



Impacts of prairie grass species restoration on plant community invasibility and soil processes in abandoned agricultural fields

Wendy M. Mahaney, Katherine L. Gross, Christopher B. Blackwood & Kurt A. Smemo

Keywords

Agricultural abandonment; Native species; Old-field restoration; Plant invasion; Plant litter; Plant traits; Soil nitrogen

Abbreviations

C = carbon; N = nitrogen; ADF = acid detergent fibre

Nomenclature

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Mahaney, W.M. (corresponding author, mahaneyw@gmail.com) & **Gross, K.L.** (kgross@kbs.msu.edu): W.K. Kellogg Biological Station and Department of Plant Biology, Michigan State University, Hickory Corners, MI 49060, USA

Mahaney, W.M.: ENVIRON International Corporation, Burton, OH 44021, USA

Blackwood, C.B. (cblackwo@kent.edu) &

Smemo, K.A. (kurt.smemo@gmail.com):

Department of Biological Sciences, Kent State University, Kent, OH 44242, USA

Smemo, K.A.: The Holden Arboretum, Kirtland, OH 44094, USA

Abstract

Question: Can plant species with particular traits be used to address common problems encountered during agricultural land restoration, including invasion by undesirable species and altered soil conditions? How does the establishment of dominant old-field and prairie grasses with different functional traits affect community invasibility and soil nitrogen (N) cycling in abandoned agricultural fields?

Location: W.K. Kellogg Biological Station, Hickory Corners, Michigan, USA.

Methods: We established seedlings of several common old-field and prairie grasses in a Trait Assessment Study to determine the magnitude of species differences in traits expected to influence community invasibility and soil processes. We also established monocultures of these species in a field experiment to determine how species with particular traits impacted community invasibility and soil processes 2 and 4 yr after restoration.

Results: The prairie species consistently produced more shoot, root and litter biomass, and had more recalcitrant tissue than the old-field species, and there were corresponding differences in invasibility and nutrient cycling. Soils under the three prairie grasses had significantly lower inorganic N after 2 yr and significantly lower potential N-mineralization after 4 yr. The prairie plots also had significantly less invasion than the old-field plots after 4 yr. Plots dominated by the old-field species had higher biomass of non-native species, and higher numbers of colonizing species than plots dominated by prairie species.

Conclusions: Restoration using prairie grasses with particular effect traits can reduce N cycling and availability, and lead to a decrease in invasion by undesirable species from adjacent unrestored sites.

Introduction

The mass ratio hypothesis (Grime 1998) predicts that ecosystem functions and processes are largely determined by the traits of the dominant species, a prediction supported by many studies (Poley et al. 2006; Vile et al. 2006; Laughlin 2011). A recent meta-analysis of empirical research found extensive evidence for dominant functional traits exerting a significant influence over ecosystem properties (de Bello et al. 2010). The relationship between dominant plant species traits and ecosystem functions/processes could be used to select specific species for use in restoration projects to strategically address common problems encountered during restorations, such as

altered soil properties and prevalence of invasive species. Selecting dominant species with traits that reduce community invasibility and/or direct particular soil functions (effect traits, or traits relating to species impact on ecosystem function, *sensu* Lavorel & Garnier 2002; Violle et al. 2007) could be an important tool early in restoration projects, prior to efforts to restore a diverse native plant community (Eviner & Hawkes 2008).

Functional effect traits related to litter chemistry and biomass are often important predictors of how different plant species affect soil processes (Wardle et al. 1998; Lovett et al. 2004; Dijkstra et al. 2006) and invasibility (Blumenthal et al. 2003; Bakker & Wilson 2004; Fynn et al. 2009; van Kleunen et al. 2010; Young et al. 2010;

Steers et al. 2011). These traits can be used to predict the effects of species composition change on soil processes (Eviner 2004; Eviner et al. 2006). A natural extension of this research is to examine whether restoration of target plant species with particular traits can alter soil conditions and reduce invasion, thereby aiding overall restoration success.

Abandoned agricultural lands present an ideal opportunity to examine these relationships. Row-crop agriculture dramatically reduces total soil carbon (C) and nitrogen (N) (Burke et al. 1995; Camill et al. 2004; DeGryze et al. 2004); in the Midwestern United States, grassland cultivation can reduce total soil organic C and N content by as much as 30–60% (Burke et al. 1995). These changes affect the competitive dynamics between species after cultivation stops, thereby influencing the recovery and restoration of native species. Abandoned ‘old-fields’ are typically dominated by a successional sequence of non-native C₃ species, whereas the native C₄ prairie grasses are slow to establish and are often excluded (Foster & Gross 1997; Averett et al. 2004; Emery & Gross 2006; Gross & Emery 2007).

Grass species that are common in successional old-fields often differ from native prairie grasses in several traits expected to influence soil processes and invasibility; native prairie grasses typically have higher biomass and more recalcitrant tissue (i.e. high C:N and lignin:N) compared to the non-native grasses that characterize successional old-fields in the Midwestern USA (Wedin & Tilman 1990; Craine et al. 2002; Tjoelker et al. 2005; Mahaney et al. 2008). These trait differences have been shown to affect soil C and N cycling rates (Wedin & Tilman 1990; Evans et al. 2001; Baer et al. 2002; Mahaney et al. 2008) and plant community invasibility (Foster 1999; Emery & Gross 2006) in studies with differing dominant species.

In this study, we compared the biomass and tissue quality traits of six grass species – three native prairie and three non-native old-field species – and determined how each impacted soil conditions and invasibility by undesirable species. We established seedlings of several common old-field and prairie grasses in a Trait Assessment Study to determine the magnitude of differences in species functional traits. We also established monocultures of these species in a field experiment to determine whether soil processes and community invasibility differed among these species 2 and 4 yr after establishment. We hypothesized that the native prairie species would have higher and more recalcitrant biomass, and those plots would be less invulnerable (lower colonizing species biomass and richness) than the plots planted with non-native species. We also expected reduced N cycling and availability in the plots with more recalcitrant litter (i.e. the prairie grass plots via microbial C limitation).

