

# Seed limitation and the regulation of community structure in oak savanna grassland

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## Summary

**1** We present results from a long-term sowing experiment conducted in nutrient-poor savanna grassland in eastern Minnesota. We examine the effects of a one-time seed addition of 23 grassland species on plant community dynamics and structure over eight growing seasons.

**2** Our goals were to: (i) test the importance of seed availability in regulating plant colonization dynamics and species richness; (ii) assess both the initial effects of sowing on species diversity and community structure and whether these effects increased, persisted or dissipated over the long-term; and (iii) determine the long-term impacts of sown species on the structure and dynamics of the existing community, including effects on species diversity, the abundance of existing (non-sown) species, extinction rate and abundance hierarchy.

**3** Sowing led to the successful establishment of several plant species that had not been present in the plots and to increased abundance of other species that were already present.

**4** Sowing led to sustained, significant changes in community structure, including increased species richness, increased community evenness, and decreased absolute and relative abundance of non-sown species. Effects of sowing were large and significant 8 years after sowing, revealing the role of seed limitation in these grassland communities.

**5** In total, the results suggest that dispersal limitations, species pools and local biotic processes interact to regulate plant community structure.

*Key-words:* community structure, diversity, grassland, oak savanna, seed limitation, species coexistence, species richness

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## Introduction

Species diversity at the local scale (alpha diversity) is determined by the dynamic balance of local colonization and local extinction (MacArthur & Wilson 1967; Grubb 1977; Tilman 1993). Rates of extinction are primarily controlled by local ecological processes such as competitive exclusion, predation, disease or disturbance, and by demographic stochasticity (Grime 1979; Huston 1994; Grace 1999; Zobel *et al.* 2000). Although colonization dynamics can be affected by biotic interactions such as competition (Grime 1973; Huston 1994; Foster & Gross 1998; Grace 1999; Juttila & Grace 2002), litter accumulation (Carson & Peterson 1989; Facelli & Pickett 1991; Foster & Gross 1997) and seed

predation (Andersen 1989; Whelan *et al.* 1991; Myster & Pickett 1993), it may also be affected by processes that determine rates of propagule arrival (Huston 1999; Levine 2000; Turnbull *et al.* 2000; Zobel *et al.* 2000). Within plant communities, colonization of local patches may be limited by the propagule production and dispersal of those species present in adjacent patches or neighbouring habitats (Grubb 1977; Primack & Miao 1992; Pacala & Levin 1997; Turnbull *et al.* 2000; Tofts & Silvertown 2002). As a result, seed rain to a particular patch may contain propagules of only a small subset of species from the broader community pool. Species availability may also be constrained by large-scale processes that affect the composition and richness of the broader regional species pool (migration, speciation; Grime 1979; Taylor *et al.* 1990; Gough *et al.* 1994; Zobel 1997; Grace 2001).

To what degree are limitations to species availability important in the control of local species diversity? Proponents of the species pool hypothesis suggest that many communities are unsaturated and that local species richness is therefore limited by the availability of colonists from the landscape or regional species pools (Taylor *et al.* 1990; Cornell 1993; Eriksson 1993; Pärtel *et al.* 2000). In an unsaturated plant community, microsites for colonization would presumably be plentiful and species richness would thus be limited entirely by rates of species arrival via seed dispersal. Alternatively, if a community were saturated with species, so that local diversity was limited entirely by local biotic interactions and niche availability, then constraints on dispersal would be of little consequence to local diversity (Tilman 1988; Cornell 1993; Foster 2001). A dichotomy of saturated vs. unsaturated communities is perhaps too simplistic, and a more realistic view may be that local diversity is governed by multiple limitations imposed by species availability, biotic interactions and abiotic constraints (Tilman 1997; Leach & Givnish 1999; Grace 2001; Lepš 2001). Such interplay of species pools, among-patch dispersal and within-patch biotic interactions form the basis of meta-population and meta-community models of species coexistence (Skellam 1951; Hastings 1980; Nee & May 1992; Tilman 1994; Pacala & Rees 1998; Turnbull *et al.* 1999; Freckleton & Watkinson 2002).

