

Dispersal, not Understory Light Competition, Limits Restoration of Iowa Woodland Understory Herbs

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Abstract

Plant community restoration may be limited by the inability of target species to disperse to a restoration site (i.e. dispersal limitation) or by the failure of species to establish once seeds do arrive (i.e. establishment limitation). Seed additions attempt to overcome dispersal limitations; however, seed additions may fail due to establishment limitations resulting from competition with pre-existing vegetation. We tested whether dispersal and/or competition with the pre-existing understory limited restoration of 22 native deciduous woodland herbs in Iowa, United States. We employed an experiment that varied seed mix composition to contain either high densities of forbs or graminoids, coupled with clipping of pre-existing understory vegetation to reduce competition for light during establishment. We found strong support for dispersal limitations, as seed additions increased understory richness by 4 – 8 species/m². This was due to the addition of species from the seed mix, not modification to the naturally occurring plant community, which suggests the existence of an open (unsaturated) plant community. Most species in our seed mix established at high rates and there was no effect of seed mix (high vs. low density of graminoid vs. forb seeds) on the richness or persistence of species added by seed. Light competition with the pre-existing understory vegetation did not limit establishment. We recommend simple seed sowing to restore the majority of species in our study; 19/22 species readily established. Our results support the use of less expensive seed mixes containing high density of graminoids, relative to forbs.

Key words: deciduous forest, dispersal limitation, establishment limitation, oak/hickory woodland, seed addition, species diversity, understory control.

Introduction

Restoration efforts seek to reestablish populations of species that have been lost during human-induced habitat modification (SER 2004). For plants, this is most commonly carried out through seed additions (i.e. sowing) or through trans-planting (e.g. Petersen & Philipp 2001; Graae et al. 2004; Mottl et al. 2006). Across ecosystems, seed additions generally increase plant species richness, suggesting that recruitment in many communities is dispersal limited (Matlack 1994; Ehrlén & Eriksson 2000; Clark et al. 2007). However, recruitment of species may also be limited by establishment opportunities — constraints to germination and seedling survival — (Eriksson & Ehrlén 1992; Turnbull et al. 2000; Clark et al. 2007), so simply adding seeds to a site may not effectively restore populations of all species. Local site conditions that commonly limit establishment include competition with existing species (Sluis 2002; Huddleston & Young 2004; Mabry 2005), leaf litter cover (Reader 1993; Eriksson 1995), or seed predation (Reader 1993).

Due to establishment limitations, three general outcomes could follow seed additions of native species. First, seed additions might fail due to lack of suitable establishment opportunities—a poor restoration outcome. Second, added species might establish and then displace pre-existing species, providing evidence for a saturated local community (Zobel et al. 1998), but demonstrating

superior competitive ability of the added species. This outcome may be either desirable or undesirable, depending on whether or not pre-existing species are components of the target community. Finally, species added by seeds may establish and then coexist with pre-existing species, suggesting a dispersal limited, but open (i.e. unsaturated) local community (e.g. Seabloom et al. 2003). This could also produce either desirable or undesirable restoration outcomes, depending on whether pre-existing species were components of the target community. Frequently, exotic species are cited as problematic barriers to native species establishment (e.g. Seabloom et al. 2003; Mabry 2005), but it is important to note that certain dominant native species may also limit seedling establishment during restoration and this has been particularly well documented in grasslands, where forbs are limited by graminoids (e.g. Sluis 2002; Huddleston & Young 2004; Pywell et al. 2004; Dickson & Busby 2009).

Because of this wide array of causes and consequences, understanding recruitment limitations has been a major recent focus in ecological theory (Turnbull et al. 2000; Moore & Elmendorf 2006; Clark et al. 2007) and restoration ecology (Young et al. 2005). However, in practice, restoration efforts must consider additional, more pragmatic, aspects of adding seeds to restoration sites. For example, species poor mixes may fail to properly restore species diversity to levels observed in reference sites (e.g. Martin et al. 2005), which suggests that the composition of seed mixes may have implications for restoration outcomes. Relatively less is known about implications of varying species and life-form ratios in seed mixes (Dickson & Busby 2009). Restoration seed mixes frequently use a high proportion of graminoids and lower proportion of forbs, as graminoids are typically less expensive (e.g. Prairie Moon Nursery 2010). Such an approach would be justified if seed mixes with high proportions of graminoids produce similar restoration outcomes to seed mixes with high proportions of forbs or other more expensive/rarer species. However, if high- graminoid mixes result in lower species diversity due to failed establishment of seeded species, then seed mixes with higher proportions of forbs or other more expensive species should be considered.

