

UNIVERSITY OF MINNESOTA

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Date

GRADUATE SCHOOL

**Evaluation of resource-limiting strategies intended to facilitate
sedge meadow restorations by preventing
Phalaris arundinacea L. invasion**

A THESIS
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DEDICATION

This thesis is dedicated to the memory of Robert Jacobson (Bob). Without Bob's dedication to the field of restoration ecology and his efforts to improve the quality of ecosystem restorations in Minnesota, this research would not have been possible.

GENERAL ABSTRACT

Invasive species often prevent community recovery in restorations. For example, *Phalaris arundinacea* invades sedge meadow restorations, forming persistent monotypes that prevent community establishment. Further, *Phalaris* eradication leaves these ecosystems prone to reinvasion. The purpose of this research was to determine if reducing light by sowing cover crops and reducing nitrogen by incorporating soil-sawdust amendments would prevent *Phalaris* invasions, facilitating community recovery. A two-year study was conducted in two wetland basins with controlled hydrology. Seeds of a 10-species target community and *Phalaris* were sown in plots with a high diversity (five structurally varying species), low diversity (one grass species), or absent cover crop treatment in soils with or without sawdust (cedar). Environmental conditions resembled a newly restored sedge meadow or a sedge meadow after *Phalaris* eradication. To determine the effects of cover crops and sawdust amendments on resource availability, and community establishment and composition, nitrogen, light, first-year seedling emergence, establishment, and growth, second-year aboveground biomass, and C:N ratios of leaf tissue were measured. Only high diversity cover crops reduced light availability. Cedar sawdust reduced nitrogen for about 9 weeks. First and second-year data suggest that *Phalaris*-control efforts should focus on establishing perennial communities rather than implementing separate resource-limiting strategies. The target community, which reduced light and nitrogen, decreased *Phalaris* invasion as much as cover crops did. Sowing high diversity cover crops resulted in a *Phalaris*-dominated community, making cover crops an ineffective *Phalaris*-control strategy. Because sawdust did not reduce *Phalaris* invasion much beyond what the target community did,

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THESIS FORMAT

The chapters of this thesis were written in the format required by the particular peer-reviewed journals to which they will be submitted for publication. When submitted in manuscript form, Dr. Susan Galatowitsch, my advisor, will be listed as a co-author. Dr. Galatowitsch has provided valuable insights into the development of this study and the interpretation of my findings, and edited prior versions of this document. Dr. Galatowitsch will also be involved in future editing to prepare these chapters for publication. However, I was solely responsible for the experimental questions, design, and set up, the data collection and analyses, and the writing of this document.

GENERAL INTRODUCTION

Restoration sites often have abundant resources and limited vegetative cover (e.g. Adams & Galatowitsch 2005; Orr & Stanley 2006) making them prone to invasions from problematic plant species (Johnstone 1986; Davis, Grime, & Thompson 2000). Once invaded, these sites can persist in undesirable monotypic states that prevent community recovery (D'Antonio & Meyerson 2002; Mulhouse & Galatowitsch 2003; Orr & Stanley 2006). Further, efforts to eradicate invasive plants from an ecosystem can increase resource availability making the ecosystem prone to other invasive plants or to reinvasion from the original invader (Morrison 2002; Ogden & Rejmánek 2005; Adams & Galatowitsch 2006; Hulme & Bremner 2006). In order to reestablish desired plant communities in these resource-rich restoration sites, strategies are needed that prevent invasions. Once established the restored community can sequester resources possibly making the ecosystem resistant to future invasions (Seabloom et al. 2003; Barger et al. 2003; Bakker & Wilson 2004).

Phalaris arundinacea L. (hereafter *Phalaris*) invasions have increased in North American wetlands (Galatowitsch et al. 1999a; Perkins & Wilson 2004; Lavoie & Dufresne 2005). The invasive ability of this native species (Cronquist et al. 1977) has been attributed to increased fertilizer use, road expansions, possible agricultural improvements to the species, and increased genetic variation from multiple introduction of Eurasian strains (Galatowitsch et al. 1999a; Green & Galatowitsch 2002; Lavoie & Dufresne 2005, Lavergne & Molofsky 2007). *Phalaris* is particularly problematic in wetland restorations where it prevents community reestablishment (Mulhouse & Galatowitsch 2003; Hovick & Reinartz 2007). For example, when prairie pothole

wetlands are reflooded, sedge meadow species do not reestablish because of depleted seedbanks and propagule sources in the fragmented landscape (Galatowitsch & van der Valk 1996, Kettenring 2006). *Phalaris* quickly invades these moist, fertile areas (Adams and Galatowitsch 2005), forming persistent monotypes that prevent community recovery (Mulhouse & Galatowitsch 2003). *Phalaris* control, however, does not eliminate all *Phalaris* seed (Adams & Galatowitsch 2006). This remnant seedbank, dispersal of *Phalaris* seed from adjacent sources, and the moist, fertile post-eradication conditions allow *Phalaris* to reinvade quickly (Adams & Galatowitsch 2005; 2006). The most common restoration practice after reflooding or *Phalaris* removal is sowing desired species. This practice, however, usually fails to restore desired plant communities when *Phalaris* seeds are present, even at low densities (Adams & Galatowitsch 2006).

Phalaris germination, establishment, and growth are limited by light and nitrogen (N) (Lindig-Cisneros & Zedler 2001; Perry et al. 2004). Therefore, light-reducing cover crops and N-reducing soil-carbon (C) amendments have been suggested as possible *Phalaris*-control strategies (Galatowitsch et al. 1999b; Lindig-Cisneros & Zedler 2002a; Perry et al. 2004). A prior study of cover crop use in wetland restorations, however, predicted that cover crops would prevent the establishment of desired species (Perry & Galatowitsch 2003), therefore having limited utility. Given this study used single-species cover crops and Lindig-Cisneros and Zedler (2002a; b) found diverse canopies with greater structural complexity blocked more light, structural complexity of cover crops needs investigation. In contrast to studies of cover crops, a prior study of C amendment showed that sedge meadow species could outcompete *Phalaris* if N availability is reduced (Perry et al. 2004). Carbon amendments, however, have not been tested in

wetlands and the longevity of their effects on N availability is unknown. Prior studies of both cover crops and C amendments only considered competition between a single sedge meadow species (*Carex hystericina*) and *Phalaris*. Therefore, studies are needed to investigate how cover crops and C amendments would affect competition between *Phalaris* and a multi-species seed mix typically used in restorations.

The purpose of this thesis was to determine if reducing light by sowing cover crops that vary in structural complexity and reducing N by incorporating C amendments (sawdust) would facilitate community recovery in restored sedge meadows by preventing initial *Phalaris* invasions and by preventing reinvasions after *Phalaris* removal. To determine the effects of these resource-limiting strategies, I conducted a study under environmental conditions similar to a recently restored sedge meadow that was reflooded after drainage and cultivation or after *Phalaris* eradication. These conditions were created in two experimental wetland basins by depleting the existing seedbank, removing standing vegetation, and manipulating hydrology (Adams & Galatowitsch 2005; 2006). In this representative environment, I seeded 10 sedge meadow species in the presence of *Phalaris* seeds along with three possible cover crop treatments: high diversity (five species varying in structure), low diversity (one species) or absent. Sedge meadow species, *Phalaris*, and the cover crop treatments were sown in soils with or without sawdust amendments. The study lasted nearly two full years, allowing for observations across two growing seasons.

The first chapter of this thesis focused on the first growing season of the study. In this chapter, I documented the understudied transition between invasive species removal and community reestablishment. I wanted to determine if cover crops and sawdust

amendments were effective strategies for reducing light and nitrogen availability. In addition, I wanted to determine how reducing light and nitrogen in sedge meadows where *Phalaris* was recently removed affected seedling emergence, establishment, and growth of a target community (i.e. desired sedge meadow species) and remnant *Phalaris* seeds. Since seedling establishment has lasting effects on final community composition (Grubb 1977; Schupp 1995; Eriksson 2002), factors such as resource availability that affect seedling establishment are likely crucial to restoration outcomes, especially when seeds of both desired and invasive species are present. Collecting data on resource availability and seedling establishment, allowed me to determine if any treatment combinations created conditions that favored seedling establishment of the target community over *Phalaris*. Knowing the results of first-year seedling establishment provided insights into pre-seeding actions that may enhance the effectiveness of sowing native seed mixes in restorations. Additionally, first-year seedling data provided a finer resolution of sedge meadow community development than if second-year biomass data were collected alone.

The second chapter of this thesis primarily focused on the second year of the study. In this chapter, I sought to determine how the effects of cover crops and sawdust amendments on light and nitrogen availability affected community establishment and composition (i.e. competitive outcomes) after two growing seasons in a recently reflooded sedge meadow. By monitoring light and N over this two-year period, I identified how resource availability affected the transition between seedling establishment and second-year community composition. In addition, I wanted to identify periods where cover crops and sawdust amendments had particularly strong influences on resource availability and therefore competitive outcomes. Identifying these periods of

strong influence on resource availability and competition may improve our understanding of how and when resource manipulations can help or hinder the recovery of desired plant communities.

The knowledge gained from the research within this thesis is intended to provide guidance on how to control *Phalaris* and facilitate the recovery of sedge meadow wetland plant communities. This research should also increase the understanding of how resource availability and competition affect community establishment and composition in ecosystem restorations, and help to understand the importance of seedling establishment to the development of restored communities.