Sowing experiments can allow one to examine the importance of species availability and dispersal limitations in regulating species abundances (Houle & Phillips 1989; Primack & Miao 1992; Ehrlén & Eriksson 1996; Turnbull *et al.* 2000) and diversity in plant communities (Tilman 1997; Zobel 1997; Zobel *et al.* 2000; Foster 2001; Lord & Lee 2001). If sowing seeds of many plant species into field plots results in a sustained increase in local plant species richness, we may take this as evidence that the community is unsaturated and that colonization dynamics and species richness are thus seed limited. Zobel *et al.* (2000) found that a one-time sowing of 15 grassland species into Estonian alvar led to a significant increase in species richness that was still detectable after three growing seasons. Tilman (1997) found that a one-time sowing of up to 34 species in low productivity savanna resulted in a significant increase in richness that was sustained through four growing seasons. Other sowing experiments have found similar effects of sowing on richness (Foster 2001; Lord & Lee 2001), but none of these studies have reported results for more than four growing seasons.

Although previous sowing experiments have given important insights into the regulation of colonization dynamics and the maintenance of local species richness in grasslands, it is uncertain if relatively short-term results merely reflect the transient dynamics of seedlings and juveniles rather than long-term persistence. Here we present community-level responses over eight growing seasons to the sowing of 23 grassland species in savanna vegetation. Our study tests the long-term

persistence of sown species and the impacts of these species on local community structure and dynamics.

Our experiment was conducted in the diverse ground-layer vegetation of a temperate oak savanna in eastern Minnesota (USA). Upland oak savannas of the mid-western United States are typically more diverse than the open prairies and closed forests of the region (Curtis 1959; Leach & Givnish 1999). The high diversity of these ecotonal communities has been attributed to their mosaic nature and their extensive microsite heterogeneity associated with complex gradients in tree canopy coverage, light intensity, disturbance and soils (Bray 1960; Grimm 1984; Leach & Givnish 1999; Will-Wolf & Stearns 1999). Partial shading by overstorey trees provides the most obvious contrast of savannas to open prairie. It has been suggested that reduced abundance and competitive vigour of the dominant matrix grasses under shade, may partly explain the high abundance and diversity of forbs in these communities (Leach & Givnish 1999).

The objectives of this study were to: (i) test the importance of seed availability in regulating colonization dynamics and species richness in local patches; (ii) assess whether the observed initial effects of sowing on species richness dissipate or persist in the long term; and (iii) determine the long-term impacts of established sown species on the abundances of existing (non-sown) species, extinction rates, abundance hierarchy and community evenness.

## Methods

### STUDY SITE

The experiment was conducted from 1991 to 1998 at Cedar Creek Natural History Area in east-central Minnesota (45°5' N, 93°10' W). Cedar Creek lies within the ecotone between temperate deciduous forest to the east and tallgrass prairie to the west, and is located on the Anoka Sand Plain, which was formed by glacial outwash 12 000 years ago. The soils are comprised of deep, well-sorted sands (Sartell, Zimmerman and Nymore series) of low organic matter and low nitrogen content (Grigal *et al.* 1974). The climate is temperate, continental with a mean annual temperature of 6 °C and annual precipitation of 775 mm. Maximum monthly precipitation typically occurs in June. At the time of settlement by Europeans in the mid-19th century, upland vegetation of the region was most likely a combination of fire-maintained tallgrass prairie, oak savanna and oak scrub (Grimm 1984; Tester 1989). The upland savanna site where this study was conducted (known as Field D) has never been cultivated and has been free of grazing for over 50 years. Prescribed fire has been used at the site since the mid-1960s by burning in early May every 2 out of 3 years (Tilman 1987; Tester 1989). During this study, the savanna was burned in 1991, 1993, 1994, 1996 and 1997. Currently, the dominant overstorey trees are Burr Oak (*Quercus*

*macrocarpa*) and Hill's Oak (*Quercus ellipsoidalis*), while the ground-layer is dominated by the perennial grasses *Sorghastrum nutans*, *Andropogon gerardi*, *Schizachyrium scoparium* and *Stipa spartea*. However, the savanna is highly diverse, supporting a large number of forbs, woody plants and other graminoids. Abundant forbs include *Amphicarpa bracteata*, *Amorpha canescens*, *Artemisia ludoviciana* and *Lathyrus venosus* (nomenclature follows McGregor *et al.* 1986).