We conducted this study to understand dispersal and establishment limitations in how they pertain to restoring deciduous woodland understory herbs in central Iowa, United States. In spite of its recognized importance, relatively little is known about restoring woodland herbs (Honnay et al. 2002; Whigham 2004), and this is particularly true in the Midwestern United States, relative to the attention paid to prairie restoration (e.g. Sluis 2002; Martin et al. 2005; Polley et al. 2005). The most common naturally occurring understory species at our site (Table 1) were components of native deciduous woodland in the study region, and are generalist species found in a wide range of wooded habitats (Eilers & Roosa 1994). However, components of pristine woodland (i.e. species commonly found in woodlands with a minimal history of human disturbance) were missing, likely due to the history of livestock grazing at our site (Mabry 2002). Thus, the restoration goal at this site was to supplement, not displace, the naturally occurring understory community.

We sought to answer a series of both theoretical and practical questions that arise during restoration, using an experiment that varied the graminoid-to-forb ratio of seed additions, coupled with manipulation of pre-existing (e.g. naturally occurring) understory vegetation. The theoretical questions were (1) What are the relative importance of dispersal and establishment limitations during deciduous woodland restoration? We hypothesize that if the woodland community is dispersal limited, the seed addition treatments will increase understory species richness and alter community composition. However, if control of pre-existing understory vegetation increases richness, we will have evidence for establishment limitation. (2) Is the community open or saturated? If the community is open, we expect plots receiving the seed addition treatment to have greater richness, without reductions in pre-existing species. However, if the community is saturated, we expect to see either weak results of seed addition or a reduction in pre-existing species after seed addition. Questions of practical importance during restoration were (1) Are seed additions and control of naturally occurring understory vegetation effective restoration techniques for reestablishing woodland understory herbs? (2) For which species in our seed mix are these two techniques most and least effective? (3) Does the proportion (by mass) of graminoid versus forb seeds in the seed mix impact restoration outcomes? Due to increased rarity of forbs (17/22 species in the seed mix) in the high-graminoid addition treatment (75% by mass graminoid seeds), we hypothesize that the seed mix with high forb-to-graminoid ratio (75% by mass forb seeds) will result in the highest species richness and diversity. To answer these questions, we consider species diversity metrics, community composition, and individual species patterns.

Methods

Study Site

This work was conducted at the Conard Ecological Research Area (CERA), near Kellogg, IA, United States (41° 43' N, 92° 55' W). CERA is Grinnell College's 150 ha field station and situated within the North American ecotone between forest and grassland (Anderson 1983). We conducted this experiment on a 0.7 ha ridgetop, located within 5 ha of secondary deciduous woodland. This site was periodically grazed by livestock for up to 100 years prior to purchase by Grinnell College in 1968, at which point grazing and management ceased until a prescribed fire in November 2004. Soils were Lindley loam, alfisols developed in pre-Wisconsin glacial till, on 25 – 40% slopes. Overstory tree density was 1720 stems/ha (McGranahan et al. 2005), canopy cover was 85% (L. Mottl, unpublished data), and common canopy trees included oak, hickory, elm, and other deciduous tree species (e.g. *Quercus rubra*, *Q. macrocarpa*, *Carya ovata*, *C. cordiformis*, *Ulmus americana*, *Prunus serotina*, *Tilia americana*).

Common understory species are presented in Table 1. Understory cover in June 2005—at the time of the clipping treatment—was 68.5%. This cover value demonstrates (1) recovery from the previous fall burn and (2) a dense pre-existing understory, upon which our clipping treatment was imposed (see below).

Experimental Design

We used a balanced split-plot design, with a randomly applied whole-plot factor of seed addition and a split-plot factor of understory clipping. The seed addition component had three levels: two seed addition mixes (described below) and a control (no seeds added), applied to 5×5 m plots (three plots/ treatment; nine plots total). Both seed mixes were applied at a rate of 8.97 kg/ha (8 lbs/acre; Diboll 1997), or 25 g/ 5×5 m plot. All seed addition plots, aside from control plots, received seeds from 22 woodland understory plants (5 graminoids, 17 forbs; Table 2). These species were chosen based on feasibility for widespread introduction into degraded woodlands in the region based on (1) ability to produce abundant seed; (2) tolerance of dry storage; (3) high germination rates; and (4) ability, under ideal conditions, of reaching reproductive maturity in one growing season (<http://web.grinnell.edu/individuals/mottll/index.html>), except for four forbs, which do not tolerate dry storage, have exacting germination requirements and grow slowly (“trace” species in Table 2). Seeds of these species were added to plots because, as species that typify the least disturbed woodlands in the region (Mabry 2002), they are highly desirable woodland plants (Table 2). A uniform number of seeds (approximately 100/species) for these species were added to each plot, but were not used in seed mix calculations due to their large seed sizes and lower feasibility for widespread reintroduction. They were, however, included in all analyses along with the other members of the seed mix.