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CHAPTER 1

**Altering seedling emergence, establishment, and growth
by reducing light and nitrogen to prevent *Phalaris arundinacea*
reinvasions of sedge meadow wetlands**

Abstract

Efforts to eradicate invasive plants can unintentionally create conditions that favor the reestablishment of the original invader over desired species, especially when remnant invasive propagules persist. Under this scenario, limiting resources needed by the invader for seedling establishment may allow desired species to reestablish. Remnant propagules of *Phalaris arundinacea* persist after its removal from sedge meadow wetlands and reestablish quickly in fertile post-eradication conditions, hindering community recovery. A study was conducted in two experimental wetlands with controlled hydrology to determine if reducing light by sowing native cover crops or reducing nitrogen by incorporating soil-sawdust amendments would decrease *Phalaris* seedling establishment, preventing reinvasion. Seedling emergence, establishment, and growth were measured on a 10-species target community and *Phalaris* seeded under three cover crop treatments (high diversity, low diversity, or absent) in soils with or without sawdust amendments. High diversity cover crops reduced light, decreasing *Phalaris* and target community seedling establishment by 89% and 57%, respectively. Short-term nitrogen reduction in sawdust-amended plots delayed *Phalaris* seedling emergence and decreased *Phalaris* seedling establishment by 59%, but did not affect total target community seedling establishment. Surprisingly, the target community reduced *Phalaris* seedling establishment as effectively as cover crops did. The primary benefit of incorporating sawdust into soils where the target community was sown was decreased *Phalaris* growth. Results show that sowing light-limiting cover crops will reduce seedling establishment of desired species and is counterproductive to restoration goals. Further, establishing target species is more important and practical than reducing nitrogen in preventing *Phalaris* seedling establishment.

Keywords: competition, cover crops, invasion biology, resource availability, seedling establishment, soil amendments, restoration

Introduction

Eradicating invasive species can have unintended, adverse effects on ecosystems (Zavaleta et al. 2001, Courchamp et al. 2003; Chapuis et al. 2004; Harms & Hiebert 2006). One common outcome is creating environmental conditions suitable for establishment of other invasive species or reinvasion by the original invader (Morrison 2002; Ogden & Rejmánek 2005; Adams & Galatowitsch 2006; Hulme & Bremner 2006). Restoring native vegetation to prevent future invasions and to accelerate ecosystem recovery (Hulme 2006) may not be possible if invasive propagules persist through eradication and resources required for their reestablishment are abundant (e.g. Adams & Galatowitsch 2006). Alternatively, if native species establish before the invader they can provide the restored ecosystem with resiliency against future invasions by sequestering available resources (Seabloom et al. 2003; Barger et al. 2003; Bakker & Wilson 2004). The availability of resources needed for plant establishment can affect final community composition (Grubb 1977; Schupp 1995; Eriksson 2002), making resource availability an especially important factor in restoration outcomes when propagules of both invaders and the desired community are present.

Efforts to eradicate the invasive perennial grass *Phalaris arundinacea* L. (reed canary grass; hereafter *Phalaris*) from sedge meadow wetlands leaves these ecosystems prone to reinvasion (Adams & Galatowitsch 2006). *Phalaris* reinvasions occur from remnant seedbanks and dispersal from nearby seed sources. In addition, desired native plants are dispersal limited and their establishment requires direct seeding (Kettenring 2006a). Nonetheless, even when native plants are seeded, *Phalaris* dominates these ecosystems within two growing seasons because of the rapid growth and high

reproductive capacity of its remnant seedbank under the moist and fertile post-eradication conditions (Adams & Galatowitsch 2005; 2006). Limiting resources needed by *Phalaris* at early developmental stages may be an effective strategy to prevent reinvasion and restore native vegetation in sedge meadows, if native species require less of these resources to establish (*sensu* Tilman et al. 1999).

Limiting light availability in sedge meadows after *Phalaris* eradication may prevent its reinvasion. Since *Phalaris* seeds cannot germinate in the dark, intact wetland canopies reduce *Phalaris* germination (Lindig-Cisneros & Zedler 2001; 2002a; 2002b). Because of increased structural complexity, diverse canopies possibly block more light (Lindig-Cisneros & Zedler 2002a; 2002b). Based on these findings, sowing a rapidly-growing native cover crop to reduce light availability may be effective in preventing *Phalaris* germination and invasion in wetland restorations if native species require less light for germination, seedling establishment, and growth than *Phalaris* (Galatowitsch et al. 1999; Lindig-Cisneros & Zedler 2002a).

Studies of cover crop use in wetland restorations suggest that this strategy is ineffective because it might prevent the establishment of native graminoids, which have similar light requirements as *Phalaris* (Perry & Galatowitsch 2003; 2004). Yet, the only field study of cover crop use in wetland restorations considered competition between a single sedge meadow species, *Carex hystericina* Muhl. (bottlebrush sedge), and *Phalaris* grown under 2 single-species cover crops (Perry & Galatowitsch 2003). No studies have investigated how multi-species cover crops affect light competition between *Phalaris* and a typical restoration seed mix.

Because native plant species can suppress *Phalaris* in low nitrogen (N) environments (Perry et al. 2004), another resource-limiting strategy could be to limit N after *Phalaris* eradication, creating an environment that slows the establishment and development of *Phalaris* seedlings. Prairie pothole wetlands occur within agricultural landscapes, and therefore often receive excess N (Neely & Baker 1989; Brinson & Malvarz 2002). Increased N availability is responsible for the displacement of native vegetation by invasive species in other ecosystems (Dukes & Mooney 1999) and may be contributing to *Phalaris*'s ability to displace desired native wetland species (Green & Galatowitsch 2002; Lavoie & Dufresne 2005).

Perry et al. (2004) tested if N levels contributed to the competitive ability of *Phalaris* in a greenhouse experiment where *Phalaris* and *C. hystericina* were grown together in wetland soils under depleted and ambient inorganic-N levels. Inorganic-N was reduced by incorporating pine sawdust (i.e. carbon amendment), which caused microbial immobilization. Even though seedling emergence of both species occurred at higher rates in the depleted soils, *C. hystericina* outcompeted *Phalaris* because the growth rate of *Phalaris* was reduced. Results of this study suggested that native seedlings have a greater capacity to attain and assimilate N than *Phalaris* seedlings in low N environments (Perry et al. 2004). Reducing N by adding carbon has been effective in limiting invasive species establishment in other ecosystems (Zink & Allen 1998; Blumenthal et al. 2003; Averett et al. 2004), but the effects of carbon amendments on soil N levels and the longevity of these effects in sedge meadow wetlands are unknown.

The purpose of this study was to determine if reducing light and N availability with cover crops and sawdust amendments, respectively, is effective in preventing

Phalaris seedling establishment after its initial removal from invaded sedge meadows. I studied competition between *Phalaris* seeds and a target community seed mix under cover crops of varying structural complexity in plots with or without sawdust amendments. The study was conducted in two experimental wetland basins with controlled hydrology. My objectives were to: 1) determine the effectiveness of cover crops varying in structural complexity and sawdust amendments in reducing light and N availability, respectively, and 2) determine how these treatments affect seedling emergence, establishment, and growth of a target community seed mix and *Phalaris* in conditions resembling sedge meadow restorations after *Phalaris* removal.

Methods

Experimental Overview and Site Description

I designed a randomized complete block experiment with four factors. A 10-species target community seed mix (absent or present) and *Phalaris* (absent or present) were sown in plots with three possible cover crops treatments: high diversity (5 structurally different species), low diversity (1 species), or absent. These treatments were grown in soils with or without sawdust amendments. During October 2004, a row of 24-one m² plots were marked out at 1, 3, and 5 m distances from the water's edge on the western side of two experimental wetland basins. The 24 treatment combinations were randomly assigned to each row (6 repetitions blocked on basin and distance from the water).

The basins are located at the University of Minnesota Horticultural Research Center in Carver County, Minnesota, 44°51'45''N latitude, 93°36'00''W longitude. The site, which historically was a drained depressional wetland used for agriculture, is

classified as a Glencoe clay loam soil (Cumulic Endoaquoll; U.S. Department of Agriculture 1968). In 1994, the area was divided by earthen dikes into four ≈ 0.20 ha basins with separate water inlets and adjustable drainage tiles, and set aside for wetland restoration research.

Experimental Set Up and Sawdust Treatments

Site preparation began in fall of 2004 by removing vegetation, and surveying and grading the study areas to make them uniform in elevation relative to the basin bottoms. Plots were resurveyed prior to experimental start up to determine if changes in elevation had occurred. On 30 September 2004, Basamid[®] soil fumigant (Dazomet; BASF Corporation, Mt Olive, NJ, USA) was applied to deplete the seedbank. Weed fabric was affixed between plots to prevent vegetative growth in these areas.

Sawdust was incorporated during October 2004 using methods similar to Perry et al. (2004). In plots assigned a sawdust amendment, the upper 7 cm of soil was removed and replaced with cedar (*Thuja* sp.) sawdust. Sawdust was hand-tilled to a depth of 20 cm, resulting in a soil:sawdust ratio of 2:1 by volume (8.40 ± 0.13 kg dry weight plot⁻¹). The sawdust, acquired from Ser-a-Dock, Inc (Victoria, MN, USA), was 49.9% C and 1.6% N with nitrate-N and ammonium-N concentration of 15 and 141 mg kg⁻¹, respectively. Percent C and N were determined on a Skalar Primacs Carbon Furnace and a LECO FP-528 Nitrogen Analyzer, respectively (Leco Corporation, St. Joseph, MI; Yeomans & Bremmer 1991; Lee et al. 1996). Inorganic-N was extracted with 30 ml of 2 M KCL and the extract was colormetrically analyzed using an Alpkem Rapid Flow Analyzer at 660 nm (Astoria-Pacific International, College Station, TX; Keeney &

Nelson 1982). Various chemical parameters were measured on soil samples collected 1 week prior to the start of the experiment from two randomly chosen plots in each repetition, one with and one without sawdust amendments (Table 1) (See analytical methods in: Dahlquist & Knoll 1978; Baker & Amacher 1982; Keeney & Nelson 1982; Thomas 1982; Yeomans & Bremmer 1991; Lee et al. 1996; Combs & Nathan 1998; Combs et al. 1998; Gelderman & Mallarino 1998; Frank et al. 1998; Watson & Brown 1998; Whitney 1998). All soil and sawdust samples in this study were analyzed at the University of Minnesota Research Analytical Laboratory (St. Paul, MN)

During April 2005, I finished preparing the soil, basins, and plots. To promote microbial recolonization, 250 ml of water from an adjacent wetland was poured through a 106- μ m sieve (to prevent introduction of non-experimental seeds) over each plot. To prevent seed loss and between-plot migration, fiberglass screen extending \approx 15 cm above and below the soil surface was installed around each plot and reinforced with wood lathe. Two observation wells were installed to an approximate depth of 50 cm within each repetition to monitor water table depths.

