Evaluation of resource-limiting strategies intended to prevent *Phalaris arundinacea* (reed canarygrass) invasions in restored sedge meadows[1]

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Abstract: Resource-rich restoration sites are prone to invasion by aggressive plants that prevent community recovery. Reducing light by sowing non-persistent cover crops and immobilizing nitrogen by amending soils with sawdust, however, may prevent this scenario in restored sedge meadows by limiting *Phalaris arundinacea* (reed canarygrass) invasions. To determine the usefulness of these resource-reducing methods, a perennial target community and *Phalaris* were sown with a high-diversity cover crop, a low-diversity cover crop, or no cover crop in plots with or without sawdust under controlled hydrological conditions. Aboveground biomass was measured after two growing seasons, and light and soil nitrogen were measured throughout the study. Only high-diversity cover crops reduced light, and in doing so they decreased target community and *Phalaris* establishment by 73% and 68%, respectively, resulting in a *Phalaris*-dominated community. Despite only reducing nitrogen over the short term, amending soils with sawdust decreased *Phalaris* establishment by 56% without hindering target community establishment, resulting in a graminoid-rich community similar to natural sedge meadows. The target community, however, reduced both light and nitrogen, and in doing so decreased *Phalaris* establishment by 78% and 67% in plots with and without sawdust, respectively. Our results show that rapidly establishing a perennial plant community may be more important than reducing initial resource availability when trying to limit invasions of resource-rich restorations.
Keywords: competition, cover crops, high C:N amendments, invasion biology, resource reduction, restoration ecology.

Résumé : Les sites en restauration qui sont riches en ressources sont propices à l'envahissement par des plantes agressives qui empêchent le rétablissement des communautés. Semer des cultures couvre-sol non persistantes pour réduire la lumière et amender les sols avec de la sciure de bois afin d'immobiliser l'azote peut cependant empêcher ce scénario dans les prairies de carex en restauration en limitant les invasions de *Phalaris arundinacea* (l'alpiste roseau). Pour déterminer l'utilité de ces méthodes de réduction des ressources, une communauté cible de plantes vivaces et *Phalaris* ont été semés avec soit une culture couvre-sol avec une diversité élevée, une diversité faible, ou sans culture couvre-sol dans des parcelles avec ou sans sciure de bois dans des conditions hydrologiques contrôlées. La lumière et l'azote du sol ont été mesurés tout au long de l'étude et la biomasse aérienne après deux saisons de croissance. Seules les cultures couvre-sol avec une diversité élevée ont réduit la lumière et par conséquent l'établissement de la communauté cible et celui de *Phalaris* de 73 % et 68 %, respectivement, ayant pour résultat une communauté dominée par *Phalaris*. Malgré la courte durée de la réduction de l'azote causée par l'amendement des sols avec de la sciure de bois, cette méthode a réduit l'établissement *Phalaris* de 56 % sans gêner celui de la communauté cible, ayant pour résultat une communauté riche en graminées semblable aux prairies naturelles de carex. La communauté cible a quant à elle réduit à la fois la lumière et l'azote et par conséquent l'établissement de *Phalaris* de 78 % et 67 % dans les parcelles avec et sans sciure de bois, respectivement. Nos résultats démontrent que l'établissement rapide d'une communauté de plantes vivaces peut être plus important que la réduction initiale de la disponibilité des ressources afin de limiter les invasions lors de restauration de sites riches en ressources.
Mots-clés : amendements élevés en C:N, biologie des invasions, compétition, cultures couvre-sol, écologie de la restauration, réduction des ressources.

Nomenclature: Gleason & Cronquist, 1991.

Introduction

Disturbed ecosystems requiring restoration often have abundant resources and low plant cover (Adams & Galatowitsch, 2005; Orr & Stanley, 2006), making them prone to invasion by aggressive plants (Johnstone, 1986; Davis, Grime & Thompson, 2000). These plants can prevent ecosystem recovery and even change the trajectory of community development, resulting in undesirable, persistent community states (D'Antonio & Meyerson, 2002; Mulhouse & Galatowitsch, 2003; Suding, Gross & Houseman, 2004; Orr & Stanley, 2006). Decreasing the levels of abundant resources may help avoid this scenario if desired species require less of these resources for establishment than invasive species do (*sensu* Tilman *et al.,* 1999).

Phalaris arundinacea (hereafter *Phalaris*) is increasingly dominant in North American wetlands (Galatowitsch, Anderson & Ascher, 1999) and prevents the establishment of diverse plant communities in wetland restorations (Budelsky & Galatowitsch, 2000; Green & Galatowitsch, 2002; Hovick & Reinartz, 2007). Propagule availability of *Carex* species, which typically characterize sedge meadows, is very limited because of depleted seedbanks and reduced propagule sources in the fragmented landscape (Galatowitsch & van der Valk, 1996; Kettenring, 2006). Therefore, when hydrology is restored, *Phalaris* quickly invades and forms persistent monotypes in these moist nonvegetated areas (Mulhouse & Galatowitsch, 2003). Even after *Phalaris* control and seeding of desired species, *Phalaris* typically dominates the system again within 2 y (Adams & Galatowitsch, 2006). Since *Phalaris* establishment is limited by light and nitrogen (N) (Lindig-Cisneros & Zedler, 2001; Lindig-Cisneros & Zedler, 2002a,b; Perry, Galatowitsch & Rosen, 2004), reducing these resources in restorations may create environmental conditions suitable for the establishment of a diverse plant community over persistent *Phalaris* monotypes.

Researchers have suggested sowing native cover crops in wetland restorations to reduce light availability, thereby preventing *Phalaris* invasions (Galatowitsch, Budelsky & Yetka, 1999; Lindig-Cisneros & Zedler, 2002a). This suggestion is reasonable given that *Phalaris* germination is light-triggered and intact wetland canopies limit *Phalaris* germination by blocking light (Lindig-Cisneros & Zedler, 2001; Lindig-Cisneros & Zedler, 2002a,b). Canopies that are more diverse possibly intensify this effect via greater structural complexity (Lindig-Cisneros & Zedler, 2002a,b). Cover crops have been successful in reducing undesired species in both agriculture and restorations (Ilnicki & Enache, 1992; Shebitz & Kimmerer, 2005). Studies of cover crop use in wetland restorations, however, suggest that cover crops will limit the establishment of desired species, which have light requirements similar to those of *Phalaris* (Perry & Galatowitsch, 2003; 2004). The only prior field study of cover crop use in wetlands tested competition between *Phalaris* and *Carex hystericina* (a desired native species) seeded beneath canopies of 2 single-species cover crops (Perry & Galatowitsch, 2003). No studies have considered how cover crops differing in structural complexity and possibly below-canopy light levels will affect competition between *Phalaris* and a typical restoration seed mix.