Seeds were hand collected from woodlands within 80 km of the study site and air dried prior to creation of seed mixes. The high-forb mix contained 75% by mass (pure live seed) forb seeds and 25% by mass graminoid seeds. The high-graminoid mix had the mass of forbs and graminoids reversed. The control treatment had no seeds experimentally added. Seed additions were performed in December 2004, after a fall prescribed understory fire. Seeds were broadcast by hand into plots that had been lightly raked to expose the soil surface and then lightly trampled by foot to ensure contact between seeds and the soil surface (Packard 1997). Control plots were both raked and trampled. Within each whole plot, we established eight 1×1 m permanently marked subplots. Subplots were randomly assigned one of two split-plot level understory clipping treatments. The goal of this treatment was to evaluate establishment limitation by reducing understory competition for light (pre-existing understory cover was approximately 70% at the time of clipping). Four subplots per whole plot received the clipping treatment, where all understory plants were clipped with hand shears to a level of approximately 5 cm during June 2005. Clipped biomass was removed from plots following clipping. This occurred after germination of seeds in seed addition plots and following the first round of data collection; however, newly germinated seedlings were unclipped because they were shorter than the clipping level. The remaining four subplots/ main plot received no understory manipulation.

Data Collection

We conducted surveys of all subplots during April 2005 and annually in June from 2005 to 2007. We identified all nonwoody vascular plant species rooted within each subplot and assigned each species to one of eight cover abundance classes (1=1%; 2=1–5%; 3=6–10%; 4=11–15%; 5= 16–25%; 6 = 26–50%; 7 = 51–75%; 8 = 76–100%). The April 2005 survey was to account for a group of spring ephemeral species from our region that senesce before the June survey period. Because our study plots contained only one spring flowering species, which was still visible in June, this survey period was discontinued and all analyses are based on data from June sampling only. All nomenclature follows Gleason and Cronquist (1991).

Data Analysis

We determined impacts of seed addition and clipping treatments using univariate and multivariate tests and inspection of individual species trends. We compared overall species richness, evenness, and Simpson’s diversity (Magurran 2004) of species from the seed addition mix, and richness of naturally occurring species (species not in the seed addition mix, but present in plots) separately, using repeated measures split-plot analysis of variance (ANOVA; PROC GLM; SAS 2002), with seed addition treatment as the whole-plot factor, clipping treatment as the split-plot factor, and year as the repeated effect. Following significant full models, we used independent linear contrasts to compare between seed addition treatments, clipping treatments, and interactions between seed addition and clipping treatments.

To understand how the seed addition and clipping treatments altered community composition, we used multiresponse permutation procedure (MRPP; McCune & Mefford 1999). MRPP is a nonparametric multivariate test of differences between pre-defined groups (McCune & Grace 2002). We defined groups as subplots grouped two ways: by seed addition treatment (24 subplots in each of 3 groups) and by clipping treatment (36 subplots in each of two groups). We ran separate MRPPs for each year of study, using cover class data for each species and considered treatment effects significant at $\alpha < 0.05$. We used Sørensen distance as the MRPP distance measure to avoid the influence of outliers (McCune & Grace 2002), because numerous species

were rare and occurred at low densities in only a few plots, whereas other species were common and/or locally abundant in our experiment.

Results

Competition with Pre-Existing Understory Vegetation

We found no evidence that competition with pre-existing understory vegetation for light limited establishment in our experiment. There was no effect of the clipping treatment on overall species richness ($F_{1,2} = 0.04$, mean square [MS] = 91.4, $p = 0.85$) or Simpson's diversity ($F_{1,2} = 1.78$, MS = 20.4, $p = 0.19$), richness of species in the seed addition mix ($F_{1,2} = 0.09$, MS = 0.35, $p = 0.76$; Table 3), richness of naturally occurring species in the plots ($F_{1,2} = 0.20$, MS = 1.7, $p = 0.66$; Table 3), or plant community composition in any year (2005 : $A = -0.00227$, $p = 0.92$; 2006: $A = -0.00015$, $p = 0.47$; 2007 $A = 0.0030$, $p = 0.13$). Furthermore, we found no evidence for interactions between the seed addition and clipping treatments (maximum $F = 2.2$, MS = 0.001, $p = 0.13$; evenness). All ensuing results combine clipping treatments to compare seed addition treatments.

Dispersal Limitation

We found evidence for dispersal limitation, as the seed addition treatments altered understory diversity and composition for the duration of our study. Furthermore, we found support for an open community, as pre-existing species were not displaced by our seed addition treatments.

