the other hand, regressions of FUE vs MAP at some levels of fertilization (FertN = 5 and 20), Maximum Response vs MAP, and Relative Response vs both MAP and AAP were either not significant or were negatively correlated (Table 6). These indices do not indicate that the degree of N limitation necessarily increases as water availability increases. Furthermore, production responses to N were generally greater than production responses to water addition across the precipitation gradient (Figure 8) and there were significant N × water interactions across the entire gradient, indicating co-limitation by both resources.

Either way, our results differ from the modeling analysis of Seagle and McNaughton (1993), who found water to be primarily limiting and N to be secondarily limiting in both dry and mesic regions of the Serengeti. In both regions, they saw no response to additional N supply until precipitation was at least 120% above average. In contrast, most of the studies we surveyed showed at least some response to N addition even at dry locations (Figures 5, 6, and 7) and even in years of below average precipitation (Figure 11).

Which index to use?

There is probably no one "best" measure of N limitation; each index sheds light on a different aspect of the question. Which index is best depends upon which aspect of production response to N is most relevant. For example, greater absolute increases in production in response to N addition agrees with the experience of range managers where fertilization pays for itself in wetter sites and/or wetter years in terms of increased forage production; it may not pay in drier sites or years (Kilcher 1958; Thomas and Osenbrug 1959; Seligman et al. 1986). In this sense, the Relative Response results agree with that experience – the same Relative Response across the precipitation gradient still means greater absolute production in wetter regions or years because of the greater control production under wetter conditions.

But what do these results tell us about how the degree of N limitation changes across the temporal and spatial gradients of water availability? The different responses of the different indices emphasize that this question is not as simple as it might at first appear. Our discussion will therefore focus on trying to interpret our results mechanistically to further understand the underlying interactions among N availability, water availability and plant growth. The questions we need to address are: (1) why might absolute ANPP responses to N increase with precipitation, both geographically and temporally, but Relative Response to N does not? (2) How can low precipitation sites with, on average, much lower rates of ANPP actually have equal Maximum Responses to N? (3) Why did ANPP have a higher slope in response to MAP across sites than to AAP across years in nonfertilized sites, but a higher AAP response than MAP response in fertilized sites? (4) What does each index tell us about the strength of N limitation in response to precipitation?

Several factors complicate the assessment of N limitation by using plant growth response to fertilization, especially when looking at natural ecosystems across broad gradients of environmental conditions. Our different indices help shed light on these complications. First, because the degree of microbial immobilization may change across geographic precipitation gradients (Zak et al. 1994), enough N must be added to saturate microbial demands and assure that plants are actually experiencing significantly enhanced N supply (Chapin et al. 1986; Jackson et al. 1989; Schimel et al. 1989). The Maximum Response index answers the question “No matter how much N is added, and even with changes in species, what is the greatest absolute gain in plant biomass that can be achieved?” It estimates the maximum degree to which plants can compensate for and utilize the different resources at a given site for increased biomass production. By this criterion, the degree of N limitation does not increase with increasing precipitation (Figure 7), even when taking differences in species composition (exotics vs natives) into account.

However, does one define the degree of N limitation by the Maximum Response (e.g., some index of site limitations independent of the plant community), or by the extent to which potential gains in production of the original community are limited by N supply versus other resources? A second complication is that species changes often occur with fertilization so that after multiple years of N addition, community composition can shift dramatically from the original state of the ecosystem (Tilman 1987). This is a critical question in many range studies attempting to improve grazing yields, but where weeds and unpalatable species may invade following high levels of fertilization. In many cases, species replacement in fertilization experiments follow predictable patterns, such as the increase in C3 species at the expense of C4 species in many prairie sites (Moser & Anderson 1965; Johnston et al. 1967; Goetz 1969; Rogler & Lorenz 1974), the loss of N fixers in N fertilized plots and gains in N fixers in P fertilized plots (Russel et al. 1965; Thomas & Osenbrug 1959), or the increase in ruderal species at high levels of N fertilization (Kilcher et al. 1965; Johnston et al. 1969; McLendon & Redente 1991). Such changes in species composition could be responsible for the unexpected results we saw for the Maximum Response index.

The FUE index helps to assess the extent to which production of given communities might be limited by N relative to other potentially limiting resources (specifically, water) across the precipitation gradient. The FUE index measures how absolute changes in biomass responded to fertilization at lower levels of N addition, where species shifts are less of a problem and where plant response has not yet saturated. The significant negative response of FUE to MAP at FertN = 5 (Figure 6) may result because of greater microbial immobilization in more mesic sites (resulting from higher SOM and microbial biomass), so that less added N actually reached those plants at high MAP. At FertN = 10, greater FUE at higher precipitation indicates that plants are able to convert a given amount of N into greater absolute biomass at wetter sites than at drier sites. This is similar to the positive responses seen for FUE versus AAP (see below), and in contrast to the Maximum Response index, indicates greater N limitation at sites with greater water availability. Lack of a similar response at FertN = 20 is difficult to explain.

The Relative Response to fertilization allows assessment of N response independent of initial plant size. A third complication is that despite having low nutrient supplies, plant responses to added N could be smaller on more nutrient limited sites than in more nutrient rich sites because of intrinsically low relative growth rates (RGR) of species commonly found in N limited sites (Chapin et al. 1986). If low precipitation sites had a lower absolute productivity increase in response to fertilization, does this mean that low precipitation sites are not as limited by N supply as high precipitation sites, or are the individuals just smaller and/or slower growing? Relative Response could still be influenced by differences in growth strategies if RGR differs substantially among species; however, the negative correlation of Relative Response and MAP indicates that this is not the case (see below). A similar result for Relative Response was seen in data from Johnston et al. (1969). For 5 native grassland sites in Canada ranging in MAP from ≈300 to ≈600 mm (MAT = 4.6–5.6 °C), there was a negative correlation of Relative Response to fertilizer with increasing MAP.

