

REPORT

Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability

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Abstract

An important goal in ecology is to discern under what habitat conditions community structure is primarily regulated by local ecological interactions and under what conditions community structure is more regulated by the pool of available colonists. I conducted a seed addition experiment in successional grassland to evaluate the relative significance of neighbourhood biotic interactions and propagule availability in regulating plant colonization and species richness along a natural gradient of grassland productivity. In undisturbed field plots, seed additions of 34 species led to an increase in species richness in locations of low productivity, an effect that declined in magnitude as productivity increased. In disturbed plots, seed additions led to a relatively constant increase in species richness at all levels of productivity. The results support the hypothesis that the role of propagule availability in regulating colonization dynamics and species richness declines in significance relative to local-scale competitive interactions as habitat productivity increases.

Keywords

Colonization, grassland, productivity gradient, propagule availability, species pools, species richness, standing crop.

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INTRODUCTION

There is growing evidence that many ecological communities are unsaturated with species such that their richness is constrained more by species pools and by species availability than by local ecological processes (Taylor *et al.* 1990; Cornell 1993; Eriksson 1993; Pärtel *et al.* 1996; Tilman 1997; Zobel *et al.* 2000). From the growing literature on species pools, important questions have emerged: under what habitat conditions are local colonization dynamics, species coexistence and species richness regulated more by the availability of colonists, and under what habitat conditions are these attributes of communities limited more by local biotic interactions and niche availability? (Zobel 1997; Huston 1999; Grace 2001; Safford *et al.* in press). It has been hypothesized for plant communities that species pools are most important in limiting colonization and richness in relatively unproductive habitats where competitive exclusion is slow and recruitment microsites are abundant, but also that competitive exclusion becomes more important in limiting colonization and richness as productivity increases

(Grime 1979; Huston 1994, 1999; Pärtel *et al.* 2000; Zobel *et al.* 2000). According to this hypothesis, unless regularly disturbed, productive habitats will be saturated and thus largely closed to colonization no matter how large the pool of potential colonists. Previous tests of saturation in plant communities have been based primarily on correlations between local and regional species richness (Zobel & Liira 1997; Cantero *et al.* 1999; Pärtel *et al.* 2000). However, experiments are necessary to properly evaluate the relative significance of local interactions and species availability in regulating colonization dynamics and diversity along environmental gradients (Grace 2001). Using a factorial propagule addition and disturbance experiment in successional grassland I demonstrate that species availability limits colonization and small-scale species richness at low productivity, but declines in significance as productivity increases.

METHODS

The study was conducted at the Nelson Environmental Studies Area (University of Kansas), located in the

prairie-forest ecotone of north-eastern Kansas, U.S.A. The experiment was established within a 20-ha field dominated by introduced C3 grasses, *Bromus inermis* Leyss and *Festuca arundinacea* Schreb. The field site is undergoing succession following abandonment in 1984 from use as a hay field, and is currently being colonized by native plants from a nearby prairie.

In September 1999, 40, 2.5 × 2.5 m blocks of four, 1 × 1 m plots were distributed throughout the field using a stratified random approach. This was done to assure that a wide array of microhabitats was sampled within the field. Within each block plots were separated by 0.5 m buffer strips. To each block, a 2 × 2 factorial arrangement of treatments was randomly assigned: two levels of seed addition of 34 grassland species (seeds added, no seeds added; Table 1), and two levels of moderate disturbance designed to remove biomass and alter microsite availability (disturbance, no disturbance). Disturbances were applied by (1) removing litter and scarifying the soil with a rake in January 2000 and February 2001; and (2) clipping the canopy to a height of 15 cm in April and June of both years. Seeds were added in January 2000 (400 seeds per species). Each of the added species is a member of the regional pool and can be found growing within 2 km of the study site. Added species represent a range of life histories, functional groups, origins and habitat affinities (Table 1). To test the hypothesis that colonization and species richness are not limited by species availability in productive local sites it is necessary to introduce propagules of species from productive habitats. Of the 34 added species, 14 are present in either productive lowland prairies or fertile old-fields of the region (Table 1; McGregor *et al.* 1986; Kettle & Whitmore 1991).