Methods

Study area

The studies were performed at the W.K. Kellogg Biological Station (KBS) in southwestern Michigan, USA (Kalamazoo County; 42°24' N, 85°24' W). The area has glacial, sandy loam soils (Foster & Gross 1997) in the Kalamazoo Series (Typic Hapludalfs). Mean annual precipitation is 890 mm, mean annual temperature is 9.7 °C, and land elevation is ca. 280 m.

Species selection

We selected three native prairie grasses [*Andropogon gerardii* (Vitman), Big bluestem; *Sorghastrum nutans* (L), Indian grass; *Schizachyrium scoparium* (Michx), Little bluestem]; and three non-native old-field grasses [*Bromus inermis* (Leyss), Smooth brome; *Poa pratensis* (L), Kentucky bluegrass; *Elymus repens* (L), Quackgrass] for these analyses; naming follows USDA PLANTS Database (<http://plants.usda.gov>). The prairie species were common in southwest Michigan prior to agricultural development (Gotshall 1972) and often dominate prairie restorations in the upper Midwest (Burbank et al. 1992; Foster 1999). The old-field grasses are common dominant species in Midwestern old-fields abandoned from cultivation-based agriculture (Burbank et al. 1992; Foster 1999). Plants were started from seed in a greenhouse.

Trait assessment study

We conducted a field traits assessment study of these six species to determine the magnitude of differences in traits between species. We buried 30 pots (PVC pipe: 15.24-cm diameter, 100-cm deep) to a depth of ca. 97 cm in a fenced field (five rows of six pots) with 1.5 m mowed buffer strips between pots. The pots were filled with a 3:1 mixture of pure sand and sandy loam topsoil collected from an old-field at KBS. The soil was sieved (6.35 mm) to remove large rocks and roots and then mixed with sand. After filling the pots, the soil was supersaturated with water to achieve similar bulk densities among pots (Craine et al. 2002), and refilled with the sand/soil mixture to within 3 cm of the top of the pot. We randomly assigned five replicate pots to each species and transplanted one 7-wk-old seedling to the centre of each pot in June 2006. Pots were watered equivalently, as necessary, throughout the summer.

In late September 2006, we clipped plants at ground level, dried the material for 72 h at 65 °C, and weighed it (± 0.01 g). Shoot tissue was coarse-ground in a Wiley mill, then ground to <2 mm in a Tecator Cyclotech sample mill

(Foss North America, Eden Prairie, MN, US). Dried tissue (2–3 mg) was then packed in tin capsules to determine percentage C and N using an elemental analyser (Costech Analytical, Ventura, CA, US). We determined leaf lignin and hemicellulose composition using acid detergent fibre analyses on ground plant tissue using an Ankom 2000 fibre analyser (Macedon, NY, US). To determine root biomass, we removed the pots from the ground, cut them in half lengthwise without disturbing the soil core, and separated the core into 0–10, 10–20 and 20–80 cm depth intervals. Soils from each depth interval were kept in plastic bags at 3 °C until processed. Root biomass was estimated by removing roots >0.6 mm in diameter from soil cores placed in water, and then repeatedly washing them to remove remaining soil. Roots were dried for 48 h at 65 °C and weighed (± 0.01 g). For each species, we determined the absolute biomass and proportion of total root biomass in each depth interval.

Field monoculture experiment

Species and study sites

We established experimental monocultures of these same six species in spring 2005 at two old-fields that were abandoned over 35 yr ago following decades of row crop agriculture (Burbank et al. 1992; Foster & Gross 1997). Both fields were dominated by non-native grasses, but differed in species composition and productivity. Turkey Meadow is dominated by *B. inermis* (72% cover) and *P. pratensis* (23%); McKay Field is dominated by *E. repens* (94%) with patches of *Achillea millefolium* (L; 5%). Turkey Meadow has higher above-ground biomass ($362 \pm 30 \text{ g}\cdot\text{m}^{-2}$ vs $241 \pm 27 \text{ g}\cdot\text{m}^{-2}$), total soil C ($2815 \pm 150 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}$ vs $1638 \pm 225 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}$), and total soil N ($288 \pm 12 \text{ g}\cdot\text{N}\cdot\text{m}^{-2}$ vs $169 \pm 18 \text{ g}\cdot\text{N}\cdot\text{m}^{-2}$) than McKay Field (Mahaney 2007).

We established experimental monocultures of the species in each field in late spring 2005 in three randomized blocks (each 11 m \times 14 m), with each block containing 30 1 m² plots separated by 1-m walkways. We treated each block with a glyphosate herbicide (Roundup®) in April 2005 to kill existing vegetation, and then removed surface litter and hand-clipped standing dead tissue. To minimize soil disturbance, we left highly fragmented surface litter in place. In May 2005, we covered each plot with landscape fabric to minimize weed growth, and planted 16 7-wk-old seedlings into each plot (16 plants \cdot m⁻² plot). In each block, we randomly assigned six (1 m²) plots to each species. We planted five of the species in both sites, but were only able to obtain enough seed of *Elymus* to plant it in one site (Turkey Meadow). The transplants were watered as needed for several weeks to aid establishment, and the landscape fabric was removed after 1–2 mo. In total, each site had 18

replicate monocultures of each species, six in each of three blocks.