Cover Crop Treatments and Native Seeding

Five native species were chosen as cover crops; all were annuals or short-lived perennials so they would not be persistent competitors. I sought to create two different below-canopy light environments by using cover crop species that varied structurally (*sensu* Lindig-Cisneros & Zedler 2002a, b). The high diversity cover crop seed mix consisted of *Beckmannia syzigachne* (Steud.) Fern. (American sloughgrass), *Carex vulpinoidea* Michx. (fox sedge), *Bidens cernua* L. (bur-marigold), *Polygonum lapathifolium* L. (dock-

leaved smartweed), and *Epilobium glandulosum* Lehm. (northern willow-herb) sown at equal densities. The low diversity cover crop seed mix consisted solely of *B. syzigachne*. Target community species were selected from a seed mix used in restorations by Minnesota State Agencies (Jacobson 2003). The target community seed mix consisted of 10 C₃ perennial species sown at equal densities (listed in Table 7). Nomenclature followed Gleason and Cronquist (1991).

All study species were common, native sedge meadow species of central Minnesota. Cover crop and target community seed mixes were sown at 2,100 and 2,250 viable seeds m⁻², respectively. The cover crop density was based on recommendations for Minnesota State Agencies (Jacobson 2003) and the target community density was based on seed densities of natural sedge meadows (Galatowitsch & Biederman 1998). *Phalaris* was sown at a density representative of a remnant *Phalaris* seedbank after its removal in restorations, 60 viable seeds m⁻² (Adams & Galatowitsch 2006).

Prior to the start of the experiment, seeds were tested for viability and cold stratified. Viability was estimated on 200 seeds of each species using tetrazolium analysis (Grabe 1970). Seeds were then stratified in moist steam-sterilized wetland soil at 4⁰C for 4 months to mimic outdoor conditions and aid in breaking dormancy (Baskin & Baskin 1998; Kettenring 2007). Seeds were sown on 4 and 5 May 2005, which marked the start of the experiment.

Seeds were acquired from suppliers in Minnesota and Iowa. *P. lapathifolium*, *E. glandulosum*, and *C. hystericina* were purchased from Prairie Moon Nursery (Winona, MN). *B. syzigachne* and *Phalaris* were donated by Shooting Star Native Seed (Spring

Grove, MN) and the University of Minnesota Department of Agronomy (St. Paul, MN), respectively. All other seeds were bought from Ion Exchange, Inc. (Harper Ferry, IA).

Site Maintenance and Data Collection

Site maintenance consisted of manipulating water levels to mimic the hydrology of an adjacent restored wetland and weeding for 10 weeks after seeding. To determine treatment effects on N and light availability, I measured soil nitrate-N and ammonium-N at weeks 9 and 18, and the proportion of photosynthetically active radiation (PAR) blocked by plant canopies at weeks 7, 10, 13, and 16. All measurements were taken from the inner 0.8 m² of the plots to avoid edge effects. Soil nitrate-N and ammonium-N were measured on a moist 3 g subsample taken from three homogenized 1.5-cm diameter x 20-cm soil cores. Inorganic-N was extracted with 30 ml 2 M KCl (Keeney & Nelson 1982). The extract was then analyzed using an Alpkem Rapid Flow Analyzer at 660 nm (Astoria-Pacific International, College Station, TX). Nitrogen values were adjusted to account for soil moisture. Soil cores were collected from three random points in all plots of four randomly chosen repetitions (two from each basin). The percentage of PAR blocked was estimated in all plots by dividing the average of two perpendicular ground-level PAR readings by an above-canopy PAR reading and subtracting the value from 1. PAR readings were made between 1100 and 1400 on cloudless days using a line quantum sensor attached to LI-250A light meter (LiCOR[®] Biosciences, Lincoln, NE).

By extrapolating shoot counts from five randomly placed 10 x 10 cm subplots every 3 weeks, shoot densities of individual species in all plots were estimated to determine seedling emergence and establishment. Cumulative proportion of seedling

emergence was estimated each sampling period by adding any increase that occurred in shoot density to the prior week's density and dividing this value by the number of viable seeds sown. This estimate was treated as a minimum value since unobserved seedling emergence and mortality likely occurred between sampling periods. The assumptions were made that all seeds emerged when proportions reached 1.0; values > 1.0 resulted from clonal growth. Shoot densities at week 16 were considered final seedling establishment.

To estimate growth, individual species cover, total plant cover, and canopy heights were measured in all plots every 3 weeks. Covers of individual species were made using the following ordinal cover class system: 0 = 0%; 1 = < 1%; 2 = 1-4%; 3 = 5-24%; 4 = 25-49%; 5 = 50-74%; and 6 ≥ 75%. Total plant cover was visually estimated to 10% increments. To limit observer bias, I made all cover estimates. Canopy height was estimated by averaging the vegetation heights at 10 random points.

Statistical Analyses

Treatment effects on average nitrate-N and ammonium-N levels for the length of the study and on changes in nitrate-N and ammonium-N levels were determined by analysis of covariance (ANCOVA) on the averages and differences of values from weeks 9 and 18, respectively. Two outliers, having ammonium-N levels 5 and 19 x greater than any other values in their treatment combinations, were removed from analyses. A randomized mixed-effects model was used to determine treatment effects on the percentage of PAR blocked. Linear regression was used to test for a relationship between total vegetative cover from weeks 7-16 and percent PAR blocked. Treatment effects on *Phalaris* and total

target community seedling emergence were determined graphically while differences between treatment levels at each week were determined by Kruskal-Wallis or Wilcoxon rank-sum tests. ANCOVA and logistic regression were used to test for treatment effects on shoot densities and ordinal cover classes, respectively. Bonferroni adjustments were made for the whole-model test of individual target community species ($\alpha/10$). The effects of sawdust amendments on total vegetative cover for weeks 7-16, and canopy heights at week 16 were analyzed by Wilcoxon rank-sum tests. Model terms and transformations used in analyses are given in the appropriate tables.

Statistical analyses were done with JMP 6.0 (SAS Institute), excluding analysis of PAR blocked, which was done with “R” (Ihaka & Gentleman 1996). All models contained plot elevation as a covariate, since plot settling occurred between experimental set up and seeding. During analyses, insignificant terms were removed from models hierarchically (Oehlert 2000). Differences were considered significant at $P < 0.05$ except for Bonferroni-adjusted test ($\alpha = 0.05/10$). Differences between treatment levels were determined using Tukey’s HSD test ($\alpha = 0.05$). For reporting, all values were back-transformed and expressed as mean \pm SE unless otherwise noted. Some significant model terms were not reported or discussed if significant higher-order interactions provided an explanation of the response.

Results

Soil N and Light Availability

Sawdust amendments initially reduced nitrate-N levels from 8.6 to 3.8 mg kg⁻¹ (56%), and ammonium-N levels from 14.7 to 5.9 mg kg⁻¹ (60%), while having little effect on

other soil parameters (Table 1). These effects on soil N were short-lived. After 9 weeks, differences between nitrate-N levels in plots with vs. without sawdust amendments decreased to 25% (6.0 ± 0.4 vs. 7.9 ± 0.5 mg kg⁻¹, respectively) and by the end of the experiment (wk 18), were not observed (Tables 2 & 3). After 9 weeks, sawdust amendments raised ammonium-N levels 46% (4.9 ± 0.9 to 7.2 ± 0.9 mg kg⁻¹) (Table 2). Higher ammonium-N was observed in most treatments with sawdust amendments by week 9 and all treatments with sawdust amendments by the end of the study (Table 3).

Vegetation strongly influenced soil N (Tables 2 & 3). Throughout the study, plots with low diversity cover crops had higher ammonium-N (8.2 ± 1.6 mg kg⁻¹) than plots with high diversity and no cover crops (4.4 ± 0.6 and 5.7 ± 0.9 mg kg⁻¹, respectively) and high diversity cover crops marginally reduced nitrate-N levels from 10 ± 0.8 to 8.4 ± 0.4 mg kg⁻¹ (16%) (Tables 2 & 3). The target community reduced nitrate-N levels from 10 ± 0.6 to 8.4 ± 0.4 mg kg⁻¹ (16%) across all treatments and ammonium-N from 11 ± 2.8 to 5.1 ± 1.3 mg kg⁻¹ (54%) in plots with low diversity cover crops (Tables 2 & 3; cover crops x target community). By the end of the experiment, the target community reduced nitrate-N in plots with low diversity and no cover crops from 14 ± 1.5 and 18 ± 2.2 to 9.1 ± 0.9 and 8.9 ± 1.2 mg kg⁻¹ (35% and 52%), respectively (Tables 2 & 3; cover crops x target community). *Phalaris* reduced nitrate-N levels from 10 ± 0.6 to 8.7 ± 0.4 mg kg⁻¹ (13%) in all treatments and ammonium-N from 8.4 ± 1.3 to 6.1 ± 1.3 mg kg⁻¹ (27%) in sawdust-amended plots (Tables 2 & 3; *Phalaris* x sawdust).