Mechanisms

We suggest that mechanisms at several levels could lead to no change in Relative Response or Maximum Response but significant increases in FUE as precipitation increases. Potential mechanisms include growth response to multiple resources of individual plants, plant community dynamics, and biogeochemical feedbacks at the ecosystem level. At the ecosystem level, water and N availability covary strongly across broad precipitation gradients because of linkages in their biogeochemical cycles (Schimel et al. 1997). Increasing precipitation and soil water availability positively affect atmospheric N inputs, decomposition, N mineralization, and physical transport of N ions in the soil, all of which should lead to greater plant available N (Vitousek et al. 1994; Zak et al. 1994; Burke et al. 1997; Schimel et al. 1997). Greater water availability (either geographically or temporally) could lead to greater gains in plant biomass per amount of added N (FUE) for three potential reasons: (a) more moisture makes that N more mobile and physically available in the soil (Nye & Tinker 1977), (b) plant N demand is linked to water availability (Chapin et al. 1987; Chapin 1991), or (c) individual plants are able to put acquired N into more efficient biomass production (i.e., greater carbon gain per N acquired) because of greater water availability. All of these mechanisms could potentially operate simultaneously. In the first two mechanisms, however, plants in more arid sites may be "seeing" a smaller amount of the added N, because N acquisition scales with water availability. If so, similar Relative Response to N across the geographic gradient may indicate similar capacities for species at sites of different MAP to utilize N for growth. In the last mechanism, growth response to acquired N also would be limited by water availability at low MAP. In that case, we would expect greater Relative Response of plant production to N fertilization as precipitation increases, which we did not see. Mechanisms (a) and (b) should lead to little change of plant %N with precipitation, whereas for mechanism (c), wetter sites should have lower plant %N. In a preliminary analysis of our data, fertilization up to 20 g $N \cdot m^{-2} \cdot yr^{-1}$ increased average foliar N concentrations across the entire geographical precipitation gradient, however, there were no significant effects of MAP on either the magnitude of this response or on control levels of foliar N ($P_{MAP} = 0.20$, $P_{FertN} < 0.001$, $n = 31$). In contrast to conclusions drawn by Seagle and McNaughton (1993), our results therefore suggest that mechanisms (a) and (b) are most important.

At the individual level, plants compensate for resource imbalances by allocating nonlimiting resources to the acquisition of limiting resources, with the consequence that they often are co-limited by multiple resources (Chapin et al. 1987; Chapin 1991). At the community level, those species that dominate production under a given set of conditions are presumably those that are able to convert available resources most efficiently into biomass. When changes in resource balance exceed the physiological compensation ability of the extant species, species that are able to more efficiently convert the available resources into biomass will account for a larger proportion of total production. Such changes in species composition (Lauenroth et al. 1978; Tilman 1987; Briggs & Knapp 1995) could have the effect of maintaining multiple resource limitations of the plant community as a whole. We suggest that these shifts play a large role in the patterns of ecosystem productivity in response to N that we saw across the precipitation gradient. Similarly, shifts in species dominance from year to year in response to variation in rainfall could help explain why Relative Response to fertilization did not show a significant response to AAP within sites, though more data on annual species composition is necessary to investigate this.

The lack of a geographic precipitation effect on both Relative Response to fertilization and Maximum Response to fertilization appears to negate the hypothesis that species of low resource environments have intrinsically low relative growth rates in response to addition of limiting resources (Chapin 1980; Chapin et al. 1986). Because variability in rainfall increases as MAP decreases (Noy-Meir 1973) and because plant N availability is closely tied to water availability (Chapin et al. 1987; Chapin 1991), native species in arid and semiarid systems may have the capacity to quickly respond to pulses of water and N availability, despite living in a chronically resource deficient environment. On the other hand, the original dominants of the site may indeed have low responses to added nutrients whereas the new dominants after species shifts (either invaders or previous subdominants) are better able to utilize the new balance of resources following N addition. More detailed studies that assess both production response and species changes over time across the precipitation gradient would shed more light on this.

Reasons for variation in response

Despite the strong relationship of ANPP to MAP described above, all indices of N limitation varied widely even at similar levels of MAP. This suggests that differences in site characteristics besides precipitation exert strong control over the extent to which plant growth is limited by N supply. The variation results from at least three primary factors:

a) factors that modify the relationship of plant available water to precipitation. These are primarily geophysical features, including climate (e.g., site temperature), timing and distribution of precipitation, soil texture and depth, and topography (slope and aspect).
b) factors that modify plant N availability and other resources that might limit plant growth. These include disturbance and management regimes (e.g., fire, grazing).
c) differences in plant community composition (e.g., Cooper 1959; Power 1980, 1985; Contreras & Gasto 1986).

With regard to (a), above, we had expected that MAT might help explain the variation in response to precipitation. Indeed, increasing MAT significantly decreased response to added N for the Relative Response index for FertN = 10 when looking at a restricted realm of MAP (Figure 5(b)). This is consistent with similar effects of MAT on production in unfertilized systems (Epstein et al. 1996), because increasing temperature in arid and semi-arid systems tends to decrease plant water availability. In general, however, differences among sites in other characteristics, such as grazing regime, fire regime, and plant composition influenced production response to fertilization as much as, or more than, site temperature did.

Plant production in tallgrass prairie (the primary ecosystem for which we had data at the wetter end of the gradient) is strongly affected by litter accumulation that reduces light availability and early season growing temperatures at the soil surface (Knapp & Seastedt 1986; Seastedt & Knapp 1993). Such litter feedbacks and light limitation could be one reason that we see, on average, lower Relative Response to N at higher precipitation. It is a limitation of this study that the wet end of the precipitation gradient depends so heavily on this one location and ecosystem. At the same time, this indicates that in undisturbed systems, any simple tradeoff in water and N limitation across precipitation gradients may be overwhelmed in moister regions by light limitation resulting from litter accumulation.

Production response to spatial vs temporal variation in precipitation

We originally hypothesized that interactions between N and water availability would differ for temporal versus geographic gradients in precipitation. Specifically, we expected that the production response to N addition would increase more across geographic gradients in precipitation (wet vs dry locations) than it would across temporal gradients in precipitation (i.e., wet vs dry years within a site). We predicted this based on previous studies (Lauenroth & Sala 1992; Burke et al. 1997) that found that under *control* (unfertilized) conditions, for a given increase in annual precipitation, production increased more with geographic variation in precipitation than it did with year-to-year variation in precipitation within a given site. Our literature review from control conditions (unfertilized) agrees with those findings (compare slopes for FertN = 0 in Table 2 and Appendix 2). Fertilization changes this picture, however. Temporal variation in precipitation (wet vs dry years on the same site) had a larger effect on plant response to N than did geographic variation in precipitation (wet vs dry locations) (Table 6). The slopes of ANPP vs AAP were similar to or greater than those across the geographic gradient at similar levels of N addition (compare Table 2 and Appendix 2). The same pattern holds for FUE response to geographic (Table 5) versus temporal (Appendix 4) variation in precipitation.