Field sampling

We removed (clipped at ground level) species that had not been planted in that particular plot for two growing seasons (2005–2006). In 2005, weeding was minimal as the landscape fabric prevented colonization. In 2006, we clipped and removed colonizing species every 6–7 wk; the biomass removed from each plot was bagged, dried and weighed (± 0.01 g). Weeding was discontinued in August 2006 and species from the seed bank and surrounding landscape were allowed to colonize. In August 2006 and 2008, three plots of each species were randomly selected in each block to sample ($n = 9$ per species, three per block). We randomly selected one quadrat (four 0.25 m \times 0.25 m quadrats per plot) within each of these plots for vegetation and soil sampling (the same quadrat was not resampled in 2008). Vegetation was clipped at ground level and separated into the target (planted) species and colonizer (any species other than the target, identified to species level in 2008) biomass. We then collected the surface litter. For soil chemical analyses, we collected and composited two cores (0–10-cm deep, 3.8-cm diameter) from sampled quadrats in 2006 ($n = 6$ per species, two per block) and 2008 ($n = 9$ per species, three per block). In 2006, we estimated root biomass in a subset of harvested quadrats in both fields ($n = 6$ per species, two per block) by collecting one soil core (0–20-cm deep, 6.35-cm diameter) immediately after the shoot biomass harvest. The core was split into two depths (0–10 and 10–20 cm) and refrigerated until processed in the laboratory.

Sample processing and laboratory analyses

In 2006 and 2008, above-ground biomass and surface litter was dried for at least 72 h at 65 °C, and target species biomass, colonizer biomass and surface litter mass was recorded (± 0.01 g). Tissue chemistry was only analysed in 2006 because the results after 2 yr were consistent with the results found by Mahaney et al. (2008) for these same species after being grown for 11 yr in these same study sites. Shoot tissue of each species, from both sites, was ground and packed in tin capsules, as described above, and analysed for percentage C and N using an ANCA-GSL elemental analyser (SerCon, Crewe, UK) at the UC Davis Stable Isotope Facility. Root biomass was estimated for each depth interval (0–10 and 10–20 cm) as described above.

Soils collected for soil chemistry analyses were passed through a 2-mm sieve prior to analysis to homogenize the sample and remove large roots and rocks. In 2006 and 2008, we extracted inorganic N from 20-g subsamples

processed within 24 h of sample collection using 50 ml of 1 M KCl. The extractions were stored at 3 °C until analysis on an O.I. Analytical Flow Solution IV analyzer (O.I. Analytical, College Station, TX, US) in 2006 and a BioTek Synergy HT micro-plate reader (BioTek Instruments, Winooski, VT, US) in 2008. In 2008, we estimated potential N mineralization rates from 28-day laboratory incubations (modified from Robertson et al. 1999). Inorganic N at day 0 and day 28 was determined from soil extracts processed as described above and analysed using a BioTek Synergy HT micro-plate reader. In both years, we determined gravimetric soil moisture on a subsample of soil (ca. 25 g fresh weight) by drying soils at 105 °C for 48 h. We ground a subsample of air-dried soil (ca. 50 mg) to a flour-like texture and oven-dried it for C and N analyses. In 2006, analyses for percentage C and N were performed at UC Davis on an ANCA-GSL elemental analyser (SerCon). In 2008, percentage C and N analyses were performed using a Costech CHNSO analyser (Costech Analytical, Ventura, CA, US).

Data analysis

We used non-metric multidimensional scaling (NMS) to group species simultaneously according to multiple traits measured in the Trait Assessment Study (shoot biomass; % C, %lignin, C:N and lignin:N; %total root biomass in surface 10 cm of soil; total root biomass; root:shoot; plant height) using PCOrd 5. NMS was based on Sørensen distance calculated from log transformed trait values (Fig. 1). Significance of the difference between prairie and old-field species in multivariate trait space was tested using a permutation test implemented through the capscale method (constrained analysis of principal coordinates; Anderson & Willis 2003) in the vegan package in the software R (R Foundation for Statistical Computing, Vienna, AT). The ordinations indicated that prairie and old-field species were distinct groups, so we included these two groups in an ANOVA with nested treatment structure and a completely randomized design (Milliken & Johnson 2009) in SAS 9.1 Proc Mixed (SAS Institute, Cary, NC, US). Fixed effects included plant type (prairie vs old-field) and species nested within plant type. Significant effects of species nested within plant type were interpreted by performing *post-hoc* pair-wise comparisons among species using Tukey's HSD test.

To test for differences in plant and soil variables (C and N chemistry, biomass) measured in the Field Monoculture Experiment, we used a nested ANOVA as described above. Site and block (nested within site) were included as random factors. Degrees of freedom were estimated using the Kenward–Roger method, and are reported rounded to the nearest whole number. The significance of random factors

was examined using a Wald Z test in Proc Mixed. The effects of site and block were not significant ($P > 0.05$) and are not reported further. The significance of each experimental factor was assessed using Type 3 tests available in Proc Mixed.

Total plant species richness and non-native species richness were analysed assuming Poisson distributed errors for count data using the lme4 package (<http://CRAN.R-project.org/package=lme4>) in the software R. Fixed and random effects were specified as described above, and their significance was tested using separate likelihood ratio tests. Pearson's product moment correlations were performed to examine relationships between richness and variables relating to light and nutrient availability (i.e. biomass, litter, soil nutrients) and *P*-values were adjusted using the Holm method in the software R.

Results

Trait assessment study

Ordination of plant traits (shoot biomass; %C, %lignin, C:N, lignin:N; %total root biomass in the surface 10 cm of soil; total root biomass; root:shoot; plant height) indicated that grouping the three prairie species and the three old-field species was appropriate (Fig. 1). Permutation testing using the capscale command in R indicated that the positions of prairie and old-field species in this ordination were significantly different ($P < 0.05$). Axis 1 separated species primarily based on root ($r = 0.87$, $P < 0.001$) and shoot biomass ($r = 0.90$, $P < 0.001$), and axis 2 separated species by tissue C:N ($r = 0.93$, $P < 0.001$) and lignin:N ($r = 0.93$, $P < 0.001$). The three prairie species had significantly larger shoot biomass, height and more recalcitrant tissue chemistry than the old-field species (Table 1, Fig. 2). The prairie species also had significantly higher root biomass between 10 and 80 cm soil depths, but not in the top 10 cm or total root biomass (Table 1). The old-field species had a significantly higher root:shoot than the prairie species, and a significantly larger proportion of their total root biomass (50%) in the surface soil (0–10 cm) than the prairie species (41%). There were some significant differences among species within each plant type, primarily between *Andropogon gerardii* and the other prairie species or *Bromus inermis* and the other old-field species (Table 1, Fig. 2).