#### EXPERIMENTAL DESIGN

In the spring of 1991, a grid of 501 5 × 1.5 m plots that were separated from each other by 1-m walkways was established in a relatively homogeneous upland prairie opening in the savanna. In early June 1991, seeds of 23 native grassland species (Table 1) were sown into each of 20 randomly chosen plots. Seeds were obtained from a local seed supplier (Prairie Restoration, Princeton, Minnesota, USA) and were not stratified before sowing. Of these 23 species, only 11 were present within some of the experimental plots at the start of the study in 1991. As a result, these 11 species were considered to be members of the local community species pool (species in bold in Table 1). The 12 remaining sown species occur elsewhere in the savanna or within the surrounding

prairies and old-fields at Cedar Creek and are thus considered to be members of the landscape pool, but not the local community pool. All sown species are forbs except *Rosa arkansana*, a native shrub.

Seeds of each species, with dispersal structures attached, were sown into the 20 seed addition plots at a rate of 2.9 g per species. All seeds were thoroughly mixed before sowing and then sprinkled by hand as uniformly as possible across the plot. Although the total number of seeds added per plot was *c.* 10 000, the number of seeds per species varied considerably due to variation in seed mass. It is important to note that in choosing the sowing rate for this study the goal was not to mimic natural levels of potential seed arrival into the experimental plots, but to use high levels to eliminate (or significantly reduce) the likelihood that seed availability would be a constraint to establishment of any sown species. After sowing, the vegetation and litter in each of the 20 sown plots and in 20 randomly chosen control plots were gently shaken with a rake to assist movement of seeds downward onto the soil surface. Detailed percentage cover surveys were conducted in all plots in August 1992–94 and August 1998. During each survey, the cover of every species was visually estimated within a 1 × 1 m frame placed in the middle of each sown and control plot. We also utilized cover data

**Table 1** Species characteristics, occurrence (number of plots occupied), and percentage cover (mean value) for each sown species in each treatment (1992 and 1998 vegetation surveys only). In the occurrence column, an italicized value indicates a significant difference in occurrence for the given species between control and sown plots within a given year ( $P < 0.05$ , binomial test). In the cover column, a value in italics indicates a significant difference in mean cover for the given species between control and sown plots within a given year ( $P < 0.05$ , Mann–Whitney *U*-test). Species in bold are members of the landscape and local community species pool. All other species are members of the landscape pool, but not the community pool. Taxonomy follows McGregor *et al.* (1986)

Species	Family	*Life form	Seed mass (mg seed <sup>-1</sup> )	Occurrence 1992		Cover (%) 1992		Occurrence 1998		Cover (%) 1998	
				Control	Sown	Control	Sown	Control	Sown	Control	Sown
<i>Achillea millefolium</i>	Asteraceae	PF	0.05	0	6	0	0.750	0	3	0	0.016
<i>Agastache foeniculum</i>	Lamiaceae	PF	0.23	0	0	0	0	0	5	0	0.303
<i>Allium stellatum</i>	Liliaceae	PF	2.11	0	0	0	0	0	11	0	0.089
<i>Amorpha canescens</i>	Fabaceae	PL	2.26	10	7	1.312	2.462	6	11	2.0	2.938
<i>Antennaria neglecta</i>	Asteraceae	PF	0.09	1	19	0.400	0.337	1	7	0.25	0.124
<i>Asclepias tuberosa</i>	Asclepiadaceae	PF	5.27	10	20	1.237	2.112	9	14	0.449	0.728
<i>Aster azureus</i>	Asteraceae	PF	0.17	2	8	0.075	0.537	6	14	0.47	1.665
<i>Aster ericoides</i>	Asteraceae	PF	0.06	0	0	0	0	0	0	0	0
<i>Coreopsis palmata</i>	Asteraceae	PF	1.41	2	2	0.30	0.062	3	19	0.71	1.203
<i>Dalea purpureum</i>	Fabaceae	PL	1.53	0	0	0	0	0	0	0	0
<i>Heliopsis helianthoides</i>	Asteraceae	PF	3.88	0	0	0	0	0	18	0	5.310
<i>Helianthus petiolaris</i>	Asteraceae	PF	2.97	5	17	0.062	0.37	0	0	0	0
<i>Heuchera richardsonii</i>	Saxifragaceae	PF	0.05	2	20	0.025	0.612	0	7	0	0.355
<i>Houstonia longifolia</i>	Rubiaceae	PF	0.07	0	18	0	0.262	0	12	0	0.692
<i>Lespedeza capitata</i>	Fabaceae	PL	2.42	2	9	0.212	0.187	4	16	0.197	0.407
<i>Liatris aspera</i>	Asteraceae	PF	2.40	1	1	0.013	0.20	1	2	0.007	0.012
<i>Penstemon gracilis</i>	Scrophulariaceae	PF	0.2	0	0	0	0	0	0	0	0
<i>Penstemon grandiflorus</i>	Scrophulariaceae	PF	1.98	0	18	0	0.487	0	9	0	0.320
<i>Rosa arkansana</i>	Rosaceae	W	14.60	5	20	0.475	1.187	4	4	0.410	0.310
<i>Rudbeckia hirta</i>	Asteraceae	PF	0.15	2	20	0.062	2.912	1	11	0.007	0.230
<i>Solidago rigida</i>	Asteraceae	PF	0.49	1	9	0.037	0.30	2	18	0.125	3.770
<i>Verbena stricta</i>	Verbenaceae	PF	0.94	0	0	0	0	0	0	0	0
<i>Zizia aurea</i>	Apiaceae	PF	2.02	0	0	0	0	1	19	0.005	4.070
Total occurrence				43	194			38	200		