Together, these results indicate that (a) in control plots, productivity increases more with geographic than with temporal variation in precipitation; (b) absolute (but not relative) increases in productivity with N addition are greater in wet years than dry years, (c) absolute (but not relative) increases in productivity with N addition are greater in wet sites than dry sites (at least for FertN = 10), and (d) for a given increase in precipitation, response b is greater than response c. A couple of different explanations could cause these results.

First, for the pattern in control sites, plant production response to rainfall variation within a given location may be constrained because plants in more arid sites are intrinsically slow growing (Chapin et al. 1986; Lauenroth & Sala 1992; Burke et al. 1997). Our fertilization results, which showed large gains in biomass even in relatively dry sites, do not support this explanation.

Alternatively, production in unfertilized plots could be co-limited by both N and water because of temporal shifts in the relative availability of these resources. If water is limiting in dry years, but N is limiting in wet years, this will moderate overall production response to variation in precipitation (Van Keulen & Seligman 1992; Huston 1997). While N mineralization may increase with increasing AAP, the higher N availability may not keep pace with plant demand under greater water availability (Seagle & McNaughton 1993). With fertilization, however, N limitation is eliminated (or reduced) so that plant growth becomes singly limited by water, leading to a greater dependence of production on AAP within sites (Seligman et al. 1986). Modeling studies also show co-limitation of production by water and nitrogen when AAP is average or greater than average, indicating that alleviation of N limitation will make production more sensitive to temporal variation in annual precipitation (Van Keulen & Seligman 1992; Seagle & McNaughton 1993).

In contrast to the temporal variation, as precipitation increases across the geographic gradient, both water and N may become more available in proportion to plant demand so that co-limitation by both resources persists at different sites (Schimel et al. 1997). This could arise, for example, if greater MAP leads to greater amounts of SOM per m^2 as well as increased rates of mineralization per amount of SOM. Fertilization alleviates the N restrictions to growth, but dry years within those sites could still lower the *average* response to N (because our geographic results were means over several years of data for some sites).

In light of the modeling results that show both greater absolute and relative responses of productivity to N with increased AAP (Van Keulen & Seligman 1992; Seagle & McNaughton 1993), our results showing no such effect for Relative Response were surprising. Whereas we might have expected no relationship between Relative Response and MAP across the geographic gradient because of water and N co-limitation of production, the results from temporal variation in precipitation seem to suggest a shift from water to N limitation depending on AAP within sites. Lag effects from previous seasons' precipitation could account for some of the variability in Relative Response to N, but whether lags increase or decrease production is a topic of debate. On one hand, greater plant biomass (Lauenroth

& Sala 1992), moisture carried over from the previous year (Johnston et al. 1969), and more mineralization from previous years' senesced biomass (Burke et al. 1997) are potential mechanisms leading to greater plant growth in years following wet years. On the other hand, excess N availability in years following dry years (Risser 1988; Seligman & van Keulen 1989) or litter buildup in wet years (Burke et al. 1997) could lead to a negative correlation of previous year's precipitation with current years growth. Still other experiments report no significant carryover effects (Noy-Meir & Walker 1986). Whether positive or negative, time lags could be an important source of variation in year to year response to fertilization using current year's precipitation only. Other contributing factors to our lack of relationship between Relative Response and AAP could be that yearly shifts in species dominance within communities maintain multiple resource limitations or that other indices of water availability (e.g., growing season precipitation) are more relevant to production response to N addition than is total annual precipitation.

Conclusions

Clearly, many questions remain about how N limitation changes with water availability. We have to be cognizant of several limitations in our data set. Having information on site AET and PET would be the best way to improve our estimates of relative water availability across sites. Our survey approach did not allow us the control to closely investigate some of the substantial variation in response to N resulting from management practices that we observed. Finally, having a better representation of sites in the intermediate and mesic range of precipitation would lessen the dependence of the results on the Konza studies. This survey points out the need for further investigation, especially multi-year data sets and manipulations to investigate N × water interactions.

Despite its limitations however, we believe that this survey was able to clearly demonstrate several key points. First, mechanisms at the level of the individual, community and ecosystem all influence the response of ecosystems to changing resource availability. Second, using several indices of production response to fertilization can help give a better understanding of those mechanisms and controls of N limitation. And, third, there is not necessarily a shift of primary limitation from water to N across the geographic water availability gradient. Instead, our results support the hypothesis of co-limitation by both resources.

Acknowledgements

For motivating these questions and for discussion in the formulation of preliminary hypotheses, we would like to thank Osvaldo Sala and the other members of the Drylands group at the Termas de Chillan SCOPE N meeting: Greg Asner, Amy Austin, Tim Crews, Victor Jaramillo, Manuel Maass, Ivan Ortiz-Monasterio, Everardo Sampaio, and Eugenio Sanhueza. Several people (John Blair, Terry Chapin, Alan Knapp, Peter Vitousek, and especially Howard Epstein and an anonymous reviewer) gave extensive comments that substantially improved on an earlier draft. We would also like to thank Alan Townsend and Bob Howarth for their editorial assistance (and patience). Jesse Nippert and J.R. Matchett helped track down climate information. Unpublished data for Konza Prairie came from the LTER database. Dr. J. Krupinsky of the Northern Great Plains Research Lab provided unpublished precipitation data for Mandan, ND.

Appendix

Appendix 1. Sites and references for data used in this study. NA = data not available.