Field monoculture experiment

Plant production and chemistry

In both 2006 and 2008, total shoot biomass (2006: $F_{1,86} = 142.9$, $P < 0.001$; 2008: $F_{1,90} = 151.5$, $P < 0.001$), shoot biomass of the target species (Fig. 3) and litter layer mass (2006: $F_{1,86} = 17.4$, $P < 0.001$; 2008: $F_{1,89} = 65.4$, $P < 0.001$; Table 2) were significantly higher for prairie

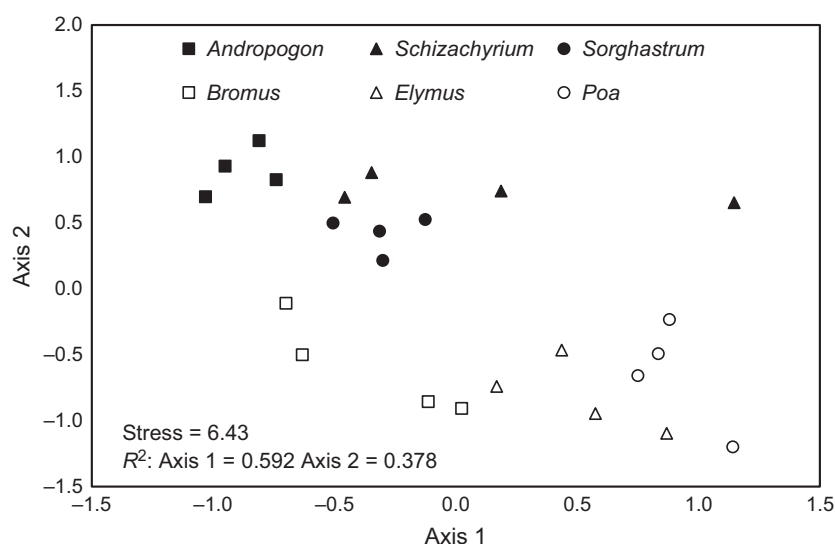


Fig. 1. Non-metric multidimensional scaling (NMS) of species traits from the Trait Assessment Study using Sørensen distance calculated from log-transformed trait values. Plant traits included in the analysis were: shoot biomass; tissue %C, lignin, C:N, lignin:N; proportion of roots in the top 10 cm of soil; total root biomass; root:shoot ratio; shoot height. Filled symbols are native prairie grasses, while open symbols are old-field grasses.

Table 1. Trait Assessment Study biomass ($\text{g} \cdot \text{plant}^{-1}$) at each depth interval and plant height (mean \pm SE; $n = 5$ for shoot, $n = 4$ for root). Group refers to prairie grass species (P) or old-field grass species (O). Shaded columns indicate significant differences between species group (P, O). Where species nested within group explained significant additional variation, significant differences between species within each group ($P < 0.05$) are denoted by lowercase (prairie species) or uppercase (old-field species) letters.

Species	Group	Shoot biomass	Shoot height (cm)	Root biomass (by depth interval)			
				0–10 cm	10–20 cm	20–80 cm	Total Root
<i>Andropogon</i>	P	13.5 \pm 1.3	165.4 \pm 1.4a	5.2 \pm 0.7	2.7 \pm 0.3a	5.7 \pm 1.0	13.5 \pm 1.8a
<i>Schizachyrium</i>	P	11.2 \pm 2.5	82.2 \pm 15.3b	2.4 \pm 0.8	1.0 \pm 0.3b	3.1 \pm 0.8	6.5 \pm 1.8b
<i>Sorghastrum</i>	P	10.4 \pm 1.2	111.0 \pm 10.1b	4.7 \pm 0.5	1.1 \pm 0.1b	3.9 \pm 0.5	9.7 \pm 0.9ab
<i>Bromus</i>	O	9.5 \pm 2.1	59.2 \pm 7.2	5.5 \pm 1.4	1.6 \pm 0.5A	4.9 \pm 1.0A	12.1 \pm 2.8A
<i>Poa</i>	O	3.2 \pm 0.6	38.5 \pm 4.9	2.6 \pm 0.6	0.6 \pm 0.1B	1.6 \pm 0.2B	4.8 \pm 0.9B
<i>Elymus</i>	O	4.3 \pm 0.6	45.6 \pm 3.5	3.5 \pm 0.8	0.6 \pm 0.1B	2.5 \pm 0.5AB	6.6 \pm 1.3AB
Group	df	1,23	1,23	1,18	1,18	1,18	1,18
	F	26.0	128.6	0.10	14.0	5.39	2.93
	P-value	<0.001	<0.001	0.75	0.002	0.032	0.104

than for old-field species. Among the prairie species, litter biomass in 2008 was higher for *Andropogon gerardii* than *Sorghastrum nutans* ($F_{4,89} = 4.2$, $P = 0.004$; Table 2); there were no other significant differences in traits among species within each plant type. Root biomass (2006) at both depth intervals (0–10 and 10–20 cm; Fig. 3) and total root biomass (0–20 cm; $F_{1,57} = 6.9$, $P = 0.011$) was significantly higher for prairie species than old-field species.

