

Chapter 12

INTERACTIONS OF WATER AND NITROGEN ON PRIMARY PRODUCTIVITY ACROSS SPATIAL AND TEMPORAL SCALES IN GRASSLAND AND SHRUBLAND ECOSYSTEMS

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1. The driving influence of water on spatial patterns of global and regional scale primary productivity in grasslands and shrublands

Soil moisture, and hence precipitation, exerts a dominant control on net primary productivity (NPP; the rate of carbon accumulation by autotrophs) in semiarid to sub-humid ecosystems, such as grasslands and shrublands. At the global scale, mean annual precipitation has been shown to account for >50% of the variance in aboveground net primary production (ANPP) in grassland ecosystems (Lauenroth 1979, Le Houérou et al. 1988). Within specific regions, numerous investigators have demonstrated strong positive relationships between mean annual precipitation and primary productivity (or some surrogate variable) for various ecosystems globally, including the Great Plains grasslands (Sala et al. 1988, Epstein et al. 2002), the Patagonian steppe (Austin and Sala 2002, Jobbágy et al. 2002), African grasslands and savannas (Bremen and de Wit 1983, McNaughton et al. 1993, Scanlon et al. 2002) and grasslands and shrublands of Inner Mongolia and northeastern China (Gao and Yu 1998, Yu et al. in press). Environmental factors other than precipitation, yet directly related to soil moisture, such as temperature and soil texture, have also been shown to be important regional-scale controls over primary productivity in grasslands and shrublands (Noy-Meir 1973, Sala et al. 1988, Epstein et al. 1996, 1997, Lane et al. 1998, Jobbágy et al. 2002).

2. Moisture controls on the interannual variability in primary productivity for grasslands and shrublands

Interannual variability in net primary productivity for grasslands and shrublands is also substantially controlled by precipitation and soil moisture. Growing season rainfall explained 43% of the interannual variance in forage production for a northeastern Colorado shortgrass steppe ecosystem over a 52-year period (Lauenroth and Sala 1992), and annual precipitation explained 37% of net primary production for a northeastern Kansas tallgrass prairie, from a 19-year dataset (Briggs and Knapp 1995). Using irrigation treatments over an 8-year period, Knapp et al. (2001) found that 81% of ANPP was explained by the annual water inputs, also for tallgrass prairie in Kansas.

Lauenroth and Sala (1992) noted that the interannual response of ANPP to changes in precipitation (in this case for a shortgrass steppe ecosystem of northeastern Colorado) was less than the spatial response for an equivalent precipitation change (e.g. Sala et al. 1988) (Figure 1), suggesting that at a given site, there were constraints on productivity responses to changing moisture. This idea was examined further for temperate grasslands globally using ANPP field data, and for grasslands along a mean annual precipitation gradient in the U.S. Great Plains, using remote sensing data (Paruelo et al. 1999b). Both the field data and the remote sensing data (which used the Normalized Difference Vegetation Index [NDVI] as a surrogate for ANPP) demonstrated that the temporal responses of ANPP to changes in moisture availability were constrained relative to spatial patterns at both the dry and wet extremes of the precipitation gradient (Figure 2).

The explanation for these findings was related to both vegetation and biogeochemical constraints on ecosystem response to fluctuating moisture conditions (see also Chapters 2, 3, and 11). At the dry end of the precipitation gradient (approximately $<400 \text{ mm yr}^{-1}$), the plant community is dominated, as would be expected, by drought-resistant species. These species have traits such as high allocation of tissue to belowground structures (e.g. roots and rhizomes) rather than leaves, low leaf area relative to leaf mass, and low stomatal conductance to restrain water loss. These plant traits, coincident with drought-tolerance, are the same traits that would constrain the rates of photosynthesis and growth of these plants in response to variable moisture (Tilman 1988, Keddy 1992, Grime 1977).

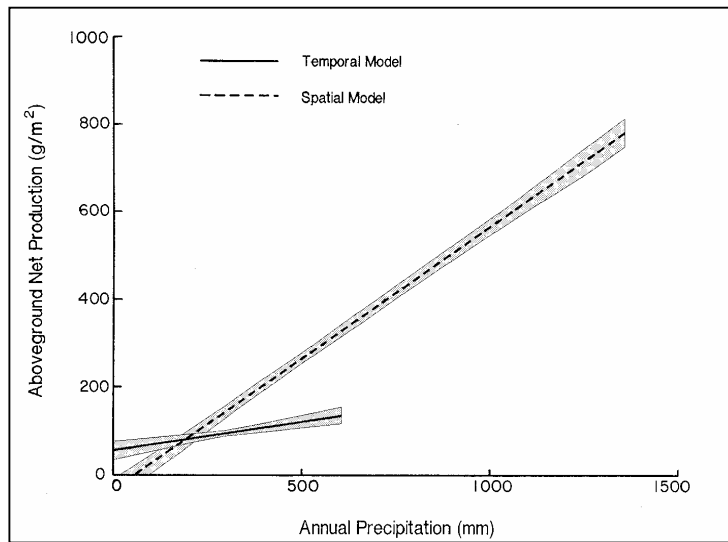


Figure 1. Temporal and spatial response of aboveground net primary production (g m^{-2}) to changes in annual precipitation (from Lauenroth and Sala 1992).

