

The role of topography and soil characteristics in the relationship between species richness and primary productivity in a Kansas grassland

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Environmental conditions influence patterns of local-scale plant productivity and species richness. We sampled soils and plant communities at a topographically-diverse, mid-successional old field site in Kansas to better understand the abiotic factors underlying a natural plant productivity gradient. We related soil texture, pH, percent nitrogen and carbon, and soil moisture to elevation, plant productivity, and species richness. Most soil qualities were significantly correlated with elevation. The four soil texture classes we identified — clay, silty clay, silty clay loam, and silt loam — were spatially clustered according to topography. The lowest elevation sites, characterized by high C and N, low pH, low light penetration, and soils containing more silt and sand which supported the most productive and least diverse plant communities. We suggest that topography drives spatial heterogeneity in soils at our site. We also suggest that although richness is influenced directly by the filtering effects of the abiotic environment on the species pool, the indirect effects environmental factors have on richness via biomass production are more important for governing plant species richness in our system.

Key Words: Succession, productivity, diversity

INTRODUCTION

Understanding the processes that generate and maintain species diversity is a central goal of ecological research. In particular, ecologists have focused on the relationship between species richness and primary productivity (e.g. Tilman 1982; Abramsky and Rosenzweig 1984; Gough, Grace and Taylor 1994; Oksanen 1996; reviewed in Mittelbach et al. 2001). While many reports focus on productivity as the single factor governing richness, environmental factors almost certainly play a major role (Gough, Grace and Taylor 1994; Grace 1999; Weiher 2003). The ability to manage and restore native plant communities in the face of human-induced landscape change may rely on our ability to predict how richness and productivity respond to environmental variables. However, such predictions are

complicated by the fact that diversity, productivity, and the abiotic environment can influence each other directly, indirectly, or both (Grace 1999).

Abiotic environmental variables are generally thought to influence plant species richness in two different ways (Gough, Grace and Taylor 1994). First, abiotic properties provide a selective ecological filter which determines the subset of species from the regional pool that can survive in a given habitat (Keddy 1992; Zobel 1997). In this way, the environment *directly* influences plant community richness and composition. Using multivariate statistical techniques, recent studies have shown that direct effects of abiotic factors often account for a substantial amount of variation in local species richness (Grace and Pugsek 1997; Grace, Allain and Charles 2000; Grace et al. 2007).

Second, environmental variables may *indirectly* influence species richness by influencing biomass production, which in turn affects richness. Net primary productivity has long been invoked as a driver of plant species richness: at extremely high productivities, reduced colonization and increased local extinction rates due to competitive exclusion can result in low diversity (Grime 1973; Grime 1979; Huston 1979; Tilman 1982). Therefore, if abiotic conditions increase primary productivity, species richness may decline.

In searching to understand the factors that govern plant productivity and diversity, it makes sense to examine environmental variables that have direct influence on plant physiology and resource availability (Pausas and Austin 2001). For example, physical soil characteristics impact nutrient and water availability to plants by influencing soil drainage, water-holding capacity, and cation exchange capacity (CEC) (Burke et al. 1998). Soil pH influences nutrient levels as well because many macro- and micro-nutrients are most accessible by plants within specific pH ranges (Schuster and Diemann 2003). Until recently, few studies have attempted to disentangle the relative role abiotic environmental factors, versus productivity, play in determining species richness along environmental gradients.

In undulating landscapes like those characteristic of northeastern Kansas, water and tillage erosion induce large differences in physical soil properties on hilltops compared with the foot of slopes (Govers et al. 1994; Li et al. 2007). Specifically, low-lying areas accumulate water and sediment derived from nearby hilltops (Pimentel et al. 1995). To the extent that soil environments govern plant establishment, growth, and persistence, such spatial variability in soils may be reflected in plant community richness and productivity. For example, long-term studies in grasslands have shown that both nutrient availability and

soil properties associated with topographic position influence both diversity and productivity (Schimel, Stillwell and Woodmansee 1985; Briggs and Knapp 1995; Baer et al. 2003).