Tissue N was significantly higher for old-field species than prairie species ($F_{1,33} = 51.3$, $P < 0.001$), and *Poa pratensis* had higher N content than the other two old-field species ($F_{4,36} = 8.8$, $P < 0.001$; Table 3). Tissue C did not differ between plant types ($F_{1,38} = 2.0$, $P = 0.165$; Table 3). Tissue C:N was significantly higher for prairie

species ($F_{1,37} = 57.7$, $P < 0.001$), and *Poa pratensis* had lower C:N than *Bromus inermis* ($F_{4,36} = 5.03$, $P = 0.002$; Table 3).

Soil properties and processes

In 2006, soils collected from plots with old-field species had higher inorganic N levels than soils under prairie species ($F_{1,86} = 9.0$, $P = 0.004$). Among the old-field species, *Bromus inermis* had significantly higher inorganic N than *Poa pratensis* ($F_{4,86} = 3.9$, $P = 0.006$; Fig. 4). Potential N mineralization rates were twice as high in soils under old-field species compared to soils under prairie species in 2008 ($F_{1,88} = 9.4$, $P = 0.003$), and there were differences among

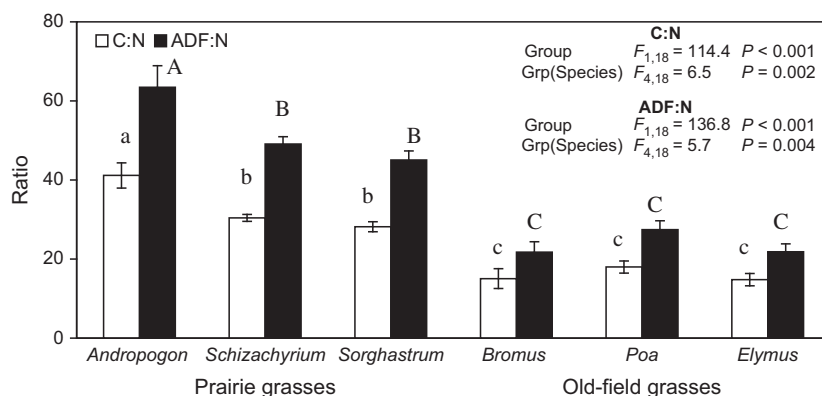


Fig. 2. Tissue chemistry data (mean \pm SE; $n = 4$) for six grass species grown in the Trait Assessment Study. Acid detergent fibre (ADF) is a measure of recalcitrant compounds, primarily lignin and hemicellulose, which are typically used as a measure of litter quality. Uppercase (ADF:N) and lowercase (C:N) letters indicate significant differences between species within each group.

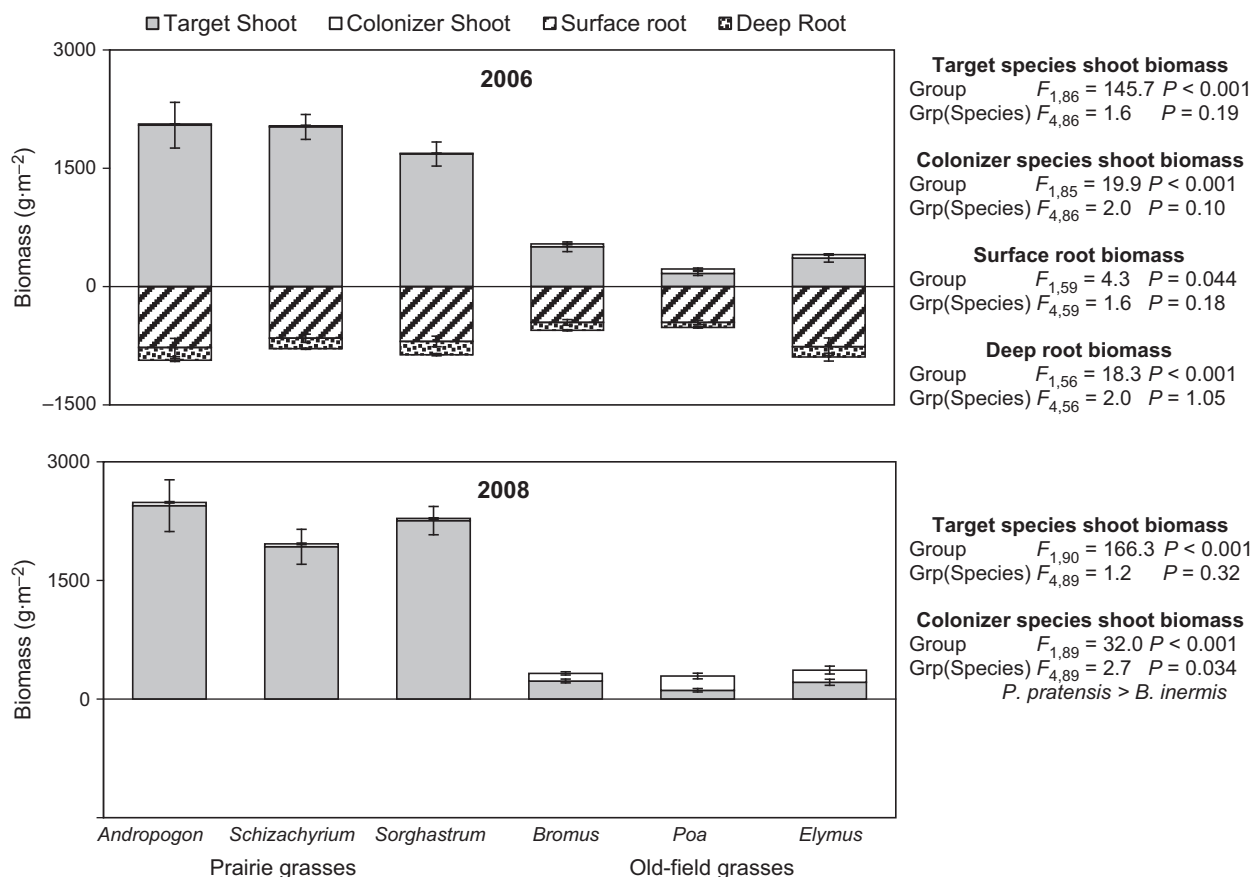


Fig. 3. Shoot and root production estimates for the grass species grown in the Field Monoculture Experiment, averaged across the two sites. Mean (\pm SE) root biomass for each depth interval ($n = 6$) is shown for 2006, and shoot biomass (separated into the target species and colonizer species; $n = 9$) is shown for both 2006 and 2008.