At the wet end of the precipitation gradient (approximately $>800 \text{ mm yr}^{-1}$), primary productivity also does not respond substantively to interannual variability in precipitation (Hooper and Johnson 1999, Paruelo et al. 1999b). These constraints in the vegetation response to moisture, however, may not be related to plant traits (as is hypothesized for the drier end of the gradient). The dominant plant species at the wet end of the mean annual precipitation gradient (typically tallgrasses) tend to have greater plasticity in their photosynthetic and growth-related properties than do the drought-tolerant species. Paruelo et al. (1999a) illustrate this for grass

species that dominate in different portions of the typical mean annual precipitation gradient for grassland regions. In a greenhouse experiment using species from grasslands of both North and South America, they showed that the magnitude of plant response to drought, in characteristics such as relative growth rate, transpiration, tiller production and leaf expansion, increased from arid to sub-humid ecosystems (Figure 3).

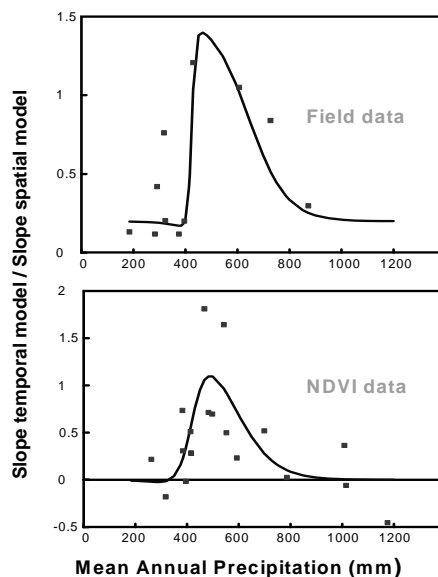


Figure 2. Temporal response of aboveground net primary productivity (from field data and represented by the normalized difference vegetation index [NDVI]) to interannual precipitation variability, along a spatial gradient of increasing mean annual precipitation (from Paruelo et al. 1999b). Points represent the slopes of the regression between MAP and either ANPP (top) or NDVI (bottom) for specific sites (temporal relationship) normalized by the slope of the spatial relationship between MAP and either ANPP (0.64) or NDVI (0.48). Lines are double logistic functions fitted to the data.

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In the absence of vegetation-related constraints to primary productivity responses, an alternative explanation was proposed related to biogeochemical properties of these systems, with a particular emphasis on nitrogen (Breman and de Wit 1983, Burke et al. 1997, see next section).

