Water and fertilizer have opposite effects on plant species richness in a mesic early successional habitat

M. Henry H. Stevens[1,]*, Rebecca Shirk[2] and Claire E. Steiner[1]
[1]*Department of Botany, Miami University, Oxford, OH, 45056, USA; [2]Oberlin College, Oberlin, OH, USA;
*Author for correspondence (e-mail: stevenmh@muohio.edu)

Abstract

Herbaceous plant species richness typically declines with increasing productivity, but differences in the resources underlying these gradients are often ignored. This study adds to the small number of studies examining the effects of water and mineral nutrients on biomass and richness in oldfield communities. We established 60 4 m² plots in a goldenrod-dominated oldfield to test the differential effects of water and mineral nutrients on community properties. Species richness declined with added nutrients, but increased with added water. Aboveground biomass increased only when both nutrients and water were added. Leaf area index increased with added nutrients alone, although the increase was greater when water was also added. Understory light levels decreased with added nutrients, but not with added water; however, the per-gram effect of biomass on understory light levels did not vary significantly among nutrient and water treatments. Our results suggest that water tends to enhance productivity, but does not cause the common decline in species richness that typically accompanies nitrogen additions. Rather, water increased richness through positivie effects on either germination and establishment, or increased survival. These results are consistent with either increased light limitation or increased water limitation causing loss of species from nitrogen-rich habitats.

Introduction

Herbaceous plant species richness frequently declines as productivity rises, but perhaps in our search for generality we have overlooked many of the details of this phenomenon. The models of resource competition thought to explain this pattern (Grime 1973, 1979; Newman 1973; Huston, 1979; Tilman 1982; Goldberg and Miller 1990; Tilman and Pacala 1993; Oksanen 1996; Cahill 1999; Stevens and Carson 1999; Rajaniemi 2003) do not typically differentiate between different resources regarding their effects on biomass: increased "soil resources" are thought to drive down

diversity through their influence on above- and belowground biomass. This assumption of equivalence of resources and equivalence of biomass, however, does not always seem consistent with available data (DiTomasso and Aarssen 1989; Carson and Pickett 1990; Goldberg and Miller 1990), and effects of different types of resources on species richness requires further investigation.

Mineral nutrients differ in the details of their uptake and utilization by plants, and in their effects on plant structures (Larcher 1995; Marschner 1995), but not nearly so radically as the differences between mineral nutrients and water. Plant water requirements differ radically from

mineral nutrient requirements; plants retain only a tiny fraction of the water they take up, requiring large amounts to maintain energy balance, and to transport nutrients and the products of photosynthesis and metabolism. Goldberg and Novoplansky (1997) point out that plants typically cannot store or recycle water as well as they can mineral nutrients (Chapin III et al. 1990), and may therefore suffer greater mortality during low water periods than during low nutrient periods.

Mineral nutrients and water may interact in their effects on individuals. Adding mineral nutrients may increase individual aboveground biomass, leading to increased water requirements, and ultimately increased mortality (Owensby et al. 1970; Goldberg and Novoplansky 1997). Huston (1997) pointed out that adding limiting mineral nutrients will make plant populations more responsive to fluctuations in water availability, for example if adding nutrients reduces drought tolerance by increasing size (Goldberg and Novoplansky 1997), especially if resources tend to be nearly co-limiting (Gleeson and Tilman 1992). Added water has the potential to not only enhance growth, but also to enhance seedling germination (Regehr and Bazzaz 1979) and establishment (Inouye et al. 1980; Weller 1985), especially in early successional plant communities (Bazzaz 1996).