the old-field species; soils from *Elymus repens* plots had higher N mineralization rates than the other old-field species ($F_{4,88} = 5.4$, $P = 0.006$; Fig. 4). Total soil C and N did

not differ between old-field and prairie species groups (Table 4). Soil C:N was higher under prairie species than old-field species in 2006 ($F_{1,45} = 13.8$, $P < 0.001$), but not

Table 2. Mean (\pm SE) surface litter mass in 2006 and 2008 for each species averaged across sites, and mean species richness (total and non-native richness \pm SE) for each site in 2008, in the Field Monoculture Experiment. Shaded columns indicate significant ($P < 0.05$) differences between species group [prairie grass species (P) and old-field grass species (O)]. For surface litter in 2008, there was also a significant difference between *Andropogon* and *Sorghastrum* within the prairie grass group ($P < 0.05$), as indicated by lowercase letters.

Species	Group	Surface litter ($\text{g}\cdot\text{m}^{-2}$)		Total richness		Non-native richness	
		2006	2008	Turkey meadow	McKay field	Turkey meadow	McKay field
<i>Andropogon</i>	P	154 \pm 19	288 \pm 28a	4.0 \pm 0.5	2.0 \pm 0.4	2.6 \pm 0.4	0.9 \pm 0.3
<i>Schizachyrium</i>	P	113 \pm 14	234 \pm 24ab	2.4 \pm 0.4	2.2 \pm 0.2	1.3 \pm 0.4	1.2 \pm 0.2
<i>Sorghastrum</i>	P	113 \pm 14	189 \pm 20b	2.4 \pm 0.4	2.0 \pm 0.4	1.3 \pm 0.4	0.9 \pm 0.4
<i>Bromus</i>	O	98 \pm 17	111 \pm 15	5.6 \pm 0.4	3.2 \pm 0.3	3.3 \pm 0.6	1.8 \pm 0.2
<i>Poa</i>	O	54 \pm 9	73 \pm 12	6.1 \pm 0.4	3.3 \pm 0.4	4.1 \pm 0.3	2.2 \pm 0.3
<i>Elymus</i>	O	71 \pm 13	112 \pm 33	4.8 \pm 0.6	n.a.	2.9 \pm 0.6	n.a.

Table 3. Plant tissue chemistry (mean \pm SE) for each species ($n = 4$) in 2006 averaged across sites, for the Field Monoculture Experiment. Shaded columns indicate significant ($P < 0.05$) differences between species groups [prairie grass species (P) and old-field grass species (O)]. Significant differences between species within each group ($P < 0.05$) are denoted by lowercase (prairie species) or uppercase (old-field species) letters.

Species	Group	%N	%C	C:N
<i>Andropogon</i>	P	0.76 \pm 0.08	45.12 \pm 0.16	63.67 \pm 6.42
<i>Schizachyrium</i>	P	0.83 \pm 0.05	44.46 \pm 0.25	55.20 \pm 3.54
<i>Sorghastrum</i>	P	0.74 \pm 0.06	45.03 \pm 0.34	63.28 \pm 4.49
<i>Bromus</i>	O	1.06 \pm 0.12A	44.84 \pm 0.20	45.22 \pm 4.27A
<i>Poa</i>	O	1.65 \pm 0.16B	43.86 \pm 0.43	27.89 \pm 2.36B
<i>Elymus</i>	O	0.92 \pm 0.08A	44.80 \pm 0.44	49.44 \pm 4.29AB

in 2008 ($F_{1,88} = 5.7$, $P = 0.114$; Table 4). Soils under *B. inermis* had lower C:N than the other two old-field species in 2008 ($F_{4,88} = 5.7$, $P < 0.001$).

Invasibility

There was significantly more colonizing species biomass in old-field plots than prairie plots in both 2006 ($F_{1,85} = 19.9$, $P < 0.001$) and 2008 ($F_{1,89} = 32.0$, $P < 0.001$; Fig. 3). Within the old-field species, *Poa pratensis* had higher colonizer biomass than *Bromus inermis* in 2008 ($F_{4,89} = 2.7$, $P = 0.034$). Most of the colonizer biomass was from non-native species that are common in old-fields, and as a result the biomass of non-native species was also significantly higher in old-field plots than prairie plots ($F_{1,91} = 11.1$, $P = 0.001$; Fig. 5). Total and non-native species richness in 2008 was significantly higher in old-field plots compared to prairie species ($\chi^2 = 26.60$ and 23.65, respectively, $P < 0.0001$ for both; Table 2). The effect of particular species nested within plant type on invasibility (either biomass or richness) was not significant. Total richness was significantly affected by site (higher at Turkey Meadow than at McKay Field), while non-native richness was significantly affected by blocks within sites. In 2008, there were several strong correlations between invasibility

metrics (richness and biomass) and plant and soil variables relating to soil nutrients and light availability (Table 5). For both litter and target species biomass, there was a significant negative correlation with total species richness, colonizer biomass and non-native species richness (Table 5). There were significant positive correlations between potential N mineralization rates and total species richness, colonizer biomass, non-native species richness and biomass (Table 5). There was a significant negative correlation between potential N mineralization rates and litter mass (Table 5).