When situated in agricultural landscapes, wetlands typically receive excess N (Neely & Baker, 1989), possibly increasing *Phalaris* invasions (Green & Galatowitsch, 2002; Lavoie, Dufresne & Delisle, 2005). Desired plant species, however, may outcompete *Phalaris* if N is limited. In a greenhouse study, Perry, Galatowitsch, and Rosen (2004) found that *C. hystericina* outcompeted *Phalaris* if soil N was immobilized by incorporating a high carbon (C):N amendment (pine sawdust). High C:N amendments, however, have produced mixed results in restorations (Morghan & Seastedt, 1999; Blumenthal, Jordan & Russelle, 2003; Huddleston & Young, 2005; Eschen, Muller-Scharer & Schaffner, 2006; Eschen *et al.,* 2007). In addition, the effects of high C:N amendments on competition between *Phalaris* and a typical restoration seed mix and the longevity of N-depletion caused by these amendments in wetlands are unknown.

Given that low light and N reduce *Phalaris* establishment, the use of cover crops and high C:N amendments in sedge meadow restorations may limit *Phalaris* invasion and allow desired plant communities to establish. This field study was conducted to evaluate the usefulness of these resource-limiting methods as restoration strategies in sedge meadow wetlands. Specific objectives of the study were to 1) determine if cover crops varying in structural complexity and high C:N amendments will hinder *Phalaris* invasion, 2) determine if sedge meadow communities can establish in environmental conditions created by cover crops and high C:N amendments, and 3) determine how treatment effects on light and N availability shaped experimental outcomes.

Methods

EXPERIMENTAL OVERVIEW AND STUDY SITE

To meet our objectives, we designed a randomized complete-block experiment with 4 factors (target community, *Phalaris*, cover crops, sawdust). Competition between a 10-species target community seed mix (absent or present) and *Phalaris* seeds (absent or present) was studied in plots with cover crops (high diversity, low diversity, or absent) and soil-sawdust amendments (with or without) (*i.e.,* high C:N amendment). The high-diversity cover crop consisted of 5 structurally varying species, and the low-diversity cover crop consisted of one grass species. Cover crops varying in structural complexity were used to create multiple below-canopy light levels (*sensu* Lindig-Cisneros & Zedler, 2002a,b). This complete-factorial design included treatments without vegetation. After 2 growing seasons, aboveground biomass of all species was weighed to determine competitive outcomes.

This study was conducted in 2 experimental wetland basins located at the University of Minnesota Horticultural Research Center in Carver County, Minnesota, USA (44° 51' 45" N, 93° 36' 00" W). The site, which was originally a drained wetland used for agriculture, was later divided into 4 approximately 0.20-ha basins by earthen dikes and is now used for wetland restoration research. Each basin has a separate water inlet and adjustable drainage tile for hydrological control. The soil at the site is Glencoe clay loam (Cumulic Endoaquoll) (US Department of Agriculture, 1968).

SEED MIX DESIGN AND PREPARATION

All cover crop and target community species selected for this study are common sedge meadow species native to central Minnesota. The cover crop species were either annuals or short-lived perennials that would not persist in the community. The high-diversity cover crop contained *Beckmannia syzigachne*, *Carex vulpinoidea*, *Bidens cernua*, *Polygonum lapathifolium*, and *Epilobium glandulosum*. The low-diversity cover crop was *B. syzigachne*. Target community species were chosen from a seed mix used on publicly funded restorations in Minnesota (Jacobson, 2006) and contained the following C_3 species: *Calamagrostis canadensis*, *Glyceria grandis*, *Carex hystericina*, *Carex scoparia*, *Scirpus atrovirens*, *Mimulus ringens*, *Vernonia fasciculata*, *Lobelia siphilitica*, *Pycnanthemum virginianum*, and *Eupatorium maculatum*.

Seeds were acquired from area suppliers. The University of Minnesota Department of Agronomy (St. Paul, Minnesota, USA) and Shooting Star Native Seed (Spring Grove, Minnesota, USA) donated *Phalaris* and *B. syzigachne* seeds, respectively. *Polygonum lapathifolium*, *E. glandulosum*, and *C. hystericina* seeds were obtained from Prairie Moon Nursery (Winona, Minnesota, USA). All other seeds came from Ion Exchange, Inc. (Harper Ferry, Iowa, USA).

The cover crop sowing densities were based on State of Minnesota revegetation guidelines (Jacobson, 2006), and sowing densities of the target community were based on seedbank densities of natural sedge meadows (Galatowitsch & Biederman, 1998). Cover crops and target communities were sown at 2100 and 2250 viable seeds·m^{-2}, respectively. *Phalaris* was sown at 60 viable seeds·m^{-2}, a density typical after *Phalaris* removal from invaded sedge meadows (Adams & Galatowitsch, 2006). The target community and high-diversity cover crop seed mixes both contained their species at equal proportions. Tetrazolium analysis was conducted to determine seed viability (Grabe, 1970). Prior to sowing, seeds were cold stratified at 4 °C in moist steam-sterilized wetland soil for 4 months to break seed dormancy (Baskin & Baskin, 1998; Kettenring & Galatowitsch, 2007) and mimic natural conditions.

EXPERIMENTAL SET UP AND SITE MAINTENANCE

Preparation of the basins began in fall of 2004. The western sides of both basins were surveyed and graded to achieve a uniform elevation. Basamid® soil fumigant (Dazomet; BASF Corporation, Mt. Olive, New Jersey, USA) was used to deplete the seedbank. Twenty-four 1-m^2 plots were marked out at 1, 3, and 5 m from the water's edge in each basin. Weed fabric was laid between plots. The 24 treatment combinations were randomly assigned to each row of plots, resulting in 6 complete repetitions blocked on basin and distance from water. To limit edge effects, samples and measurements were collected from the inner 0.8 m^2 of each plot.