Mineral nutrients and water may have different effects on total biomass and species richness. While a large number of experiments have shown that adding nutrients causes plant biomass to increase and richness to decrease (DiTomasso and Aarssen 1989; Gough et al. 2000), relatively few experiments have assessed the relative effects of mineral nutrients and water. Water often has moderately positive effects on plant biomass, survival and fecundity, especially in desert and shortgrass prairie (Ditomasso and Aarssen 1989). For instance, Kirchner (1977) found that in a shortgrass prairie, water alone marginally increased biomass in a shortgrass prairie community and had no effect on diversity (H'), whereas when both water and nitrogen were added biomass increased two to three times and diversity declined. In a more mesic, early successional habitat, Goldberg and Miller (1990) showed that nitrogen additions increased aboveground biomass of herbaceous vegetation and decreased species richness, whereas water additions increased biomass, but decreased richness only in the presence of nitrogen. Carson and Pickett (1990) showed that

added nutrients increased total percent cover with minimal effects on richness, whereas water increased total percent cover and actually increased species richness. Kadmon (1995), however, showed that competition intensity experienced by a common desert annual grass increased with increasing soil moisture gradients, and Kochy and Wilson (2004) showed that species composition changed in response to watering in grass-dominated, but not in shrub-dominated communities. We believe that such mixed results from water addition experiments warrant further consideration for their potential impact on our understanding of productivity–diversity relations.

We created factorial water and fertilizer addition treatments in early successional vegetation to test the relative effects of water and mineral nutrients on aboveground biomass, subcanopy light levels, and species richness. We also tested whether the effect of aboveground biomass on subcanopy light levels and richness differed among water and mineral nutrient treatments. Explanations for the loss of diversity along productivity gradients suggest that regardless of whether water or mineral nutrients enhance productivity, increased biomass should reduce species richness (Rajaniemi 2003), and the per-gram effect of biomass on richness should be independent of the underlying resource. In contrast to these predictions, we present data showing differential effects of nutrients and water, and briefly discuss implications of these differences.

Methods

This study was conducted at Miami University's Ecology Research Center, in Oxford, Ohio, USA (39°30′ N, 84°44′ W) during May–September 2002. The particular oldfield habitat selected was typical for the region, and was dominated by *Solidago canadensis*. The soil at the site is Xenia silt-loam over limestone bedrock (Carson and Barrett 1988). One hundred circular 4 m^2 plots were initially established in a 20×5 array within a *Solidago*-dominated oldfield in May 2002. Each plot had a radius of 1.13 m, and each plot was separated by a 1 m buffer. All treatments were applied to the entire 4 m^2 plot. For this experiment, we selected the 60 plots with the most homogeneous vegetation on the basis of visual inspection of average height and

species composition, avoiding shrub-dominated plots in particular. At the perimeter of each plot we used a spade to cut stolons, rhizomes, and roots to a depth of at least 30 cm. An electric fence (wires at 15 and 90 cm in ht) was established around the entire study area to minimize deer browsing. Fertilizer treatments were assigned randomly to plots and received fertilizer on May 16 and June 18, 2002, with Osmocote^{TM} 18-6-12 NPK slow-release fertilizer (The Scotts Company, Marysville, OH, USA) at an annual rate of 20 g N m^{-2}.

Water amendments began on June 27, 2002, when the seasonal rainfall typically begins to decline, and ended August 30. Water was added to plots at rates of 47 and 190 mm month^{-1}. These levels correspond to the 14th and 82nd percentiles of average May precipitation, based on daily precipitation records from Miami University's weather station from 1982 to 2003 (available from http://www.oardc.ohio-state.edu/centernet/weather.htm, for the MIAMI station). High-water plots received 13 mm every other day (50 L plot^{-1}), applied by hand with a broad spray. Low-water plots also received 13 mm per watering, but at eight day intervals, and control plots received no water. Watering treatments were grouped together to reduce the chance that water additions would impact adjacent control plots. High water plots were clustered at one end of the field, the low water plots in the middle, and the control plots clustered at the other end. Thus, space and watering were almost entirely confounded. The only departure from this spatial segregation occurred where we assigned equal numbers of each water level to the randomly located fertilizer treatments. We tested whether there were any spatial trends in early season species richness prior to the start of watering treatments and whether species richness varied among plots that later received control, medium or high water treatments. We also used location (x,y distances) as a random factor in our mixed model analysis of variance (see below). The spatial analysis and use of location as a random factor helped to evaluate whether effects apparently due to water may have been due to an underlying pre-treatment variation in richness.