Richness and Diversity. Across all years of study, seed addition plots had higher species richness than control plots ($F_{2,6} = 85.9$, MS = 947.7, $p < 0.0001$; Fig. 1a). The magnitude of this difference ranged from 4 to 8 species/m² and both the high-forb and high-graminoid treatments resulted in higher overall richness than the control seeding treatment in all years (Fig. 1a). Although this pattern in overall richness was driven primarily by an increase in species from the seed addition mix ($F_{2,6} = 162.34$, MS = 620.1, $p < 0.0001$), naturally occurring species also contributed ($F_{2,6} = 14.46$, MS = 126.1, $p < 0.0001$; Table 3). Seed addition plots contained between six and eight more species from the seed addition mix (Table 3) and both the high-forb (minimum $t = 8.70$, $p < 0.0001$; 2007) and high-graminoid treatments (minimum $t = 8.83$, $p < 0.0001$; 2007) resulted in higher richness of species from the seed mix than the control treatment in all years (Table 3). The high forb seeding treatment had higher richness of species in the seed mix than the high-graminoid treatment in 2005 ($t = 5.45$, $p < 0.0001$); however, this difference disappeared over time and the high-forb and high-graminoid seed addition mixes did not differ in richness of added species in 2006 ($t = 0.30$, $p = 0.77$) or 2007 ($t = 0.12$, $p = 0.90$).

The high-graminoid seed addition treatment had 2.25–2.5 more naturally occurring species than the high-forb addition treatment (significantly more in all years, minimum $t = 2.92$, $p = 0.005$; 2005) and 2.2–2.4 more naturally occurring species than the control seed addition treatment (significant in all years, minimum $t = 2.57$, $p = 0.01$; 2005) and the magnitude of these differences increased throughout the course of the study (Table 3). The high forb and control seed addition treatments did not differ in number of naturally occurring species in any year (maximum $t = 0.35$, $p = 0.72$; Table 3).

Overall richness did not differ between the two seed addition treatments in 2005 ($t = 0.40$, $p = 0.69$), as higher richness of seed addition mix species in the high-forb treatment was offset by higher richness of naturally occurring species in the high-graminoid treatment. However, the high-graminoid treatment had greater overall richness than the high-forb treatment in 2006 ($t = 2.39$, $p = 0.02$) and the magnitude of this difference increased in 2007 ($t = 4.23$, $p < 0.0001$; Fig. 1a).

In all years, seed addition plots had higher Simpson's diversity, relative to control plots ($F_{2,6} = 53.7$, MS = 593.2, $p < 0.0001$; Fig. 1b). Simpson's diversity did not differ between the two seed addition treatments in 2005 ($t = 1.21$, $p = 0.23$), but there was some evidence that the high-graminoid treatment had higher Simpson's diversity than the high-forb treatment in 2006 ($t = 1.86$, $p = 0.07$). The high-graminoid treatment had higher Simpson's diversity than the high-forb treatment in 2007 ($t = 2.99$, $p = 0.004$; Fig. 1b).

In all years, the seed addition treatment plots had higher species evenness, relative to control plots ($F_{2,6} = 85.9$, MS = 0.009, $p < 0.0001$; Fig. 1c). Species evenness did not differ between the two seed addition treatments in any year of study (maximum $t = 1.21$, $p = 0.23$, 2007; Fig. 1c).

Community Composition. The seed addition treatments altered plant community composition in all years of study (2005: $A = 0.038$, $p < 0.0001$; 2006: $A = 0.052$, $p < 0.0001$; 2007: $A = 0.028$, $p < 0.0001$). In each year, community composition differed across all three seed addition treatments (high-forb, $p = 0.002$). high-graminoid, control; minimum $A = 0.019$, $p = 0.002$).

Dispersal Limits Woodland Restoration

Table 1. Dominant naturally occurring understory species (i.e. species present in plots, but not components of the seed mix) present in $>50\%$ of plots in ≥ 1 year, during 3 years of study. The occurrence of these species is also shown for the three experimental seeding ratios used: a high forb (F; 75% forb seeds by mass), a high graminoid (G; 75% graminoid seeds by mass), and a control (C; no seeds added) seed treatment.