Reference	Years of experiment	Location	Country	MAP (mm)	MAT (°C)
Ettershank et al. 1978	1977	Jornada, NM	U.S.A.	211	14.5
Stephens & Whitford 1993	1988	Jornada LTER	U.S.A.	230	14.5
Kilcher et al. 1965	1958–60	Kamloops, B.C.	Canada	242	8.6
Seligman et al. 1986	1962–72	Migda	Israel	250	17.4[1]
Cooper & Hyder 1958	1957	Burns, Oregon	U.S.A.	253	8.0
Kilcher et al. 1965	1958–60	Summerland, B.C.	Canada	279	9.0
McLendon & Redente 1991	1985–89	NW Colorado	U.S.A.	280	3.5
Jacobsen et al. 1996	1971, 1977	Havre, MT	U.S.A.	282	7.0
Klipple & Retzer 1959	1953	CPER, Colorado	U.S.A.	283	9.1
Klages & Ryerson 1965	1958–60	Norris, MT	U.S.A.	300	7.6
Kilcher et al. 1965	1958–60	Manyberries, Alb.	Canada	301	4.6
Hunt et al. 1988	1984	CPER, Colorado	U.S.A.	310	9.1
Lauenroth et al. 1978	1970–74	CPER, Colorado	U.S.A.	311	9.1
Johnston et al. 1967	1964–65	Manyberries, Alb.	Canada	313	4.6
Johnston et al. 1969	1962–64	Manyberries, Alb.	Canada	313	4.6
Contreras & Gasto 1986	NA	Maipu	Chile	315	14.5[1]

Appendix 1. Continued.

Reference	Years of experiment	Location	Country	MAP (mm)	MAT (°C)
Black 1968	1961–62	Montana	U.S.A.	322	6.2
Burzlaff et al. 1968	1964	E. Montana	U.S.A.	325	7.7
Wight & Black 1979	1969	E. Montana	U.S.A.	349	7.7
Kilcher 1958	1954–57	Swift Current, Sask.	Canada	355	3.5
Kilcher et al. 1965	1958–60	Swift Current, Sask.	Canada	374	3.5
Cosper & Thomas 1961	1957–59	Texas Ag. Res. Serv., USDA	U.S.A.	378	20.4
Lodge 1959	1951	Swift Creek, Sask.	Canada	380	3.5
Thomas & Osenbrug 1959	1948–51	South Dakota	U.S.A.	383	8.2
Goetz 1969	1964–66	Havre, ND	U.S.A.	392	5.2[1]
Goetz 1969	1964–66	Manning, ND	U.S.A.	392	5.2
Goetz 1969	1964–66	Rhoades, ND	U.S.A.	392	5.2[1]
Goetz 1969	1964–66	Vebar, ND	U.S.A.	392	5.2[1]
Johnston et al. 1969	1962–64	Coalhurst, Alb.	Canada	400	5.0[1]
McGinnies 1968	1962–67	Manitou Exp. Forest, CO	U.S.A.	400	11.6
Lorenz & Rogler 1972	1958–65	Mandan, ND	U.S.A.	403	5.4
Power & Alessi 1971	1963–68	Mandan, ND	U.S.A.	403	5.4
Rogler & Lorenz 1957	1951–56	Mandan, ND	U.S.A.	406	5.4
Smika et al. 1965	1958–61	Mandan, ND	U.S.A.	406	5.4
Power 1980	1968–73	Mandan, ND	U.S.A.	406	5.4
Power 1985	1970–78	Mandan, ND	U.S.A.	406	5.4
Kilcher et al. 1965	1958–60	Indian Head, Sask.	Canada	439	2.2
Johnston et al. 1969	1962–64	Magrath, Alb.	Canada	450	5.6
Russel et al. 1965	1953	Holt County, NE	U.S.A.	465	8.9
Kilcher et al. 1965	1958–60	Brandon, Man.	Canada	468	1.8
Johnston et al. 1969	1962–64	Spring Point, Alb.	Canada	475	5.0[1]
Kilcher et al. 1965	1958–60	Stavely, Alb.	Canada	573	5.0[1]
Johnston et al. 1969	1962–64	Stavely, Alb.	Canada	573	5.0[1]
Van Keulen & Seligman 1992	1976	Niono	Mali	580	NA
Hunt et al. 1988	1984	SE Wyoming	U.S.A.	600	0.1
Elisseou et al. 1995	1992	Thessaloniki	Greece	805	16.6[1]
Owensby et al. 1970	1965–68	Flint Hills, KS	U.S.A.	806	12.3
Seastedt et al. 1991	1986–89	Konza LTER, KS	U.S.A.	810	12.3
Gay & Dwyer 1965	1963	E. Oklahoma	U.S.A.	833	15.6
Moser & Anderson 1965	1963	Flint Hills, KS	U.S.A.	835	12.3
Konza LTER (unpublished data)	1986–96	Konza LTER, KS	U.S.A.	835	12.3

Appendix 1. Continued.

Reference	Years of experiment	Location	Country	MAP (mm)	MAT (°C)
Benning & Seastedt 1995	1989–90	Konza LTER, KS	U.S.A.	835	12.3
Turner et al. 1997	1994	Konza LTER, KS	U.S.A.	835	12.3
Parton & Risser 1979	NA	Osage, OK	U.S.A.	1031	14.9

[1] MAT estimated from nearby sites or cities.

Appendix 2. Response of ANPP to temporal, within-site variation in precipitation. Regression parameters are for ANPP ($g{\cdot}m^{-2}{\cdot}yr^{-1}$) versus actual annual precipitation (AAP, in mm) within sites (ANPP = $a + b{*}$AAP). Separate regressions were performed for control plots (FertN = 0) and for each level of fertilization (FertN). Also shown are the mean annual precipitation (MAP) for each site, the range of AAP during the experiment, and the number of years for which there is data. Summary regressions for all sites within a given range of fertilization are shown at the bottom of the table. Where outliers have a large effect on parameters, regressions are performed both with and without the outliers.

Reference FertN level ($g\ N{\cdot}m^{-2}{\cdot}yr^{-1}$)	MAP (mm)	AAP range (mm)	Yrs data	r^2	slope	p	intercept	p
Lauenroth et al. 1978	311	203–501	5					
0				0.38	0.30 ± 0.22	0.26	89 ± 59	0.23
5				0.04	0.16 ± 0.44	0.74	169 ± 119	0.25
Kilcher 1958	355	300–501	4					
0				0.85	0.64 ± 0.19	0.08	–166 ± 78	0.16
3.8				0.91	1.01 ± 0.22	0.04	–262 ± 89	0.09
7.5				0.98	1.70 ± 0.17	0.01	–476 ± 69	0.02
Rogler & Lorenz 1975	406	260–516	6					
0				0.46	0.20 ± 0.07	0.02	28 ± 33	0.41
2.8				0.47	0.43 ± 0.14	0.01	–71 ± 66	0.30
8.4				0.37	0.75 ± 0.31	0.04	–142 ± 144	0.34
Smika et al. 1965	406	210–365	4					
0				0.61	0.25 ± 0.14	0.21	–45 ± 41	0.39
1.9				0.87	0.61 ± 0.17	0.07	–121 ± 49	0.13
3.8				0.95	0.92 ± 0.15	0.03	–185 ± 44	0.05
7.5				0.94	1.19 ± 0.21	0.03	–238 ± 62	0.06
15.0				0.78	1.51 ± 0.57	0.10	–290 ± 167	0.22

Appendix 2. Continued.

