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LETTER

Community maturity, species saturation and the variant diversity–productivity relationships in grasslands

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Abstract

Detailed knowledge of the relationship between plant diversity and productivity is critical for advancing our understanding of ecosystem functioning and for achieving success in habitat restoration efforts. However, effects and interactions of diversity, succession and biotic invasions on productivity remain elusive. We studied newly established communities in relation to preexisting homogeneous vegetation invaded by exotic plants in the northern Great Plains, USA, at four study sites for 3 years. We observed variant diversity–productivity relationships for the seeded communities (generally positive monotonic at three sites and non-monotonic at the other site) but no relationships for the resident community or the seeded and resident communities combined at all sites and all years. Community richness was enhanced by seeding additional species but productivity was not. The optimal diversity (as indicated by maximum productivity) changed among sites and as the community developed. The findings shed new light on ecosystem functioning of biodiversity under different conditions and have important implications for restoration.

Keywords

Biotic invasion, developmental stage, diversity gradient, ecosystem functioning, experiments, productivity, restoration.

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INTRODUCTION

Understanding effects of diversity (species richness) on ecosystem productivity is important to restoration and management (Bullock *et al.* 2001; Hooper *et al.* 2005; Spehn *et al.* 2005). Results from recent grassland experiments show that annual biomass production increases with diversity and the enhanced productivity has been typically explained by species facilitation, niche complementarity or selection/sampling effects (Huston 1997; Palmer & Maurer 1997; Hector *et al.* 1999; Tilman *et al.* 2001; Cardinale *et al.* 2002; Grime 2002; Loreau *et al.* 2002; Roscher *et al.* 2005). However, experiments so far have been conducted during early development when plants were still relatively small and community evenness (measured by biomass) was relatively high (by design). Effects of range in seeded diversity (low to high), species saturation, and possible negative interactions among species in shaping the diversity–productivity relationship as the community matures are not clear (Swift &

Anderson 1994). For example, a positive, monotonic diversity–productivity relationship in a newly seeded community (i.e. early succession) does not reveal: (i) how many more species the community may possibly support; (ii) how many species are needed to achieve maximum productivity; and (iii) whether seeding additional species (or higher diversity) will produce even higher productivity. Also, species interactions are likely to switch from positive (facilitation) in early succession to negative (due to competition) as the community develops during which vegetation canopy closes and biomass accumulates (Bischoff *et al.* 2005; Guo 2005, 2006).

The role of diversity may change as the ecosystem develops; therefore, understanding ecosystem performance in relation to species saturation level in different locations and times is critical for successful land management and restoration (Vandermeer 1989). If productivity in a given location is governed primarily by diversity, the diversity–productivity relationship observed in seeded communities

should also exist in mature communities (Thompson *et al.* 2005). Unlike previous seeding experiments of diversity on bare soils or microcosms with minimal preexisting seed banks (e.g. using treated, mineral soils or with top soil removed; Hector *et al.* 1999; Tilman *et al.* 2001), we seeded species with a wide range of diversity on relatively homogeneous preexisting vegetation at four sites: Lostwood National Wildlife Refuge (LW), Devils Lake Wetland Management District (DL), Northern Prairie Wildlife Research Center near Jamestown (NP; with two additional treatments) and Sheyenne National Grassland (SH), in North Dakota, USA (Table 1). We examined the effects of number of species on productivity for seeded species, resident species, and all species combined as measured by biomass production at the end of the first, second and third growing seasons. Specifically, we examined: (i) whether productivity stabilized (species redundancy) or diminished (species saturation/competition) as diversity exceeded a certain (or optimal) level; (ii) whether seeded and resident communities showed similar diversity–productivity relationships (effects of maturity or succession); and (iii) how other factors such as site conditions and community evenness may have influenced the observed patterns.