Species richness was determined in early June and early September in a centered circular 2 m^2 subplot. Leaf area index (LAI) was measured twice during the growing season (May 31, August 25) using an LAI meter (LAI-2000, LiCor, Inc.,

Lincoln, Nebraska, USA) and based on 2 sets of 1 above-canopy and 3 below-canopy readings 3 cm above the soil surface, positioned at regular intervals within the 2 m^2 subplot. Fractional photosynthetically active radiation (hereafter FPAR, the fraction of μmol photons m^{-2} s^{-1} transmitted through the vegetation) was measured May 31 and August 25 using paired point sensors and a LI-1400 datalogger (Quantum Sensors, model no. 190, LiCor, Inc., Lincoln, Nebraska, USA). Measurements were made at 5 cm above the soil surface, and was based on six simultaneous above- and below-canopy readings per plot. Readings were taken along a 1.0 m transect running E–W and centered in the plot. Total aboveground biomass was sampled Sept. 1 and was clipped at the soil surface for a centered circular 1 m^2, and dried for three days at 60C.

Generalized linear mixed models (Pinheiro and Bates 2000; Venables and Ripley 2002) tested treatment effects on both early and late season response variables, after removing the effects of spatial autocorrelation, and row and column block effects. We also tested whether there were differences in LAI or species richness among plots that later received the control, medium, and high water treatments. After determining that no pre-water addition gradients existed, we then tested effects of water and fertilizer additions on late season response variables: aboveground biomass, LAI, FPAR, and species richness. We also tested whether per-gram effects of biomass on FPAR or species richness depended on fertilizer or water. We used a normal error distribution for all continuous variables and a Poisson error distribution (with a log link function) for species richness. All response variables were modeled interactively to determine the minimally adequate (most parsimonious) statistical model (Crawley 2002). Random effects (row, column, spatial autocorrelation, heteroscedasticity) were tested with AIC (Akaike's Information Criterion, −2 (maximized log-likelihood) + 2 (#parameters), Akaike, 1974; Venables and Ripley 2002). Random effects that resulted in the lowest AIC, given the same fixed effect terms, were retained (Pinheiro and Bates 2000). Fixed effects were tested with conditional F tests, and terms with $p < 0.05$ were retained (Pinheiro and Bates 2000). Error degrees of freedom varied among response variables, as different factors are retained in the models.

Results

We observed no spatial patterning of early season (pre-watering) species richness (Figure 1). In particular, neither early season LAI, nor early season species richness varied significantly between the control plots and the plots selected for watering (ANOVA watering terms $p > 0.10$; Figure 2). Fertilizer increased early season LAI ($F_{1,58} = 37.7$, $p < 0.0001$; Figure 2), but had no effect on early season species richness (Figure 2, ANOVA fertilizer $p > 0.10$).