Discussion

The Trait Assessment Study exhibited trait differences with respect to both tissue production and chemistry between the prairie and old-field grasses examined in this study. The functional trait differences we found are similar to those found in other studies (Wedin & Tilman 1990; Baer et al. 2002; Craine et al. 2002; Tjoelker et al. 2005; Mahaney et al. 2008). Our results clearly show that the selection of a dominant species with particular plant traits (root and shoot biomass, surface litter biomass, tissue chemistry) had the predicted effects on invasibility and soil processes. We demonstrated that restoration of species with larger amounts of recalcitrant biomass (i.e. prairie species) reduced invasibility and N cycling rates compared to old-field species. Further, species within each group were similar for many of the plant traits, and within-group trait differences did not affect soil processes or invasibility. This suggests that species that have generally similar functional effect traits can be used in restorations to produce similar results (i.e. species with a large amount of recalcitrant biomass).

We found differences in community invasibility between plots dominated by prairie and old-field species, which supports the notion that the species traits can be used to direct native prairie restoration. Blumenthal et al. (2003) found that prairie restorations dominated by the

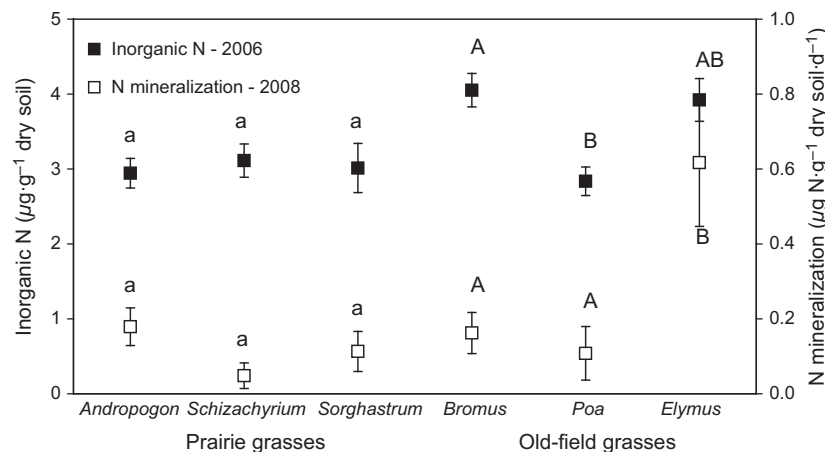


Fig. 4. Species effects on inorganic N concentrations and N mineralization rates (mean \pm SE) in the Field Monoculture Experiment, averaged across the two sites. There were significant differences between species group (prairie grass species and old-field grass species) for both variables. Significant differences between species within each group ($P < 0.05$) are denoted by lowercase (prairie species) or uppercase (old-field species) letters.

Table 4. Soil chemistry data (mean \pm SE) for soils under each species averaged across sites, for the Field Monoculture Experiment. Shaded columns indicate significant ($P < 0.05$) differences between species groups [prairie grass species (P) and old-field grass species (O)]. Significant differences between species within each group ($P < 0.05$) are denoted by lowercase (prairie species) or uppercase (old-field species) letters.

Species	Group	2006			2008		
		N (%)	C (%)	C:N	N (%)	C (%)	C:N
<i>Andropogon</i>	P	0.10 \pm 0.01	1.21 \pm 0.09	11.8 \pm 0.2	0.11 \pm 0.01	1.47 \pm 0.14	13.2 \pm 0.4
<i>Schizachyrium</i>	P	0.13 \pm 0.01	1.47 \pm 0.09	11.4 \pm 0.1	0.12 \pm 0.01	1.62 \pm 0.17	13.7 \pm 0.6
<i>Sorghastrum</i>	P	0.13 \pm 0.01	1.49 \pm 0.14	11.5 \pm 0.2	0.13 \pm 0.01	1.61 \pm 0.16	13.0 \pm 0.5
<i>Bromus</i>	O	0.14 \pm 0.01	1.55 \pm 0.11	11.2 \pm 0.1	0.13 \pm 0.01	1.59 \pm 0.18	12.6 \pm 0.4A
<i>Poa</i>	O	0.12 \pm 0.01	1.31 \pm 0.08	11.0 \pm 0.1	0.12 \pm 0.01	1.67 \pm 0.19	14.0 \pm 0.5B
<i>Elymus</i>	O	0.15 \pm 0.00	1.63 \pm 0.03	10.9 \pm 0.2	0.11 \pm 0.01	1.47 \pm 0.20	13.0 \pm 0.7B

same three prairie grasses used in our experiments had the potential to reduce weedy species biomass in restorations in Minnesota, USA. While study sites differed in their total species richness, plots within each site have the same seed bank and seed rain, suggesting that the effects in this study are a result of the planted species trait differences. We found that higher shoot and litter biomass (prairie species) corresponded to a decline in colonizer biomass, and communities dominated by old-field species were more invasible than those dominated by prairie species based on biomass and richness metrics. Invasibility (non-native biomass, colonizer richness, colonizer biomass) was positively correlated with N mineralization rates (i.e. higher in old-field plots) and negatively correlated with target species shoot biomass and surface litter (i.e. higher in prairie plots).

The lower invasibility of our prairie grass plots could be the result of several factors, including reduced N availability and light limitation. Both the higher amounts of litter and the higher above-ground biomass in the prairie plots could reduce invasion. In southwestern Michigan, Emery

& Gross (2006) found that communities dominated by *Andropogon virginicus* (a native prairie species) were the least invasible, while communities dominated by *Centaurea maculosa* and *Bromus inermis* (non-native species) were most invasible. The authors suggested that litter biomass was a strong controller of the reduced invasibility by both native and non-native species (Emery & Gross 2006). Foster & Gross (1998) found that higher litter and shoot biomass interchangeably reduced species richness in Midwestern old-fields, which they attributed to light attenuation. Litter and biomass removal studies support light limitation as an important factor limiting invasibility. McCain et al. (2010) found that a restored prairie dominated by *Andropogon gerardii* had low species richness and diversity, but this effect was reduced with experimental manipulations of *Andropogon* abundance. Within 2 yr of removing 50% of the *Andropogon* tillers, species richness had increased in the field, was negatively correlated with total grass productivity and cover, and was positively correlated with light availability at the soil surface, suggesting light limitation controlled colonization in these restorations