Species	2005				2006				2007			
	Total plots (%)	C	G	F	Total plots	C	G	F	Total plots	C	G	F
<i>Circaea quadrisulcata</i>	98.6	100.0	100.0	95.8	97.2	100.0	100.0	91.7	95.8	100.0	100.0	87.5
<i>Geum canadense</i>	94.4	91.7	91.7	100.0	72.2	62.5	87.5	66.7	44.4	45.8	45.8	41.7
<i>Anemone thalictroides</i>	93.1	87.5	95.8	95.8	43.1	45.8	50.0	33.3	70.8	61.1	62.5	50.0
<i>Hackelia</i> spp.	90.3	87.5	87.5	95.8	34.7	33.3	50.0	20.8	6.9	4.2	16.7	0.0
<i>Sanicula gregaria</i>	86.1	83.3	87.5	87.5	94.4	87.5	95.8	100.0	90.3	95.8	87.5	87.5
<i>Cryptotaenia canadensis</i>	83.3	87.5	79.2	83.3	83.3	83.3	87.5	79.2	63.9	62.5	54.2	75.0
<i>Polygonum virginianum</i>	81.9	75.0	70.8	100.0	87.5	70.8	95.8	95.8	81.9	75.0	79.2	91.7
<i>Pilea pumila</i>	79.2	75.0	83.3	79.2	36.1	50.0	8.3	50.0	27.8	33.3	25.0	25.0
<i>Phryma leptostachya</i>	77.8	70.8	87.5	75.0	83.3	83.3	79.2	87.5	79.2	70.8	100.0	66.7
<i>Eupatorium rugosum</i>	73.6	66.7	79.2	75.0	90.3	83.3	95.8	91.7	76.4	75.0	75.0	79.2
<i>Osmorhiza</i> spp.	69.4	75.0	66.7	66.7	36.1	41.7	29.2	37.5	56.9	58.3	70.8	41.7
<i>Festuca obtusa</i>	66.7	33.3	83.3	83.3	80.6	54.2	100.0	87.5	55.6	45.8	58.3	62.5
<i>Galium triflorum</i>	62.5	66.7	54.2	66.7	77.8	83.3	79.2	70.8	58.3	75.0	37.5	62.5
<i>Parthenocissus quinquefolia</i>	62.5	62.5	75.0	50.0	47.2	33.3	66.7	41.7	50.0	45.8	62.5	41.7
<i>Teucrium canadense</i>	59.7	58.3	62.5	58.3	55.6	58.3	66.7	41.7	51.4	54.2	62.5	37.5
<i>Acalypha</i> spp.	58.3	45.8	62.5	66.7	47.2	41.7	45.8	54.2	0.0	0.0	0.0	0.0
<i>Carex blanda</i>	36.1	45.8	45.8	16.7	51.4	66.7	45.8	41.7	68.1	79.2	66.7	58.3

Table 2. Species used in a seed mix to restore woodland understory in Iowa. Three seeding ratios were used: a high forb (F; 75% forb seeds by mass), a high graminoid (G; 75% graminoid seeds by mass), and a control (C; no seeds added) seed treatment. Values are rates of occurrence (% of plots per treatment where a species was observed), by seeding treatment (C: control, G: high graminoid, F: high forb) in 24 sampling plots/treatment, over 3 years of study. Because an understory clipping treatment had no effect on species composition (MRPP; $p > 0.1$), clipped and unclipped plots are combined within each seeding treatment.

	% Seed mix (G/F) ^a	# Seeds/25 m ² plot (G/F) ^a	2005			2006			2007		
			C	G	F	C	G	F	C	G	F
Graminoids	75.0/25.0	822,000/274,000									
<i>Carex davisi</i>	26.0/8.7	206,550/68,850	0	0	0	0	0	0	0	0	0
<i>Diarrhena americana</i>	2.2/0.7	4925/1640	0	0	0	0	0	0	0	0	0
<i>Elymus hystrix</i>	8.7/2.9	58,140/19,380	13	63	75	25	75	38	13	50	46
<i>Elymus villosus</i>	9.5/3.2	46,080/15,360	0	75	83	0	92	92	0	92	54
<i>Festuca obtusa</i>	28.6/9.5	506,125/168,700	38	83	83	54	100	88	46	58	63
Forbs	25.0/75.0	520,500/1,561,500									
<i>Agastache nepetoides</i>	0.5/1.6	42,425/127,270	0	8.3	42	0	8.3	37.5	0	8.3	4.2
<i>Arisaema triphyllum</i>	Trace ^b	Trace ^b	0	0	0	0	33	37.5	0	46	33
<i>Aster cordifolius</i>	0.3/1.0	15,370/46,100	0	63	92	0	46	83	0	46	83
<i>Blephila hirsute</i>	0.3/0.8	57,270/171,810	0	13	83	0	21	38	0	17	38
<i>Caulophyllum thalictroides</i>	Trace ^b	Trace ^b	0	0	0	0	4	0	4	4	0
<i>Campanula americana</i>	0.3/0.9	46,075/138,225	17	33	38	33	33	50	0	0	0
<i>Eupatorium purpureum</i>	1.7/5.0	58,735/176,210	17	71	63	4	63	38	0	13	13
<i>Polygonum virginiana</i>	6.5/19.0	28,950/86,860	75	71	100	71	54	96	75	79	92
<i>Scrophularia marilandica</i>	0.6/1.9	93,650/280,960	0	0	0	0	0	0	0	0	8
<i>Smilacina racemosa</i>	Trace ^b	Trace ^b	0	0	0	0	46	33	0	38	21
<i>Smilacina stellata</i>	Trace ^b	Trace ^b	0	0	0	0	0	0	0	0	0
<i>Solidago flexicaulis</i>	0.3/0.9	9220/27,650	0	0	0	0	46	75	0	42	54
<i>Solidago ulmifolia</i>	0.4/1.3	22,925/68,770	4	63	92	0	46	54	0	46	71
<i>Teucrium canadense</i>	3.3/10.0	44,100/132,300	58	63	58	58	67	42	63	63	38
<i>Thalictrum dasycarpum</i>	3.2/9.5	30,785/92,360	0	8	4	4	54	54	0	0	0
<i>Verbesina alternifolia</i>	0.7/2.2	4565/13,690	0	0	17	0	8	21	0	0	0
<i>Zizia aurea</i>	6.8/20.5	66,430/199,300	0	0	0	0	0	0	0	0	4

^a Based on weight of pure live seed.