Basin and distance from water affected soil N (Table 2). In one basin, both ammonium-N and nitrate-N levels were higher at 1 m from water (12 ± 2.3 and 12 ± 1.0 mg kg⁻¹, respectively) than at 3 m from water (3.7 ± 1.0 and 6.7 ± 2.8 mg kg⁻¹,

respectively) (basin x distance from water). Nitrate-N and ammonium-N levels also increased from 7.5 ± 4.1 and 3.4 ± 0.5 to 14 ± 7.3 and 14 ± 2.0 mg kg⁻¹, respectively, between weeks 9 and 18 at 1 m, but not 3 m from water (distance from water).

Total vegetative cover was strongly related to light availability ($R^2 = 0.91$; $P = < 0.0001$), explaining the high number of significant model terms (Table 4). As vegetation cover increased so did the amount of light blocked. High diversity cover crops reduced light availability by 69% throughout the experiment and 96% by the end of the experiment (Tables 4 & 5). The reduction in light availability caused by the high diversity cover crop was not attributable to structural complexity as anticipated because *B. cernua* dominated the canopy. The modal cover class of *B. cernua* was 6 ($\geq 75\%$). *Beckmannia syzigachne* had a modal cover class of 1 ($< 1\%$). All other species in the high diversity cover crop treatment had a modal cover class of 2 (1-4%). The target community reduced light availability by 52% throughout the experiment and almost as much as high diversity cover crops by the end of the experiment (90%) (Tables 4 & 5; time x cover crops x target community). The effects of low diversity cover crops and *Phalaris* on light reduction were only detected when growing alone (Tables 4 & 5; time x cover crop x target community x *Phalaris*).

Sawdust amendments indirectly affected light availability by reducing plant growth. Sawdust amendments decreased mean total cover from 60% to 32% ($X^2 = 81.52$; d.f. = 1; $P = < 0.0001$) throughout the experiment and final canopy height from 39 ± 2.5 to 23 ± 2.1 cm (41%) ($X^2 = 19.05$; d.f. = 1; $P = < 0.0001$). This decrease in growth reduced the amount of light all plant treatments blocked while having the most noticeable impact on *Phalaris* and low diversity cover crops growing alone (Tables 4 & 5; time x

target community x *Phalaris* x sawdust; time x cover crops x sawdust). By the end of the study, however, high diversity cover crops and target community were less affected (Tables 4 & 5; time x cover crops x target community x sawdust). In addition, as plot elevation increased light reduction decreased, but by week 16 this relationship reversed (Table 4; time x elevation). Although significant, these relationships were weak.

***Phalaris* Seedling Emergence, Establishment, and Growth**

Reducing light availability did not delay *Phalaris* seedling emergence, but sawdust amendments and the target community did (Figure 1). By week 7, all seeded *Phalaris* emerged in plots with high diversity and no cover crops (Figure 1A). *Phalaris* seedling emergence was delayed in plots with low diversity cover crops (Figure 1A), despite their minimal effect on light availability (Table 5). Even though sawdust had short-lived effects on soil N and the effects of the target community on resource levels were not pronounced until later in the study (Tables 3 & 5), both treatments delayed *Phalaris* seedling emergence (Figures 1B & 1C).

No treatment completely prevented *Phalaris* seedling emergence, but they did affect the extent of seedling establishment. *Phalaris* seedling establishment was reduced 87% by high diversity cover crops (from 420 ± 120 to 51 ± 14 shoots m^{-2}) and 81% by low diversity cover crops (from 420 ± 120 to 81 ± 21 shoots m^{-2}) compared to plots without cover crops ($F = 5.23$; d.f. = 2, 71; $P = 0.008$). Sawdust amendments reduced *Phalaris* seedling establishment by 61% (from 260 ± 82 to 100 ± 35 shoots m^{-2}) compared to plots without sawdust amendments ($F = 7.83$; d.f. = 1, 71; $P = 0.007$). In addition, the target community reduced *Phalaris* establishment as much as cover crops

did ($F = 5.12$; d.f. = 1, 71; $P = 0.009$; cover crops x target community). Sawdust had no effect on *Phalaris* shoot density in plots where the target community was present.

Phalaris growth was highest when growing alone in plots without sawdust amendments (Figure 2B). Under these conditions *Phalaris* cover was $\geq 50\%$ ($X^2 = 15.61$, d.f. = 2; $P = 0.0004$; cover crops x target community x sawdust). Cover crops reduced the maximum cover of *Phalaris* from $\geq 75\%$ to $\leq 24\%$, with *Phalaris*' modal cover classes being 3 (5-24%) and 2 (1-4%) in plots with low and high diversity cover crops, respectively ($X^2 = 32.08$, d.f. = 2; $P < 0.0001$). Sawdust reduced *Phalaris* growth, which decreased maximum *Phalaris* cover from $\geq 75\%$ to $\leq 24\%$ ($X^2 = 56.13$, d.f. = 1; $P < 0.0001$). The target community reduced *Phalaris* growth as much as cover crops did (Figure 2A; $X^2 = 26.92$, d.f. = 2; $P < 0.0001$; cover crop x target community) but not as much as sawdust amendments. *Phalaris* growth was most reduced in plots having both sawdust amendments and the target community present (Figure 2, $X^2 = 7.71$, d.f. = 1; $P = 0.006$; target community x sawdust).

Target Community Seedling Emergence, Establishment, and Growth

Decreasing light reduced target community seedling emergence. By the end of the experiment, high diversity cover crops reduced target community seedling emergence from 0.61 ± 0.03 to 0.33 ± 0.2 (Figure 3A). Low diversity cover crops only delayed seedling emergence, while initial N reduction caused by sawdust amendments, and competition from *Phalaris* had no effects (Figure 3A-C).

Cover crops greatly reduced target community seedling establishment. By lowering *C. canadensis*, *C. scoparia*, and *S. atrovirens* establishment, and marginally

decreasing *G. grandis* establishment ($P = 0.05$), high and low diversity cover crops decreased total graminoid establishment from 700 ± 66 to 190 ± 28 and 480 ± 63 shoots m^{-2} , respectively (Tables 6A & 7). Even though cover crops did not affect individual forb species, total forb establishment was marginally reduced by high diversity cover crops ($P = 0.06$) (Tables 6A & 7). High diversity cover crops reduced total target community establishment from 1100 ± 89 to 470 ± 37 shoots m^{-2} (Tables 6A & 7). High diversity cover crops had less effect on forb vs. graminoid seedling establishment, resulting in forbs being a higher percentage of the established target community in plots with high diversity cover crops (66%) vs. plots with low diversity (47%) or no cover crops (49%).

Phalaris and sawdust amendments had little effect on target community establishment. Although sawdust amendments reduced *C. canadensis* and *G. grandis* establishment, they had no effect on total graminoid or target community establishment (Tables 6A & 7). Sawdust amendments did, however, reduce total forb establishment from 520 ± 68 to 280 ± 52 shoots m^{-2} in plots with low diversity cover crops, decreasing their percentage in the target community from 60% to 36% (Tables 6A & 7; cover crops x sawdust). When *Phalaris* was present without cover crops, total forb establishment and percentage of forbs in the target community increased from 260 ± 31 to 560 ± 75 shoots m^{-2} , and from 32% to 48%, respectively (Tables 6A & 7; cover crops x *Phalaris*).

Cover crops reduced the growth of more target community species than sawdust did (Tables 6B & 8). High diversity cover crops had the greatest impact, lowering the modal cover classes of *C. scoparia*, *S. atrovirens*, and *M. ringens*, *V. fasciculata*, *P. virginianum*, and *E. maculatum* by 1-3 classes (Table 8). Low diversity cover crops reduced *C. scoparia* and *S. atrovirens*' modal cover classes from 3 (5-24%) to 2 (1-4%),

and only *M. ringens* experienced decreased growth from sawdust amendments (Table 8). In plots with high diversity cover crops *V. fasciculata*'s modal cover increased from 3 to 4 (25-49%) if sawdust was added (Table 6B; cover crops x sawdust), but decreased from 4 to 3 when *Phalaris* was present (Table 6B; cover crop x *Phalaris*). Other significant interaction terms regarding individual target community species growth involved species whose modal cover class never reached > 2 or marginally significant results (Table 6B).

Analyses revealed block and covariate effects on target community establishment and growth (Table 6). Forb establishment was 22% higher in one basin. As plot elevation increased the growth of two species decreased. The growth of three species also varied by repetition (basin x distance from water). Although significant, these effects were trivial to experimental outcomes.

Discussion

Cover crops and sawdust amendments were not as effective in reducing resources as expected. First, only high diversity cover crops reduced light availability. This light reduction, however, was not attributable to structural complexity (*sensu* Lindig-Cisneros & Zedler 2002a, b) as anticipated, but more likely due to the broad-leaf structure of the dominant species, *B. cernua*. Since low diversity cover crops blocked little light, their effects on target community and *Phalaris* seedling emergence, establishment, and growth was likely attributable to competition for another resource. Second, sawdust amendments only depleted N short-term and later increased ammonium-N, suggesting that practitioners must time native seeding with short periods of decreased N if relying on sawdust amendments for *Phalaris* control. However, a study comparing the effects of

different C amendments on soil N levels, conducted at the same site, revealed that sawdust with higher C:N ratios than cedar sawdust reduced nitrate-N more long-term (Appendices A-C). This finding suggests that practitioners using sawdust must also pay careful attention to the species of sawdust they use.