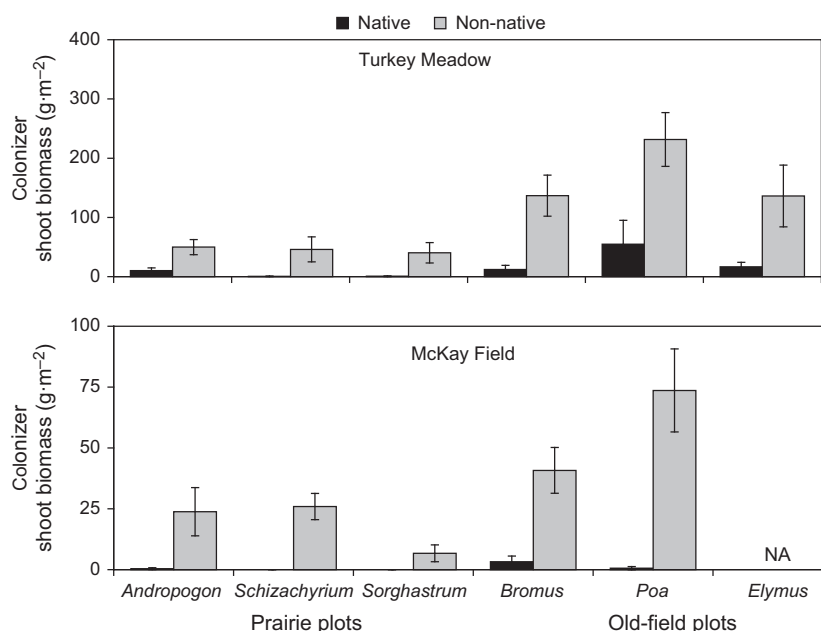


Fig. 5. Contribution of native and non-native species (mean \pm SE) to total colonizer shoot biomass in the Field Monoculture Experiment in 2008. Non-native species biomass differed significantly between species groups (prairie grass species and old-field grass species).

Table 5. Pearson correlations (r , P -value) between invasion metrics and plant and soil variables relating to light and soil nutrients. P -values corrected by the Holm method for multiple comparisons.

	Colonizer biomass	Litter mass	Total richness	Non-native biomass	Non-native richness	N Mineralization
Target biomass	-0.46	0.55	-0.55	-0.44	-0.49	-0.17
	<0.001	<0.001	<0.001	0.001	<0.001	1.00
Colonizer biomass	—	-0.36	0.71	0.93	0.69	0.42
		0.037	<0.001	<0.001	<0.001	0.002
Litter mass	—	—	-0.44	-0.35	-0.44	-0.27
			0.001	0.051	0.001	0.876
Total richness	—	—	—	0.64	0.92	0.36
				<0.001	<0.001	0.029
Non-native biomass	—	—	—	—	0.68	0.48
					<0.001	<0.001
Non-native richness	—	—	—	—	—	0.40
						0.005

(McCain et al. 2010). Patrick et al. (2008) also found that removing litter from a temperate grassland caused a significant increase in non-native species richness.

Nitrogen availability has also been associated with invasibility. Prober & Lunt (2009) found that the use of native tussock grasses in Australian woodland restorations decreased soil nitrate concentrations, and that this, in combination with C additions or burning, decreased invasive species percentage cover. We also found that lower soil N corresponded to reduced invasibility. Soil N cycling rates were significantly affected by species type; inorganic N pools (2006) and N mineralization rates (2008) were lower in soils under the native prairie grasses, suggesting rapid and overall higher N immobilization under native prairie

grasses. Other studies have also shown less inorganic N and/or reduced N mineralization rates in communities dominated by prairie grasses (Wedin & Tilman 1990; Wedin & Pastor 1993; Baer et al. 2002; Camill et al. 2004; Mahaney et al. 2008). Based on the results in Mahaney et al. (2008), which found significantly lower inorganic N under prairie species compared to old-field species after 10 yr, we expect the N cycling rate differences and their potential effect on invasibility will persist. Further study to determine the relative importance of factors affecting community invasibility in these old-field systems would improve our ability to select species traits (e.g. relating to light attenuation, N availability) with the goal of reducing N availability and invasibility by undesirable species.

Our results suggest that focusing on species traits related to invasibility and soil processes could be an effective approach for selecting species for restoration. A potential approach to test the effectiveness of this restoration strategy would utilize a species effect–response trait framework similar to that proposed by Suding et al. (2008). Their framework examined how species response traits (i.e. traits relating to how a species responds to an environmental factor; *sensu* Lavorel & Garnier 2002) would relate to their effect traits (i.e. traits relating to how a species impacts some ecosystem function; *sensu* Lavorel & Garnier 2002). The Suding et al. (2008) framework could be adapted to focus on choosing dominant species with plant effect traits that minimize invasion and restore soil conditions (Lavorel & Garnier 2002; Violle et al. 2007; Eviner & Hawkes 2008; Suding et al. 2008). However, invasibility by both desirable and undesirable species may be decreased (Howe 1994; Kindscher & Tieszen 1998; Baer et al. 2002; Camill et al. 2004; McCain et al. 2010), creating a barrier to restoring both soil conditions and diverse plant communities. This may require the subsequent use of a second restoration stage focused on selecting a diverse suite of species with plant response traits that are likely to lead to successful establishment under the restored conditions (potentially in conjunction with strategic actions to alleviate light limitation). This two-stage restoration approach recognizes and addresses some of the difficulties in restoring agricultural lands to native prairie communities: altered soil conditions and invasive species are especially problematic in the initial stages of a restoration, and re-establishment of native forb species is often difficult in the later stages.

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