^b Species included in restoration (approximately 100 seeds/species were added to each plot) but not used in calculations of seed mix, due to intolerance of dry storage, slow growth rates, and requirements of exacting germination conditions.

Table 3. Richness \pm 1 SE of species in seed mix used to restore understory flora and naturally occurring species (present in plots, but not in seed mix) in 1 m² Iowa woodland plots. Plots received three levels of seed additions with 22 understory herbs: a high-graminoid mix (75% mass graminoid seeds, 25% forb seeds), a high-forb mix (75% mass forb seeds, 25% mass graminoid seeds), and a control treatment, with no seeds added. Within each seed addition plot, subplots received an understory control treatment, where existing understory plants were clipped after establishment of added seeds (clipping treatment) or understory plants were retained (control).

Seed addition treatment	Clipping treatment	2005		2006		2007	
		Species in seed mix	Naturally occurring species	Species in seed mix	Naturally occurring species	Species in seed mix	Naturally occurring species
Control	Control	1.9 \pm 0.3	17.8 \pm 1.3	2.2 \pm 0.2	12.7 \pm 0.8	2.1 \pm 0.3	9.7 \pm 0.5
Control	Clipped	2.4 \pm 0.4	17.1 \pm 1.2	2.2 \pm 0.4	11.2 \pm 0.9	1.8 \pm 0.3	9.5 \pm 0.5
High graminoid	Control	5.8 \pm 0.5	19.6 \pm 0.8	7.9 \pm 0.5	13.9 \pm 0.6	6.0 \pm 0.7	11.3 \pm 0.5
High graminoid	Clipped	6.5 \pm 0.5	19.8 \pm 0.9	8.3 \pm 0.5	14.6 \pm 0.4	6.3 \pm 0.6	12.2 \pm 0.4
High forb	Control	8.2 \pm 0.4	17.8 \pm 0.7	8.4 \pm 0.5	12.1 \pm 0.8	6.4 \pm 0.6	9.1 \pm 0.6
High forb	Clipped	8.3 \pm 0.4	16.4 \pm 0.9	8.1 \pm 0.5	12.0 \pm 0.5	5.8 \pm 0.5	9.9 \pm 0.4