Soil was amended with cedar sawdust (*Thuja* sp.) during October 2004 using methods similar to Perry, Galatowitsch, and Rosen (2004). In the plots assigned sawdust, the upper 7 cm of soil was removed, replaced with sawdust at a rate of 8.40 ± 0.13 kg dry-weight·plot^{-1}, and then tilled to a depth of 20 cm (2:1 soil:sawdust ratio

by volume). Soil removal ensured all plots had similar soil volumes. The sawdust, acquired from Ser-a-Dock, Inc. (Victoria, Minnesota, USA), was 49.9% C and 1.6% N with ammonium-N and nitrate-N concentrations of 141 and 15 mg·kg^{-1}, respectively (University of Minnesota Research Analytical Laboratory, St. Paul, Minnesota, USA; hereafter UMRAL). Preliminary comparisons of soil chemical parameters (other than inorganic N) between soils with and without sawdust revealed no substantial differences (Iannone, 2007). To promote microbial recolonization, 250 mL of water from a neighbouring wetland was sprinkled as evenly as possible over each plot through a 106-μm sieve (to prevent introduction of non-experimental propagules). The lag between soil removal, sawdust addition, and reinoculation on the one hand and seeding on the other provided time for soil organisms to re-establish.

The experiment began in spring 2005 after site set up was completed. Plots were resurveyed. Fibreglass screen extending approximately 15 cm above and below the soil surface was installed around all plots to reduce seed loss and between-plot seed migration. Seeds were sown on 4 and 5 May 2005 (week 1). Basin hydrology was manipulated for the first growing season to mimic that of an adjacent restored wetland. Water levels during the second growing season, however, were held constant at 2 cm below the lowest plot due to a dryer than average growing season (NOAA, 2006). Non-experimental species were hand weeded during the first 10 weeks.

DATA COLLECTION AND ANALYSES

Soil nitrate-N and ammonium-N were measured throughout the study. One week prior to seeding, soil was collected from 2 random plots in each row (one with, one without sawdust) and nitrate-N and ammonium-N concentrations were determined. During weeks 9 and 18 of the first growing season and weeks 5, 9, and 14 of the second growing season, three 1.5-cm diameter × 20-cm depth soil cores were collected from random points in all plots of 4 randomly selected rows (2 per basin). Soil samples from the first growing season were analyzed at UMRAL using an Alpkem Rapid Flow Analyzer (Astoria-Pacific International, College Station, Texas, USA). Soil samples from the second growing season were analyzed using a Wescan N Analyzer (Wescan Instruments Inc., Deerfield, Illinois, USA). For both methods, inorganic-N was extracted from moist soil using 2 M KCl solution (Mulvaney, 1996). Results were adjusted for percent soil moisture. Twelve random samples from the second growing season were sent to UMRAL to confirm the comparability of results from both growing seasons.

Throughout the study, the proportion of photosynthetically active radiation (PAR) blocked by plant canopies was measured. In all plots, the average of 2 perpendicular ground-level readings was divided by an above-canopy reading and this value was subtracted from 1. PAR was measured during weeks 7, 10, 13, and 16 of the first growing season and weeks 3, 7, and 13 of the second growing season on cloudless days between 1100 and 1400 using a line quantum sensor attached to a LI-250A light meter (LiCOR© Biosciences, Lincoln, Nebraska, USA).

Establishment and growth was estimated by measuring aboveground dry-weight biomass, canopy heights, and percent

cover. During week 15 of the second growing season, plants were cut at 2 cm above the soil surface, separated by species, dried at 70 °C for 48 h, and weighed. All unplanted species excluding *Solidago canadensis*, *Verbena hastata*, and non-seeded *C. vulpinoidea* were weighed together. Dryweight litter biomass was also measured. Canopy height was estimated at the end of both growing seasons by taking the average of measurements from 10 random points in all plots. Percent total vegetative cover of all plots was estimated visually to 5% increments during weeks 4, 7, 10, 13, and 16 of the first growing season and weeks 3 and 13 of the second.

To further understand N competition, C:N ratios of leaf tissue was measured. The equivalent of 30 mg dryweight leaf tissue was collected from the target community, *Phalaris*, and both cover crop treatments at weeks 9 and 18 of the first growing season and weeks 9 and 15 of the second growing season. Except for week 9 of the first growing season, when seedlings were still emerging, tissue was collected from mature leaves. Target community and high-diversity cover crop samples included all of the species from that treatment that were present in a plot at equal proportions. Samples were dried at 70 °C for 48 h and ground through a 1-mm screen. Percent N and C were measured on a 15-mg subsample using a Vario EL III CNS elemental analyzer (Elementar Americas Inc., Mt. Laurel, New Jersey, USA). Changes in C:N ratios reflected changes in N, and therefore the latter is not reported.

Analysis of Covariance (ANCOVA) was used to analyze *Phalaris*, total forb, graminoid, and target community biomass. Soil nitrate-N and ammonium-N, PAR, and C:N ratios of target community and *Phalaris* leaf tissues were analyzed using random mixed-effects models (RME). Due to soil settling, both ANCOVA and RME models contained plot elevation as a covariate. A *t*-test was used to determine effects of sawdust on *Phalaris* biomass in plots where the target community was seeded. A Wilcoxon rank-sum test was used to test for effects of sawdust on canopy height and the biomass of litter, nonseeded species, and both target community grasses and members of the Cyperaceae family. Linear regression was used to test for a relationship between percent vegetative cover and proportion of PAR blocked. Analysis of Variance (ANOVA) was used to determine if the C:N ratios of target community, *Phalaris*, and high- and low-diversity cover crop leaf tissue were different at each sampling period. Four outliers were removed from soil ammonium-N analysis and 1 from soil nitrate-N analysis. These outliers were either 8–20 times greater or 6–10 times smaller than the next closest value for that treatment combination at the time of sample collection. Transformations and model terms for specific analyses are presented in appropriate tables. $P < 0.05$ was considered significant. Differences between or among treatment levels were determined using Tukey's HSD tests (= 0.05). Significant main effects are not generally discussed if significant higher-order interactions explained results more clearly. Model test and linear regression were done using "R" (R Development Core Team, 2008), and Tukey's HSD tests, Wilcoxon rank-sums tests, and *t*-tests were done using JMP 6.0 (SAS Institute, Cary, North Carolina, USA). All data were back-transformed and reported as mean ± SE unless noted otherwise.