Variables measured late in the growing season responded primarily to the combined effects of water and fertilizer. Aboveground biomass increased only when both fertilizer and water were applied (Figure 3, significant fertilizer × water interaction, $F_{2,42} = 7.19$, $p = 0.002$; Table 1). LAI also increased only when both fertilizer and water were applied (Figure 3, significant fertilizer × water interaction, $F_{2,54} = 5.24$, $p = 0.008$; Table 1). Biomass and LAI were also positively correlated (Spearman $\rho = 0.517$, $p = 0.002$). Understory light levels (FPAR) declined with fertilizer ($F_{1,58} = 5.49$, $p = 0.023$; Table 1; Figure 3). Neither water nor the water × fertilizer interaction had a significant negative impact on understory light levels, in spite of water's positiv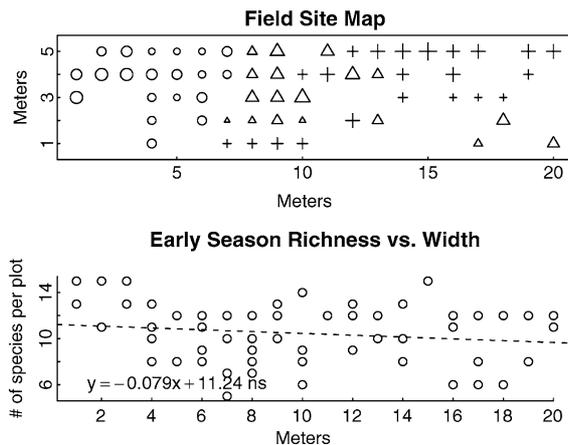e effect on both aboveground biomass and LAI (Figure 3). Species ichness declined with added fertilizer ($F_{1,54} = 5.12$, $p = 0.028$; Table 1, Figure 3) but increased with added water ($F_{2,54} = 13.5$, $p < 0.0001$; Table 1, Figure 3).

FPAR declined with increasing biomass (Figure 4a; slope of log[FPAR] vs. biomass $\beta_1 = -0.00229$; 95% CI = $(-0.00374) - (-0.00084)$). No treatment or treatment combination had a significant effect on either the y-intercept, or the slope of this relation (all $F < 1.4$, all $p > 0.25$). Species richness declined with increasing aboveground biomass (Figure 4b, slope parameter in loglinear model $\beta_1 = 0.9994$; 95% CI = $0.9991 - 0.9999$), and the intercept depended on the watering level ($F_{2,43} = 11.9559$, $p = 0.0001$), but not on fertilizer ($F_{1,43} = 0.0787$, $p = 0.7805$). The slope did not differ among either watering or fertilizer treatments. Thus the effect of fertilizer on richness seemed to operate through its effect on biomass, because the inclusion of biomass in the model caused fertilizer to become redundant (nonsignificant). In addition, there was no relation between FPAR and species richness, whether other factors were included in the model, or not ($F_{1,46} = 1.1142$, $p = 0.2967$).

Discussion

The effects of water and mineral fertilizer that we observed in this study are not consistent with the generalization that increases in productivity via resource additions reduce species richness. Indeed, in spite of the large positive interactive effects of water and fertilizer on aboveground biomass, water enhanced species richness, while fertilizer reduced species richness, with no interactive effect on species richness. These results show that different resource gradients can cause different relationships to emerge between species richness and productivity.

Our data suggest a potential decoupling of germination, growth and survival in response to water and fertilizer additions: water and fertilizer interacted to increase biomass, showing positive effects of these resources on growth, whereas water and fertilizer had opposite effects on richness, suggesting opposite effects on either germination or survival. At least two scenarios seem plausible and warrant further exploration. If increased biomass, regardless of resource, suppressed richness via
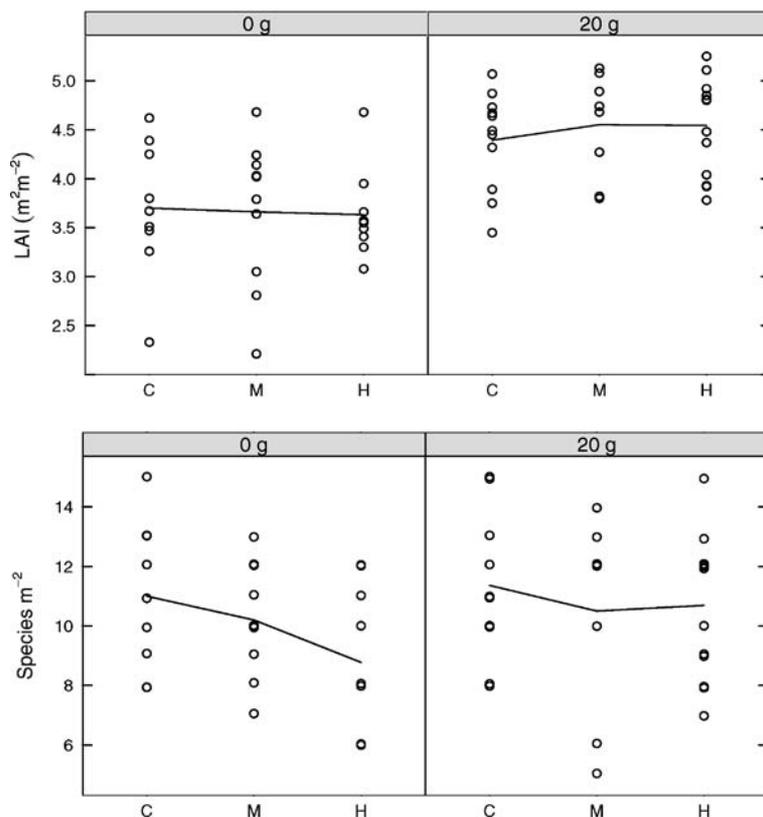