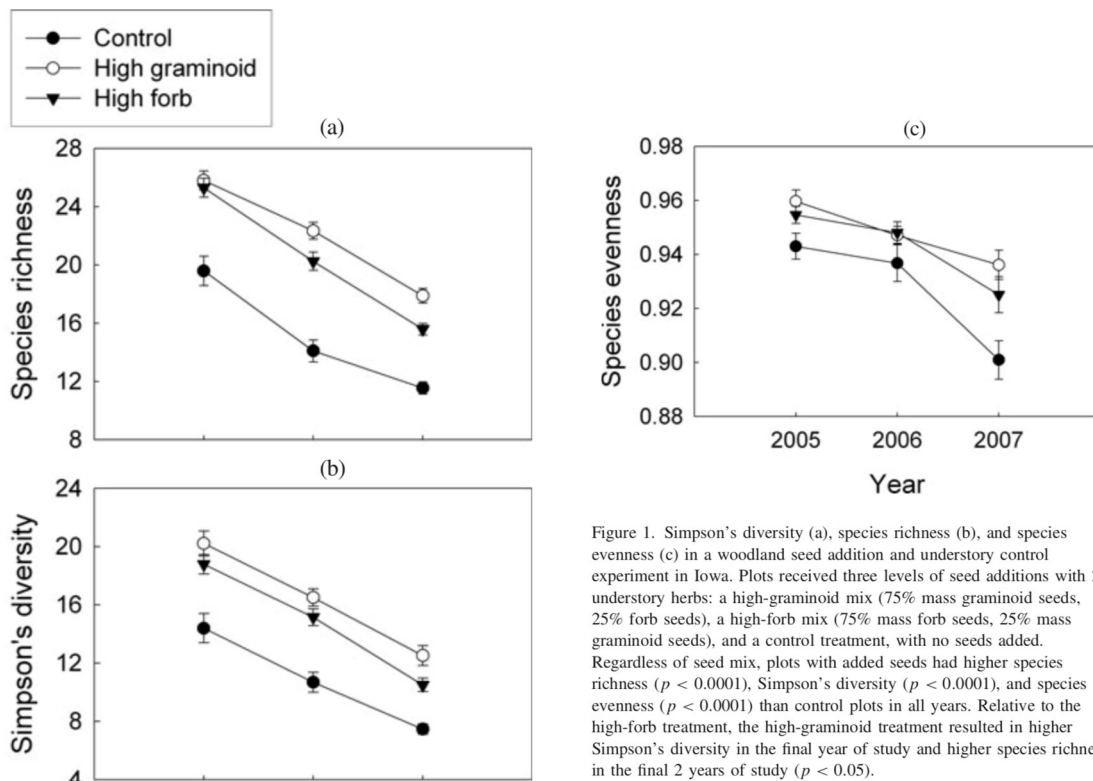


Figure 1. Simpson's diversity (a), species richness (b), and species evenness (c) in a woodland seed addition and understory control experiment in Iowa. Plots received three levels of seed additions with 22 understory herbs: a high-graminoid mix (75% mass graminoid seeds, 25% forb seeds), a high-forb mix (75% mass forb seeds, 25% mass graminoid seeds), and a control treatment, with no seeds added. Regardless of seed mix, plots with added seeds had higher species richness ($p < 0.0001$), Simpson's diversity ($p < 0.0001$), and species evenness ($p < 0.0001$) than control plots in all years. Relative to the high-forb treatment, the high-graminoid treatment resulted in higher Simpson's diversity in the final year of study and higher species richness in the final 2 years of study ($p < 0.05$).

Individual Species Trends

Seed Mix Species. Of the 22 species in our seed mix, there was a group of species that was found in all plots (*Festuca obtusa*, *Polygonum virginiana*, *Teucrium canadense*), a group of species that was found only in seed addition plots, that persisted through the course of the study (*Elymus villosus*, *Arisaema triphyllum*, *Aster cordifolius*, *Eupatorium purpureum*, *Smilacina racemosa*, *Solidago flexicaulis*, *Solidago ulmifolia*), a group of species that was found only in seed addition plots, but did not persist through the course of the study (*Agastache nepetoides*, *Campanula americana*, *Thalictrum dasycarpum*, *Verbesina alternafolia*), and a group of species that were absent or very rare in all plots, even despite being added from seed (*Diarrhena americana*, *Carex davisii*, *Schrophularia marilandica*, *Zizia aurea*; Table 2). Aside from clear cases of *Festuca obtusa*, *Polygonum virginiana*, *Teucrium canadense*, we found little evidence that species were moving from seeded into unseeded plots (e.g. appearance of seed addition species in control plots).

Naturally Occurring Species. In general, the frequency of occurrence for naturally occurring species declined throughout the course of the study (Table 1). This mirrored the results for species richness (Fig. 1; Table 3) and this pattern of a spike, followed by a decline in understory richness has been observed elsewhere after understory fire in oak/hickory woodlands (Wilhelm & Masters 1994). However, neither seed addition ($F_{2,6} = 0.24$, $MS = 0.4$, $p = 0.79$) nor understory clipping altered rates of decline of naturally occurring species ($F_{1,2} = 0.12$, $MS = 7.0$, $p = 0.73$), relative to control plots.

Discussion

In our study of central Iowa woodland restoration, we found strong support for an open, dispersal limited understory community. Reduction in dispersal limitations through the addition of native seeds increased understory Simpson's diversity and its two components—species evenness and species richness—and this altered community composition relative to control plots. In particular, species richness increased by 6–8 species/m². These changes were driven by the addition of new species from the seed mix and not accompanied by modifications to the naturally occurring plant community, thus supporting an open (not saturated) plant community (Zobel et al. 1998). Conversely, we found no evidence for understory light competition limiting establishment, although some individual species did fail to establish. Seed additions successfully produced new recruits for more than 80% of the added species, discounting seed predators, who were allowed access to our experimental plots, as major limiters of establishment. To restore the majority of species in our study to deciduous woodlands, we recommend simple seed sowing.

Although herbs display major dispersal limitations in forested ecosystems around the world (e.g. Matlack 1994; Ehrlén & Eriksson 2000), little work has been conducted to understand what consequences this has for woodland restoration and land management (e.g. Honnay et al. 2002; Whigham 2004). This is of particular importance in fragmented landscapes, like the one in which our study site was imbedded, as species differ in their abilities to disperse between patches and, for some species, movement may be rare (Damschen et al. 2008). Manual movement of seeds through seed sowing represents a means to increase movement, which in turn may increase rates of recruitment in patches, thus promoting population persistence and overall levels of plant biodiversity (Damschen et al. 2008). With a growing ability to predict species abilities to move and persist in fragmented landscapes (Damschen et al. 2008; Montoya et al. 2008), efforts can be focused on manually moving (i.e. sowing) those species lacking these capabilities. Our work clearly supports such seed sowing: 19/22 species established from seed, with 17 of these species readily establishing at high rates. Furthermore, sowing of seeds for species already present in a community may work to increase local species richness by increasing within-patch seed dispersal (Tilman 1997; Foster & Tilman 2003), thus reducing seed limitation and providing an additional benefit to this restoration technique.