METHODS

Study sites

The experiments were conducted at four sites (each *c.* 0.4 ha) in North Dakota, USA (Table 1). Each site was chosen to have high within-site homogeneity in terms of vegetation, slope, and minimal impacts from grazing or other disturbances. All sites were excluded from grazing by large herbivores and chosen to have little humus layer so that possibilities of inhibition on seed germination were reduced. The LW site was once cropland but was seeded to *Bromis inermis* Leyss. in the 1950s and remained idle for more than 20 years. In the last 5 years, the site has received periodic disturbance in the form of prescribed fires and cattle grazing. The DL site was also once cropland but is now co-dominated by *B. inermis* and is periodically hayed. The NP site was at one time cropland but has been hayed annually for the past 15 or more years; vegetation is

dominated by *Medicago sativa* L. and *B. inermis*. The SH site has sandy, poor soils with vegetation lightly invaded by *Poa pratensis* L. and *Euphorbia esula* L. Although the sites were treated by fire, haying or grazing prior to seeding, the belowground communities remained relatively undisturbed and in a mature stage during site preparation.

To remove aboveground vegetation for seedbed preparation, all sites including treatment plots were treated with a prescribed burn (LW and DL) and glyphosate (2.3 L ha⁻¹) herbicide during the 2002 growing season. Although glyphosate is a total herbicide for some species, the dose used did not kill the belowground parts of the resident community because of the compensational growth of non-target species. In late 2002, 15 evenly spaced experimental plots (5 m × 5 m) were established at LW, DL and SH sites, and 25 plots were established at the NP site. Plots were spaced 5 m apart in all cardinal directions.

Experimental design

Treatments (number of seeded species) were randomly assigned to plots (five plots/treatment) within a site. Plots were seeded in May 2003 at a rate of 11.2 kg ha⁻¹ of pure live seeds. We used a Truax eight-foot drill that had three seed boxes, and we calibrated the drill to deliver equal weights of each species in a mixture. Effects of multiple passes of the drill were minimized by passing the drill over each plot the same number of times. We seeded two, eight and 16 native perennial species at LW, DL and SH, and two, four, eight, 16 and 32 species at NP to ensure that the total diversity (seeded + resident species) in some plots exceeded diversity in nearby natural grasslands and in recent experiments. Number of seeded species on each plot was divided evenly between the two major functional groups, i.e. grasses and forbs, thus the grass-to-forb ratio in terms of seed weight was 1. The 32 species included nine C4 grasses, seven C3 grasses, three legume forbs and 13 non-legume forbs. The species seeded at each site were locally common but absent from the experimental plots, and therefore, the species mixes varied among sites. However, the same two-species mixture, consisting of *Andropogon gerardii* Vitman and *Linum lewisii* Pursh, was used at all sites. We allowed resident (preexisting, non-seeded)

Table 1 Locations and climate conditions of the four experimental study sites in North Dakota, USA

Site	Latitude (N)	Longitude (W)	Elevation (m)	January to July temperature (°C)	Annual precipitation (cm)	Growing season precipitation (May to August) (cm)
Lostwood (LW)	48.52	102.39	692	−3.5 to 10.0	41.9	33.3
Devils Lake (DL)	48.12	98.88	450	−1.6 to 9.8	45.7	14.7
Northern Prairie (NP)	46.9	98.7	455	−1.4 to 11.6	47.5	27.4
Sheyenne (SH)	46.45	97.50	327	−0.8 to 12.3	50.4	17.8

species to persist in all plots, and monitored their growth along with seeded species.

We recorded densities of each seeded and resident species in a 1-m × 1-m portion of each plot in late-summer 2003, 2004 and 2005; and all plants were clipped at the ground level for determination of biomass in the laboratory. The fresh plant material was collected species by species and was later oven-dried to determine dry weight. Two-cm diameter × 10-cm deep soil core samples were collected from opposite corners of each plot at each site in June 2003. Soil samples were analysed for nitrogen, phosphorus, potassium, pH, soluble salts, organic matter and total carbon. Vegetation was removed at the end of each growing season by mowing and hand-raking each plot.