Understanding how sawdust raised ammonium-N levels is important since increasing resource availability may affect future competition and invasions (Tilman 1982; Johnstone 1986; Davis et al. 2000). One explanation for increased ammonium-N may be the low C:N ratio and high ammonium-N levels in cedar sawdust (Appendix A). Perry et al. (2004), however, used pine sawdust (C:N \approx 187) in their study and ammonium-N still increased after 6 weeks. Further, in the study comparing the effects of different C amendments on N levels in sedge meadow soils, cedar sawdust only increased ammonium-N for 2 weeks (Appendices B & C). Other C amendments used in this study had no effect on ammonium-N levels until 24 weeks after they were incorporated. At this time, plots with red oak (*Quercus rubra* L.) sawdust had lower ammonium-N levels than plots with other C amendments (Appendices B & C). Soil-microbe interactions may also explain elevated ammonium-N. Carbon amendments, which increase bacteria populations (Paul & Clark 1989), may also increase the number of protozoa that prey on bacteria and excrete metabolic waste as ammonium-N, increasing N-mineralization (Elliott et al. 1979; Clarholm 1981; Schaetzl & Anderson 2005). Reduced vegetative growth, despite elevated N, may be explained by the timing of N depletion in sawdust-amended plots, which occurred early in the growing season when C₃ species typically experience high productivity (Ode et al. 1980).

Phalaris seedling emergence, establishment, and growth were limited more by N than light. Cover crops did not establish fast enough to achieve their intended goal of preventing *Phalaris* germination, which occurs after short photoperiods (Lindig-Cisneros & Zedler 2001). In contrast, *Phalaris* seedling emergence was delayed in plots with sawdust amendments, suggesting that *Phalaris*, like many ruderal and weedy species, requires nitrate to break seed dormancy (Fenner 1985; Pons 1989; Lambers et. al. 1998). Although cover crops reduced *Phalaris* seedling establishment, *Phalaris* seedlings growing within their canopies reached similar shoot lengths as seedlings growing alone and greater shoot lengths than seedlings growing in sawdust-amended plots (Iannone, University of Minnesota, unpublished data). These results suggest that reduced clonal expansion (Maurer & Zedler 2002) rather than individual seedling growth caused decreases in *Phalaris* densities and cover in plots with cover crops.

In contrast to *Phalaris*, target community seedling emergence, establishment, and growth were limited more by light than N. Both cover crop treatments either reduced or delayed target community seedling emergence, whereas sawdust amendments did not. The low-light environment below high diversity cover crops explains reduced seedling emergence since *Carex* spp. need long photoperiods to germinate and high levels of far red light, typical of dense plant canopies, can reverse germination induction (Kettenring 2006b). In addition, target community seedling establishment and growth were reduced more by high diversity cover crops than sawdust amendments. These results confirmed predictions that reducing light availability by sowing cover crops will prevent native species establishment (Perry & Galatowitsch 2003; 2004). Sawdust amendments did, however, reduce grass establishment, which has been noted in other studies (Averett et al.

2004; Eschen et al. 2007) and confers that practitioners using sawdust in should expect species-specific rather than community level responses (Eschen et al. 2006).

Surprisingly, the target community reduced *Phalaris* reinvasion. This result was unexpected since *Phalaris* typically outcompetes native species (Wetzel & van der Valk 1998; Green & Galatowitsch 2002; Adams & Galatowitsch 2006). These findings may be attributed to sowing densities and cold-stratifying native seeds. Most restoration seed mixes contain about 75% less native perennial seeds than used in this study (Jacobson 2003). High seed densities and cold stratifying seeds likely increased germination and establishment rates (Schutz & Rave 1999; Kettenring 2006a; 2007; Sheley & Half 2006) possibly allowing native species to competitively suppress *Phalaris* by sequestering resources (*sensu* Seabloom et al. 2003; Barger et al. 2003; Bakker & Wilson 2004). Once established, the target community reduced soil N and light availability. In addition, the broad-leafed forb *V. fasciculata* established at high densities, possibly further reducing light. This reduction in resources likely prevented clonal expansion of *Phalaris* (Maurer & Zedler 2002). These results suggest that sequestering resources by rapidly establishing native species is vital in preventing *Phalaris* reinvasion.

Experimental treatments not only affected target community seedling emergence, establishment, and growth, but they also affected community composition. The established target community had a higher proportion of forb seedlings in plots with *Phalaris* and in plots with non-amended soils and low diversity cover crops. This suggests that these treatments competed more with graminoids than forbs and restorations using grass cover crops or lacking follow-up *Phalaris* control may result in forb-rich communities atypical of natural sedge meadows (Galatowitsch & van der Valk 1996).

High forb abundance, however, in a sedge meadow restoration where grass cover crops were not used and *Phalaris* control was ongoing suggests that a forb-rich community may be a typical transitional state in the development of restored sedge meadow communities (Bohnen & Galatowitsch 2005).

Conclusion

Establishing perennial vegetation rapidly may be more important than reducing initial resource availability in preventing *Phalaris* seedling establishment. The ability of native species to reduce *Phalaris* seedling establishment may be attributed to sowing native perennial species at higher than typical densities and cold stratifying seeds prior to sowing, which increased rates of germination, establishment, and resource sequestration. Cover crops failed to impede *Phalaris* germination and prevented target community seedling establishment. Therefore, cover crops should not be used. Acquiring the volume of sawdust necessary to deplete N, transporting this volume, and incorporating it into moist soils makes utilizing sawdust amendments logistically difficult. Given the short-lived effects sawdust had on N depletion, and that sawdust did not reduce *Phalaris* seedling establishment more than the target community did, the logistical difficulties of using sawdust may outweigh the benefits. However, since the target community further reduced *Phalaris* seedling growth in sawdust-amended soils and the short-lived effects of sawdust on N depletion may have resulted from the sawdust species used, N reduction deserves further research. Even when *Phalaris* seeds are present at low densities, reducing resources and establishing perennial species does not totally prevent reinvasion, making follow-up *Phalaris* control a necessary aspect of sedge meadow restorations.

Implications for Practice

- When trying to prevent *Phalaris* reinvasions, practitioners should focus efforts on establishing native perennial species quickly, possibly by seeding at high densities and cold stratifying seeds to break dormancy.
- Cover crops are not effective for sedge meadow restorations because they will fail to prevent *Phalaris* germination while reducing seedling establishment of desired species.
- Given the logistical difficulties of incorporating sawdust and its limited effectiveness in reducing *Phalaris* seedling establishment, sawdust amendments may be an impractical *Phalaris*-control strategy in sedge meadows. Additionally, practitioners need to pay attention to the species of sawdust being used since sawdust with low C:N ratios may only reduce N short-term.
- Ongoing *Phalaris* control in sedge meadow restorations will be necessary even if *Phalaris* seed densities are low, resources availability is decreased, and native species establish.
- Future restorations that could be affected by invasive species may also benefit from research that increases rates of germination and seedling establishment of desired native species.

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Table 1. Chemical composition of soils with and without sawdust amendments one week prior to seeding experiment.

| <i>Chemical parameters</i> | <i>With sawdust</i> | <i>Without sawdust</i> |
|---|---------------------|------------------------|
| organic matter (g kg ⁻¹) | 9.5 | 6.7 |
| total C (g kg ⁻¹) | 5.46 | 4.15 |
| inorganic C (g kg ⁻¹) | 0 | 0 |
| organic C (g kg ⁻¹) | 5.46 | 4.15 |
| total N (g kg ⁻¹) | 0.37 | 0.31 |
| NO ₃ -N (mg kg ⁻¹) | 3.8 | 8.6 |
| NH ₄ -N (mg kg ⁻¹) | 5.9 | 14.7 |
| total P (mg kg ⁻¹) | 39 | 38 |
| SO ₄ -S (mg kg ⁻¹) | 24 | 34 |
| Fe (mg kg ⁻¹) | 261.6 | 199.3 |
| Mn (mg kg ⁻¹) | 41.1 | 28.4 |
| Zn (mg kg ⁻¹) | 4.7 | 3.8 |
| Cu (mg kg ⁻¹) | 3.6 | 4 |
| Pb (mg kg ⁻¹) | 3 | 2.9 |
| Ni (mg kg ⁻¹) | 4.6 | 4.1 |
| Cd (mg kg ⁻¹) | 0.2 | 0.2 |
| Cr (mg kg ⁻¹) | 0.1 | 0.1 |
| K (mg kg ⁻¹) | 154 | 137 |
| Ca (mg kg ⁻¹) | 4529 | 4540 |
| Mg (mg kg ⁻¹) | 717 | 737 |
| Na (mg kg ⁻¹) | 43 | 44 |
| % Moisture (wet wt.basis) | 49.2 | 36.4 |
| pH | 7.1 | 7.2 |

Table 2. ANCOVA results for ammonium-N and nitrate-N levels. The means of measurements from the halfway point (week 9) and the end of the first growing season (week 18) were used to test for treatment effects throughout the length of the study. Differences between the measurements at weeks 9 and 18 were used to test for treatment effects on changes in levels over the course of the experiment. Basin, distance from water, and basin x distance from water were included in the model as block-effects. Prior to analyses mean nitrate-N was log-transformed and all other values were Box-Cox-transformed. Only significant values or marginally significant values are shown. Values in *italics* were marginally significant ($0.10 > P > 0.05$).