Managers must weigh the ecological benefits of various restoration activities against their cost of implementation. One common restoration decision is the composition of seed addition mixes during plant species reintroductions (Brudvig & Mabry 2008), where seeds purchased from seed distributors vary widely in their cost. If purchased from a local seed distributor (Prairie Moon Nursery 2010), the seeds in our seed mixes range from \$3 to \$288/oz (\$0.11 – \$10.16/g), with forbs costing on average >2× as much as graminoids (\$58 vs. \$28/oz [\$0.98 vs. \$2.06/g]). As such, the use of a seed mix containing high amounts of forb seeds would only be justified if this resulted in improved understory conditions relative to seed mixes with higher relative graminoid contributions. Although we initially observed a species richness benefit to using a seed mix with higher proportions of forbs, this difference did not persist. By the final year of study, plots seeded with high proportions of graminoids contained nearly identical numbers of seed addition species as plots seeded with high proportions of forbs. Thus, in our case, a less expensive seed mix containing a high proportion of graminoid seeds is justified.

Our finding that high-graminoid and high-forb seed mixes performed similarly contrasts sharply with findings from Mid-western US prairie restoration studies. Warm season prairie grasses exhibit strong competitive abilities (Wedin & Tilman 1993), which may lead to high dominance by these species, especially when prairies are managed with fire in the absence of mowing or ungulate grazing (Collins et al. 1998). Prairie plantings frequently fail to replicate remnant prairie diversity due to the rarity of forbs relative to graminoids in seed mixes (e.g. Martin et al. 2005; Polley et al. 2005) and either increasing forb or reducing graminoid seed density may result in elevated forb species establishment (Dickson & Busby 2009). Why did our experimental plots not tend toward high-graminoid dominance? The answer may lie in the clear differences between Midwestern grassland and woodland graminoids. Warm season prairie grasses are the structurally dominant component of prairies, are highly caespitose and produce extensive amounts of detritus that can limit productivity (Knapp & Seastedt 1986), which may reduce establishment opportunities for subordinate forb species. Conversely, the graminoid species in our study are not highly caespitose, are generally only a relatively minor component of Midwestern woodland communities both in structure and diversity (Curtis 1959), and produce far less above ground biomass and detritus.

Seed additions in this experiment had an overall positive impact on woodland understory diversity, and there was not a general pattern of establishment limitation; however, outcomes of individual species varied. These individual species patterns were not

predicted by the number of seeds added per species in the seed mix—there was no relationship between seed number and plot occupancy in any year (maximum $r^2 = 0.08$, $p = 0.2$). The vast majority of species established in at least some plots, but two species of graminoids — *Carex davisii* and *Diarrhena americana* — did not establish and this may have been due to a number of causes ranging from nonviable seed to higher seed predation rates relative to the other species in our seed mix. It is important to note, though, that two forb species — *Schrophularia marilandica* and *Zizia aurea* — began to establish only during the final year of study, suggesting that the two graminoid species may yet establish. Four additional species — *Agastache nepetoides*, *Campanula americana*, *Thalictrum dasycarpum*, *Verbesina alternifolia* — readily established, but then declined or did not persist through the study. However, the first three species are species of open woodlands and woodland edges (Eilers & Roosa 1994), and it is possible that the light environment was not favorable for them in the relatively dense canopy of our study site. Under- and overstory competition by canopy trees can limit performance of reintroduced understory herbs in some forested systems (e.g. Harrington et al. 2003). *Verbesina* typifies alluvial woods (Eilers & Roosa 1994), and our study site was possibly too dry for it to persist.

In spite of longstanding calls for stronger coupling of restoration research and land management, especially during community restoration (Clewell & Rieger 1997; Palmer et al. 1997), such a unification is poorly realized (Cabin 2007). Of particular importance are the needs for ecological theory to inform restoration activities and for restoration research to address key questions faced by land managers. Our research team, representing both academic research and land management, tested questions of theoretical (e.g. dispersal vs. establishment limitation; open vs. saturated community dynamics) and practical importance, resulting in strategies for the restoration of 19 woodland herbs and a woodland preserve.

Implications for Practice

- Simple seed sowing reestablished 19/22 native Iowa deciduous woodland herbs.
- Seed mixes with high-forb and high-graminoid densities performed similarly.
- Because forbs cost on average twice as much as graminoids, we recommend using a diverse seed mix with a high density of graminoids.
- Understory clipping had no effect on species establishment and is not recommended as a restoration measure.

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