Data analyses

The experimental design allowed us to examine the consistency of treatment effects across sites. Because the aboveground plant materials of both seeded and resident species were totally removed prior to each growing season, the annual biomass production (aboveground) of these species provided an estimate of productivity. Response of seeded species, resident species, and both seeded and resident species combined were analysed separately by site and year.

Because the functional form of the relation between number of sown species and productivity was unknown, we considered five possible models: (i) no relation (i.e. constant productivity); (ii) linear relation; (iii) log-linear relation; (iv) quadratic relation; and (v) means model (i.e. one-way ANOVA). Models 4 and 5 are indistinguishable with only three treatment levels; thus we did not fit quadratic models to data from DL, LW and SH. We used information-theoretic methods and computed Akaike weights to quantify the evidence for each model relative to the others (Burnham & Anderson 2002). We used multimodel inference and model averaging to estimate productivity for each treatment (Burnham & Anderson 2002). By averaging productivity estimates across models, weighting each estimate by the Akaike weight for that model, we explicitly accounted for uncertainty over which model was most appropriate. Thus, our inferences are not conditional on model choice. This is important because model choice can have a large bearing on resulting inferences.

We used analysis of covariance techniques to investigate whether seeding treatments altered diversity–productivity relations of resident species. We first modelled resident productivity as a function of resident diversity considering each of the functional forms described above except for the ANOVA model, and pooling across all treatments by site and year. We next considered models that allowed the diversity–productivity relation to vary among treatments. This process

resulted in eight models for each site and year. We used information-theoretic methods described above to judge the relative evidence for each model.

RESULTS

Productivity of seeded species exhibited much variation among sites and among years (Fig. 1). Seeded species accounted for about half the species at all sites but their biomass increased over time from 5%, 24%, 44% and 27% of the total biomass in 2003 to 26%, 42%, 45% and 75% in 2005 at the LW, DL, NP and SH sites respectively. Species richness and productivity of resident species (including exotic species) also varied among the four study sites (see Appendix 1). In 2003, diversity and productivity of resident species were greatest at DL and the productivity of seeded species was highest at NP. The diversity patterns were generally the same in 2004 and 2005, but seeded species at NP and SH showed significantly higher productivity than at the other two sites (paired *t*-tests, $P < 0.05$). Richness and productivity (relative to the total biomass of all resident species) of exotic species were lowest at the SH site (Appendix 1).

We observed some similarities but also some marked differences in annual productivity of seeded species in relation to seeded species richness among the four sites and 3 years. In 2003, the ‘constant’ diversity–productivity model received the greatest weight for LW and SH sites (Table 2). Model selection uncertainty was substantial, however, and model averaging suggested that productivity may have increased with eight sown species and then levelled off or decreased with 16 sown species (Fig. 1). The constant model also received considerable weight for NP in 2003, but was second to the quadratic model. Model-averaged predictions indicated that productivity may have increased and then decreased beyond 16 species (Fig. 1). Linear and log-linear models received most of the weight for DL, suggesting that productivity increased at a steady or near-steady rate as sown species increased. In 2004, log-linear models received most of the weight for DL and SH, where as linear and ANOVA models were most supported for LW and NP respectively. Productivity of seeded species at NP was clearly greatest with 16 sown species and then dropped markedly with 32 species. Diversity–productivity patterns in 2005 were similar to 2004 (Fig. 1), but the model weights were somewhat different between the 2 years (Table 2). We found little evidence that productivity of resident communities and of both seeded and resident communities combined were related to resident species diversity or overall community diversity (data not shown). However, competition between seeded and resident species became evident at NP in 2003 and all sites except LW in 2004–2005 as indicated by the negative correlations between biomass of