In a Kansas grassland undergoing secondary succession, Foster (2001) documented a decline in plant species diversity along a natural gradient of increasing plant productivity. He observed that plant productivity varied over an order of magnitude at the site and suggested that the underlying soil resource and topography gradient may regulate spatial variation in primary productivity and/or plant diversity. We studied the same grassland to evaluate the influence of physical soil properties, soil nutrients and topographic position on plant communities. Our objectives were to (i) characterize the patterns and inter-relationships among soils, plant productivity and plant species richness across a complex soil-topographic gradient in an old field and (ii) evaluate the extent to which the relationship between plant species richness and plant productivity reflect direct or indirect influences of landscape topography and underlying soil variables.

METHODS

Study site

This study was conducted at the Nelson Environmental Studies Area (NESA), 12 km north of Lawrence in north-eastern Kansas (39°03'N, 95°12'W). The 20-hectare study area, which was once a hayfield, was abandoned in 1984. The site is currently undergoing secondary succession. The landscape is dominated by perennial grasses such as *Bromus inermis* Leyss. (introduced C₃ grass), *Lolium arundinaceae* Schreb. (introduced C₃ grass), *Poa pratensis* L. (introduced C₃ grass), and *Adropogon virginicus* L. (native C₄ grass). The site has rolling topography, forming the typical ridge-to-swale geomorphology of the region. The

mean annual temperature at NESA is 12.9°C; minimum temperatures in winter can dip to -29°C and maximum summer temperatures can reach 43°C. Precipitation peaks in June, with an annual mean of 930 mm.

Plant data collection

In September 1999, 40 2.5 x 2.5 m blocks were established throughout the topographically diverse field. Block locations were assigned according to a stratified random design to include adequate numbers of ridge, mid-slope, and swale sites. The elevation difference between the lowest and highest site was 8.32 m; we used a Garmin eTrex® handheld GPS receiver to determine a baseline elevation, and used differential leveling to establish relative topographic differences among plots.

Each block included four 1 x 1 m plots with 0.5 m buffers between them. In 2000, experimental seed addition and disturbance treatments were assigned to three of the four plots in each block as part of an earlier study. In this paper we focus only on measurements taken in control plots.

In July, 2003, plant richness and productivity were assessed for each plot. Plant species richness was determined by counting the number of plant species per square meter. Percent cover, our measure of abundance, was determined by visual estimation. We used cardboard cutouts of known cover amounts to calibrate our estimates. Aboveground plant biomass, our index for productivity, was measured by harvesting a 0.8 x 1 m strip of vegetation next to each plot. The harvested sample was sorted into living and litter components, then dried for 24 h in a 74°C oven and weighed.

In early June and late July we measured canopy penetration of photosynthetically active radiation (%PAR Penetration) in all plots using a 0.8m Accupar® Ceptometer probe (Decagon Devices, Pullman, Washington, USA). Multiple measurements

below and above the plant canopy were made within each plot. PAR Penetration was calculated as a percentage of full sun (PAR below canopy/PR above canopy x 100) and averaged across dates.

Soil data collection

For 38 of 40 plots, we measured the particle size, pH, carbon, and nitrogen for soils collected from between 17 and 28 cm below the soil surface. We chose to sample the A-horizon of grassland soils, which typically extends to at least 27 cm, because it contains the peak rooting depth of many dominant grassland plants (Weaver 1958). We also wanted to avoid sampling the litter and organic layer which we expect to vary with biomass production. Two of the plots were eliminated from the sampling due to ambiguity concerning precise plot location. Soil samples were collected over the course of five days in October, 2004. Because it rained intermittently over the sampling period, and soil moisture was likely to vary daily, only particle size and pH were assessed from the October samples. Additional samples from 10 plots that represented the topographic gradient were collected in November to measure gravimetric soil moisture content. As precipitation varies considerably with season, we interpreted soil moisture estimates as a relative measure among plots at a single point in time.

We used the hydrometer method (Black 1965) to determine textural class for all 38 soil samples. Soils were dried in a 100°C oven for 24 h and crushed to a fine dust using a mortar and pestle. We added 100 ml 5% sodium hexametaphosphate ((NaPO₃)₆) to disperse the particles in 50 g soil. After 12 h, we combined the solution with 880 ml distilled water in a large graduated cylinder. We took hydrometer readings at 40 s (% silt) and 2 h (% clay) to determine the relative proportion of each particle type. We used a blank control to calibrate the hydrometer and account for air and water temperature changes. Once we

obtained the percentages of each soil particle size, we determined the textural class of each soil using the USDA textural triangle (Weil 1998).