Species richness data reported here are from surveys conducted during September 2000 and June 2001. A single index of productivity was obtained for each block in July 2000 by harvesting the aboveground standing crop in the unmanipulated spaces between plots. Light penetration to the soil was measured in each plot on four occasions during the 2000-growing season using a PAR Ceptometer. Soil moisture was measured using time domain reflectometry on June 18, 2000, 4 days after rainfall.

Regression was used to examine relationships between plot-level species richness (S) and block standing crop (log-transformed). Nested analysis of covariance was used to evaluate the effects of experimental manipulations, and their interactions with standing crop, on species richness and resource availability. To estimate richness change in response to seed additions, ΔS was calculated (for undisturbed and disturbed treatments separately) as the difference in richness between plots that received seeds and plots that did not ($S_{\text{seeds added}} - S_{\text{seeds not added}}$).

RESULTS AND DISCUSSION

Of the 34 added species, 31 were recorded in at least one plot during at least one of the two surveys (Table 1). Of these 31 species, 17 were present exclusively in the seed addition plots, suggesting that establishment of these species is constrained by seed availability throughout much of the study area. In the September 2000 survey, species richness declined significantly and monotonically with increasing standing crop in all treatments (Fig. 1A and 1B). However, the slope of the relationship between richness and standing crop was affected by the experimental manipulations, as indicated by a significant three-way interaction in the analysis of covariance ($F = 10.49$, $P < 0.01$). In the absence of disturbance, the slope of the richness-standing crop relationship was significantly more negative in plots that had received seeds compared with those that did not (seed addition × standing crop: $F = 15.47$, $P < 0.001$; Fig. 1A). This reflected an increase in richness in response to seed addition at low standing crop that diminished in magnitude as standing crop increased (negative correlation between ΔS and standing crop; Fig. 1C). In the presence of disturbance, seed addition significantly increased richness ($F = 7.21$, $P < 0.01$), but had no effect on the slope of the richness-standing crop relationship (seed addition × standing crop: $F = 0.16$, $P > 0.05$; Fig. 1B). This reflected a constant-magnitude increase in richness across low, intermediate, and high standing crop blocks (no correlation between ΔS and standing crop; Fig. 1D).

Responses measured in the June 2001 survey were similar to those measured in 2000 except that richness was much greater overall. This probably reflected: (1) the early season sampling time (June vs. September); and (2) a pronounced pulse of germination and emergence from the resident and augmented seed reservoir in response to above-average spring rainfall. In the absence of disturbance the slope of the richness-productivity relationship in 2001 was made significantly more negative by seed addition (seed addition × standing crop: $F = 19.28$, $P < 0.001$; Fig. 1E). In the presence of disturbance, seed addition led to a highly significant increase in richness ($F = 73.40$, $P < 0.001$; Fig. 1F), but there was no seed addition × standing crop interaction ($F = 0.63$; $P > 0.05$). As in 2000, ΔS was negatively correlated with standing crop in the absence of disturbance (Fig. 1G), but varied independently of standing crop in the presence of disturbance (Fig. 1H).

To eliminate the influence of seedlings on assessments of species richness, the 2001 data were reanalysed after excluding from the calculations of richness those species recorded in plots exclusively as seedlings. When seedlings were removed from consideration, results were largely unchanged: (1) the slope of the richness-productivity relationship was made significantly more negative by seed

Table 1 Species added as seed, their life form, historical origin, primary habitat and frequency of occurrence in the experimental plots.