Figure 1. Spatial array of plots. Field Site Map: Symbol type (circle, triangle, cross) corresponds to water addition level (Control, Moderate, High). Symbol size increases with species richness. Early Season Richness vs. Location: no apparent trend in initial species exists between control plots (0–7 m) and watered plots (7–20 m). See text for relevent ANOVAs and Figure 2 for differences among treatments.

Figure 2. Early season variation among plots selected for watering amendments (Control, Moderate, High) at two fertilizer levels (0 and 20 g m^{-2}). Water treatments commenced after these data were collected, and plots selected for watering did not differ in either LAI or mean species richness; fertilizer increased LAI; see text for additional details. Points jittered slightly for display, lines connecting means.

reduced survival of subordinate species, then water must have increased germination and establishment to such a large degree that it more than compensated for the loss of richness due to increased biomass. This is at least plausible, as water can be an important germination cue for some species in early successional habitat (Regehr and Bazzaz 1979; Bazzaz 1996). It is hard to imagine, however, how water could both decrease survival of some individuals, but increase establishment of seedlings. Alternatively, water and fertilizer may have had different effects on plant growth. Fertilizer may have increased biomass in a way that caused the increased biomass to reduce survival or germination, thereby reducing richness, whereas water may have increased biomass in a way that avoided negative effects of the additional biomass on survival and germination. In this case, water and fertilizer acted differently in the mechanisms by which they increased biomass, with cascading

differential effects on survival and germination. We discuss mechanisms associated with this alternative below.

At least two mechanisms may explain possible differential effects of fertilizer and water on growth and biomass. First, nitrogen addition may cause plants to intercept more light per gram of biomass. Several studies (Goldberg and Miller 1990; Carson and Pickett 1990; this study) showed that nutrients have larger negative effects on understory light levels than does water. In particular, if nitrogen soil amendments increase foliar nitrogen, and allow plants to make more chlorophyll (Larcher 1995), this may cause plants to intercept more light for a given leaf area and biomass. In addition, if water and nitrogen additions result in different carbon allocation patterns, this could cause different leaf area: stem ratios. Some of our data contradict this hypothesis: per-gram effects of biomass on light do not differ significantly among

Table 1. Estimates (and 95% confidence intervals) of late season treatment effects, based on treatment linear contrasts.