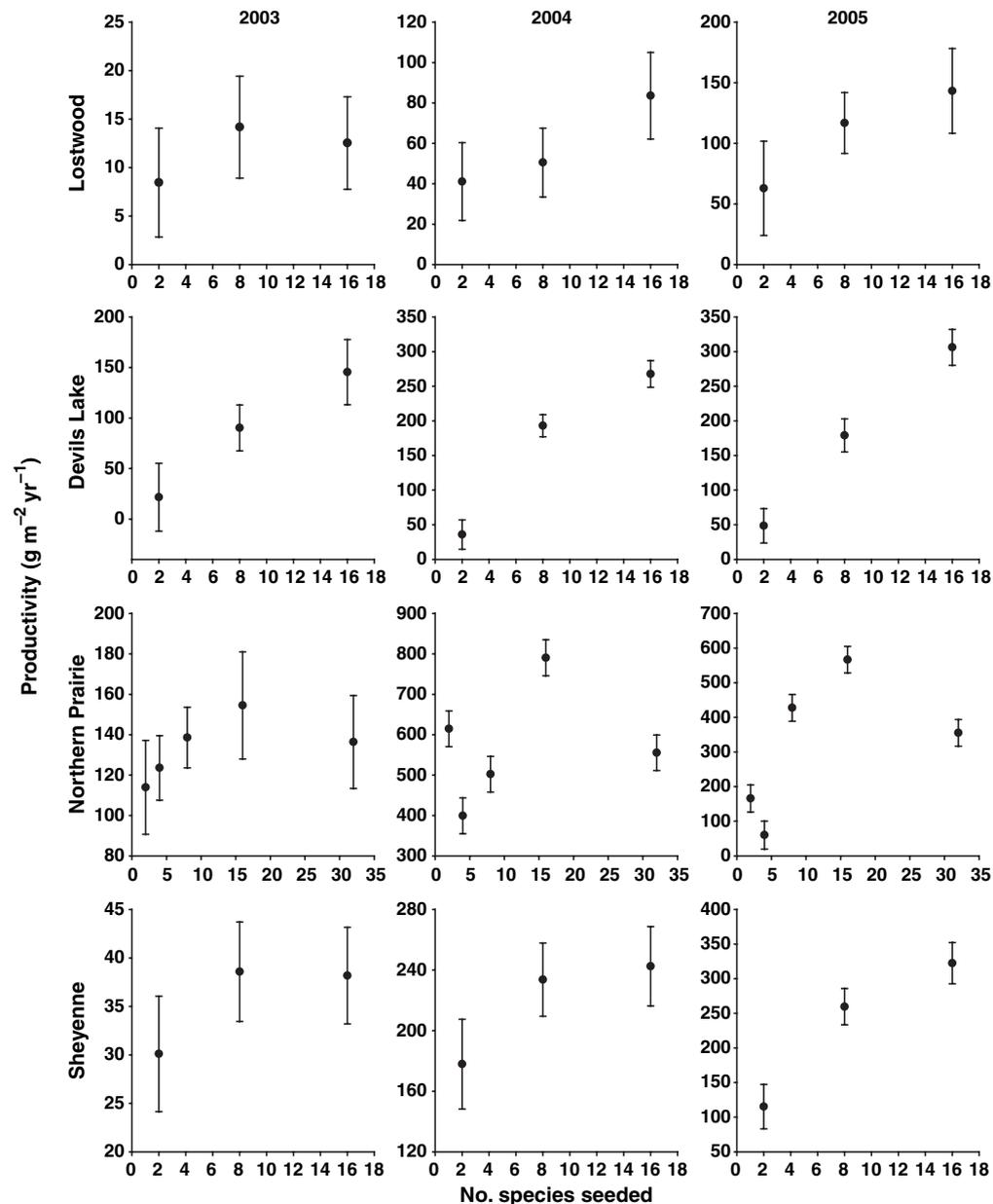


Figure 1 Diversity–productivity relationships for the seeded communities at the four experimental sites during 2003–2005 based on averaging of models shown in Table 2 (mean \pm SE). Standard errors reflect both sampling variability and model selection uncertainty. Note that scales of the horizontal axes vary. No diversity–productivity relationship was detected for the resident communities or seeded and resident communities combined at all sites and in all years.

resident and seeded species that strengthened with time (Table 3).