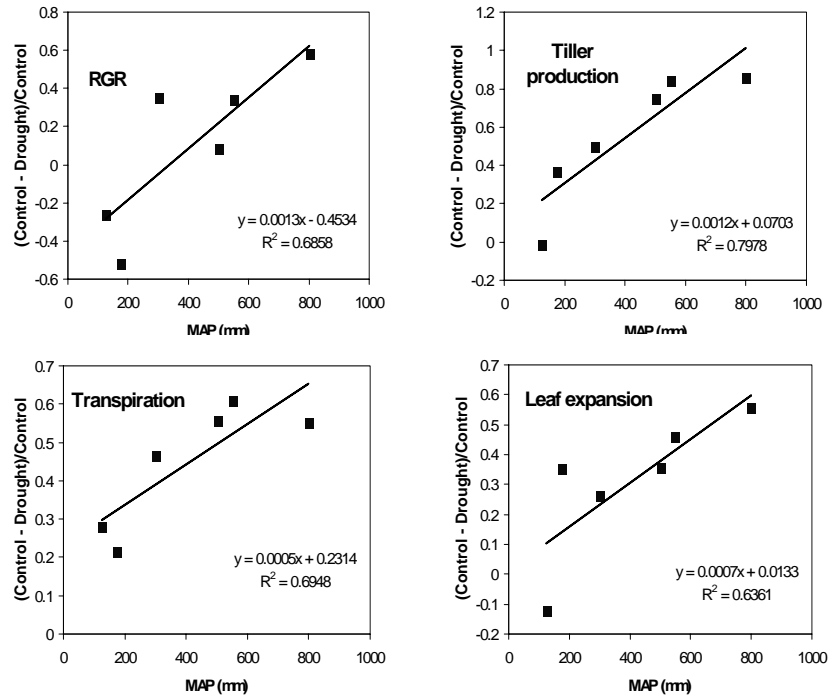


Figure 3. Responses of relative growth rate (RGR), tiller production, transpiration and leaf expansion to drought conditions along a spatial gradient of mean annual precipitation. The y-axis represents the response of the particular function to drought (control – drought) normalized by the rate of the function under control conditions, i.e. the relative response of the function to drought. The species analyzed are dominant at the mean annual precipitation level indicated on the x-axis in South American (SA) and North American (NA) grasslands. The species included in the analysis are *Stipa humilis* (SA), *Poa ligularis* (SA), *Festuca pallescens* (SA), *Hilaria jamesii* (NA), and *Stipa viridula* (NA). Reconstructed from Paruelo et al. (1999a).

3. The relationship between soil water and soil nitrogen availability at the regional scale and the relative limitations of these factors to primary productivity

While soil moisture clearly exerts a strong positive effect on net primary productivity in grasslands and shrublands, water also positively influences plant-available nitrogen in soils (e.g. Drury et al. 2003, Paul et al. 2003; see also Chapter 11); this in turn can stimulate primary productivity across a variety of ecosystems, as demonstrated in numerous experimental studies (see Hooper and Johnson 1999 for a comprehensive list) and in simulation modeling (Schimel et al. 1997b). Burke et al. (1997) found that mean annual precipitation explained 94% of the spatial variability in simulated net nitrogen (N) mineralization (the rate at which plant-available forms of nitrogen accumulate in soils), using the CENTURY model (Parton et al. 1987) for sites with

constant mean annual temperature in the U.S. Great Plains. They also found that 40% of the interannual variability in simulated net N mineralization could be explained by annual rainfall.

One field study in Patagonian grasslands, shrublands and forests found that mean annual precipitation was positively associated with, and explained 96% of the variability in, soil ammonium (NH_4^+) levels (Austin and Sala 2002). Not surprisingly, ANPP was also strongly and positively related to total inorganic soil nitrogen in that study. Other field studies, however, conducted in the Great Plains to evaluate the relationships among interannual variability in precipitation, nitrogen availability and productivity across a transect from semiarid to sub-humid sites have been much less conclusive (Barrett et al. 2002), suggesting that net nitrogen mineralization rates may not vary systematically across precipitation gradients. In general it is very difficult to assess nitrogen availability across regional and landscape spatial gradients (Zak et al. 1994, Hook and Burke 2000, Barrett et al. 2002). As net primary production, soil organic matter and soil microbial biomass all increase with increasing precipitation, so does the nitrogen immobilization potential of the soil (Barrett and Burke 2000, 2002). Thus net nitrogen mineralization, or perhaps our ability to estimate it, may not necessarily change across these moisture gradients.

So, it is rather apparent that water has a strong positive relationship with primary productivity in semiarid to sub-humid ecosystems. Water may also have a positive relationship with net nitrogen mineralization and plant-available soil N. However some field studies have shown otherwise for regional moisture gradients (Barrett and Burke 2000, Barrett et al. 2002) and have suggested that while gross N mineralization might increase along precipitation gradients, N immobilization by decomposers might increase as well. Since several studies have found that ANPP is more responsive than net N mineralization to spatial increases in precipitation (Seagle and McNaughton 1993, Burke et al. 1997, Austin and Sala 2002, Barrett et al. 2002), this suggests that nitrogen may become more limiting to grassland and shrubland ecosystems as water availability is augmented. There are several pieces of evidence supporting this idea that N limitation increases with available water in grasslands and shrublands.

First, there are more data demonstrating nitrogen limitations to primary productivity in tallgrass prairie ecosystems (e.g. Owensby et al. 1970, Risser and Parton 1982, Knapp and Seastedt 1986, Tilman 1987, Seastedt et al. 1991, Benning and Seastedt 1995, Turner et al. 1997) than there are in shortgrass steppe or desert ecosystems (Ettershank et al. 1978, Lauenroth et al. 1978, Dodd and Lauenroth 1979, Horn and Redente 1998). Tallgrass prairie in the Great Plains of the U.S. typically receives approximately 50-100% more annual rainfall than shortgrass steppe (Paruelo et al. 1995). Additionally, N amendments to shortgrass steppe ecosystems showed greater responses under wetter conditions (Dodd and Lauenroth 1979), whereas tallgrass prairie exhibited large responses to N additions in all but the driest years (Owensby et al. 1970).