We used the gravimetric method to measure soil moisture for 10 plots that represented the gradient of plant species productivity. For all 38 plots, we measured soil pH by mixing 25 g of soil from each plot with 30 ml distilled water. After one hour we recorded pH using a microprocessor-based pocket-size pHTestr 1 by Oakton that was calibrated with buffer solution of known pH 7.0. Percent nitrogen and percent carbon measurements for all plots were analyzed by Kansas State University Soil Testing Laboratory.

Data analyses

There are several statistical approaches for analyzing multivariate studies along ecological gradients. Because we did not have the sample size required for structural equation modeling (Kline 2005)—one popular approach for identifying the relative contribution of several correlated variables—we opted for a combination of methods: principal component analysis (PCA) and stepwise multiple regression, in addition to simple correlation and regression analyses.

We first used Spearman's rank correlation to identify associations among soil variables. Because many of the soil variables were highly correlated, we conducted a Principal Components Analysis of the soil data set to ordinate the soil data. Using a Scree plot, we identified three ordination axes that contributed significantly to explaining variation in soil qualities.

We conducted simple linear regression to quantify the influence of elevation on species richness and log-transformed biomass, as well as the influence of biomass on species richness.

Table 1. Spearman's rank correlation (ρ) for pH, % of each particle size (clay, silt, sand), % carbon (% C), and % nitrogen (% N). Statistically significant relationships ($\alpha = 0.05$, two-tailed tests) are denoted as * $0.01 < p < 0.05$ and ** $p < 0.01$.

	pH	% Clay	% Silt	% Sand	% C	%N
pH	1					
% Clay	0.268	1				
% Silt	-0.344*	-0.922**	1			
% Sand	-0.201	-0.769**	0.527**	1		
% C	-0.597**	-0.258	0.325*	-0.432**	1	
% N	-0.597**	-0.324*	0.281	0.396*	0.933**	1

To characterize the relative effect of environmental variables on biomass and richness, we used backward stepwise multiple regression with significance level for remaining in the model set to 0.05.

Analyses were conducted using SPSS Statistical Package Version 14 (Spearman's rank correlation and regression) and Minitab Statistical Package version 14.1 (PCA).

RESULTS

Soil properties

Most soil properties were correlated significantly to one another (Table 1) and to elevation (Fig. 1). Although not significant at $\alpha=0.05$, there still existed evidence for a relationship between silt and elevation (Fig. 2). Soil pH ranged from 4.8 to 6.3 (median = 5.45). The most frequent pH value among sampling plots was 5.1, low enough to classify these soils as strongly acidic.

Clay, silt, and sand combined in different proportions to form four soil textural classes; of the 38 plots surveyed, 16 (42%) were classified as clay, nine (24%) were silt loam, seven (18%) were silty clay, and the remaining six (16%) were silty clay loam. Silt loam and silty clay loam soil types were