Species	Life form*	Origin†	Habitat‡	Frequency, undisturbed plots		Frequency, disturbed plots	
				No seed	Seed added	No seed	Seed added
<i>Achillea millefolium</i>	PF	N	G-O-P	0	11	1	20
<i>Amorpha canescens</i>	PL	N	P	1	22	0	27
<i>Andropogon gerardi</i>	PG	N	G-P	0	7	1	11
<i>Asclepias tuberosa</i>	PF	N	G-P	3	19	1	25
<i>Aster novae-angliae</i>	PF	N	P	0	8	0	5
<i>Bouteloua curtipendula</i>	PG	N	P	0	1	0	0
<i>Chrysanthemum leucanthemum</i>	PF	I	P	0	5	0	17
<i>Dactylis glomerata</i>	PG	I	G-O-F	0	3	0	7
<i>Desmanthus illinoensis</i>	PL	N	G-P	0	23	0	35
<i>Echinacea pallida</i>	PF	N	P	0	18	0	21
<i>Elymus canadensis</i>	PG	N	G-P-F	0	1	0	5
<i>Eragrostis trichodes</i>	PG	N	P	0	0	0	0
<i>Festuca arundinacea</i>	PG	I	G	14	17	15	19
<i>Festuca ovina</i>	PG	N	O	0	0	0	2
<i>Lespedeza capitata</i>	PL	N	P	0	21	0	27
<i>Liatris pycnostachya</i>	PF	N	G-P	0	2	0	6
<i>Medicago sativa</i>	PL	I	G-O	0	4	0	9
<i>Melilotus officinalis</i>	BL	I	G-O	0	7	1	23
<i>Monarda fistulosa</i>	PF	N	G-P-F	3	30	0	37
<i>Panicum virgatum</i>	PG	N	G-P	1	6	0	5
<i>Petalostemum candidum</i>	PL	N	P	0	17	0	19
<i>Petalostemum purpurea</i>	PL	N	P	0	11	0	13
<i>Phleum pratense</i>	PG	I	G-O	0	2	0	10
<i>Poa pratensis</i>	PG	I	G-O-P	35	35	33	36
<i>Ratibida columnifera</i>	PF	N	P	0	11	0	6
<i>Ratibida pinnata</i>	PF	N	G-P	0	0	0	0
<i>Rudbeckia hirta</i>	PF	N	G-O-P	6	21	9	30
<i>Salvia azurea</i>	PF	N	P	0	17	0	22
<i>Schizachyrium scoparium</i>	PG	N	G-P	0	6	2	4
<i>Sorghastrum nutans</i>	PG	N	P	2	7	0	9
<i>Sporobolus cryptandrus</i>	PG	N	G	0	0	0	0
<i>Trifolium pratense</i>	PL	I	G-O	0	15	1	19
<i>Trifolium repens</i>	PL	I	G-O	2	9	6	12
<i>Tripsacum dactyloides</i>	PG	N	O-P	0	4	0	2

Frequency refers to the number of plots within a treatment ($n = 40$) where a given species was recorded in either 2000 or 2001. Species in bold are present in either productive lowland prairies or fertile old-fields of the region. Habitat refers to the habitat type(s) in the surrounding landscape in which a given species has been recorded (habitat classifications follow Kettle & Whitmore 1991). Taxonomy follows McGregor *et al.* (1986).

*P, perennial; B, biennial; L, legume; F, nonlegume forb; G, grass.

†N, native; I, introduced.