| <i>Model term</i> | <i>df</i> | <i>Mean NH₄-N</i> | | <i>Difference in NH₄-N</i> | | <i>Mean NO₃-N</i> | | <i>Difference in NO₃-N</i> | |
|--|-----------|--------------------------------|----------------|---------------------------------------|----------------|------------------------------|----------------|---------------------------------------|----------------|
| | | <i>(x)^{-0.8} * -1</i> | <i>P-value</i> | <i>(x + 50)⁻² * -1</i> | <i>P-value</i> | <i>log (x)</i> | <i>P-value</i> | <i>(x + 50)² / 100</i> | <i>P-value</i> |
| Basin | 1 | - | - | - | - | - | - | - | - |
| Distance from water | 2 | - | - | 0.04 | - | - | - | 0.02 | - |
| Basin x Distance from water | 2 | 0.002 | - | - | 0.0009 | - | - | - | - |
| Elevation | 1 | - | - | - | - | - | - | - | - |
| Cover crops | 2 | 0.04 | - | - | - | 0.05 | - | - | - |
| Target community | 1 | - | - | - | - | 0.002 | - | < 0.0001 | - |
| <i>Phalaris</i> | 1 | - | - | - | - | 0.04 | - | - | - |
| Sawdust | 1 | < 0.0001 | - | - | - | - | - | 0.01 | - |
| Cover crops x Target community | 2 | 0.03 | - | - | 0.002 | - | - | < 0.0001 | - |
| Cover crop x <i>Phalaris</i> | 2 | - | - | - | - | - | - | - | - |
| Cover crops x Sawdust | 2 | - | - | - | - | - | - | - | - |
| Target community x <i>Phalaris</i> | 1 | - | - | - | - | - | - | - | - |
| Target community x Sawdust | 1 | - | - | - | - | - | - | - | - |
| <i>Phalaris</i> x Sawdust | 1 | 0.001 | - | - | - | - | - | - | - |
| Cover crops x Target community x <i>Phalaris</i> | 2 | - | - | - | - | - | - | - | - |
| Cover crops x Target community x Sawdust | 2 | - | - | - | - | - | - | - | - |
| Cover crops x <i>Phalaris</i> x Sawdust | 2 | - | - | - | - | - | - | - | - |
| Target community x <i>Phalaris</i> x Sawdust | 1 | - | - | - | - | - | - | - | - |
| Cover crops x Target community x <i>Phalaris</i> x Sawdust | 2 | - | - | - | - | - | - | - | - |

Table 3. Mean ammonium and nitrate-N levels in plots with different vegetative treatment combinations grown in soils with and without sawdust amendments. Values are from samples collected at the halfway point (week 9) and end of the first growing season (week 18).

| <i>Vegetation in plot</i> | <i>Mean NH₄-N ± SE (mg x kg⁻¹)</i> | | | | <i>Mean NO₃-N ± SE (mg x kg⁻¹)</i> | | | |
|---|--|----------------|---------------------------|----------------|--|----------------|---------------------------|----------------|
| | <i>Plots without sawdust</i> | | <i>Plots with sawdust</i> | | <i>Plots without sawdust</i> | | <i>Plots with sawdust</i> | |
| | <i>Week 9</i> | <i>Week 18</i> | <i>Week 9</i> | <i>Week 18</i> | <i>Week 9</i> | <i>Week 18</i> | <i>Week 9</i> | <i>Week 18</i> |
| High diversity, Target community, <i>Phalaris</i> | 12 ± 7.4 | 1.7 ± 0.2 | 7.1 ± 2.3 | 3.2 ± 1.2 | 6.8 ± 0.9 | 11 ± 1.8 | 6.7 ± 1.2 | 13 ± 1.9 |
| High diversity, Target community | 3.2 ± 0.6 | 1.6 ± 0.2 | 9.8 ± 4.2 | 2.0 ± 0.2 | 6.5 ± 1.5 | 11 ± 2.6 | 6.5 ± 0.5 | 9.7 ± 1.5 |
| High diversity, <i>Phalaris</i> | 3.7 ± 0.4 | 1.5 ± 0.2 | 6.2 ± 1.2 | 2.5 ± 0.6 | 6.6 ± 1.0 | 8.4 ± 1.0 | 5.6 ± 0.7 | 10 ± 1.2 |
| High diversity | 3.7 ± 0.7 | 1.6 ± 0.2 | 9.2 ± 1.8 | 2.0 ± 0.2 | 7.3 ± 1.4 | 8.9 ± 1.2 | 5.8 ± 1.1 | 10 ± 1.8 |
| Low diversity, Target community, <i>Phalaris</i> | 14 ± 8.8 | 1.4 ± 0.1 | 6.8 ± 2.8 | 3.0 ± 0.7 | 7.9 ± 2.1 | 7.8 ± 0.9 | 5.5 ± 1.8 | 9.5 ± 3.2 |
| Low diversity, Target community | 3.5 ± 0.7 | 1.6 ± 0.1 | 7.7 ± 2.4 | 2.6 ± 0.4 | 6.5 ± 0.8 | 10 ± 1.1 | 5.7 ± 1.3 | 8.7 ± 1.7 |
| Low diversity, <i>Phalaris</i> | 16 ± 11 | 2.8 ± 0.8 | 20 ± 12 | 4.4 ± 1.8 | 7.3 ± 0.6 | 14 ± 3.1 | 4.9 ± 1.3 | 10 ± 2.1 |
| Low diversity | 15 ± 12 | 2.8 ± 1.1 | 19 ± 9.3 | 9.3 ± 3.8 | 11 ± 2.5 | 16 ± 4.4 | 7.9 ± 2.7 | 14 ± 1.7 |
| Target community, <i>Phalaris</i> | 5.2 ± 1.1 | 1.6 ± 0.1 | 7.0 ± 2.1 | 2.4 ± 0.3 | 9.3 ± 3.2 | 6.9 ± 2.5 | 6.2 ± 2.6 | 9.8 ± 1.2 |
| Target community | 9.2 ± 5.6 | 1.6 ± 0.1 | 14 ± 7.3 | 2.3 ± 0.2 | 9.6 ± 1.8 | 9.0 ± 1.3 | 7.1 ± 1.3 | 10 ± 4.1 |
| <i>Phalaris</i> | 4.2 ± 0.7 | 1.5 ± 0.4 | 7.4 ± 2.5 | 3.1 ± 0.6 | 5.9 ± 1.6 | 14 ± 3.2 | 4.7 ± 0.3 | 17 ± 5.2 |
| No vegetation | 4.4 ± 1.8 | 1.7 ± 0.3 | 15 ± 6.7 | 7.3 ± 1.3 | 11 ± 2.5 | 20 ± 2.2 | 4.7 ± 1.5 | 22 ± 6.7 |
| Weekly experimental mean ± SE | 8.1 ± 1.7 | 1.8 ± 0.1 | 11 ± 1.6 | 3.3 ± 0.5 | 7.9 ± 0.5 | 11 ± 0.8 | 6.0 ± 0.41 | 12 ± 0.97 |

Table 4. Results of randomized mixed-effects model analysis for % PAR blocked. Basin and distance from water were included into the model as random-effects. Time was included as a continuous variable. Values were arcsine square root-transformed prior to analysis. Only significant or marginally significant values are shown. Values in *italics* were marginally significant ($0.10 > P > 0.05$).

| <u>Model term</u> | <u>df</u> | <u>P-values</u> | <u>Model term</u> | <u>df</u> | <u>P-values</u> |
|--|-------------------|-----------------|---|-------------------|-----------------|
| Basin | 1 | - | | | |
| Distance from water | 2 | - | Time | 1 | - |
| Elevation | 1 | 0.001 | Time x Elevation | 1 | 0.0007 |
| Cover crops | 2 | < 0.0001 | Time x Cover crops | 2 | 0.009 |
| Target community | 1 | 0.0004 | Time x Target community | 1 | < 0.0001 |
| <i>Phalaris</i> | 1 | - | Time x <i>Phalaris</i> | 1 | < 0.0001 |
| Sawdust | 1 | - | Time x Sawdust | 1 | - |
| Cover crops x Target community | 2 | 0.05 | Time x Cover crops x Target community | 2 | < 0.0001 |
| Cover crop x <i>Phalaris</i> | 2 | - | Time x Cover crop x <i>Phalaris</i> | 2 | 0.003 |
| Cover crops x Sawdust | 2 | < 0.0001 | Time x Cover crops x Sawdust | 2 | < 0.0001 |
| Target community x <i>Phalaris</i> | 1 | 0.02 | Time x Target community x <i>Phalaris</i> | 1 | < 0.0001 |
| Target community x Sawdust | 1 | - | Time x Target community x Sawdust | 1 | - |
| <i>Phalaris</i> x Sawdust | 1 | - | Time x <i>Phalaris</i> x Sawdust | 1 | 0.0009 |
| Cover crops x Target community x <i>Phalaris</i> | 2 | - | Time x Cover crops x Target community x <i>Phalaris</i> | 2 | 0.02 |
| Cover crops x Target community x Sawdust | 2 | 0.07 | Time x Cover crops x Target community x Sawdust | 2 | 0.07 |
| Cover crops x <i>Phalaris</i> x Sawdust | 2 | - | Time x Cover crops x <i>Phalaris</i> x Sawdust | 2 | - |
| Target community x <i>Phalaris</i> x Sawdust | 1 | 0.02 | Time x Target community x <i>Phalaris</i> x Sawdust | 1 | 0.0009 |
| Cover crops x Target community x <i>Phalaris</i> x Sawdust | <i>Error term</i> | | Time x Cover crops x Target community x <i>Phalaris</i> x Sawdust | <i>Error term</i> | |

Table 5. The mean percentage of PAR blocked by different vegetative treatment combinations grown in plots with and without sawdust amendments. Starting at week 7 measurements were made every 3 weeks during the first growing season.