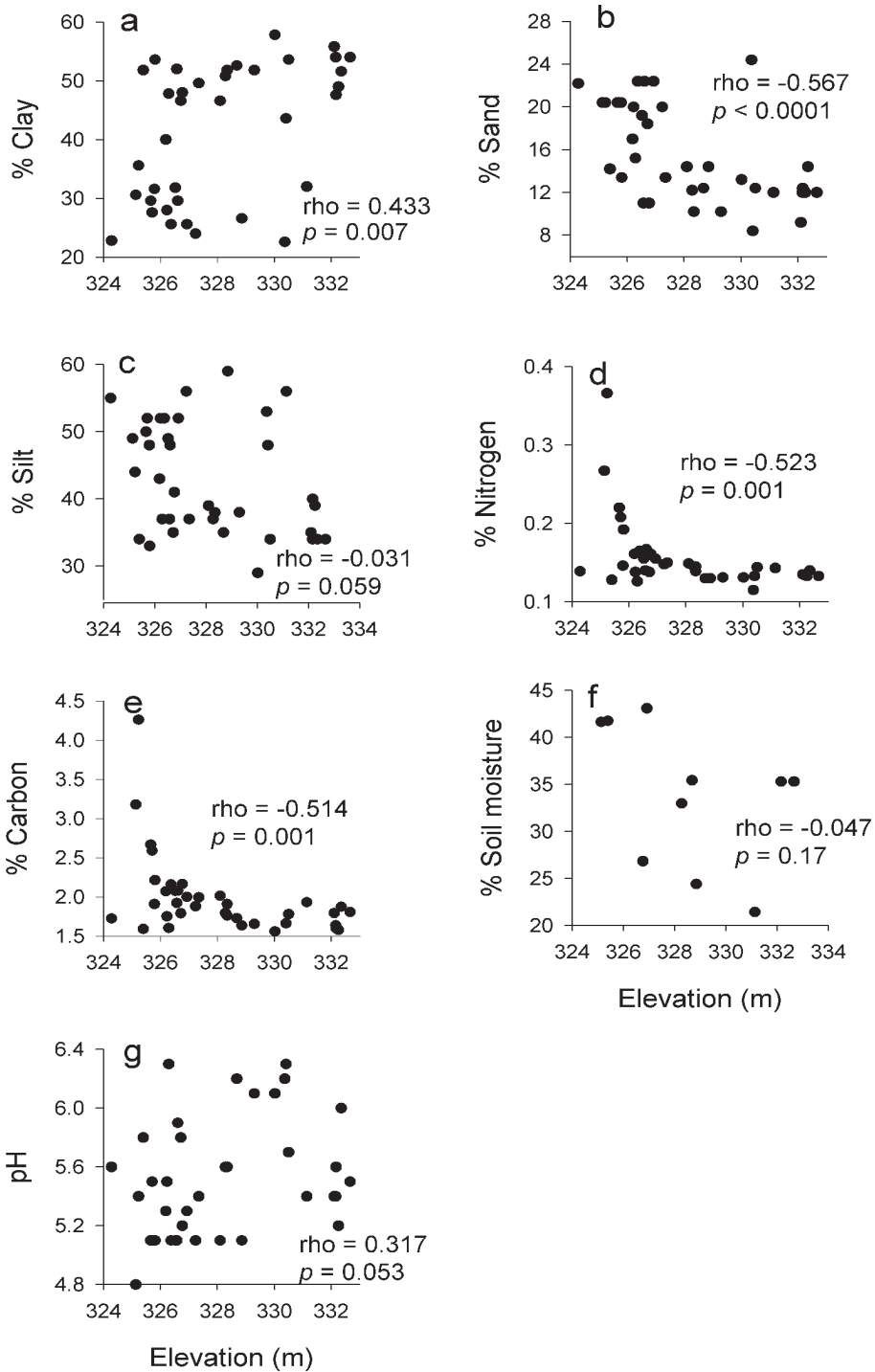


Figure 1. Bivariate plots of soil variables versus elevation. Each point indicates percent soil measurement for a single sample taken from a 1-m plot. Spearman's rank correlation statistics are presented for each figure.