\*PF = perennial forb; PL = perennial legume; W = woody.

gathered in 1991 in these plots to assess which sown species were initially present as established members of the community pool. However, difficulties with the identification of sown species as small seedlings in 1991 preclude any other use of the 1991 data.

#### DATA ANALYSES

We examined the effects of sowing on plot occupancy and cover of individual sown species (binomial test for occupancy, Mann and Whitney *U*-test for cover) for the 1992 and 1998 surveys. We used repeated measures analysis of variance (ANOVA) to examine the effects of sowing on several community-level variables, including richness of sown species in aggregate, richness of non-sown species in aggregate, total species richness, community evenness (*E*), cover of sown species in aggregate, cover of non-sown species in aggregate and total vegetative cover. Finally, we used one-way ANOVA to examine the effects of sowing on species gains (the number of species present in a plot in 1998 that were not present in 1992) and species losses (the number of species present in 1992, but not in 1998). This approach does not account for species that were gained or lost after 1992, but that were subsequently lost or re-gained, respectively, before 1998. Variance in cover was successfully homogenized among treatments by log<sub>10</sub>-transformation, and the square-root transformation was used to improve the normality of species richness data. All analyses were conducted using SPSS for Windows (Version 9.0).

### Results

#### INDIVIDUAL SPECIES RESPONSES

Across all survey years, all but two of the 23 sown species, *Aster ericoides* and *Verbena stricta*, were recorded in at least one plot in one year. In August 1992, 15 months after sowing, 15 of the 23 sown species were recorded in at least one plot: 12 in the control plots and all 15 in the sown plots (Table 1). Of the sown species present, 12 were found more frequently in the sown plots than in the controls, nine significantly so ( $P < 0.05$ , binomial test). Only four of the sown species recorded in 1992 were not members of the local community pool (*Achillea millefolium*, *Antennaria neglecta*, *Houstonia longifolia* and *Penstemon grandiflorus*). The total number of sown species occurrences in the sown plots (194) was significantly greater than that of the controls (43:  $P < 0.0001$ , binomial test). Of the 12 species common to both treatments in 1992, nine had greater mean cover in the sown plots than in the controls, seven significantly so ( $P < 0.05$ , Mann–Whitney *U*-test; Table 1).

In August 1998, eight growing seasons after sowing, 18 of the 23 sown species were recorded in at least one plot: 11 in the control plots and all 18 in the sown plots (Table 1). Four of the 18 sown species present in 1998