The most striking observation occurred at the NP site where the range in number of sown species was greater than at the other three sites. Productivity of the seeded community increased with seeding diversity, but only to a certain point (eight to 16 species); when diversity exceeded this level, productivity was reduced (Fig. 1). At remaining sites, productivity of the seeded community generally

increased as number of sown species increased from two to 16 species (Fig. 1). Thus the diversity–productivity relationships were dependent on the range in number of sown species, site and year.

Another significant observation was that optimal diversity levels that led to the greatest productivity were different among sites and changed somewhat over time. The levelling-off of productivity with increasing richness was less visible at DL than at the other three sites (Fig. 1). When

Table 2 Results of Akaike's information criterion-based model selection and relative rankings for both seeded and resident communities at the four study sites

Model	Model weight											
	2003				2004				2005			
	LW	DL	NP	SH	LW	DL	NP	SH	LW	DL	NP	SH
Seeded												
Constant	0.46	0.07	0.30	0.31	0.21	0.00	0.00	0.17	0.22	0.00	0.00	0.00
Log-linear	0.19	0.45	0.20	0.29	0.14	0.79	0.00	0.41	0.45	0.30	0.00	0.68
Linear	0.12	0.41	0.11	0.13	0.38	0.03	0.00	0.14	0.21	0.59	0.00	0.09
ANOVA	0.23	0.07	0.02	0.28	0.27	0.18	0.99	0.28	0.12	0.11	0.98	0.22
Quadratic			0.38				0.00				0.02	
Resident												
Constant	0.68	0.34	0.53	0.62	0.37	0.52	0.57	0.41	0.44	0.41	0.07	0.00
Log-linear	0.15	0.31	0.15	0.18	0.08	0.23	0.19	0.23	0.25	0.21	0.44	0.39
Linear	0.14	0.30	0.16	0.18	0.08	0.21	0.19	0.17	0.27	0.25	0.22	0.53
Quadratic	0.03	0.05	0.17	0.03	0.47	0.04	0.05	0.19	0.04	0.13	0.27	0.08

Boldface type indicates the model with the highest model weight among the models evaluated. ANOVA model was not used for resident community because resident richness was not fixed.

Table 3 Correlations between resident and seeded community biomass at the four study sites

Year	Site			
	LW	DL	NP	SH
2003	-0.44	-0.13	-0.55**	-0.45
2004	-0.48	-0.62*	-0.76**	-0.63*
2005	-0.48	-0.65**	-0.80**	-0.77**

* $P < 0.05$, ** $P < 0.01$.

the number of germinated species was used in place of number of seeded species, the patterns were similar. We observed an initial positive relationship in seeded communities and negative relationship in resident communities between forbs and grasses in terms of biomass (Fig. 2). Such relationships were only observed in 2003 when seeded plants were still relatively small and shallow-rooted, therefore avoiding belowground competition with resident species that had deeper and larger roots. In 2004–2005, as the shoots and roots of seeded species grew larger and the competition with resident species became stronger, the forb–grass relationship measured by biomass at each site became weaker (no longer significant) or disappeared (data not shown).

We found no evidence that our treatments altered the diversity–productivity relationship in resident communities and there was no clear relationship between diversity and productivity in resident communities, especially in 2003. Analysis of covariance models involving treatment received essentially no support and the best model indicated that productivity of resident species was unrelated to diversity of

resident species (i.e. constant model; Table 2). We observed no significant effects of soil chemical properties (N, P, C and K) on the productivity of either seeded, resident or combined communities at any site (data not shown), possibly due to the high within-site homogeneity. Community dominance, measured in terms of biomass, was clearly higher in resident communities than in newly seeded communities (Fig. 3). Productivity of the seeded community was generally positively related to community evenness measured by biomass at all sites, whereas productivity of the resident community showed the opposite pattern (data not shown).