Results

PHALARIS AND TARGET COMMUNITY ESTABLISHMENT

Cover crops, sawdust amendments, and the target community all reduced *Phalaris* establishment (Table Ia). High-diversity and low-diversity cover crops reduced *Phalaris*

TABLE I. ANCOVA results for (a) *Phalaris* and (b) total graminoid, forb, and target community biomass. Data was cube root-transformed prior to analyses ($X^{0.33}$).

a) Model term	df	*Phalaris* (*P*-value)		
Basin (block-effect)	1	-		
Distance from water (block-effect)	2	-		
Elevation	1	-		
Cover crop	2	0.003		
Target community	1	<0.0001		
Sawdust	1	<0.0001		
Cover crop × target community	2	<0.0001		
Cover crop × sawdust	2	-		
Target community × sawdust	1	-		
Cover crop × target community × sawdust	2	-		
b) Model term	df	Total graminoid (*P*-value)	Total forb (*P*-value)	Total target community (*P*-value)
Basin (block-effect)	1	-	-	-
Distance from water (block-effect)	2	-	-	-
Elevation	1	0.0004	0.01	-
Cover crop	2	0.01	<0.0001	<0.0001
Phalaris	1	-	-	-
Sawdust	1	0.03	-	-
Cover crop × *Phalaris*	2	-	-	-
Cover crop × sawdust	2	-	0.02	<0.0001
Phalaris × sawdust	1	-	-	-
Cover crop × *Phalaris* × sawdust	2	-	-	-

biomass by 68% (270 ± 41 g·m^{-2}) and 38% (520 ± 98 g·m^{-2}), respectively, compared to plots without cover crops (840 ± 180 g·m^{-2}). Sawdust-amended plots had 56% less *Phalaris* (330 ± 74 g·m^{-2}) than plots without sawdust (760 ± 120 g·m^{-2}). On average, the target community reduced *Phalaris* biomass by 78% (1100 ± 160 to 250 ± 68 g·m^{-2}) in plots with low-diversity or no cover crops but did not reduce *Phalaris* in plots with high-diversity cover crops (Table Ia; cover crop × target community). In plots where the target community was sown, *Phalaris* biomass was reduced (68%) (380 ± 82 to 120 ± 32 g·m^{-2}) by sawdust amendments (additive effect; $t_{34} = -2.99$, $P = 0.003$).

On average, the high diversity cover crop reduced total forb, graminoid, and target community biomass compared to other cover crop treatment levels (Tables Ib & II). Sawdust amendments did not affect total target community biomass (Tables Ib & II). Sawdust, however, decreased the combined biomass of the target community grasses (*C. canadensis* and *G. grandis*) by 62% (78 ± 12 to 30 ± 6.6 g·m^{-2}) ($X^2_1 = 15.102$, $P = 0.0001$) while doubling the combined biomass of the target community species belonging to the Cyperaceae family (*C. hystericina*, *C. scoparia*, and *S. atrovirens*) (190 ± 30 to 400 ± 55 g·m^{-2}) ($X^2_1 = 7.864$, $P = 0.005$), resulting in a 37% net increase of graminoids. In sawdust-amended soils, forb biomass decreased by 26% and 32% in plots with low-diversity or absent cover crop treatments, respectively, but more than doubled in plots with high-diversity cover crops (Tables Ib & II; cover crop × sawdust). Total target community biomass also more than doubled in plots with high-diversity cover crops when sawdust was incorporated (Tables Ib & II; cover crop × sawdust). Nonetheless, forb and target community biomass were still greatly reduced compared to plots with other cover crop treatment levels. Graminoid biomass decreased as plot elevation increased, allowing forb biomass to increase slightly. Elevation, however, did not affect total target community biomass (Table Ib).

Besides affecting both *Phalaris* and target community biomass, treatments also affected community composition. Target community species comprised the highest percentage of the established community in plots without cover crops (75–81%) (Figure 1). In contrast, target community species only comprised 20–43% of the established community in plots with high-diversity cover crops (Figure 1). In these plots, total biomass was also reduced compared to other cover crop treatment levels (Figure 1). Only 2 of the 5 cover crop species established during the second growing season, *C. vulpinoidea* and *E. glandulosum*, and their biomass was 27–28% of the established community (Figure 1). When *Phalaris* was present in plots with high-diversity cover crops and no sawdust, it comprised 44% of the established community (Figure 1). Sawdust amendments increased biomass of non-seeded species from 190 ± 30 to 440 ± 63 g·m^{-2} (231%) ($X^2_1 = 11.038$, $P = 0.0009$), increasing their percentage in the community from 8–11% to 19–33% (Figure 1).

TREATMENT EFFECTS ON RESOURCE AVAILABILITY

Sawdust amendments affected soil N in ways that were not anticipated. Ammonium-N and nitrate-N concentrations were initially reduced from 14.7 to 5.9 mg·kg^{-1} (60%) and 8.6 to 3.8 mg·kg^{-1} (56%), respectively. After 9 weeks, however, sawdust increased ammonium-N concentrations from 3.9 ± 0.40 to 5.4 ± 0.40 mg·kg^{-1} (28%) and did not affect nitrate-N concentrations (Table IIIa). These trends persisted through the end of the study.

Vegetation had more persistent effects on soil N than sawdust did. Early in the second growing season, plots with high-diversity cover crops had marginally higher ($P = 0.06$) ammonium-N concentrations (3.3 ± 0.5 mg·kg^{-1}) than plots with low-diversity or no cover crops (2.2 ± 0.2 and 2.3 ± 0.2 mg·kg^{-1}, respectively). In plots without *Phalaris*, the target community reduced ammonium-N concentrations from 5.9 ± 0.7 to 3.9 ± 0.4 mg·kg^{-1} (33%) (Table IIIa; target community × *Phalaris*). Plots that had *Phalaris* growing alone or with the target community had ammonium-N concentrations equivalent to non-vegetated plots (Table IIIa; target community × *Phalaris*).