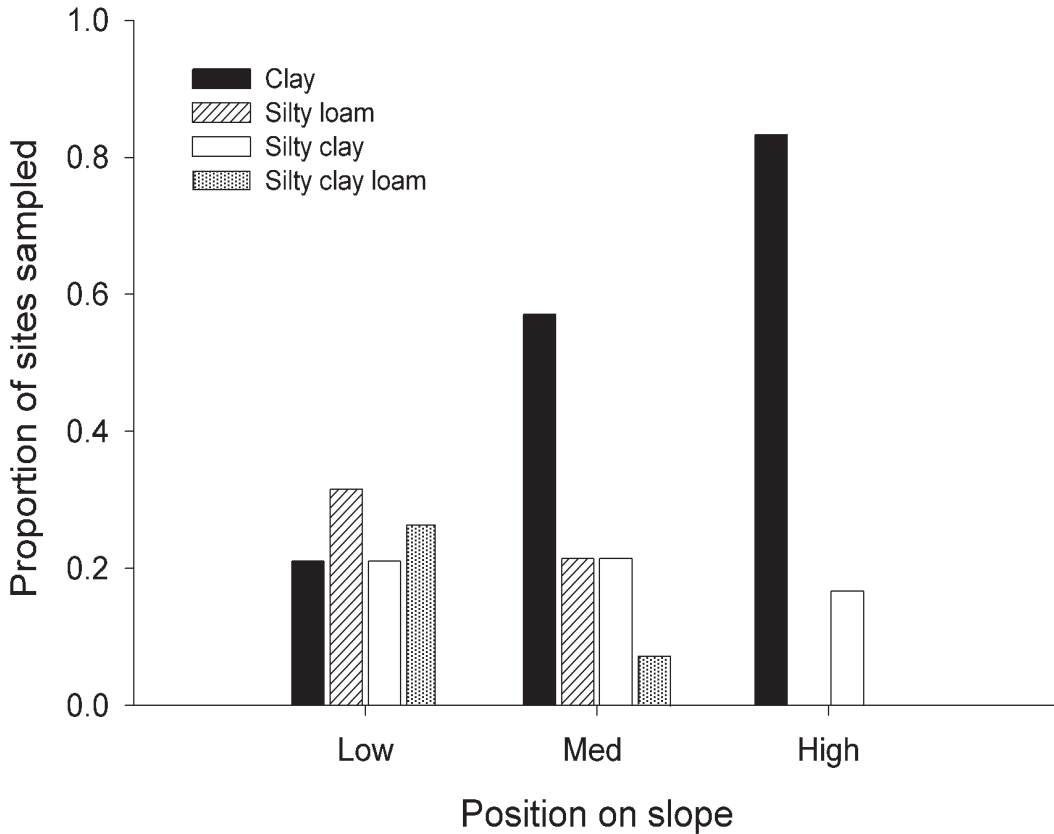


Figure 2. Proportion of soils types present at low (322.0-324.9 m), middle (325.0-328.9 m), and high (329.0-330.4 m) topographic positions.

located in the lowest areas (swales) or at medium elevations. By contrast, plots with clay soils were near the top of the ridge (Fig. 2).

Three principal components summarized 91% of the variation in soils among sites (Table 2). The first principal component (PC1), which accounted for 55% of the variation among sites, represents soil texture. This axis was significantly related to elevation ($R^2 = 0.58$, $t = 4.25$, $p < 0.001$). The second axis, which reflects soil nutrient properties (C and N), was not correlated with elevation ($R^2 = 0.16$, $t = 0.56$, $p > 0.05$). The third axis, determined primarily by pH, also did not significantly relate to elevation ($R^2 = 0.06$, $t = 0.48$, $p > 0.05$).

Plant species richness and productivity

Mean plant species richness at the site was 7.13 species/m² (± 1 SD = 4.4), ranging from 3 to 16 species/m². Mean biomass for the site was 379.6 g/m² (± 1 SD = 159.9) and ranged between 363.3 and 865.7 g/m².

Species richness increased with elevation ($t_{37} = 2.97$, $p < 0.01$, $R^2 = 0.19$; Fig. 3a), while plant biomass decreased ($t_{37} = -2.97$, $p < 0.01$, $R^2 = 0.20$; Fig. 3b). As found in the previous study at this site, species richness was negatively related to biomass ($t_{35} = -6.99$, $p < 0.001$, $R^2 = 0.58$; Fig. 3c).

All soil properties except soil moisture were significantly associated with species richness

Table 2. Eigenvectors and eigenvalues for the first three principal component (PC) axes. Soil variables analyzed included % organic matter (OM), % of each particle size (clay, silt, sand), pH, % carbon (% C), and % nitrogen (% N).

	PC1	PC2	PC3
% Clay	0.477	-0.391	0.035
% Silt	-0.429	0.419	0.119
% Sand	-0.447	0.244	-0.304
pH	0.293	0.204	-0.897
% C	-0.390	-0.537	-0.180
% N	-0.389	-0.531	-0.234
Eigenvalue	3.302	1.589	0.783
Variance explained	55.0%	26.5%	13.0%

(Table 3). By contrast, only silt, pH, C and N were significantly related to biomass (Table 3). In a multiple stepwise regression including biomass, soil PCA's, and elevation as predictors for plant species richness, biomass and PC1 were the only two predictor variables that remained in the final model (partial correlation coefficient for ln biomass = -0.622, $t_{\text{biomass}} = -4.694$, $p < 0.0001$; partial correlation coefficient for PC1 = 0.404, $t_{\text{PC1}} = 2.614$, $p = 0.013$). Together, biomass and PC1 explained 63% of the variation in plant species richness. Using simple linear regression to predict richness with biomass and PC1 separately, biomass accounted for 56% of the variation in richness ($t = -6.51$, $p < 0.001$) and PC1 accounted for 40% ($t = 4.9$, $p < 0.001$).