Treatment	Biomass	LAI	FPAR	S
Control[a]	544 (398, 690)	3.35 (2.91, 3.79)	0.138 (0.089, 0.188)	5.64 (4.67, 6.82)
Fertilizer	−80.0 (−246, 86.3)	**0.475 (0.115, 0.806)**	**−0.043 (−0.080, −0.006)**	**−0.839 (−0.962, −0.731)**
Moderate water	−12.5 (−179, 154)	0.063 (−0.024, 0.150)	na	**1.32 (1.09, 1.59)**
High water	−74.5 (−243, 94.5)	0.061 (−0.036, 0.157)	na	1.57 (1.33, 1.87)
Moderate water, w/Fert	**267 (49.0, 485)**	−0.125 (−0.611, 0.361)	na	na
High water, w/Fert	**416 (194, 639)**	**0.632 (0.14, 1.12)**	na	na

Table includes only contrasts in the minimally adequate models. When terms (e.g., interactions) are eliminated, respective treatments are pooled. Nonsignificant terms were retained when higher order interactions were significant. Bold indicates treatment effects significantly different than zero.[a]Only the "Control" reflects the mean among respective plots; the remainder are added effects due to treatments, relative to the controls.

treatments, and richness was unrelated to light levels. We reject this hypothesis with some caution, however, for several reasons. First, fertilizer alone had a positive effect on LAI and water alone did not. Second, fertilizer alone had a negative effect on FPAR, and water did not. Third, nonsignificant trends were consistent with this hypothesis: the per-gram effect of biomass on FPAR was higher (less negative) in the water-added treatment than in the fertilizer treatment (Figure 4a). Last, our test for differences in slopes lacked a high degree of power, as evidenced by the apparent differences in slopes that were not significantly different (Figure 4a).

A second mechanism explaining the differential effects of fertilizer and water on richness is that fertilizer additions may make plants more sensitive to drought stress (Gleeson and Tilman 1992; Huston 1997), especially if fertilizer increases aboveground plant biomass and therefore increases maintenance requirements (Goldberg and Novoplansky 1997). In addition, alleviating shortages of mineral nutrients may increase competition for water, and lead to exclusion of subordinate species experiencing heightened water stress. This could be assessed with an individual-based demographic approach (e.g., Suding et al. 2003) that measures individual survival and growth, total germination, and includes a careful assessment of soil moisture.

Although the results of this 5-month study should not be generalized to any great degree, it does warrant a little further speculation regarding several of its implications. First, we speculate that any limiting mineral nutrient may cause increased competition for water and put individuals at greater risk of drought stress. Such an effect will be most apparent for those resources (typically N in these habitats) that limit growth to a large degree. Second, if we can believe that the per-gram effect of biomass on richness (i.e., the slope) does not differ among mineral nutrients, then generalizations
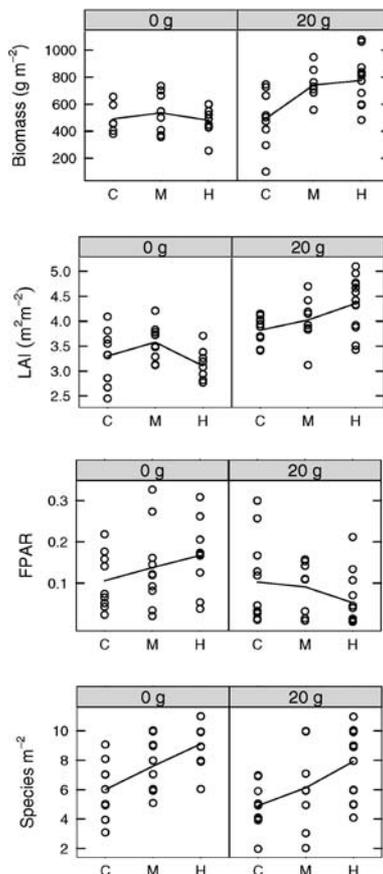