Vegetation had greater impacts on nitrate-N concentrations than ammonium-N concentrations. Non-vegetated plots had higher nitrate-N concentrations than vegetated

TABLE II. The effects of cover crops and sawdust on biomass of individual target community species, target community graminoids and forbs, and the total target community (mean g·m^{-2} ± SE).

| Cover crop:	High diversity		Low diversity		Absent	
Sawdust:	With	Without	With	Without	With	Without
TARGET COMMUNITY GRAMINOIDS						
Calamagrostis canadensis	3.2 ± 1.3	16 ± 4.8	1.5 ± 0.5	8.8 ± 1.7	2.8 ± 1.0	67 ± 19
Glyceria grandis	38 ± 14	41 ± 15	17 ± 5.7	40 ± 14	27 ± 13	62 ± 20
Carex hystericina	21 ± 9.1	8.2 ± 1.6	41 ± 7.8	17 ± 5.1	44 ± 15	32 ± 9.1
Carex scoparia	52 ± 12	30 ± 5.3	130 ± 30	81 ± 17	160 ± 26	130 ± 32
Scirpus atrovirens	260 ± 89	29 ± 8.7	200 ± 110	96 ± 29	280 ± 88	150 ± 35
Total graminoids	380 ± 100	121 ± 21	390 ± 110	240 ± 48	520 ± 99	440 ± 73
TARGET COMMUNITY FORBS						
Mimulus ringens	10 ± 3.1	3.5 ± 1.4	57 ± 19	50 ± 15	60 ± 18	99 ± 21
Vernonia fasciculata	150 ± 48	67 ± 15	560 ± 150	860 ± 100	690 ± 180	910 ± 160
Pycnanthemum virginianum	3.3 ± 1.5	0.6 ± 0.2	15 ± 5.4	10 ± 3.1	9.9 ± 4.0	15 ± 6.9
Lobelia siphilitica	0.2 ± 0.1	0.2 ± 0.1	0.6 ± 0.4	1.6 ± 0.8	0.0 ± 0.0	1.3 ± 0.9
Eupatorium maculatum	18 ± 10	10 ± 7.7	30 ± 9.8	55 ± 17	48 ± 26	64 ± 25
Total forbs	190 ± 54	81 ± 20	670 ± 140	980 ± 110	810 ± 180	1100 ± 150
TOTAL TARGET COMMUNITY	560 ± 74	210 ± 23	1100 ± 130	1200 ± 100	1300 ± 130	1500 ± 130
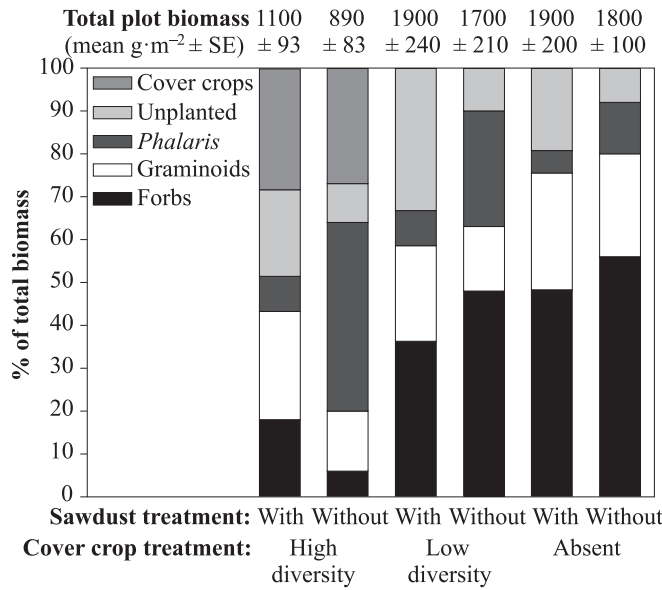
FIGURE 1. Final community composition in plots with both the target community and *Phalaris* growing under different sawdust and cover crop treatment combinations.

plots throughout the study (Tables IIIa & IV; cover crop × target community × *Phalaris*). Early in the second growing season (week 5), plots with high-diversity cover crops had higher nitrate-N concentrations than plots with other vegetative treatments (Tables IIIb & IV; year × week × cover crop). In plots without high-diversity cover crops, the target community reduced nitrate-N concentrations (Tables IIIa & IV; cover crop × target community). When grown alone, *Phalaris* was able to reduce nitrate-N concentrations as much as the cover crops and the target community did (Tables IIIa & IV; cover crop × *Phalaris*; target community × *Phalaris*).

Light availability was strongly correlated to total vegetative cover ($R^2 = 0.89$, $P < 0.0001$), explaining the high quantity of significant model terms in the PAR analysis (Table III). Throughout the study, high-diversity cover crops reduced light availability by 75%. During the first growing season, the effects of low-diversity cover crops on light availability were only detected in plots without the target community (Figure 2; Table IIIb; year × week × cover crop × target community). Decreased light levels during the second growing season in plots where the low-diversity cover crop was seeded alone (Figure 2) were likely attributable

TABLE III. Results of RME model analyses of soil nitrate-N and ammonium-N concentrations, and percent PAR blocked. Models contained basin, distance from water, and plot as random-effects, and year and week as continuous variables. Part (a) shows results of test for treatment effects across the entire experiment and part (b) shows results of test for changes in treatment effects over time.

	Transformation: df	NH_4-N $[(x^{-0.4}) - 1] * -1$ (P-value)	NO_3-N $\log(x+1)$ (P-value)	% PAR Blocked arcsinesqrt (x) (P-value)
a) MODEL TERM				
Elevation	1	-	-	-
Cover crop	2	-	-	<0.0001
Target community	1	0.002	<0.0001	<0.0001
Phalaris	1	-	0.001	<0.0001
Sawdust	1	<0.0001	-	-
Cover crop × target community	2	-	<0.0001	<0.0001
Cover crop × *Phalaris*	2	-	0.0003	<0.0001
Cover crop × sawdust	2	-	-	0.002
Target community × *Phalaris*	1	0.04	0.0008	<0.0001
Target community × sawdust	1	-	-	-
Phalaris × sawdust	1	-	-	<0.0001
Cover crop × target community × *Phalaris*	2	-	0.01	<0.0001
Cover crop × target community × sawdust	2	-	-	-
Cover crop × *Phalaris* × sawdust	2	-	-	0.0009
Target community × *Phalaris* × sawdust	1	-	-	0.005
b) MODEL TERM				
Year	1	0.008	<0.0001	<0.0001
Year × week	1	0.001	<0.0001	<0.0001
Year × week × elevation	1	-	-	-
Year × week × cover crop	2	-	0.006	0.003
Year × week × target community	1	-	-	0.03
Year × week × *Phalaris*	1	-	-	0.02
Year × week × sawdust	1	-	-	0.03
Year × week × cover crop × target community	2	-	-	0.007
Year × week × cover crop × *Phalaris*	2	-	-	-
Year × week × cover crop × sawdust	2	-	-	0.002
Year × week × target community × *Phalaris*	1	-	-	0.03
Year × week × target community × sawdust	1	-	-	-
Year × week × *Phalaris* × sawdust	1	-	-	-
Year × week × cover crop × target community × *Phalaris*	2	-	-	-
Year × week × cover crop × target community × sawdust	2	-	-	-
Year × week × cover crop × *Phalaris* × sawdust	2	-	-	-
Year × week × target community × *Phalaris* × sawdust	1	-	-	-