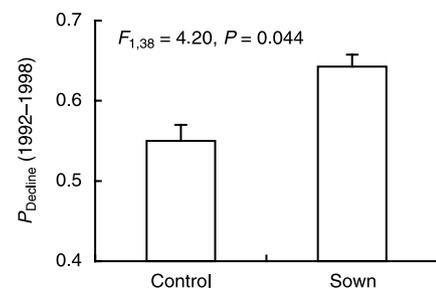
(*Agastache foeniculum*, *Allium stellatum*, *Heliopsis helianthoides* and *Ziza aurea*) had been initially absent from the community in 1992, probably due to initial seed dormancy or unfavourable establishment conditions for these species during the first years of the study. Of the sown species present in 1998, 17 were found more frequently in the sown plots than in the controls, 10 significantly so ( $P < 0.05$ , binomial test). The total number of sown species occurrences in the sown plots (200) was significantly greater than that of the controls (38:  $P < 0.0001$ , binomial test). Of the 11 species common to both treatments in 1998, nine had greater mean cover in the sown plots than in the controls, six significantly so ( $P < 0.05$ , Mann–Whitney *U*-test; Table 1).

We found no significant effects of sowing on the plot occupancy or mean cover of any non-sown species in either 1992 or 1998. These results do not necessarily mean that sowing had no effect on the abundances of non-sown species in individual plots, because it is possible that the identity of those species affected may have differed from plot to plot. We therefore calculated the proportion of all non-sown species initially present in a plot in 1992 that exhibited a decline in cover between 1992 and 1998 ( $P_{\text{Decline}}$ ) in that plot. On average, in both the control and sown plots, a greater proportion of non-sown species declined in cover than increased ( $P_{\text{decline}} > 0.5$ ). However, a significantly greater proportion of non-sown species declined in the sown plots than in the controls (Fig. 1).

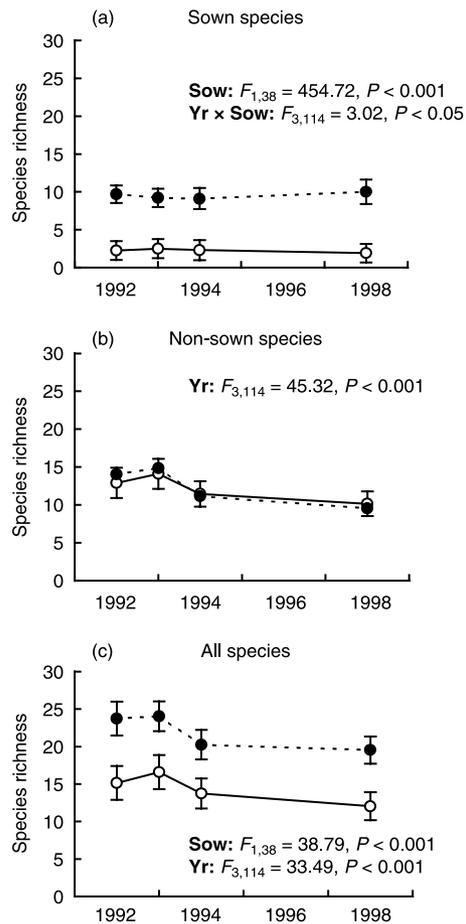
#### COMMUNITY RESPONSES

##### Species richness

The richness of sown species varied significantly in response to sowing (control vs. sown plots) and with the interaction between sowing and year, reflecting a positive effect of sowing on richness that varied slightly, but significantly, in magnitude over time (Fig. 2a). The richness of non-sown species varied significantly among years, but was unaffected by sowing (Fig. 2b). Total species richness (richness of all species combined) was increased significantly by sowing and varied significantly



**Fig. 1** Declines in cover of non-sown species ( $P_{\text{Decline}}$ ; means + 1 SE) in control and sown plots.  $P_{\text{Decline}}$  was calculated for each individual plot as the proportion of all non-sown species initially present that exhibited a decline in cover from 1992 to 1998.