Figure 3. Late season treatment effects. Significant effects: Biomass: water × fertilizer interaction; LAI: water×fertilizer interaction; FPAR: negative effect of fertilizer; Species Richness: positive effect of water, negative effect of fertilizer. See Table 1 and text for additional details. Lines connect means.
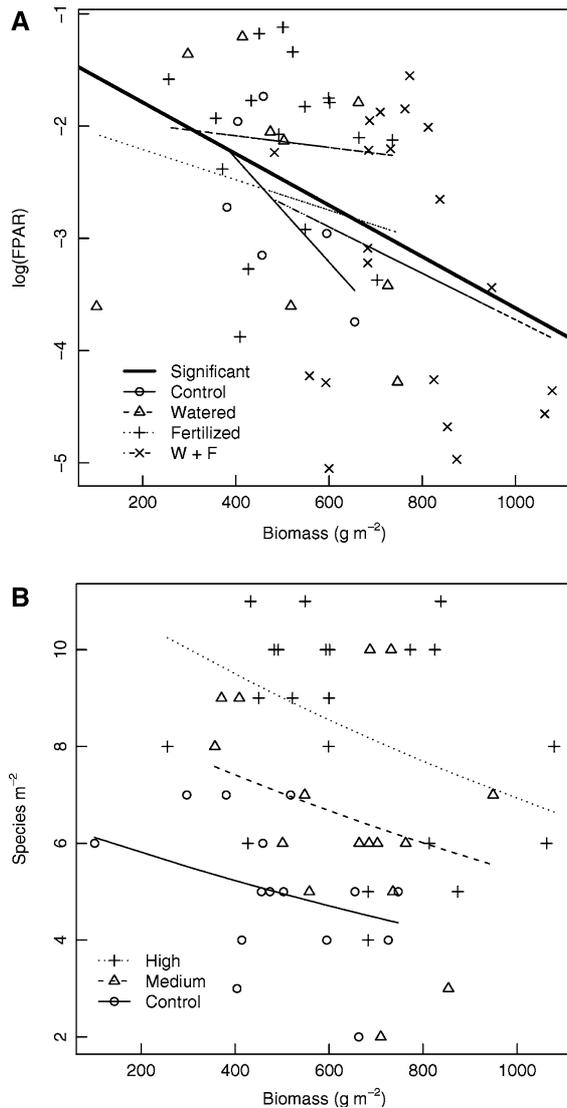
Figure 4. Per-gram effects of aboveground biomass on understory light levels and species richness. (a) Effects on understory light levels. Bold line shows significant relation. No treatment combination had significant effects on this overall slope (all $p > 0.25$), but lines included for clarity. Added water levels (medium and high) were pooled because they did not differ in their effects on light levels, with the pooled model having a lower AIC and greater log-likelihood. (b) Effects on species richness. Each watering level differed significantly, but fertilizer had no effect.

controlling germination or by ameliorating drought stress. These relations are further complicated along natural productivity gradients, because increased soil moisture tends to enhance nitrogen mineralization rates (Chapin III et al. 2002). Thus, water is likely to have positive and negative, direct and indirect effects on plant species richness. Plant diversity and composition also have effects on both soils and productivity, further complicating the picture (Loreau et al. 2002). Manipulative experiments are likely to play an important role in teasing apart the many facets of the regulation of species richness along productivity gradients. Additional research should include (i) testing the generality of the water effect, (ii) understanding the relations between water and mineralization rates along both experimental and natural gradients, (iii) teasing apart the effects of nutrients and water on carbon allocation within plants, (iv) measuring the effects of mineral nutrients and water on imposition and alleviation of drought stress and light limitation, (v) measuring the effects of water on germination in intact vegetation, and (vi) understanding how these effects are moderated by life history stages (e.g., Suding it et al. 2003) and the ecophysiological traits of forbs, C3 and C4 grasses, and shrubs (Reich et al. 1997; Craine et al. 2002; Kochy and Wilson 2004).

Acknowledgements

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regarding productivity –diversity or standing crop – richness relations are conditionally independent of the nutrient. The condition, or context, however, may be set by water availability, which could control the mean level of richness (e.g., the intercept of the biomass-richness relation) by either

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