Second, there is evidence that plant nitrogen-use efficiency increases with increasing water availability in the U.S. Great Plains (Schimel et al. 1991, Vinton et al. 1993, Vinton and Burke 1995, Murphy et al. 2002) and in the Sahel and savannas of West and Central Africa (Breman and de Wit 1983), suggesting increased N limitations to plant productivity (Vitousek 1982) with increasing soil moisture. Oyarzabal et al. (submitted) analyzed 12 grass species from areas differing in mean annual precipitation and found that N conservation within plants [as indicated by N resorption efficiency from leaves, defined as $(\text{N in green leaves} - \text{N in senescent leaves}) / \text{N in green leaves}$] increased significantly across an annual rainfall gradient (Figure 4) (see Austin and Sala 2002 however for opposing results). So, if the efficiency of nitrogen-use increases along a precipitation gradient then N availability need not increase to the same extent as water availability, and the increase in ANPP will still occur. Therefore there is some information supporting the idea that vegetation constraints limit primary productivity responses to moisture changes in drier areas and that resources (possibly nitrogen) exhibit greater limitations to primary productivity as water limitations decline.

4. Examining the hypothesis that nitrogen limitation in grasslands and shrublands increases as water limitation declines

It has been assumed that as annual precipitation increases in dryland ecosystems, so will plant demand for nitrogen (Seagle and McNaughton 1983, Hooper and Johnson 1999). N availability may or may not increase with mean annual precipitation, yet if any increase in N availability does not meet the increasing plant demand for nitrogen (Seagle and McNaughton 1993, Burke et al. 1997, Barrett et al. 2002), then nitrogen will become more limiting as precipitation increases.

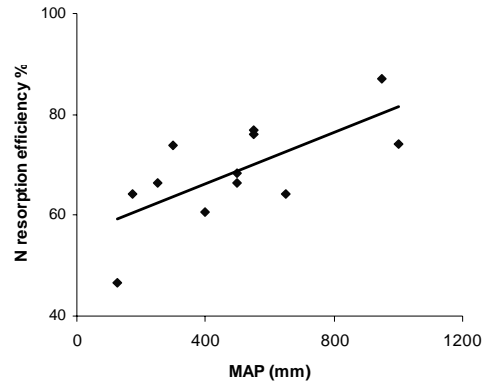


Figure 4. Relationship between the nitrogen resorption efficiency % [defined as $(N \text{ in green leaves} - N \text{ in senescent leaves}) / N \text{ in green leaves}$] and the mean annual precipitation where the species is dominant for 12 grasses of North and South America. (Redrawn from Oyarzabal et al. submitted)

Hooper and Johnson (1999) used a meta-analytical approach to test this hypothesis that nitrogen limitation increases with increasing soil moisture in dryland ecosystems. In their analysis of over 50 studies of nitrogen fertilization experiments in grasslands and shrublands globally, they found that neither the relative response nor the maximum response of ANPP to N fertilization increased with increasing moisture. Fertilizer-use efficiency, and hence an absolute response, did however increase significantly with spatial and temporal increases in moisture. Their conclusions were that water and nitrogen co-limit ANPP along spatial and temporal gradients of moisture, and there is likely no switch from water-limited to nitrogen-limited systems as moisture increases.

Two alternative hypotheses that arise from these results are: 1) ANPP, plant N demand and N availability all increase similarly along moisture gradients (this is the scenario proposed by Hooper and Johnson 1999) or 2) plant N demand and N availability vary similarly along moisture gradients, yet increase to a lesser extent than does ANPP with increasing precipitation. The latter of the two hypotheses, with regard to changes in N availability along precipitation gradients, is better supported by the published data, as mentioned above (Seagle and McNaughton 1993, Burke et al. 1997, Austin and Sala 2002, Barrett et al. 2002). In addition, nitrogen-use efficiency has been shown to increase (i.e. relative plant N demand decreases) with increasing precipitation (Breman and de Wit 1983, Schimel et al. 1991, Vinton et al. 1993, Vinton and Burke 1995, Murphy et al. 2002). The relative lack of response to N additions in sub-humid grasslands along the precipitation gradient implies that the demonstrated increase in N-use efficiency with increasing moisture may not be the result of nitrogen limitation, but rather could be inherent in the structure and function of the taller vegetation.