Reference FertN level (g N·m^{-2}·yr^{-1})	MAP (mm)	AAP range (mm)	Yrs data	r^2	slope	p	intercept	p
Lorenz & Rogler 1972	406	304–593	6					
0				0.73	0.34 ± 0.10	0.03	53 ± 43	0.28
4.5				0.77	0.65 ± 0.18	0.02	16 ± 72	0.83
9.0				0.66	0.84 ± 0.31	0.05	20 ± 124	0.87
18.0				0.44	0.59 ± 0.33	0.15	117 ± 135	0.43
Power & Alessi 1971	403	376–593	6					
0				0.23	0.12 ± 0.01	0.33	1 ± 49	0.98
0.6				0.17	0.12 ± 0.13	0.42	10 ± 59	0.87
1.1				0.09	0.11 ± 0.17	0.56	34 ± 77	0.68
2.2				0.11	0.17 ± 0.24	0.53	13 ± 109	0.91
4.5				0.30	0.43 ± 0.13	0.26	–51 ± 147	0.74
9.0				0.20	0.41 ± 0.41	0.38	1 ± 184	0.99
Power 1985	403	242–532	9					
0				0.11	0.32 ± 0.34	0.38	347 ± 59	0.0007
4.5 (w outlier)				0.06	0.49 ± 0.71	0.51	116 ± 286	0.69
4.5 (w/o outlier)				0.87	1.76 ± 0.27	0.007	–324 ± 107	0.02
22.5 (w outlier)				0.02	0.43 ± 0.99	0.68	293 ± 399	0.48
22.5 (w/o outlier)				0.75	2.14 ± 0.51	0.006	–298 ± 196	0.17
Owensby et al. 1970	806	366–1050	4					
0				0.91	0.43 ± 0.09	0.045	–43 ± 80	0.64
5.6				0.95	0.74 ± 0.12	0.03	–98 ± 104	0.45
Konza LTER	835	483–1227	10					
0 – burned (all cases)				0.43	0.10 ± 0.04	0.041	223 ± 34	0.0002
0 – burned (no outlier)				0.43	0.10 ± 0.04	0.054	224 ± 37	0.0005
10 – burned (all cases)				0.41	0.81 ± 0.34	0.047	83 ± 295	0.78
10 – burned (no outlier)				0.58	0.85 ± 0.27	0.017	99 ± 81	0.68
0 – unburned				0.02	0.51 ± 0.11	0.64	222 ± 90	0.03
10 – unburned				0.07	–1.80 ± 2.3	0.45	627 ± 198	0.01
All studies, FertN > 0 (n = 129)		203–1227		0.48	0.73 ± 0.07	0.0001	–73 ± 36	0.05

Appendix 2. Continued.

FertN level (g N·m^{-2}·yr^{-1})	r^2	slope	p	intercept	p
All sites by fertilization level:					
FertN 0 ($n = 63$) (excludes Konza unburned)	0.55	0.33 ± 0.04	0.0001	–15 ± 21	0.47
FertN 1–3 ($n = 25$)	0.33	0.30 ± 0.07	0.0003	–36 ± 32	0.27
FertN 3–5 ($n = 33$)	0.51	0.63 ± 0.11	0.0001	–23 ± 48	0.63
FertN 5–10 ($n = 45$) (excludes Konza unburned)	0.55	0.74 ± 0.08	0.0001	–52 ± 52	0.32
FertN 5–10 (no Konza outlier)	0.75	1.04 ± 0.09	0.0001	–191 ± 54	0.0009
FertN 10–22.5 ($n = 18$)	0.51	1.56 ± 0.40	0.0009	–206 ± 148	0.18

Appendix 3. Relative Response index of N limitation as a function of temporal variation in AAP within sites. Equations are presented as % increase in ANPP in fertilized plots = a + b∗AAP. Separate regressions are performed for each fertilizer level. Table variables are as in Appendix 2. Summary regressions for all sites within a given range of fertilization are shown at the bottom of the table. Where outliers have a large effect on parameters, regressions are performed both with and without the outliers.

Reference FertN level (g N·m^{-2}·yr^{-1})	MAP (mm)	AAP range (mm)	Yrs data	r^2	slope	p	intercept	p
Lauenroth et al. 1978	311	203–501	5					
5				0.02	–0.07 ± 0.32	0.84	46 ± 84	0.62
Kilcher 1958	355	300–501	4					
3.8				0.10	0.06 ± 0.13	0.68	36 ± 50	0.54
7.5				0.46	0.55 ± 0.42	0.32	–103 ± 17	0.60
Rogler & Lorenz 1957	406	260–516	6					
2.8				0.07	0.11 ± 0.12	0.42	40 ± 56	0.49
8.4				0.04	0.17 ± 0.26	0.54	125 ± 121	0.33
Smika et al. 1965	406	210–365	4					
1.9				0.29	0.34 ± 0.38	0.46	3 ± 110	0.98
3.8				0.10	0.57 ± 1.19	0.68	53 ± 347	0.89
7.5				0.23	0.99 ± 1.27	0.52	5 ± 373	0.99
15.0				0.08	0.48 ± 1.14	0.72	272 ± 333	0.51

Appendix 3. Continued.