DISCUSSION

Our results suggest that many seeded species can survive and establish in the presence of preexisting vegetation, including invasive exotic plants. This finding has important implications for restoration efforts worldwide. The diversity of the whole community could be elevated by seeding additional species, although productivity may not change. The optimal diversity level as indicated by maximum ecosystem productivity is likely to change as the community develops over time. Our experimental study delivers three central messages: (i) the diversity–productivity relationship varies among sites, years and the gradients of seeding diversity; (ii) the relationship is likely to change as the ecosystem reaches maturity; and (iii) to a certain degree, the biomass produced by sown species essentially replaces resident biomass. We consider each of these in detail below.

First, diversity–productivity relationships can vary substantially among sites and years, and observed relationships

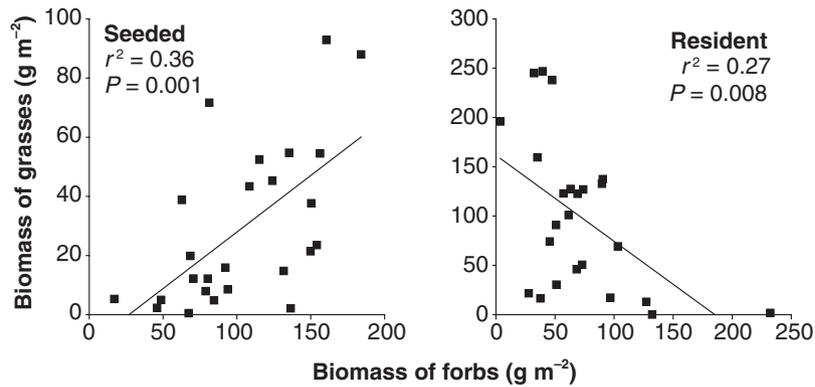


Figure 2 An example of the relationships between biomass of forbs and grasses in seeded (left) and resident communities (right) at the NP site in 2003. In the first year, the seeded species were still small and had small and shallow roots; therefore, little competition existed but facilitation led to a positive relationship between forbs and grasses. In mature vegetation, however, both above- and belowground plant components were much larger, and thus competition led to a negative relationship. Other sites and other years showed similar results (not shown).

depend heavily on the range in number of seeded species. Results from the NP site suggest that when seeded diversity spans a sufficiently broad range (i.e. two to 32 species), the diversity–productivity relationship may be non-monotonic, i.e. in newly established communities, productivity first increases with diversity and then declines when diversity reaches a certain level (saturation). This finding is in contrast with the other three sites and most (if not all) previous grassland experiments that may not have exceeded the

species saturation level, and therefore showed positive monotonic diversity–productivity relationships (Fig. 1; Fukami & Morin 2003). In mature communities, species dominance is well established and the role of aboveground species diversity might become less important than species composition (identity effect). By creating a sufficiently broad range in diversity of seeded species at the NP site, we were able to determine that saturation for that site occurred somewhere between 16 and 32 species, although such levels