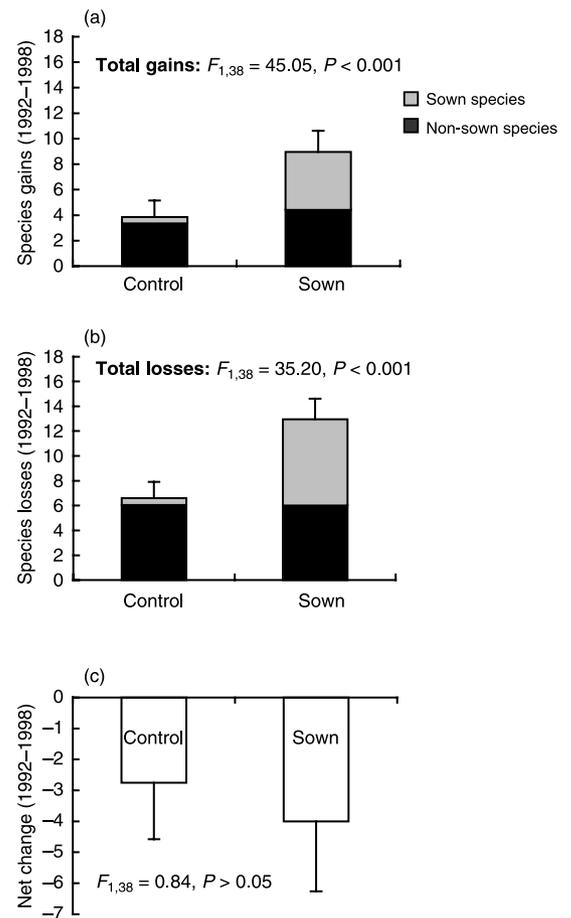
**Fig. 2** Effects of sowing on species richness (means  $\pm$  1 SE) in control (○) and sown (●) plots.

among years (Fig. 2c). At the end of the study period there was an average of 7.5 more species in the sown plots than in the controls.

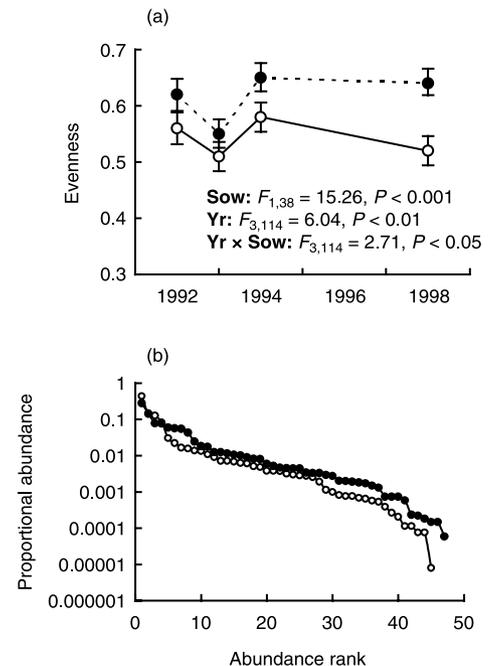
Total species gains and losses between 1992 and 1998 were significantly greater in the sown plots than in the controls (Fig. 3a,b) as a result of significantly higher rates of both gain and loss of sown species (sown species gains:  $F_{1,38} = 27.03, P < 0.001$ ; sown species losses:  $F_{1,38} = 32.30, P < 0.001$ ). The gain and loss of non-sown species did not differ significantly between treatments (non-sown species gains:  $F_{1,38} = 1.02, P > 0.05$ ; non-sown species losses:  $F_{1,38} = 0.87, P > 0.05$ ). There was a statistically similar net loss of species between 1992 and 1998 in the two treatments (Fig. 3c).

#### Changes in community evenness and abundance hierarchy

The distribution of cover among species, or community evenness, varied significantly in response to sowing, with year and with the interaction between sowing and year, reflecting a positive effect of sowing on evenness that increased in magnitude over time (Fig. 4a). The positive effect of sowing on the equitability of cover is evident from the dominance-diversity curves



**Fig. 3** Effects of sowing on species gain and loss (means  $\pm$  1 SE) between 1992 and 1998 in sown (light grey) and non-sown (black) species.



**Fig. 4** (a) Effects of sowing on community evenness from 1992 to 1998 (means  $\pm$  1 SE) in control (○) and sown (●) plots. (b) Mean dominance-diversity curves for the control (unsown) (○) and sown (●) treatments in 1998.

constructed from 1998 data (Fig. 4b). In 1998, six of the 10 most abundant species present in the sown plots were species that had been experimentally sown (*Helopsis helianthoides*, *Zizia aurea*, *Solidago rigida*, *Amorpha canescens*, *Aster azureus*, *Coreopsis palmata*, ranked 3, 5, 7, 8, 9 and 10, respectively). In the control plots, only one of the 10 most abundant species was a species that had been sown (*Amorpha canescens*, ranked 5). Twenty-two of the 29 non-sown species common to both treatments in 1998 had a lower abundance rank in the sown plots than in the controls ( $P < 0.001$ , binomial test).