Stepwise regression analyses also revealed that ln biomass was significantly influenced by all three soil principle components; together they accounted for 43% of the variation in biomass (Table 4).

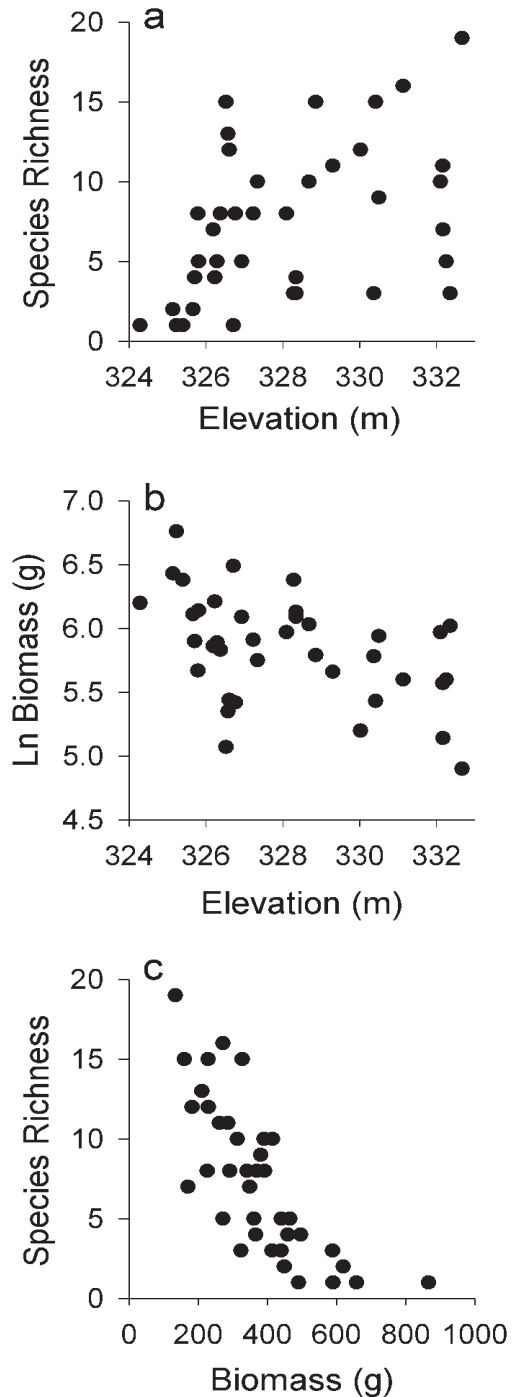


Figure 3. Bivariate relationships between species richness, biomass, and elevation. Regression statistics reported in text.

Table 3. Spearman's rank coefficients (ρ) that reflect the relationship of plant community richness and productivity (measured as standing biomass) with environmental variables: % of each particle size (clay, silt, sand), % carbon (% C), and % nitrogen (% N). Statistically significant relationships ($\alpha = 0.05$, two-tailed tests) are denoted as: * $0.01 < p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

	n	Richness	Biomass
pH	38	0.477**	-0.606***
% Clay	38	0.429**	-0.305
% Silt	38	-0.401*	0.341*
% Sand	38	-0.443**	0.287
% C	38	-0.585**	0.627**
% N	38	-0.627***	0.694***
Light	38	0.624**	-0.724**
Elevation	39	0.556**	-0.510**
Soil moisture	10	-0.401	0.585

DISCUSSION

Our study illustrates the strong correlations that exist at our site among abiotic environmental factors, plant species richness, and primary productivity. Moreover, our data suggest that both soil texture and biomass contribute significantly and independently to plant species richness. We interpret these patterns as evidence that abiotic environmental factors act both directly (filtering the species pool) and indirectly (via direct effects on biomass) to govern richness at our site.