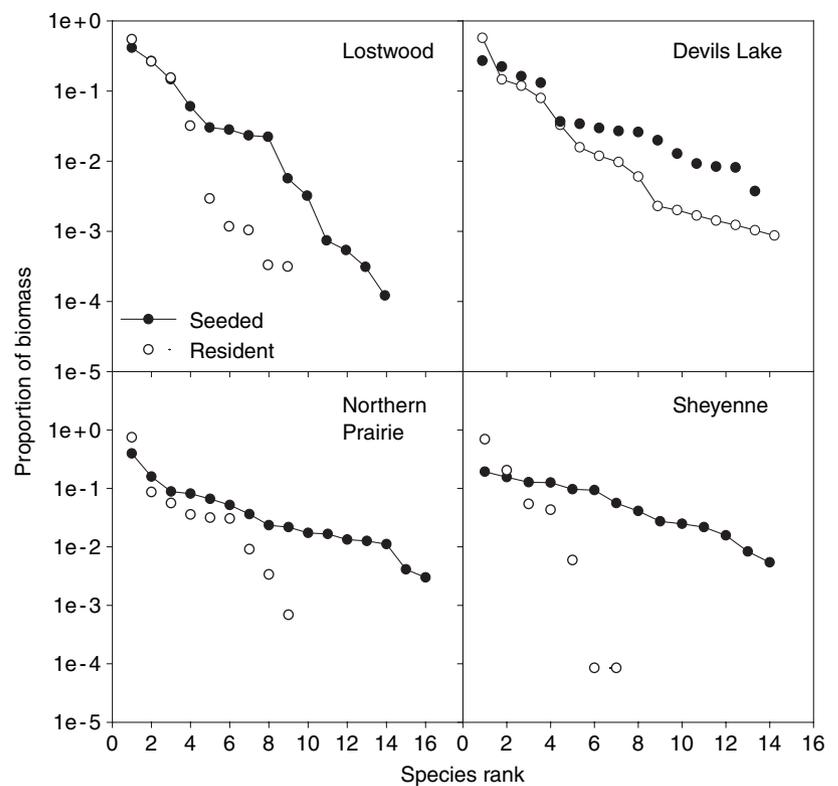


Figure 3 Comparison of dominance curves between seeded and resident communities at the four study sites in 2003. Note that the species ranks were based on biomass (not density) and each symbol represents a species. For comparative consistency, data on plots seeded with 32 species at the NP site were excluded. Resident communities exhibited higher dominance at all sites. Data from 2004 and 2005 provided similar results (not shown).

probably vary somewhat with species composition. The saturation level at remaining sites is less clear, but may also be greater than 16 species (Fig. 1).

To our knowledge, this is the first experimental study to document a non-monotonic diversity–productivity curve (i.e. at the NP site). The underlying mechanisms may include: (i) species saturation – no niche remains in the habitat and therefore additional species may not perform as well as in species-unsaturated environments; (ii) species (functional) redundancy (Grime 2002) – however, our results are counter to earlier claims that after diversity increases to a certain level, adding more species has little effect on ecosystem productivity (Symstad *et al.* 1998); and (iii) negative interactions among species or seeds (e.g. competition and allelopathic inhibition; Hooper *et al.* 2005). The downturn in productivity was not caused by fewer seeds being sown in more diverse plots because the total density of seeds increased with the number of species seeded (data not shown), although the number of seeds of any given species decreased with seeding diversity. The positive monotonic diversity–productivity relationship at the other three sites could be because these sites could potentially support more species than were seeded (i.e. 16 species). More species would need to be seeded to identify the species saturation level at these sites, particularly at the DL site.

The second important finding from this study is that the diversity–productivity relationship is likely to change as the ecosystem develops and reaches different successional states, as community evenness declines (Fig. 3), and as resources (nitrogen, space and light) become limited (Grace 1999). Seeded diversity may play a critical role only in early community development when community biomass evenness is relatively high (Fig. 3). Different numbers (and combinations) of species in different stages of development (Mouquet *et al.* 2003) may be necessary for the community to perform optimally. If diversity in nature is well below the highest diversity seeded in our experiments, high seeding diversity would lead to high productivity in early stages of community development, and in later stages, it would ensure the selection of suitable dominant species that may be highly competitive with reduced resources. In mature vegetation, community performance (e.g. stability) may also reflect the greater role of the belowground community including both the diversity (and composition) and abundance of seed banks and well-developed root systems (Wardle 2002).

Seeding additional species into existing vegetation is a common practice in restoration. Although many of the sown species can indeed persist, few studies have examined the changes in resident biomass. Our study showed that productivity from seeded species can essentially replace the biomass of residents (Table 3). The lack of a diversity–productivity relationship in resident species at all sites may