TABLE IV. The effects of vegetative treatment combinations on soil nitrate-N concentrations (mean ± SE) over time.

	Mean NO$_3$-N (mg·kg^{-1})				
Year:	2005		2006		
Vegetation in plot	Week 9	Week 18	Week 5	Week 9	Week 14
High diversity, target community, *Phalaris*	6.7 ± 0.68	12 ± 1.3	4.8 ± 0.73	0.92 ± 0.21	0.14 ± 0.09
High diversity, target community	6.5 ± 0.71	10 ± 1.4	5.4 ± 0.82	0.61 ± 0.14	0.07 ± 0.04
High diversity, *Phalaris*	6.1 ± 0.60	9.3 ± 0.81	4.4 ± 0.84	0.80 ± 0.10	0.14 ± 0.09
High diversity	6.6 ± 0.86	9.6 ± 1.0	4.7 ± 0.67	0.86 ± 0.18	0.04 ± 0.03
Low diversity, target community, *Phalaris*	6.7 ± 1.4	8.6 ± 1.6	2.3 ± 0.47	0.66 ± 0.13	0.19 ± 0.14
Low diversity, target community	6.1 ± 0.72	9.6 ± 1.0	2.5 ± 0.39	0.60 ± 0.09	0.05 ± 0.05
Low diversity, *Phalaris*	6.1 ± 0.79	12 ± 1.8	2.8 ± 0.48	0.62 ± 0.11	0.41 ± 0.25
Low diversity	9.4 ± 1.8	15 ± 2.2	2.9 ± 0.66	0.93 ± 0.14	1.0 ± 0.45
Target community, *Phalaris*	7.7 ± 2.0	8.3 ± 1.4	1.8 ± 0.35	0.38 ± 0.10	0.12 ± 0.11
Target community	8.4 ± 1.1	9.7 ± 2.0	2.1 ± 0.50	0.48 ± 0.09	0.06 ± 0.04
Phalaris	5.3 ± 0.80	16 ± 2.9	2.9 ± 0.70	0.44 ± 0.09	0.16 ± 0.09
No vegetation	7.7 ± 1.8	21 ± 3.3	10 ± 2.0	4.8 ± 1.2	7.1 ± 2.5
Weekly experimental mean ± SE	6.9 ± 0.35	12 ± 0.63	3.9 ± 0.32	1.0 ± 0.16	0.80 ± 0.28

to colonization by non-seeded species since *B. syzigachne* establishment was low at this time. The target community reduced light almost as much as the high-diversity cover crop did by the end of the first growing season and more than the high-diversity cover crop did by the beginning of the second growing season (Figure 2; Table IIIb; year × week × cover crop × target community). During the second growing season *Phalaris* reduced PAR as much as the target community did (Figure 2; Table IIIb; year × week × target community × *Phalaris*), but only when growing alone or with the low-diversity cover crop (Figure 2; Table IIIa; cover crop × target community × *Phalaris*).

Although the reduction in soil N caused by sawdust was short-lived, sawdust indirectly increased light availability. Canopy heights were 41% smaller in sawdust-amended plots (23 ± 2.1 cm) than in non-amended plots (39 ± 2.5 cm) ($X^2_1 = 19.10$, $P < 0.0001$) at the end of the first growing season. This decrease in plant growth increased light availability by 25–79% and reduced the amount of PAR that cover crops, target community, and *Phalaris* blocked during the first growing season (Figure 2; Table III). Sawdust-amended plots also had less litter than plots without sawdust (100 ± 11 and 210 ± 16 g·m^{-2}, respectively) ($X^2_1 = 22.89$, $P < 0.0001$), resulting in 15% more light at the beginning of the second growing season (week 3) (Figure 2; Table IIIb; year × week × sawdust). Beyond week 3 of the second growing season, sawdust amendments did not affect light availability.

LEAF C:N RATIOS

Experimental treatments had no effect on C:N ratios of target community or *Phalaris* leaf tissue ($P > 0.10$). However, at each particular sampling period, C:N ratios of target community, *Phalaris*, and high- and low-diversity cover crop leaf tissue varied significantly from each other ($P < 0.0001$) (Figure 3). Throughout the study, target community leaf tissue had C:N ratios 24-47% higher than the low-diversity cover crop and 19–40% higher than *Phalaris* (Figure 3). Similarly, high diversity cover crop leaf tissue had C:N ratios 14–49% higher than the low-diversity cover crop and 8–49% higher than *Phalaris* (Figure 3). During the second growing season, the C:N ratios of target community and high-diversity cover crop leaf tissue were equivalent (Figure 3). C:N ratios of target community and high-diversity cover crop leaf tissue steadily increased throughout the

study, while the C:N ratios of *Phalaris* and low-diversity cover crop leaf tissue did not (Figure 3).

Discussion

Cover crops and sawdust amendments both reduced *Phalaris* invasion, but cover crops will not be an effective restoration tool, and using sawdust amendments may not be practical. By reducing light, the high-diversity cover crop prevented target community establishment, confirming predictions that limiting light to control *Phalaris* in sedge meadow restorations will prevent the establishment of desired species (Perry & Galatowitsch, 2003; 2004). The reduction in light caused by the high-diversity cover crop was not attributable to structural complexity as intended since *B. cernua* dominated this treatment during the first growing season (Iannone, 2007) and only 2 species dominated the treatment during the second growing season (*C. vulpinoidea* and *E. glandulosum*). Sawdust amendments only reduced N over the short term, later increased ammonium-N, and did not decrease *Phalaris* invasion much beyond what the target community did. Since incorporating sawdust into moist sedge meadow soils at the volume necessary for N depletion will be difficult, the cost of using sawdust may outweigh the benefits. Sawdust from species with higher C:N ratios than cedar, however, can deplete N longer (Iannone, 2007), making the species that the sawdust comes from an important consideration when using sawdust to deplete N.