Hooper and Johnson (1999) found several other intriguing results in their analysis. The first is that, with few exceptions, nitrogen was equally or more limiting than water in terms of the

relative response of ANPP across the entire precipitation gradient, and secondly, the relative responses of ANPP to water, nitrogen, and water plus nitrogen were all greatest at moderate levels of mean annual precipitation ($\sim 500 \text{ mm yr}^{-1}$) (Figure 5). This at the very least corroborates the Paruelo et al. (1999b) findings of greatest response to moisture at intermediate levels of annual precipitation, and also suggests a constraint to productivity in addition to water and nitrogen in dry areas (vegetation properties, for example). However the nature of the constraint at the sub-humid end of the gradient remains puzzling, as it appears not to be nitrogen.

Light limitation and grazing may explain the response of ANPP to soil moisture variability in subhumid ecosystems. At the wettest extreme of the precipitation gradient, light could constrain the ANPP response to both water and nitrogen. Altesor et al. (in press) found, for tallgrass prairies of Uruguay, that the ANPP in ungrazed sites was less than ANPP in grazed sites, even though quantities of soil nitrogen and water were greater under ungrazed conditions. When standing dead biomass was experimentally removed, effectively increasing the within-canopy light level, the ungrazed sites produced more than both grazed sites and intact grazing exclosures.

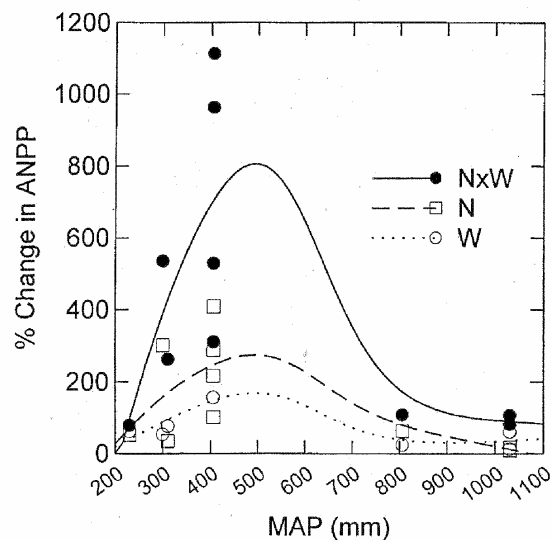


Figure 5. Relative response of aboveground net primary production (ANPP) to additions of water, nitrogen and water plus nitrogen, along a gradient of mean annual precipitation (MAP) (from Hooper and Johnson 1999). Points represent the relative response of ANPP from a variety of water addition and N fertilization studies conducted in grasslands receiving differing levels of annual precipitation. Curves are fitted by a distance weighted least squares procedure for nitrogen and water additions (N x W), nitrogen additions only (N) and water additions only (W).

Grazing can also obscure water and nitrogen relationships at the regional scale, because herbivores may consume the greatest proportions of ANPP at the wet extreme of the precipitation gradient (Oesterheld et al. 1992). Piñeiro et al. (submitted) showed using simulation modeling that the reduction in N mineralization induced by grazing increases from the dry to the wet end of the precipitation gradient (Figure 6), thereby modifying water and nitrogen relationships. Hence both light and grazing could be constraining ANPP responses to water and nitrogen at the wet extreme of the precipitation gradient.

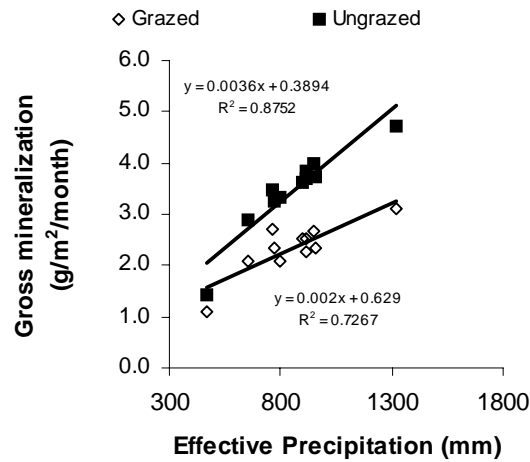


Figure 6. Changes in gross nitrogen mineralization rates for heavily grazed and ungrazed sites over 400 years along a precipitation gradient in South America, as simulated by the CENTURY model (Parton et al., 1987) (from Piñeiro et al. submitted).

So clearly, this is not the final say in the matter, and several questions beg for further examination. Do water and nitrogen co-limit productivity in dryland ecosystems across the range of annual precipitation values? Is nitrogen equally as limiting as (or even more limiting than) water in arid and semi-arid grasslands and shrublands? What does constrain ecosystem response to changes in water and nitrogen availability in sub-humid grasslands and shrublands? Figure 7 summarizes the available evidence into a new conceptual framework describing the relative importance of different types of constraints on the response of ANPP along a precipitation gradient.