Soil and Topography

Substantial variation in physical and chemical characteristics of soil accompanies small-scale topographic changes at our site in northeast Kansas. Specifically, soil texture classes varied with topography. The highest elevation

plots had the most clay, possibly because the topsoil (A horizon) has been reduced over time as a result of tilling and water erosion (Govers et al. 1994). Our results are consistent with the catena model, which generally asserts that soil variation across a slope reflects long-term geomorphic processes (such as erosion and deposition) that redistribute soil particles (Aandahl 1948; Hooke and Burke 2000). Sampling at the same depth across elevations increases the likelihood of detecting a catenary sequence. Specifically, samples taken at a given depth from plots near the ridge top may contain B horizon soils exposed by erosion, while samples taken from that same depth at the bottom of the slope contain more depositional A horizon soils, thereby accounting for observed differences in clay proportions and soil types.

The lowland plots were enriched in N and C relative to upland plots. Accumulation of fine organic matter and nutrients that are transported downhill with eroding sediments can increase C and N in downslope soils (Schimel et al. 1985; Burke, Elliot and Cole 1995). Further, the lowland plots experience higher in situ inputs of organic matter due to the increased water availability and biomass associated with swales. The observation that the highest elevation sites had the most clay—which is known to increase retention of organic matter and therefore soil C and N (Tisdall and Oades 1982)—suggests a strong role for in situ feedback processes that increase lowland C and N.

All soil variables we measured correlated with elevation, supporting the notion that elevation reflects a gradient in a suite of abiotic variables that may act individually or collectively to influence plant communities. Thus, it comes as no surprise that both richness and biomass were correlated with topographic position. Where this pattern has been documented previously, authors concluded that it is not elevation *per se* that

Table 4. Stepwise regression analyses of In biomass as a function of environmental variables.

Variable Entered	Partial Correlation Coefficient	t	p-value
Elevation			
PC1	-0.607	-4.453	<0.0001
PC2	-0.426	-2.746	0.01
PC3	0.371	2.331	0.026
Constant		127.414	<0.0001

influences plant communities, but rather the abiotic factors associated with elevation (Grace 2000 and references therein). In our regression analyses, elevation was not retained in the model as a predictor for either plant richness or biomass. This suggests that abiotic variables affect species richness independent of elevation, and that the primary role of topography for plant communities at our site is through soil developmental processes and soil erosion which create variation in soil properties across the landscape.

Linking soil variables to the species richness-productivity relationship

Primary production was highest in the lowland plots characterized by low pH, low light penetration, and soils containing more silt and sand than low productivity sites. Other studies have documented shifts in biomass that occur with elevation in both natural (e.g. Abrams et al. 1986; Briggs and Knapp 1995) and agricultural systems (Papiernik et al. 2005). In hilly landscapes where water and nutrient runoff from ridge tops may collect at lowland sites, it comes as no surprise that lowlands are more productive. However, we also found that lowlands are also less diverse.

Species richness and primary productivity were strongly negatively related at our site. Positive, negative, and hump-shaped relationships between productivity and diversity have been documented at a variety of spatial scales (see reviews in Waide et al. 1999; Mittelbach 2001; Gillman and Wright 2006). We interpret the observed decline in species richness as the descending arm of the hump-shaped curve often observed at larger spatial scales. Further, we suggest the negative relationship between productivity and richness at our site is driven primarily by environmental variables that directly influence biomass, and secondarily by direct effects of abiotic factors on richness.

We did find evidence that abiotic variables play a role in determining richness independent from biomass. Soil texture, in particular, had a significant effect on species richness. Dodd et al. (2002), too, found that soil texture strongly influenced vegetation structure. In their study, coarse and fine-grained soils supported different functional groups of plants. Given that texture has a profound impact on nutrient and water flow in soils, the relative amounts of clay and sand could also impact the number of species from the local pool that can establish and grow. However, filtering effects that abiotic gradients impose on the species pool are often detected at environmentally stressful extremes that few species tolerate (e.g. Grace and Pugsek 1997). It is difficult to conceive of potential stressors that act as filtering mechanisms in our low-richness sites which were characterized by silty, nutrient-rich soils. Thus, while soil may serve as an environmental filter for the species pool, we believe biomass is the larger contributor to richness patterns at our site.