| <u>Vegetation in plot</u> | <u>Mean % PAR blocked ± SE</u> | | | | | | | |
|---|--------------------------------|----------------|----------------|---------------------------|---------------|----------------|----------------|----------------|
| | <u>Plots without sawdust</u> | | | <u>Plots with sawdust</u> | | | | |
| | <u>Week 7</u> | <u>Week 10</u> | <u>Week 13</u> | <u>Week 16</u> | <u>Week 7</u> | <u>Week 10</u> | <u>Week 13</u> | <u>Week 16</u> |
| High diversity, Target community, <i>Phalaris</i> | 68 ± 8.6 | 83 ± 4.1 | 93 ± 2.2 | 99 ± 0.24 | 19 ± 10 | 37 ± 11 | 65 ± 10 | 93 ± 2.3 |
| High diversity, Target community | 73 ± 9.4 | 83 ± 5.6 | 93 ± 1.5 | 98 ± 0.62 | 10 ± 3.6 | 43 ± 4.9 | 70 ± 4.6 | 96 ± 11 |
| High diversity, <i>Phalaris</i> | 66 ± 9.3 | 83 ± 3.6 | 90 ± 1.2 | 98 ± 0.76 | 13 ± 2.9 | 35 ± 5.8 | 69 ± 6.6 | 93 ± 3.2 |
| High diversity | 70 ± 6.8 | 78 ± 7.2 | 91 ± 2.0 | 97 ± 0.60 | 8.7 ± 3.6 | 30 ± 3.2 | 62 ± 6.0 | 91 ± 2.7 |
| Low diversity, Target community, <i>Phalaris</i> | 18 ± 4.5 | 39 ± 5.1 | 69 ± 6.7 | 93 ± 1.9 | 4.0 ± 1.7 | 7.1 ± 1.4 | 34 ± 3.4 | 84 ± 4.2 |
| Low diversity, Target community | 12 ± 0.81 | 45 ± 8.7 | 73 ± 4.3 | 94 ± 1.6 | 4.9 ± 2.1 | 9.1 ± 4.3 | 28 ± 8.6 | 65 ± 9.6 |
| Low diversity, <i>Phalaris</i> | 8.7 ± 2.3 | 27 ± 7.9 | 45 ± 7.9 | 62 ± 7.0 | 3.1 ± 1.8 | 2.0 ± 0.21 | 1.9 ± 1.3 | 9.3 ± 4.1 |
| Low diversity | 18 ± 7.4 | 33 ± 11 | 43 ± 11 | 59 ± 8.1 | 5.7 ± 4.4 | 5.1 ± 3.1 | 9.6 ± 5.0 | 15 ± 5.3 |
| Target community, <i>Phalaris</i> | 16 ± 5.6 | 47 ± 6.7 | 80 ± 4.2 | 97 ± 0.58 | 1.8 ± 0.80 | 5.9 ± 1.9 | 27 ± 6.1 | 85 ± 5.9 |
| Target community | 8.6 ± 3.7 | 37 ± 3.6 | 78 ± 4.1 | 95 ± 1.4 | 4.4 ± 1.5 | 6.0 ± 3.0 | 27 ± 3.5 | 84 ± 5.0 |
| <i>Phalaris</i> | 8.4 ± 1.5 | 23 ± 5.4 | 53 ± 5.9 | 76 ± 2.9 | 0.58 ± 0.54 | 1.4 ± 0.61 | 1.2 ± 0.71 | 6.4 ± 2.1 |
| No vegetation | 0.0 ± 0.80 | 0.0 ± 1.8 | 0.1 ± 1.1 | 2.0 ± 0.63 | 0.0 ± 0.76 | 0.0 ± 0.78 | 1.0 ± 1.2 | 1.0 ± 1.1 |
| Weekly experimental mean ± SE | 31 ± 3.7 | 48 ± 3.6 | 67 ± 3.5 | 81 ± 3.4 | 6.3 ± 1.2 | 15 ± 2.2 | 33 ± 3.4 | 60 ± 4.7 |

Table 6. Results of analyses of shoot densities (establishment) (A) of individual target community species and total graminoids, forbs, and target community, and results of analyses of individual species cover class (growth) (B). Basin, distance from water, and basin x distance from water were included in the model as block-effects. Individual species densities were rank-transformed and total graminoid, forb, and target community densities were square root transformed prior to analysis. Only components of the target community having significant whole-model test results are presented. Only significant and marginally significant values are shown. Values in *italics* were marginally significant ($0.10 > P > 0.05$).

| | | <i>P-values from analyses of shoot densities (N = 72)</i> | | | | | | |
|--|-------------|---|-------------------------|-----------------------|---------------------------|------------------|-------------|------------------------|
| A. <i>Model term</i> | <i>d.f.</i> | <i>Catamagrostis canadensis</i> | <i>Glyceria grandis</i> | <i>Carex scoparia</i> | <i>Scirpus atrovirens</i> | Total graminoids | Total forbs | Total target community |
| Basin | 1 | - | - | - | - | - | 0.02 | - |
| Distance from water | 2 | - | - | - | - | - | - | - |
| Basin x Distance from water | 2 | - | - | - | - | - | - | - |
| Elevation | 1 | - | - | - | - | - | - | - |
| cover crops | 2 | 0.03 | 0.05 | < 0.0001 | 0.001 | < 0.0001 | 0.06 | < 0.0001 |
| <i>Phalaris</i> | 1 | - | - | - | - | - | 0.02 | - |
| Sawdust | 1 | 0.003 | 0.007 | - | - | - | - | - |
| Cover crops x <i>Phalaris</i> | 2 | - | - | - | - | - | 0.003 | - |
| Cover crops x Sawdust | 2 | - | - | - | - | - | 0.004 | - |
| <i>Phalaris</i> x Sawdust | 1 | - | - | - | - | - | - | - |
| Cover crops x Target community x <i>Phalaris</i> | 2 | - | - | - | - | - | - | - |

| | | <i>P-values from analyses of ordinal cover classes (N = 72)</i> | | | | | | |
|--|-------------|---|---------------------------|------------------------|-----------------------------|---------------------------------|-----------------------------|--|
| B. <i>Model term</i> | <i>d.f.</i> | <i>Carex scoparia</i> | <i>Scirpus atrovirens</i> | <i>Mimulus ringens</i> | <i>Vernonia fasciculata</i> | <i>Pycnanthemum virginianum</i> | <i>Eupatorium maculatum</i> | |
| Basin | 1 | - | - | - | - | - | - | |
| Distance from water | 2 | - | - | - | - | - | - | |
| Basin x Distance from water | 2 | - | 0.006 | 0.01 | 0.004 | - | - | |
| Elevation | 1 | - | 0.02 | - | - | < 0.0001 | - | |
| cover crops | 2 | < 0.0001 | 0.005 | < 0.0001 | < 0.0001 | < 0.0001 | < 0.0001 | |
| <i>Phalaris</i> | 1 | - | 0.05 | - | - | - | - | |
| Sawdust | 1 | - | - | 0.007 | - | 0.06 | - | |
| Cover crops x <i>Phalaris</i> | 2 | - | - | 0.02 | 0.007 | - | - | |
| Cover crops x Sawdust | 2 | - | - | 0.05 | 0.02 | - | 0.003 | |
| <i>Phalaris</i> x Sawdust | 1 | - | - | 0.02 | 0.002 | - | - | |
| Cover crops x Target community x <i>Phalaris</i> | 2 | - | - | - | 0.05 | - | - | |

Table 7. The effects of cover crops, sawdust amendments, and *Phalaris* on establishment of individual target community species and total graminoid, forb, and target community establishment. Values recorded are shoots m⁻² ± SE.