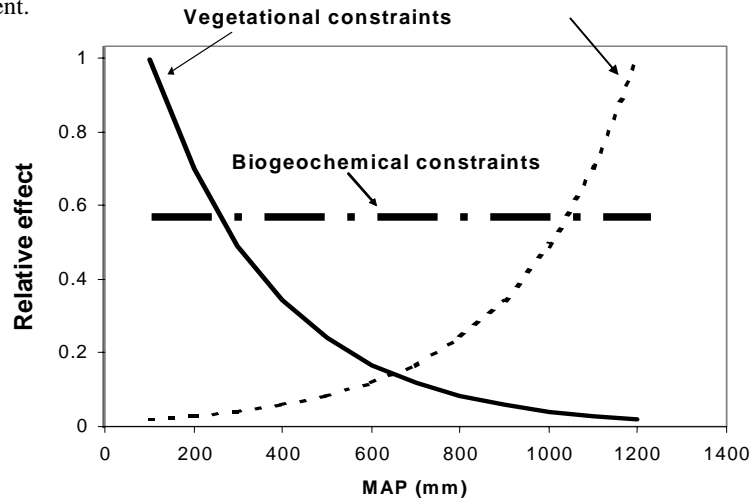


Figure 7. Conceptual diagram of the relative effects of the proposed constraints on primary productivity along a gradient of mean annual precipitation (MAP). While plant properties constrain the productivity response to water in dry ecosystems, the evidence suggests that nitrogen limitation does not vary along a precipitation gradient. A resource other than available nitrogen is likely constraining the productivity response to water in subhumid ecosystems (e.g. light).

5. Landscape-scale relationships between water and nitrogen

In order to assess the co-limitation of water and nitrogen to primary productivity in grasslands and shrublands, we can attempt to examine the relationships between water and nitrogen across topographic, soil texture and disturbance gradients within a landscape. Topography affects water redistribution, which modifies soil moisture (see Chapter 7) and is an important control of the spatial and interannual variability in net primary production at the landscape scale (Schimel et al. 1985, Briggs et al. 1989, Milchunas et al. 1989, Knapp et al. 1993, Briggs and Knapp 1995, Singh et al. 1998). As an example, lowland topographic positions in tallgrass prairie in northeastern Kansas generally have greater aboveground net primary productivity than upland topographic positions (Briggs and Knapp 1995), likely due to greater soil moisture (Knapp et al. 1993). The responses of both total ANPP and grass ANPP were controlled to a greater extent by precipitation (both total and growing season) in upland tallgrass prairie compared to lowland tallgrass prairie (Briggs and Knapp 1995), and interannual variability in ANPP was greater in the upland sites relative to the lowland sites (Knapp et al. 2001). These results suggest that rainfall exhibits a greater limitation to productivity at the dry uplands sites compared to wetter lowland sites, at the landscape scale.

In addition to controlling net primary production, topography (through its effects on soil moisture and other ecosystem properties) can influence rates of gross and net nitrogen mineralization (e.g. Schimel and Parton 1986, Burke et al. 1989, Verchot et al. 2002). However, while it seems reasonable that landscape-scale gradients of water availability and nitrogen availability should be spatially correlated (and controlled largely by topography), this is frequently not the observed pattern; several studies have shown that whereas soil moisture increases from upper to lower slope positions, the same is not always true for nitrogen availability. Hook and Burke (2000) found that, for the shortgrass steppe, net N mineralization rates were not significantly related to topography. Results from Turner et al. (1997) for the tallgrass prairie showed that net N mineralization rates were substantially greater in the drier uplands than the wetter lowlands. Many additional studies demonstrate that direct effects of soil texture, soil organic matter, fire and grazing on net N mineralization rates are often greater than those of topographically-driven soil moisture (Burke 1989, Turner et al. 1997, Tracy and Frank 1998, Augustine and Frank 2001, Delin and Linden 2002).

Landscape-scale topographic gradients therefore may not be very conducive for studying the relative limitations of water and nitrogen on primary productivity in dryland ecosystems. Nitrogen fertilization experiments conducted across topographic gradients of soil moisture may have highly variable initial conditions with respect to levels of soil organic and inorganic N, and net N mineralization rates; and given the current state of the science, these pools of nitrogen and net N mineralization rates are not necessarily predictable across topographic moisture gradients. Either spatially extensive (encompassing a wide range of initial conditions) or very controlled experiments would need to be done to assess the relative limitations of water and nitrogen to primary productivity across landscape-scale moisture gradients.