Reducing light with cover crops or N with sawdust amendments elevated the other manipulated resource, increasing community invasibility. The low-light environment beneath the high-diversity cover crop prevented target community establishment, resulting in less total community biomass (Figure 1). This less productive community had elevated inorganic soil N concentrations during the beginning of the second growing season (likely the result of decreased plant uptake) (Table IV). Since *Phalaris* growth responds strongly to increased N (Green & Galatowitsch, 2002), this period of elevated soil N potentially contributed to the high proportion of *Phalaris* in these plots (Figure 1). Sawdust amendments reduced soil N in early summer of the first growing season. This period of N reduction occurred when C$_3$ plants are most
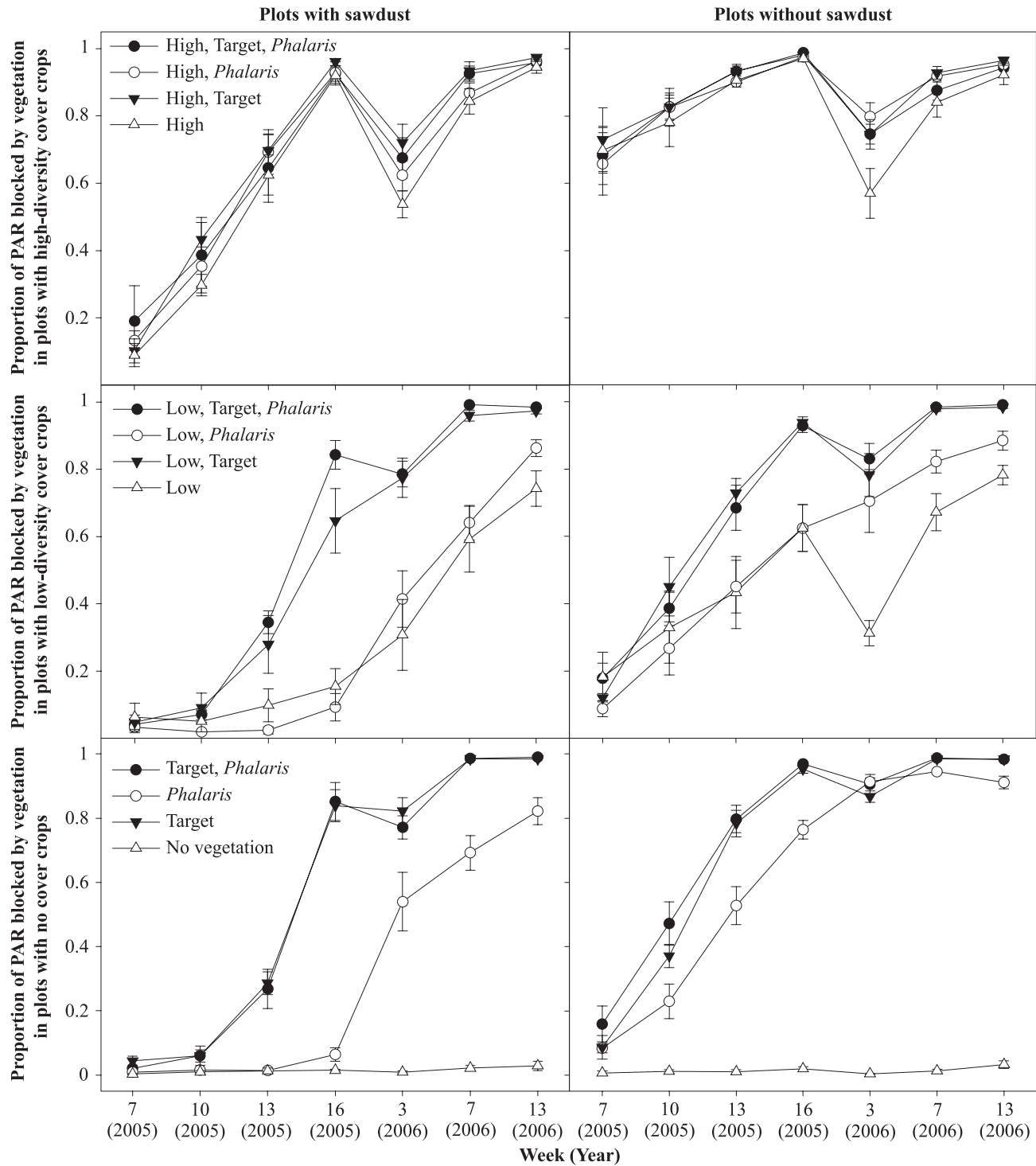
FIGURE 2. The effects of vegetation on the proportion of PAR blocked throughout the experiment in plots with and without sawdust amendments.

productive (Ode, Tieszen & Lerman, 1980), resulting in decreased first-season growth and less litter accumulation. Litter reduction increased light availability during the beginning of the second growing season (Figure 2), allowing more non-seeded species (some invasive; Iannone, 2007) to colonize. Because litter can prevent plant establishment (Carson & Peterson, 1990; Perry & Galatowitsch, 2003), sawdust amendments may facilitate the colonization

of other invasive species that occur in the surrounding area by decreasing litter accumulation. Despite higher light levels, *Phalaris* establishment was still reduced in sawdust-amended plots, suggesting that N plays a more important role than light in *Phalaris* invasion of sedge meadows.