Reference FertN level (g N·m^{-2}·yr^{-1})	MAP (mm)	AAP range (mm)	Yrs data	r^2	slope	p	intercept	p
Lorenz & Rogler 1972	406	304–593	6					
4.5				0.11	0.07 ± 0.09	0.52	18 ± 38	0.66
9.0				0.26	0.12 ± 0.09	0.31	40 ± 40	0.38
18.0				0.001	–0.01 ± 0.11	0.95	88 ± 43	0.11
Power 1971	403	376–593	6					
0.6				0.16	–0.07 ± 0.08	0.43	57 ± 37	0.20
1.1				0.38	–0.25 ± 0.16	0.19	177 ± 70	0.06
2.2				0.08	–0.16 ± 0.26	0.59	144 ± 118	0.29
4.5				0.002	0.04 ± 0.52	0.94	168 ± 230	0.50
9.0				0.03	–0.23 ± 0.67	0.75	377 ± 299	0.28
Power 1985	403	242–532	9					
4.5 (no effect of outlier)				0.18	–0.33 ± 0.26	0.25	250 ± 106	0.05
22.5 (no effect of outlier)				0.21	–0.62 ± 0.46	0.22	491 ± 186	0.03
Owensby et al. 1970	806	366–1050	4					
5.6				0.33	–0.02 ± 0.02	0.43	50 ± 14	0.07
Konza LTER	835	483–1227	10					
10 – burned (all cases)				0.27	0.19 ± 0.12	0.12	–17 ± 98	0.87
10 – burned (no outlier)				0.41	0.21 ± 0.10	0.06	–12 ± 81	0.88
10 – unburned				0.10	–0.09 ± 0.10	0.34	163 ± 85	0.09
All studies, all FertN (n = 129)		203–1227		0.01	–0.06 ± 0.05	0.18	163 ± 23	0.0001
All sites by fertilization level:								
FertN 1–3 (n = 33)				0.01	–0.05 ± 0.08	0.51	94 ± 33	0.008
FertN 3–5 (n = 33)				0.01	0.06 ± 0.16	0.70	86 ± 62	0.17
FertN 5–10 (n = 45)				0.07	–0.11 ± 0.05	0.06	218 ± 34	0.0001
FertN 5–10 (no Konza unburned)				0.04	–0.08 ± 0.07	0.26	233 ± 42	0.0001
FertN 10–22.5 (n = 18)				0.18	–0.67 ± 0.35	0.07	479 ± 133	0.002

Appendix 4. Response of Fertilizer Use Efficiency (FUE) to variation in actual annual precipitation (AAP) within sites. FUE is the change in ANPP/added N. Equations are presented as FUE = $a + b*$AAP. Separate regressions are performed for each fertilizer level. Table variables are as in Appendix 2. Summary regressions for all sites within a given range of fertilization are shown at the bottom of the table. Where outliers have a large effect on parameters, regressions are performed both with and without the outliers.

Reference FertN level ($g N\cdot m^{-2}\cdot yr^{-1}$)	MAP (mm)	AAP range (mm)	Yrs data	r^2	slope	p	intercept	p
Lauenroth et al. 1978	311	203–501	5					
5				0.02	–0.027 ± 0.101	0.8	16.00 ± 27.1	0.59
Kilcher 1958	355	300–501	4					
3.8				0.98	0.098 ± 0.010	0.009	–25.40 ± 3.8	0.02
7.5				0.98	0.142 ± 0.015	0.01	–41.40 ± 5.9	0.02
Rogler & Lorenz 1957	406	260–516	6					
2.8				0.34	0.079 ± 0.035	0.046	–15.50 ± 16.1	0.36
8.4				0.30	0.065 ± 0.032	0.066	–13.60 ± 14.7	0.37
Smika et al. 1965	406	210-365	4					
1.9				0.87	0.191 ± 0.053	0.069	–40.40 ± 15.5	0.12
3.8				0.89	0.177 ± 0.045	0.059	–36.90 ± 13.13	0.10
7.5				0.96	0.125 ± 0.017	0.02	–25.70 ± 4.9	0.03
15.0				0.80	0.083 ± 0.030	0.11	–16.30 ± 8.7	0.20
Lorenz & Rogler 1972	406	304-593	6					
4.5				0.48	0.068 ± 0.036	0.13	–8.12 ± 14.5	0.61
9.0				0.56	0.055 ± 0.025	0.09	–3.60 ± 10.1	0.73
18.0				0.20	0.014 ± 0.014	0.37	3.59 ± 5.6	0.55
Power 1971	403	376–593	6					
0.6				0.00	–0.002 ± 0.084	0.97	19.30 ± 37.4	0.63
1.1				0.00	–0.008 ± 0.080	0.92	32.00 ± 35.5	0.41
2.2				0.02	0.022 ± 0.080	0.79	6.43 ± 35.9	0.86
4.5				0.23	0.069 ± 0.063	0.33	–11.20 ± 28.1	0.71
9.0				0.14	0.032 ± 0.040	0.469	0.38 ± 17.8	0.98
Power 1985	403	242–532	9					
4.5 (all cases)				0.02	0.038 ± 0.092	0.69	22.60 ± 37.2	0.56
4.5 (no outlier)				0.87	0.198 ± 0.046	0.005	–32.80 ± 17.8	0.11
22.5 (all cases)				0.00	0.005 ± 0.032	0.89	12.40 ± 17.7	0.36
22.5 (no outlier)				0.55	0.057 ± 0.021	0.037	–5.39 ± 8.2	0.53

Appendix 4. Continued.

Reference FertN level (g N·m^{-2}·yr^{-1})	MAP (mm)	AAP range (mm)	Yrs data	r^2	slope	p	intercept	p
Owensby et al. 1970	806	366–1050	4					
5.6				0.95	0.132 ± 0.022	0.03	–17.50 ± 18.6	0.45
Konza LTER	835	483–1227	10					
10 – burned (all cases)				0.35	0.072 ± 0.035	0.074	–14.00 ± 29.6	0.64
10 – burned (no outlier)				0.71	0.102 ± 0.010	0.0001	–25.10 ± 5.8	0.0001
10 – unburned (all cases)				0.12	–0.024 ± 0.023	0.30	40.50 ± 19.6	0.07
10 – unburned (no outlier)				0.12	–0.023 ± 0.024	0.37	40.80 ± 20.4	0.09
All studies, all fert. Combined (n = 121)		203–1227		0.49	0.083 ± 0.007	0.001	–14.50 ± 3.5	0.001
All sites by fertilization level:								
FertN 1–3 (n = 33)				0.11	0.046 ± 0.023	0.055	0.50 ± 10.1	0.96
FertN 3–5 (n = 33)				0.13	0.066 ± 0.033	0.056	–2.60 ± 13.3	0.84
FertN 5–10 (n = 45) (excludes Konza unburned)				0.64	0.092 ± 0.010	0.0001	–20.70 ± 5.3	0.0003
FertN 10–22.5 (n = 18)				0.32	0.039 ± 0.014	0.015	–2.30 ± 5.3	0.67