Grazing and fire are recurrent disturbances in dryland ecosystems and both have a strong influence on water and nitrogen dynamics across landscapes; the effects of these particular disturbances on N and water availability are not always easily predictable. For example, grazing has been shown to either increase (Frank & Evans 1997) or decrease (Verchot et al., 2002) N mineralization rates at Yellowstone National Park depending on the age of the grazing exclosures.

Fire can increase N availability in the first few months after the disturbance (Laterra et al. 2001) yet decrease overall soil N content after several years of recurrent fires (Oesterheld et al., 1999). Spatial heterogeneity of grazing may contribute to nutrient patchiness through positive feedbacks on nutrient cycling in heavily grazed locations (McNaughton et al. 1997). Interactions among disturbances and landscape features therefore provide additional complexity to the analysis of nitrogen and water interactions. As an example, grazing could reverse the expected patterns of

plant nitrogen content generated by water availability along a topographic sequence. In the Mesopotamic Pampa of Argentina the nitrogen content of both litter and aboveground biomass generally increases from uplands to lowlands in ungrazed areas, however grazing has been shown to alter this pattern (Figure 8, G. Piñeiro et al. unpublished data).

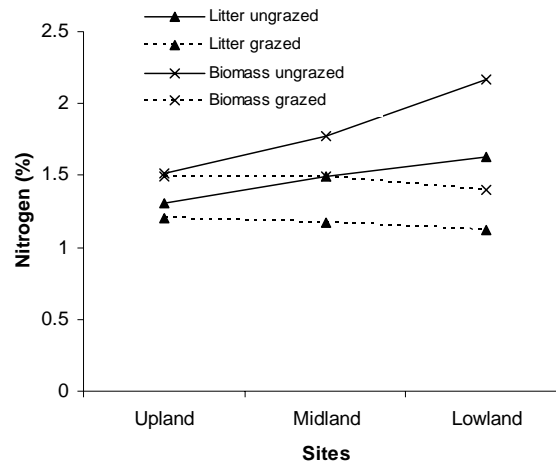


Figure 8. Changes in nitrogen content of litter and aboveground plant biomass in grazed and ungrazed grassland plots across a topographic gradient, at El Palmar National Park, Argentina.

6. Fine temporal scale relationships between water and nitrogen – pulses of resources and the relative limitations of water and nitrogen on plant growth

One other approach for addressing the relative limitations of these plant resources is to examine how water and nitrogen vary over fine temporal scales at a given site, and how individual plants may be limited temporally by either water or nitrogen. The logistics and costs involved with taking frequent *in situ* measurements of either gross or net nitrogen mineralization limit the data available for determining how plant-available N varies over fine temporal scales (e.g. hours, days, weeks) in response to variable soil moisture. Fluxes of NO and N₂O from soils, however, have been measured more frequently, and the data suggest pulse accelerations of nitrogen cycling processes with temporal increases in soil water content (e.g. Parton et al. 1988, Davidson et al. 1993, Hutchinson et al. 1993, Epstein et al. 1998, Martin et al. 1998, Smart et al. 1999).

Laboratory incubation studies examining the effects of soil moisture on nitrogen mineralization do show strong positive effects of soil water content on nitrogen mineralization rates across the range of unsaturated conditions; the relationships found between soil water content and nitrogen mineralization are generally non-linear and may have threshold values, where the nature of the relationship changes (Linn and Doran 1984, Low et al. 1997, Drury et al. 2003, Paul et al. 2003). Simulation models typically use first-order kinetics to describe nitrogen mineralization, where the decay rate terms (which act on dead organic matter pools) are functions of soil temperature, soil moisture, dead organic matter C:N ratio and microbial biomass (Herlihy 1979, Cabrera and Kissel 1988, Parton et al. 1988, Das 1995, Vigil et al. 2002, Porporato et al. 2003).

Applying these concepts to the field, of course, is difficult. Grassland and shrubland ecosystems are characterized by low annual rainfall with a high frequency of low precipitation events (< 10mm) and frequent dry periods lasting several days or longer (Sala and Launroth 1982,

Sala et al. 1992). How this temporal variability in moisture relates to the temporal variability in plant-available nitrogen is still extremely unclear. At the seasonal scale, rainfall and soil water status may dictate the seasonality of nitrogen mineralization rates (Jamieson et al. 1999), however at finer temporal scales the relationship is more complex. Schimel and Parton (1986) suggested that additional small rainfall events in shortgrass steppe ecosystems would not increase the total N mineralized, however some studies in the Great Basin of the U.S. have found that not only did rainfall events temporarily stimulate nitrate production (Cui and Caldwell 1997a), but plants were also able to capitalize on the pulses of available nitrogen following small precipitation episodes (Cui and Caldwell 1997b, Ivans et al. 2003).