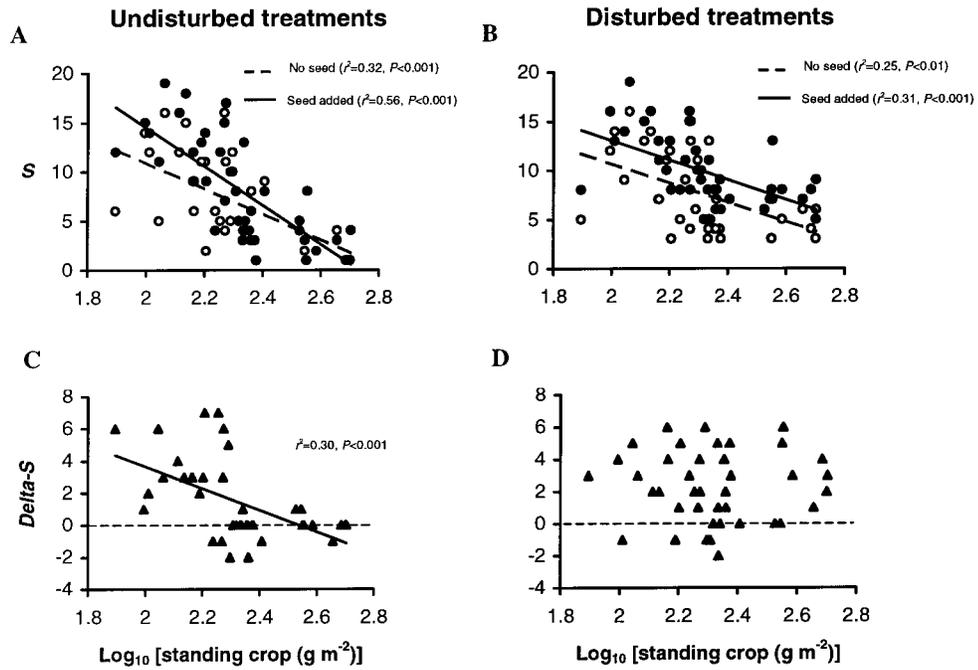
‡G, cool-season grassland; O, successional and disturbed areas; P, prairie; F, forest.

addition only in the absence of disturbance (seed addition \times standing crop: $F = 21.43$, $P < 0.001$); and (2) *Delta-S* was negatively correlated with standing crop only in the undisturbed plots ($r^2 = 0.37$, $P < 0.001$).

The results of this study are consistent with the findings of several propagule addition experiments showing that seedling establishment, colonization rate and small-scale species richness are limited by propagule availability in relatively unproductive grasslands (Filman 1997; Zobel *et al.*

2000). However, the experiment described here represents the first to explicitly test how propagule availability and local interactions vary in their relative significance to colonization and richness along natural gradients of productivity. The findings support the hypothesis that propagule availability declines in significance relative to local competitive control as productivity increases (Grime 1979; Cantero *et al.* 1999; Huston 1999; Zobel *et al.* 2000) and shows that the relationship between richness and productivity can be

September 2000 Survey



June 2001 Survey

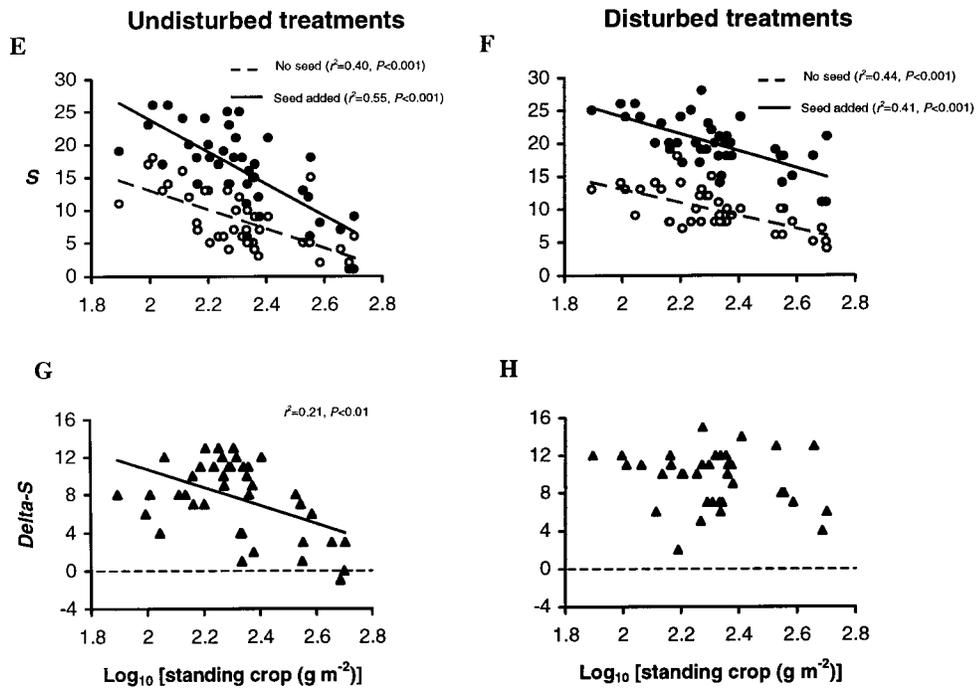


Figure 1 Responses of species richness (S) and ΔS to seed additions as a function of block standing crop in the undisturbed and disturbed treatments (September 2000 and June 2001 surveys). In A, B E and F, plots with no seeds added are represented by open circles and dashed regression lines, while plots with seeds added are represented by solid circles and solid regression lines.