References

Benning TL & Seastedt TR (1995) Landscape-level interactions between topoedaphic features and nitrogen limitation in tallgrass prairie. Landscape Ecology 10: 337–348

Black AL (1968) N and phosphorus fertilization for production of crested wheatgrass and native grass in northeastern Montana. Agron. J. 60: 213–216

Blair JM (1997) Fire, nitrogen availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecol. 78: 2359–2368

Briggs JM & Knapp AK (1995) Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. Am. J. Bot. 82: 1024–1030

Burke IC, Kittel TGF, Lauenroth WK, Snook P & Yonker CM (1991) Regional analysis of the central Great Plains: sensitivity to climate variability. BioSci. 41: 685–692

Burke IC, Lauenroth WK & Parton WJ (1997) Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecol. 78: 1330–1340

Burzlaff DF, Fick GW & Rittenhouse LR (1968) Effect of nitrogen fertilization on certain factors of a western Nebraska range ecosystem. J. Range Manage. 21: 21–23

Chapin FS, III (1980) The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11: 233–260

Chapin FS, III (1991) Effects of multiple environmental stresses on nutrient availability and use by plants. In: Mooney HA, Winner WE & Pell EJ (Eds) Response of Plants to Multiple Stresses (pp 67–88). Academic Press, San Diego, U.S.A.

Chapin FS, III, Bloom AJ, Field CB & Waring RH (1987) Plant responses to multiple environmental factors. BioSci. 37: 49–57

Chapin FS, III, Vitousek PM & Van Cleve K (1986) The nature of nutrient limitation in plant communities. Am. Nat. 127: 48–58

Contreras DL & Gasto JM (1986) Rangeland type and fertilization comparison in the Mediterranean part of central Chile under grazing conditions. In: Joss PJ, Lynch PW & Williams OB (Eds) Rangelands: A Resource Under Siege. Proceedings of the Second International Rangeland Congress (pp 316–317). Cambridge University Press, Cambridge

Cooper CS & Hyder DN (1958) Adaptability and yield of eleven grasses grown on the Oregon high desert. J. Range Manage. 11: 235–237

Cosper HR & Thomas JR (1961) Influence of supplemental run-off water and fertilizer on production and chemical composition of native forage. J. Range Manage. 14: 292–297

Detling JK (1979) Processes controlling blue grama production on the shortgrass prairie. In: French NR (Ed.) Perspectives in Grassland Ecology (pp 25–42). Springer-Verlag, New York, U.S.A.

Detling JK (1988) Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. In: Pomeroy LR & Alberts JJ (Eds) Concepts of Ecosystem Ecology (pp 131–148). Springer-Verlag, New York, U.S.A.

Elisseou GC, Veresoglou DS & Mamolos AP (1995) Vegetation productivity and diversity of acid grasslands in Northern Greece as influenced by winter rainfall and limiting nutrients. Acta Oecologica 16: 687–702

Epstein HE, Lauenroth WK & Burke IC (1997) Effects of temperature and soil texture on ANPP in the U.S. Great Plains. Ecol. 78: 2628–2631

Epstein HE, Lauenroth WK, Burke IC & Coffin DP (1996) Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. J. Veg. Sci. 7: 777–788

Ettershank G, Ettershank J, Bryant M & Whitford WG (1978) Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. J. Arid Envir. 1: 135–139

Gay CW & Dwyer DD (1965) Effects of one year's nitrogen fertilization on native vegetation under clipping and burning. J. Range Manage. 18: 273–277

Goetz H (1969) Composition and yields of native grassland sites fertilized at different rates of nitrogen. J. Range Manage. 22: 384–390

Hunt HW, Ingham ER, Coleman DC, Elliott ET & Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecol. 69: 1009–1016

Huston, MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110: 449–460

Jacobsen JS, Lorbeer SH, Houlton HAR & Carlson GR (1996) Nitrogen fertilization of dryland grasses in the northern great plains. J. Range Manage. 49: 340–345

Jackson LE, Schimel JP & Firestone MK (1989) Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. Soil Biol. and Biochem. 21: 409–415

Johnston A, Smoliak S, Smith AD & Lutwick LE (1967) Improvement of southeastern Alberta range with fertilizers. Can. J. Plant Sci. 47: 671–678

Johnston A, Smoliak S, Smith AD & Lutwick LE (1969) Seasonal precipitation, evaporation, soil moisture, and yield of fertilized range vegetation. Can. J. Plant Sci. 49: 123–128

Kilcher MR (1958) Fertilizer effects on hay production of three cultivated grasses in southern Saskatchewan. J. Range Manage. 11: 231–234

Kilcher MR, Smoliak S, Hubbard WA, Johnston A, Gross ATH & McCurdy EV (1965) Effects of inorganic nitrogen and phosphorus fertilizers on selected sites of native grassland in western Canada. Can. J. Plant Sci. 45: 229–237

Klages MG & Ryerson DE (1965) Effect of nitrogen and irrigation on yield and botanical composition of western Montana range. Agron. J.: 78–81

Klipple GE & Retzer JL (1959) Response of native vegetation of the central great plains to applications of corral manure and commercial fertilizer. J. Range Manage. 12: 239–243

Knapp AK & Seastedt TR (1986) Detritus accumulation limits production of tallgrass prairie. BioSci. 36: 662–668

Lauenroth WK, Dodd JL & Sims PL (1978) The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36: 211–222

Lauenroth WK & Sala OE (1992) Long-term forage production of North American shortgrass steppe. Ecol. Appl. 2: 397–403

Le Houerou HN, Bingham RL & Skerbek W (1988) Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. J. Arid Environ. 15: 1–18

Le Houerou HN & Hoste CH (1977) Rangeland production and annual rainfall relations in the Mediterranean Basin and in the African Sahelo-Sudanian zone. J. Range Manage. 30: 181–189

Lodge RW (1959) Fertilization of native range in the northern great plains. J. Range Manage. 12: 277–279

Lorenz RJ & Rogler GA (1972) Forage production and botanical composition of mixed prairie as influenced by nitrogen and phosphorus fertilization. Agron. J. 64: 244–249

McGinnies WJ (1968) Effects of nitrogen fertilizer on an old stand of crested wheatgrass. Agron. J. 60: 560–562

McLendon T & Redente EF (1991) Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. Ecol. 72: 2016–2024

McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. Ecol. Monogr. 55: 259–294

Moser LE & Anderson KL (1965) Nitrogen and phosphorus fertilization of bluestem range. Trans. Kans. Acad. Sci. 67: 613–616

Noy-Meir I (1973) Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 4: 25–51

Noy-Meir I & Walker BH (1986) Stability and resilience in rangelands. In: Joss PJ, Lynch PW & Williams OB (Eds) Rangelands: A Resource under Siege. Proceedings of the Second International Rangeland Congress (pp 21–25). Cambridge University Press, Cambridge

Nye, P.H. & Tinker, P.B. 1977. Solute Movements in the Root-Soil System. Blackwell, Oxford

Owensby CE, Hyde RM & Anderson KL (1970) Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. J. Range Manage. 23: 341–346

Parton WJ & Risser PG (1979) Simulated impact of management practices upon the tallgrass prairie. In: French NR (Ed) Perspectives in Grassland Ecology (pp 135–155). Springer-Verlag, New York, U.S.A.