So, small rainfall events in dryland ecosystems may stimulate the mineralization of nitrogen during brief periods when water is not directly limiting for photosynthesis. Other than event size, additional attributes of temporal precipitation patterns will influence water-nitrogen interactions as well. The length of the dry period between rainfall events may affect nutrient pulses during wetting, as a substantial portion of microorganisms may desiccate and die during these dry periods, entering a labile pool of soil organic matter (Bottner 1985, Kieft et al. 1987, Olf et al. 2004). The frequency of drying and rewetting cycles can also influence the cumulative quantities of net nitrogen mineralized and nitrified (Fierer and Schimel 2002, Olf et al. 2004, Burke et al. unpublished data).

7. Limitations of water and nitrogen across temporal scales

The co-limitation of water and nitrogen with respect to photosynthesis and plant growth has been demonstrated by field studies (Klages and Ryerson 1965, Smika et al. 1965, Lauenroth et al. 1978, Hamerlynck et al. 2004), laboratory experiments (Heitholt et al. 1991, Ciompi et al. 1996), and ecophysiological and ecosystem models (Peri et al. 2003 and Friend 1995, respectively). One interesting aspect of the relationship between these two resources is the timeframe of their limitations in arid to sub-humid ecosystems, which is related to the nature of their storage mechanisms. Water in plants and near-surface soils has a relatively short residence time (although certain plant types such as succulents can increase the duration of residence), and therefore the degree of water limitation can vary substantially over fine temporal scales, especially in dryland ecosystems. Deeply-rooted plants in dry ecosystems, however, can tap into soil reservoirs with high water content including groundwater, thereby reducing the variability of water limitations and at times eliminating water stress completely, when precipitation is low (Soriano and Sala 1983, Sala et al. 1989, Knoop and Walker 1985, Dodd et al. 1998). Nitrogen, on the other hand, can have relatively long residence times in plant tissue, and therefore nitrogen limitations to plant productivity may be less variable than water limitations (Schimel et al. 1997a).

In addition, plants may take up excess nitrogen during periods when it is not the limiting resource for use under future conditions (Chapin et al. 1986, Seastedt and Knapp 1993). Soil organic matter represents an even longer-term storage pool for nitrogen.

Therefore changes in water limitations in dryland ecosystems most often occur over fine temporal scales (e.g. minutes to days – with the exception of very deep-rooted plants), whereas nitrogen limitations have a more historical nature, resulting from the integration of plant-soil processes that occurred under prior conditions (e.g. days to years). Given the complexity of these dynamics, the effect of the co-limitation of water and nitrogen on primary productivity in dryland ecosystems, where precipitation is relatively low yet variable across many time scales (at least minutes through years), is still a subject worthy of extensive research.

8. Summary

At the regional scale, it has been thought that water limitations to primary production decrease, and nitrogen limitations to primary production increase, with increasing mean annual precipitation in dryland ecosystems. Hooper and Johnson (1999), in a comprehensive review of fertilization experiments across precipitation levels, found that the relative response of primary productivity to N fertilization does not increase with increasing precipitation, suggesting that sub-humid ecosystems are no more N-limited than semiarid ecosystems. They reasoned that if net primary productivity, N availability and plant nitrogen demand all increase similarly along precipitation gradients, then the relative response of plants to N fertilization will not vary along these gradients.

Since the Hooper and Johnson study in 1999, however, several studies have added to the evidence that N-availability either does not vary or increases to a lesser extent than net primary productivity along precipitation gradients (Austin and Sala 2002, Barrett and Burke 2002, Barrett et al. 2002); this begs for an alternative explanation of why the NPP response to N fertilization does not vary along precipitation gradients. One potential explanation is that plant nitrogen demand either does not vary or increases to a lesser extent than NPP along these gradients, an idea already supported by greater C:N ratios in wetter areas along moisture gradients (e.g. Murphy et al. 2002). Greater nitrogen-use efficiencies, in general, might not necessarily be indicative of nitrogen limitation, but may indicate less of a demand for nitrogen by plants.

Both Paruelo et al. (1999b) and Hooper and Johnson (1999) found that primary productivity responses to changes in water and N were greatest at intermediate levels of mean annual precipitation (~400-700 mm yr⁻¹), areas that are likely to be composed of a mixture of shorter and taller plant species. These results also suggest constraints to primary productivity responses at lower and higher levels of annual precipitation; structural and functional properties of the vegetation may be the culprits at both ends of gradient, although more work is clearly necessary here. The interactions between water and nitrogen over space and time, and their effects on plant productivity, are quite complex, and past research efforts have only scratched the surface of underlying mechanisms.

9. Acknowledgements

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