#### VEGETATIVE COVER

The cover of sown species in aggregate varied significantly in response to sowing, with year and with the interaction between sowing and year, reflecting a positive effect of sowing that increased in magnitude over time (Fig. 5a). The cover of non-sown species in aggregate was reduced significantly by sowing and varied significantly among years (Fig. 5b). Total vegetative cover varied significantly among years, but was unaffected by sowing (Fig. 5c).

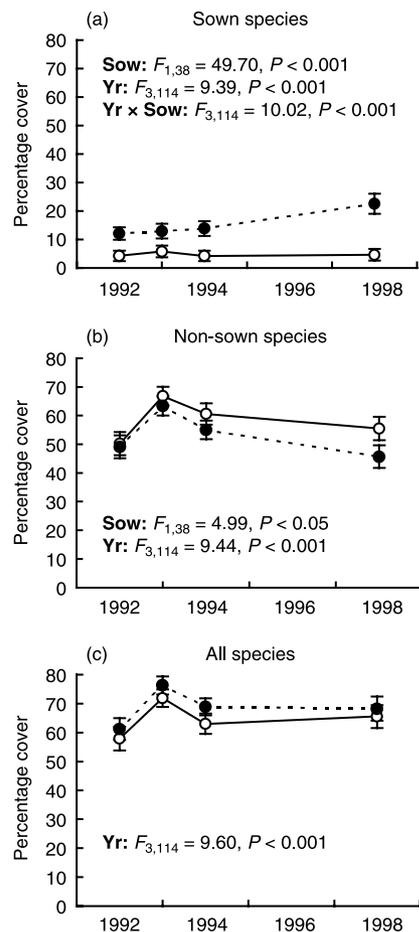


Fig. 5 Effects of sowing on species cover (means  $\pm$  1 SE) in control (○) and sown (●) plots.

#### Discussion

In this study, experimental sowing led to the successful establishment of several plant species that were not initially present and led to the increased abundance of several species that were initially present, manifest as increased occurrence in the community (plot occupancy) and increased cover at the neighbourhood scale ( $1.5 \times 1.5$  m plots). This resulted in sustained significant changes in community structure, including increased species richness and community evenness, as well as decreased absolute and relative abundance of some non-sown species. The effects of sowing on the community, which were evident during the first few years of the study, were still apparent and, in some cases had become magnified, 8 years after sowing.

Our findings are consistent with the hypothesis that local plant neighbourhoods in this savanna grassland are unsaturated with species and thus limited by seed availability. If this is indeed the case, then we may assume that more species can establish and coexist within local patches in this grassland than are typically observed within them and that this occurs as a result of constraints on seed arrival. Constraints on the diversity of colonists available to any local patch within this community could be influenced by a variety of processes that operate at different spatial scales, such as spatial segregation of source populations within the community, limited seed production of species, limited dispersal around parent plants, seed mortality at the source (pre-dispersal seed predation and disease), isolation from novel seed sources in the landscape and diversity of the broader regional species pool (Grubb 1977; Harper 1977; Primack & Miao 1992; Pacala & Levin 1997; Zobel *et al.* 2000). Because local patches in this savanna are apparently open to colonization by new species, spatial patterns of seed rain generated by the above processes might explain much of the within-community spatial variation in composition and richness that cannot be accounted for by underlying environmental gradients.

Our results suggest that seed limitation is an important factor constraining local diversity within the least disturbed and most diverse plant communities of the region, the native oak savannas, as well as in the more disturbed successional communities where seed limitation is expected. Similarly, Zobel *et al.* (2000) found that seed availability limited small-scale species richness in the extraordinarily diverse alvar communities of Estonia. Dispersal constraints are thus of fundamental importance to the regulation of diversity in many grassland communities.