be due to: (i) the resident community is more mature than the seeded community and the competition is much stronger than in the newly seeded community because of accumulated belowground biomass (roots; Fig. 2); (ii) the resident community has low evenness compared with the newly seeded community in which density or weights of seeds are more evenly distributed among species, and high dominance order (or species rank) has not been well established (Mulder *et al.* 2004; Pfisterer *et al.* 2004; Fig. 3). This is apparent from the larger variation (SD and coefficient of variation) in biomass among resident species than among seeded species at all sites (paired *t*-tests, $P < 0.01$). Also, a positive relationship existed between plant density and biomass for seeded species at all four sites (linear regressions, $P < 0.05$) but not for resident species ($P > 0.05$); and (iii) all sites except SH were heavily invaded and dominated by a few exotic species (Mulder *et al.* 2004). Although native species are capable of forming monocultures under certain conditions, native species never reached the dominance level that invasive species did at any of our study sites (field observation). Natural selection has resulted in a few, most suitable species at the sites (e.g., *Medicago sativa* at NP, a highly persistent and dominant exotic species). Conversely, not enough time has elapsed for natural selection to shape the newly seeded community and many seeded species will likely disappear in the future. Yet, initial higher evenness in a young community might lead to greater complementary use of resources and thus higher productivity, although such evenness effects may become weaker as the community matures (Nijs & Roy 2000; Mulder *et al.* 2004).

Although seed weight or seed density was kept constant across treatments in previous experiments (Naeem *et al.* 1996; Hector *et al.* 1999; Tilman *et al.* 2001; Brown & Fridley 2003; Wilsey & Polley 2003), variation in seed size among species can affect both plant size and germination rate. Evidence exists that, while seed density clearly limits plant density, high seed density generally leads to increased productivity, but very high seed density could also have adverse effects (e.g. through phytochemical inhibition; Brown & Fridley 2003).

Because site conditions and characteristics (e.g. location and climate) can also influence the diversity–productivity relationship (Huston 1997; Huston *et al.* 2000), by simultaneously conducting the same experiment at four sites, we could examine the consistency in results among sites and between young and mature communities. We observed the species saturation level of our species pool at the NP site during the 3 years of study. However, communities in natural settings in different successional stages support different numbers of aboveground species, and species diversity in a mature community is not indicative of diversity or saturation level in early successional stages (Mouquet

et al. 2003). Therefore, it may be misleading to infer how many species should be seeded to achieve the greatest productivity based on observations of a mature community. Optimal species richness also depends on species composition (identity) and relative abundance, however, and identifying optimal species combinations along with optimal amounts and per cent composition poses even greater challenges for future experimenters (Naeem *et al.* 1996; Benedetti-Cecchi 2004; Guo 2006).

Our results have important implications for native prairie restoration. It appears that at least 16 native species must be seeded on plots of 5 × 5 m to achieve maximum productivity within the mixed-grass prairie region of North Dakota, USA. Furthermore, seeding too many species may jeopardize the long-term success of a seeding project. Therefore, a community might indeed have an ‘optimal’ diversity that can promote productivity and stability under various site/time conditions and disturbance regimes (i.e. including enough species that can tolerate fire, heavy grazing, flooding or other disturbances), and yet at the same time can avoid negative inter-specific interactions. We are monitoring changes in the diversity–productivity relationship over time by continuing to observe both seeded and resident vegetation and soil conditions at the four study sites. We expect different patterns to emerge in the future as seeded communities grow, mature and compete, especially below-ground (Wardle 2002; see also Briggs & Borer 2005). We will examine how biomass accumulation in turn affects diversity and species composition, that is, what species will disappear or invade in the future and why (Cleland *et al.* 2004)? Future research that combines theoretical work and long-term field studies that span multiple successional stages and disturbance regimes are needed to gain insights for improving ecosystem restoration and management (Bullock *et al.* 2001; Temperton *et al.* 2004; Zhou *et al.* 2006). Finally, variation in species saturation levels among and within ecoregions points to the need for more experiments like this one to inform restoration efforts in other areas.

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APPENDIX 1

Comparisons of species richness and biomass between seeded and resident (including exotic species) communities at the four study sites in all 3 years. Mean values and standard deviations across all plots at a site are shown. Total included both planted and resident species and residents included both native and exotic species. Differences between open and solid bars depict the contributions of the seeded community. All sites except SH were heavily invaded by exotics, although the exotics did not represent the same proportion when measured by richness, density and biomass within each site.