Even if N plays a more important role in *Phalaris* invasion than light, both resources control *Phalaris* germination and growth (Lindig-Cisneros & Zedler, 2001;
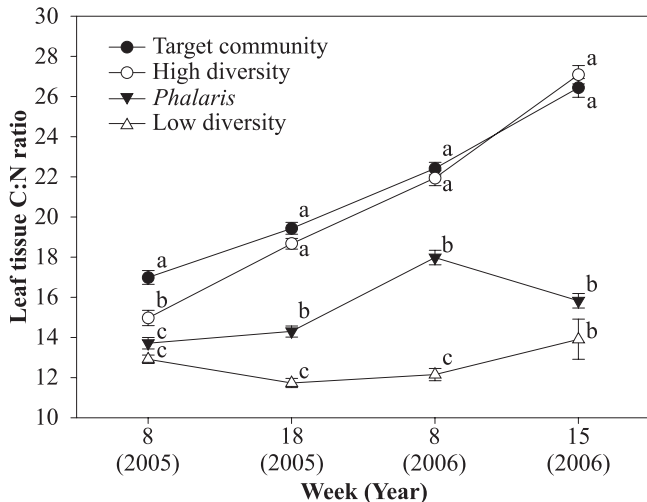
FIGURE 3. Leaf tissue C:N ratios of the target community, *Phalaris*, and low- and high-diversity cover crops. Data points at each individual sampling period that have different letters are significantly different ($P < 0.05$).

Perry, Galatowitsch & Rosen, 2004). Therefore, preventing *Phalaris* invasion over the long term will require reducing both resources. Neither cover crops nor sawdust amendments met this requirement, but once established the target community did (Figure 2; Table IV). Reduction of both N and light is likely the reason that the target community decreased *Phalaris* invasion as much as the high-diversity cover crop did, which is surprising given that *Phalaris* typically outcompetes sedge meadow species (Budelsky & Galatowitsch, 2000; Green & Galatowitsch, 2002; Adams & Galatowitsch, 2006). The target community's ability to limit *Phalaris* invasion may have been affected by the sowing density, which was 4 times higher than what is often used in restorations (Jacobson, 2006), and cold stratifying target community seeds. High-density seeding and cold stratification likely minimized lag times to germination (Baskin & Baskin, 1998; Schutz & Rave, 1999; Sheley & Half, 2006; Kettenring & Galatowitsch, 2007), allowing the target community to sequester resources faster than if these actions were not taken. These results emphasize the importance of establishing a perennial community quickly to achieve long-term reduction of resources and *Phalaris* invasion.

Target community establishment was reduced by high-diversity cover crops but not by sawdust amendments (Table II), suggesting that light limits the establishment of these species. Although both cover crops and sawdust reduced *Phalaris* biomass, only sawdust reduced *Phalaris*' proportion in the community (Figure 1). These results show that *Phalaris* could outcompete target species in low-light but not low-N environments, suggesting that N was more limiting to *Phalaris* establishment. Further, target community leaf tissue had higher C:N ratios than *Phalaris* leaf tissue (Figure 3), suggesting that target species are better competitors for N (*sensu* Tilman *et al.,* 1999). *Phalaris*' inability to outcompete the target community in sawdust-amended plots confirmed Perry, Galatowitsch, and Rosen's (2004) prediction that desired species would suppress *Phalaris* if N were reduced. Additionally, since sawdust only reduced N during the first part of the study, N reduction can probably

be short term as long as it coincides with seedling establishment. The difference between the resources that limited target community and *Phalaris* establishment (*i.e.,* light and N, respectively) may explain *Phalaris*' ability to dominate sedge meadows, since a species will have greater invasive success the more its resource needs differ from those of the constituent species where it invades (Vitousek & Walker, 1989; Fargione, Brown & Tilman, 2003).

Phalaris growth responded more to changes in nitrate-N than to changes in ammonium-N, supporting the hypothesis that fertilizer use, which increases nitrate-rich runoff and subsurface drainage (Neely & Baker, 1989), is a major contributor to *Phalaris* invasions (Green & Galatowitsch, 2002; Lavoie, Dufresne & Delisle, 2005). *Phalaris* establishment and proportion in the community decreased in sawdust-amended plots despite elevated ammonium-N concentrations. Additionally, the target community, which decreased nitrate-N but not ammonium-N when growing with *Phalaris*, still reduced *Phalaris* establishment. Because *Phalaris* exhibits rapid growth and vegetative expansion (Adams & Galatowitsch, 2005) and responds more to increased nitrate than the desired sedge meadow species do (Green & Galatowitsch, 2002), *Phalaris* can easily outcompete desired species for light in nitrate-rich environments. This scenario may explain *Phalaris*' dominance in the low-light environment plots with high-diversity cover crops since these plots had high nitrate-N concentrations in the first part of the second growing season. Since increased nutrient loads can shift wetland communities to states dominated by a few fast-growing species (Verhoeven *et al.,* 2006), *Phalaris* will likely continue to dominate restored sedge meadows and invade natural ones within agricultural landscapes.

Reducing N resulted in the community most similar to natural sedge meadows (*sensu* Galatowitsch & van der Valk, 1996) by increasing both the colonization of non-seeded wetland species and the establishment of target community species in the Cyperaceae family. This reaffirms that diverse, graminoid-rich communities can establish at low N concentrations (Green & Galatowitsch, 2002). Outcomes of natural colonization, however, depend on which species and propagules are present in the surrounding landscape. In contrast, reducing light by planting a high-diversity cover crop mixture resulted in a community dominated by *Phalaris*, *C. vulpinoidea*, and *E. glandulosum*. Target communities grown without cover crops or sawdust amendments had low *Phalaris* invasion but higher than typical forb abundance (Galatowitsch & van der Valk, 1996). Forb-rich communities, however, are typical of new sedge meadows (Bohnen & Galatowitsch, 2005) and may shift to graminoid-rich communities over time.

Our study shows that reducing initial resource levels is less important than the rapid establishment of perennial communities when trying to prevent invasions of restorations. Establishment of *Phalaris* and sedge meadow species were most limited by N and light, respectively, possibly explaining *Phalaris*' dominance in low-light environments and the target community's dominance in low-N environments. This range of outcomes illustrates the importance of determining that a resource is more limiting

to the establishment of invasive species than desired species before reducing that resource. Seeding at high densities and cold stratifying seeds prior to sowing likely enhanced the target community's ability to reduce light and N and thereby limit *Phalaris* invasion. Regardless of the cause, the fact that the target community suppressed *Phalaris* is consistent with a growing body of literature that shows native species, once established, can reduce invasions by sequestering resources (Barger *et al.,* 2003; Seabloom *et al.,* 2003; Bakker & Wilson, 2004). These findings, coupled with our own, suggest that the rapid establishment of desired plant communities is the most important step in limiting invasions of resource-rich restorations.

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