Power JF (1971) Evaluation of water and nitrogen stress on bromegrass growth. Agron. J. 63: 726–728

Power JF (1980a) Response of semiarid grassland sites to nitrogen fertilization: I. Plant growth and water use. Soil Sci. Soc. Am. J. 44: 545–550

Power JF (1980b) Response of semiarid grassland sites to nitrogen fertilization: II. Fertilizer recovery. Soil Sci. Soc. Am. J. 44: 550–555

Power JF (1985) Nitrogen-and water-use efficiency of several cool-season grasses receiving ammonium nitrate for 9 years. Agron. J. 77: 189–192

Power JF & Alessi J (1971) Nitrogen fertilization of semiarid grasslands: plant growth and soil mineral N levels. Agron. J. 63: 277–280

Risser PG (1988) Abiotic controls on primary productivity and nutrient cycles in North American grasslands. In: Pomeroy LR & Alberts JJ (Eds) Concepts of Ecosystem Ecology (pp 115–129). Springer-Verlag, New York, U.S.A.

Rogler GA & Lorenz RJ (1957) Nitrogen fertilization of northern great plains rangelands. J. Range Manage.: 156–160

Rogler GA & Lorenz RJ (1974) Fertilization of mid-continent range plants. In: Mays DA (Ed.) Forage Fertilization (pp 231–254). American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI, U.S.A.

Russel JS, Brouse EM, Rhoades HF & Burzlaff DF (1965) Response of sub-irrigated meadow vegetation to application of nitrogen and phosphorus fertilizer. J. Range Manage. 18: 242–247

Sala OE, Parton WJ, Joyce LA & Lauenroth WK (1988) Primary production of the central grasslands region of the United States. Ecol. 69: 40–45

Schimel DS, Braswell BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ & Townsend AR (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochemical Cycles 8: 279–293

Schimel DS, VEMAP Participants & Braswell BH (1997) Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol. Monogr. 67: 251–271

Schimel JP, Jackson LE & Firestone MK (1989) Spatial and temporal effects on plant-microbial competition for inorganic nitrogen in a California annual grassland. Soil Biol. Biochem. 21: 1059–1066

Seagle SW & McNaughton SJ (1993) Simulated effects of precipitation and nitrogen on Serengeti grassland productivity. Biogeochemistry 22: 157–178

Seastedt TR, Briggs JM & Gibson DJ (1991) Controls of nitrogen limitation in tallgrass prairie. Oecologia 87: 72–79

Seastedt TR & Knapp AK (1993) Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. Am. Nat. 141: 621–633

Seligman NG, Spharim I & Benjamin RW (1986) Nitrogen fertilizer application and income stability in semi-arid pastoral systems. In: Joss PJ, Lynch PW & Williams OB (Eds) Rangelands: A Resource under Siege. Proceedings of the Second International Rangeland Congress (pp 278–279). Cambridge University Press, Cambridge

Seligman NG & van Keulen H (1989) Herbage production of a Mediterranean grassland in relation to soil depth, rainfall, and nitrogen nutrition: A simulation study. Ecological Modeling 47: 303–311

Seligman NG, van Keulen H & Spitters CJT (1992) Weather, soil conditions and the inter-annual variability of herbage production and nutrient uptake on annual Mediterranean grasslands. Agricultural and Forest Meteorology 57: 265–279

Smika DE, Haas HJ & Power JF (1965) Effects of moisture and nitrogen fertilizer on growth and water use by native grass. Agron. J. 57: 483–486

SPSS Inc. (1997) SYSTAT for Windows: Graphics, Version 7.0 Edition. Chicago, Illinois, U.S.A.

Stephens G & Whitford WG (1993) Responses of *Bouteloua eriopoda* to irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. J. Arid Environ. 24: 415–421

Thomas JR & Osenbrug A (1959) Effect of manure, nitrogen, phosphorus, and climatic factors on the production and quality of bromegrass-crested wheatgrass hay. Agron. J. 51: 63–66

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol. Monogr. 57: 189–214

Turner CL, Blair JM, Schartz RJ & Neel JC (1997) Soil N and plant responses to fire, topography and supplemental N in tallgrass prairie. Ecol. 78: 1832–1843

Van Keulen H & Seligman NG (1992) Moisture, nutrient availability and plant production in the semi-arid region. In: Alberda T et al. (Eds) Food from Dry Lands (pp 25–81). Kluwer Academic, Dordrecht, The Netherlands

Vitousek PM, Aplet G, Turner D & Lockwood JJ (1992) The Mauna Loa environmental matrix: foliar and soil nutrients. Oecologia 89: 372–382

Vitousek PM, Turner D, Parton W & Sanford R (1994) Litter decomposition on the Mauna Loa Environmental Matrix, Hawaii: Patterns, mechanisms and models. Ecol. 75: 418–429

Wight JR (1976) Range fertilization in the northern great plains. J. Range Manage. 29: 180–185

Wight JR & Black AL (1979) Range fertilization: Plant response and water use. J. Range Manage. 32: 345–349

Wilkinson SR & Langdale GW (1974) Fertility needs of the warm-season grasses. In: Mays DA (Ed.) Forage Fertilization (pp 119–145). American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI, U.S.A.

Zak DR, Tilman D, Parmenter RR, Rice CW, Fisher FM, Vose J, Milchunas D & Martin CW (1994) Plant production and soil microorganisms in late-successional ecosystems: A continental scale study. Ecol. 75: 2333–2347