sensitive to species availability. That competition limited the response of productive locations to propagule availability in this study was indicated by the positive effect of disturbance on invasability within the most productive blocks. This suggests that high productivity sites in this grassland are capable of responding to an enhanced pool of colonists, but only when disturbances free resources and increase availability of recruitment microsites. Although there were no detectable effects of disturbance on soil moisture ($F = 0.73$; $P > 0.05$), disturbance greatly increased the availability of light (Fig. 2), an effect that increased in magnitude with increasing standing crop (disturbance \times standing crop: $F = 12.55$; $P < 0.01$). Extreme light attenuation in the undisturbed plots probably played an important role in restricting colonization within the most productive blocks.

It has been noted previously that richness-productivity relationships often take the form of a unimodal envelope exhibiting uniformly low richness at high productivity, but highly variable richness at low productivity (Marrs *et al.* 1996; Grace 1999). Consistently low richness within highly productive, but undisturbed plant communities, may reflect spatially homogeneous effects of light limitation (Goldberg & Miller 1990; Foster & Gross 1998; Cantero *et al.* 1999) and litter accumulation (Tilman 1993; Foster & Gross 1998) and thus homogeneous competitive exclusion in space. High variability in richness at low productivity may reflect high spatial heterogeneity in resources or abiotic conditions (Tilman & Pacala 1993; Grace 1999), or variation in the size of local species pools (Gough *et al.* 1994; Zobel *et al.* 2000; Grace 2001). The results of this study, and the sowing experiments of Tilman (1997), Zobel *et al.* (2000) and Lord & Lee (2001), suggest that much of the variation in richness within low productivity communities that cannot be explained by productivity may be accounted for by spatial heterogeneity in the density and richness of seed rain reaching local patches. Such heterogeneity might be

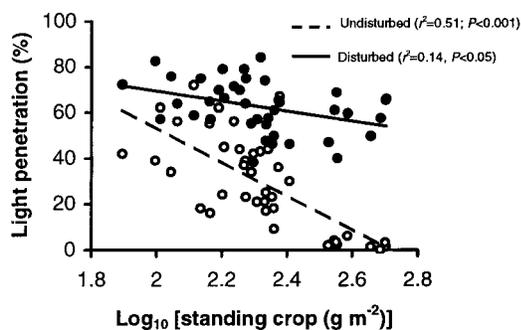


Figure 2 Light penetration to the soil surface (%; mean calculated across four sampling dates) in 2001 as a function of block standing crop in undisturbed plots (open circles, dashed regression line) and disturbed plots (solid circles, solid regression line).

generated by segregation of source populations in space and limitations on the seed production and dispersal abilities of species (Grubb 1977; Harper 1977; Primack & Miao 1992; Pacala & Levin 1997). In the undisturbed treatments of this study, seed additions led to a considerable increase in the proportion of variance in richness explained by standing crop (24% additional variance in 2000, 15% additional variance in 2001; Fig. 1A and 1E), primarily due to increases in richness in low productivity blocks. This provides further evidence that dispersal limitations and heterogeneity of local species pools contribute to unexplained variation in richness-productivity relationships.

There is a growing recognition of the role of spatial segregation, propagule limitations and species pools in regulating species coexistence and diversity in communities (Tilman 1994; Zobel 1997; Loreau & Mouquet 1999). The results of this study provide experimental evidence that propagule availability constrains colonization and small-scale species richness in grassland, but to a diminishing degree as standing crop or productivity increases.

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