Three additional lines of evidence suggest biomass is a dominant factor in governing biomass. First, biomass alone explained 57.6% of the variation in the final regression model, approximately the same level of

variation explained by many variables in multivariate studies (Grace 1999). Second, in studies that implicate abiotic factors as the primary drivers of richness, biomass is typically not well correlated with environmental conditions (e.g. Gough et al. 1994; Grace, Allaine and Allen 2000), indicating weak indirect effects of abiotic factors mediated through biomass. In our study, soil variables explained a substantial amount of variation in biomass. However, we cannot identify which soil trait most influences primary productivity because soil properties influence one another and because all soil variables (as summarized by principal components) explained a significant proportion of the variation in biomass. Most likely, the effect of soil texture on nutrient and water availability, the location at the base of the slope, and the nutrient feedbacks caused by substantial biomass contributing to organic matter in situ, all act collectively to promote to plant growth. Finally, the decline in richness we observed at high productivities in this natural gradient is consistent with studies that experimentally manipulate primary productivity using fertilizer (Tilman 1987; Foster and Gross 1998; Stevens and Carson 1999; Mittelbach et al. 2001).

In nutrient addition experiments, light competition is often cited as the mechanism driving declines in richness that accompany biomass increases (Wilson and Tilman 1993). If productivity was the primary factor driving richness at our site, we might expect light to predict changes in richness. Although light was correlated with biomass and richness in our study (negatively and positively, respectively), it was not retained in the multiple regression model as a predictor for richness.

Importantly, light competition is not the only mechanism that may cause reductions in species richness; limited soil nutrients, space or water may drive competition. In our study,

the high productivity sites at lower elevations were dominated by *Bromus inermis*, a rhizomatous C₃ grass that was planted uniformly across our study site prior to 1980. It is possible that this invasive, clonal, and fast-growing grass takes advantage of the water and nutrients collected at the slope bottom to outcompete other species, thereby decreasing richness. We also know that once established, brome monocultures are difficult to invade even for sown seeds (Foster 2001; Foster et al. 2004). Regardless of the resource (i.e. nutrients or space), in all cases competition by brome provides a mechanism for reducing richness that is consistent with our results. Thus, the legacy of historic hay management at our site is reinforced by environmental variables that maintain primary productivity; and we see this expressed in the productivity-richness relationship.

Our conclusions contrast with recent findings that implicate abiotic variables as the primary factors which drive plant species richness (Gough, Grace and Taylor 1994; Grace and Pugsek 1997). Many of the studies that show a strong role for abiotic variables in determining local species have been conducted in herbaceous communities (Gough, Grace and Taylor 1994; Grace and Pugsek 1997; Weiher et al. 2004, Mancera et al. 2005), often in coastal and wetland environments. It seems plausible that the degree to which abiotic variables govern richness will depend on the prevalence of resource limitation and other abiotic stresses (Grace and Pugsek 1997). In coastal wetlands where salinity and periodic flooding define the environmental gradient, abiotic factors may provide a strong filter for species from the available pool. In successional Kansas grasslands where soils are relatively resource-rich, responses of biomass to the environment may play a more direct role in determining richness than the environment itself.

However, it is worth noting that the elevation gradient at our site spanned only ten meters. While undulations in our landscape are enough to induce significant correlations between soil and elevation, soil conditions may not vary enough to provide strong differential filtering effects on the species pool. Still, richness patterns have been observed over much smaller gradients (e.g. 60 cm, Grace and Pugsek 1997); it is possible that the environmental differences represented at small scales in those studies may exceed those observed at larger spatial scales in studies such as ours. Moreover, Weiher (2003) suggested that opposing effects on richness, such as a positive effect on richness via a species pool effect but a negative effect on richness via biomass, can result in weak bi-variate relationships between soils and richness because they cancel each other out. If this is the case, soil variables may indeed be more important at our site than we conclude.

We believe the low species richness we observed at low elevations is due primarily to high plant biomass that was, in turn, a result of the effects topography and soils have on water and nutrient availability. Following Grace's suggestion (1999), our interpretation is consistent with the idea that when abiotic limitation is low, biotic interactions will be more important in governing plant communities (Grime 1979).

CONCLUSIONS

We found that even topographical changes of less than 10 m generate measurable differences in soil texture. We also found that elevation and soil traits related to productivity and plant species richness. Environmental factors influenced richness both directly and indirectly at our site. However, our data are consistent with the view that biomass reflects the underlying abiotic variables associated with elevation, and the primary effect of the environment on richness in our system is indirect, acting through primary production.

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