In our study, sowing increased species richness for eight growing seasons without increasing the local extinction rate of non-sown species. Sowing simply added to the existing richness of the plots without causing competitive exclusions. At first glance this result seems to support the strict view of the species pool hypothesis that competition is unimportant in regulating

local species richness and that species availability is of overwhelming importance. However, the apparent additive effect of sowing on richness is not necessarily indicative of competitive interactions being unimportant because this grassland is dominated by long-lived perennials. Although sowing did increase the rate of species loss between 1992 and 1998, this was due entirely to the loss of sown species, probably reflecting high mortality of sown species that were initially present only as young and vulnerable seedlings. Although sowing had no detectable impact on the extinction rate or the richness of non-sown species as of the eighth growing season, sowing did have a demonstrable negative impact on the absolute and relative cover of non-sown species and a positive impact on community evenness. The positive effect of sowing on sown species cover (in aggregate) and the negative effect of sowing on non-sown species cover (in aggregate) increased in magnitude over time, suggesting that competitive suppression, and perhaps exclusion, of non-sown species might be underway in the sown plots. Our finding that a greater proportion of non-sown species declined in abundance between 1992 and 1998 in the sown plots than in the controls provides further evidence for competitive suppression. Only a much longer study can determine if such suppression eventually leads to local extinction or to persistence at lower than initial population densities.

It is thus plausible that the greater evenness observed in sown plots in 1998 reflects a community in a state of dynamic transition brought about by the establishment of new species and their suppression of initial resident species. If richness were eventually to fall back to ambient levels as a result of this suppression, then these communities would, indeed, have been saturated with species in the sense that resource competition and niche-availability limited their diversity. Regardless, our results suggest that at the very least there is substantial opportunity for transient coexistence at the scale of the local plant neighbourhood once recruitment limitation is overcome.

A variety of mechanisms undoubtedly operate simultaneously in plant communities to regulate species coexistence and diversity (Grubb 1977; Grime 1979; Huston 1994; Tilman 1997; Holt 2001). Numerous vegetation removal experiments have revealed the importance of neighbourhood competition in structuring plant communities and in limiting diversity (Goldberg 1987; Gurevitch & Unnasch 1989; Carson & Pickett 1990; Wilson & Tilman 1991; Gurevitch & Collins 1994; Collins *et al.* 2002). The finding that local diversity can be seed limited in intact vegetation does not diminish the importance of competition, but rather indicates that local species interactions are likely to combine with among-site dispersal to govern local species composition and diversity. Meta-community models of species coexistence identify both within-neighbourhood interactions and among-neighbourhood dispersal dynamics as being important in the regulation of diver-

sity in spatial habitats (Shmida & Ellner 1984; Tilman 1994; Pacala & Rees 1998; Holt 2001). For example, the competition-colonization trade-off model predicts that, although superior competitors exclude inferior ones locally, limited dispersal ability of the superior competitors will ensure that there will always be microsites available throughout a spatial habitat that inferior competitors can exploit (Skellam 1951; Levins & Culver 1971; Tilman 1994). Consistent with this theory, our experimental findings and those of Tilman (1997), Zobel *et al.* (2000) and Foster (2001) suggest that the availability of establishment microsites is not the primary limiting factor to colonization and richness in unproductive grasslands. The competition-colonization trade-off thus allows many species to coexist at the scale of the whole community by ensuring that inferior competitors are spatially segregated from superior competitors. It is important to note that the simplifying assumptions of the model do not permit transient coexistence of competitors within a local patch: when a superior competitor disperses to a local patch, exclusions of inferior species are instantaneous (Tilman 1994). Such instantaneous exclusion is clearly unrealistic for communities of long-lived perennial plants (Huston 1994; Pacala & Rees 1998) and our results suggest that within a 1-m<sup>2</sup> quadrat, the amount of time it takes for inferior residents to be excluded could be quite protracted, if indeed such exclusion does occur. Thus, although spatially mediated mechanisms of species coexistence, classic local niche partitioning and local competitive exclusion are all likely to be important, transient coexistence may also contribute to the maintenance of local diversity.

Our findings indicate the local patches within this grassland are open to colonization and are thus unsaturated with species in the sense that some new species may invade, increase in abundance and add to the existing diversity for many years if barriers to dispersal are eliminated. By following community dynamics for eight growing seasons we show that local competitive exclusion is likely to limit species richness, but that because exclusions may take many years to complete, there is ample opportunity for transient coexistence. It appears that dispersal limitations, species pools and local biotic processes interact to regulate plant community structure in this grassland. An important goal for future work will be to determine how these differently scaled processes vary in their relative importance under different habitat conditions or along environmental gradients.

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