| Species | Cover crop treatment: | | | | | | Low diversity | | | | | | High Diversity | | | | | | Sawdust amendment: | | | | | | | |
|---|-----------------------|----------|----------|----------|------------|-----------|---------------|-----------|---------|------------|-----------|------------|----------------|--------|---------|--------|---------|--------|--------------------|--------|---------|--------|---------|--------|--------|--|
| | Phalaris: | | Without | | With | | Present | | Absent | | Present | | Absent | | Present | | Absent | | Present | | Absent | | Present | | Absent | |
| | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | Present | Absent | | |
| <i>Calamagrostis canadensis</i> (Michx.) P. Beauv (bluejoint) | 3 ± 3 | 7 ± 7 | 7 ± 4 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 7 ± 4 | 20 ± 14 | 3 ± 3 | 27 ± 27 | 40 ± 26 | 77 ± 43 | | | | | | | | | | | | | |
| <i>Glyceria grandis</i> S. Watts (American mangrass) | 50 ± 36 | 33 ± 20 | 33 ± 20 | 30 ± 14 | 47 ± 16 | 13 ± 10 | 33 ± 15 | 100 ± 54 | | 13 ± 10 | 93 ± 52 | 160 ± 51 | 93 ± 27 | | | | | | | | | | | | | |
| <i>Carex hystericina</i> Muhl. (bottlebrush sedge) | 20 ± 16 | 17 ± 6 | 27 ± 20 | 7 ± 4 | 73 ± 22 | 93 ± 57 | 33 ± 18 | 3 ± 3 | | 40 ± 17 | 30 ± 20 | 40 ± 19 | 77 ± 47 | | | | | | | | | | | | | |
| <i>Carex scoparia</i> Schk. (broom sedge) | 73 ± 28 | 170 ± 33 | 70 ± 39 | 97 ± 40 | 460 ± 130 | 310 ± 100 | 220 ± 45 | 230 ± 51 | | 460 ± 91 | 350 ± 160 | 360 ± 96 | 400 ± 120 | | | | | | | | | | | | | |
| <i>Scirpus atrovirens</i> Willd. (green bulrush) | 47 ± 33 | 63 ± 28 | 10 ± 10 | 17 ± 13 | 83 ± 32 | 67 ± 47 | 57 ± 23 | 77 ± 20 | | 140 ± 87 | 190 ± 69 | 63 ± 29 | 140 ± 43 | | | | | | | | | | | | | |
| Total graminoids | 190 ± 86 | 270 ± 45 | 150 ± 29 | 150 ± 51 | 660 ± 160 | 480 ± 140 | 350 ± 79 | 440 ± 100 | | 660 ± 40 | 690 ± 170 | 660 ± 190 | 780 ± 100 | | | | | | | | | | | | | |
| <i>Minulus ringens</i> L. (Allegheny monkeyflower) | 17 ± 8 | 27 ± 19 | 10 ± 4 | 7 ± 4 | 57 ± 16 | 50 ± 20 | 90 ± 40 | 120 ± 66 | | 110 ± 53 | 63 ± 35 | 70 ± 21 | 27 ± 14 | | | | | | | | | | | | | |
| <i>Vernonia fasciculata</i> Michx. (prairie ironweed) | 210 ± 56 | 290 ± 52 | 190 ± 30 | 270 ± 24 | 280 ± 81 | 120 ± 27 | 360 ± 55 | 350 ± 93 | | 490 ± 120 | 170 ± 42 | 350 ± 72 | 170 ± 42 | | | | | | | | | | | | | |
| <i>Pycnanthemum virginianum</i> L. (Virginia mountainmint) | 7 ± 4 | 10 ± 7 | 7 ± 4 | 0 ± 0 | 17 ± 6 | 0 ± 0 | 7 ± 4 | 17 ± 9.5 | | 7 ± 4 | 3.3 ± 3.3 | 7 ± 4 | 3 ± 3 | | | | | | | | | | | | | |
| <i>Lobelia siphilitica</i> L. (great blue lobelia) | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | | | | | | | | | | | | | |
| <i>Eupatorium maculatum</i> L. (spotted joe-pye weed) | 37 ± 33 | 10 ± 4 | 17 ± 8.0 | 10 ± 10 | 20 ± 7 | 13 ± 7 | 33 ± 11 | 63 ± 29 | | 67 ± 23 | 50 ± 17 | 33 ± 16 | 33 ± 7 | | | | | | | | | | | | | |
| Total forbs | 270 ± 95 | 340 ± 49 | 230 ± 27 | 290 ± 30 | 380 ± 83 | 180 ± 37 | 490 ± 65 | 550 ± 130 | | 670 ± 120 | 290 ± 49 | 460 ± 79 | 230 ± 41 | | | | | | | | | | | | | |
| Total target community | 460 ± 110 | 610 ± 52 | 370 ± 45 | 440 ± 53 | 1000 ± 220 | 670 ± 160 | 840 ± 140 | 990 ± 210 | | 1300 ± 150 | 980 ± 210 | 1100 ± 220 | 1000 ± 110 | | | | | | | | | | | | | |

Table 8. The effects of cover crops, sawdust amendments, and *Phalaris* on growth of individual target community species. Values recorded are modal cover class (# of plots sampled with that cover class) at the end of the first growing season (week 16). The total number of plots sampled is listed on top of each column. If two values are listed then the data was bimodal. Ordinal cover classes are 0 = 0%; 1 = < 1%; 2 = 1-4%; 3 = 5-24%; 4 = 25-49%; 5 = 50 -74%; and 6 = or > 75%. Values in bold text are significantly different and values in *italics* are marginally different ($0.10 > P > 0.05$).

| <u>Target community species</u> | <u>Cover crops</u> | | <u>Sawdust amendment</u> | | <u>Phalaris</u> | | |
|---------------------------------|----------------------------|---------------------------|--------------------------|-----------------|-----------------|---------------------|--------------------|
| | High diversity (N = 24) | Low diversity (N = 24) | Absent (N = 24) | Yes (N = 36) | No (N = 36) | Present (N = 36) | Absent (N = 36) |
| <i>Calamagrostis canadensis</i> | 0 (13) | 0 (18) | 0 (12) | 0 (26) | 0 (17) | 0 (21) | 0 (22) |
| <i>Glyceria grandis</i> | 0 (10) | 2 (10) | 2 (13) | 0 (19) | 2 (20) | 2 (16) | 2 (16) |
| <i>Carex hystericina</i> | 0,1 (9) | 2 (10) | 2 (10) | 2 (16) | 1 (13) | 1 (15) | 2 (12) |
| <i>Carex scoparia</i> | 2 (15) | 2 (14) | 3 (15) | 2 (19) | 2 (17) | 2 (20) | 2 (16) |
| <i>Scirpus atrovirens</i> | 0 (11) | 2 (12) | 3 (14) | 3 (15) | 2 (17) | 0,2 (13) | 3 (15) |
| <i>Mimulus ringens</i> | 1 (15) | 2 (16) | 2 (10) | 1 (14) | 2 (18) | 1 (16) | 2 (18) |
| <i>Vernonia fasciculata</i> | 3,4 (10) | 5 (11) | 5 (12) | 5 (13) | 5 (13) | 5 (14) | 4 (13) |
| <i>Pycnanthemum virginianum</i> | 0 (14) | 1 (15) | 1 (15) | 1 (23) | 1 (17) | 1 (24) | 1 (16) |
| <i>Lobelia siphilitica</i> | 0 (24) | 0 (23) | 0 (21) | 0 (33) | 0 (35) | 0 (36) | 0 (32) |
| <i>Eupatorium maculatum</i> | 0 (12) | 2 (10) | 2 (10) | 1 (18) | 0,2 (12) | 1 (13) | 2 (12) |

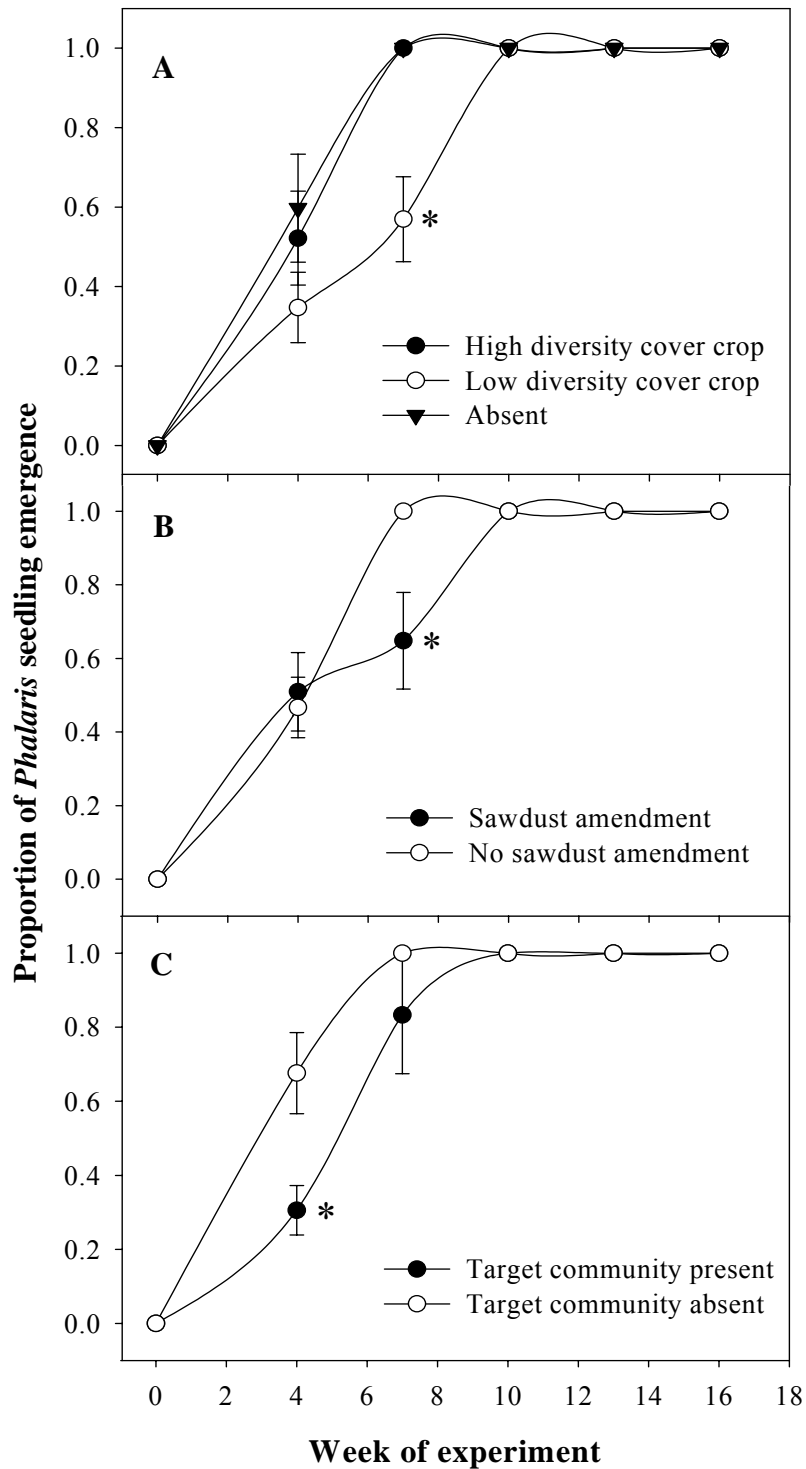


Figure 1. The effects of cover crops (A), sawdust amendments (B), and target community (C) on the cumulative proportion of *Phalaris* seedling emergence. Proportions that were greater than 1.0 were graphed as 1.0 with no SE bars. Data points with an (*) next to them signify that the point is significantly different from the other data points at that particular week, based on $P < 0.05$.

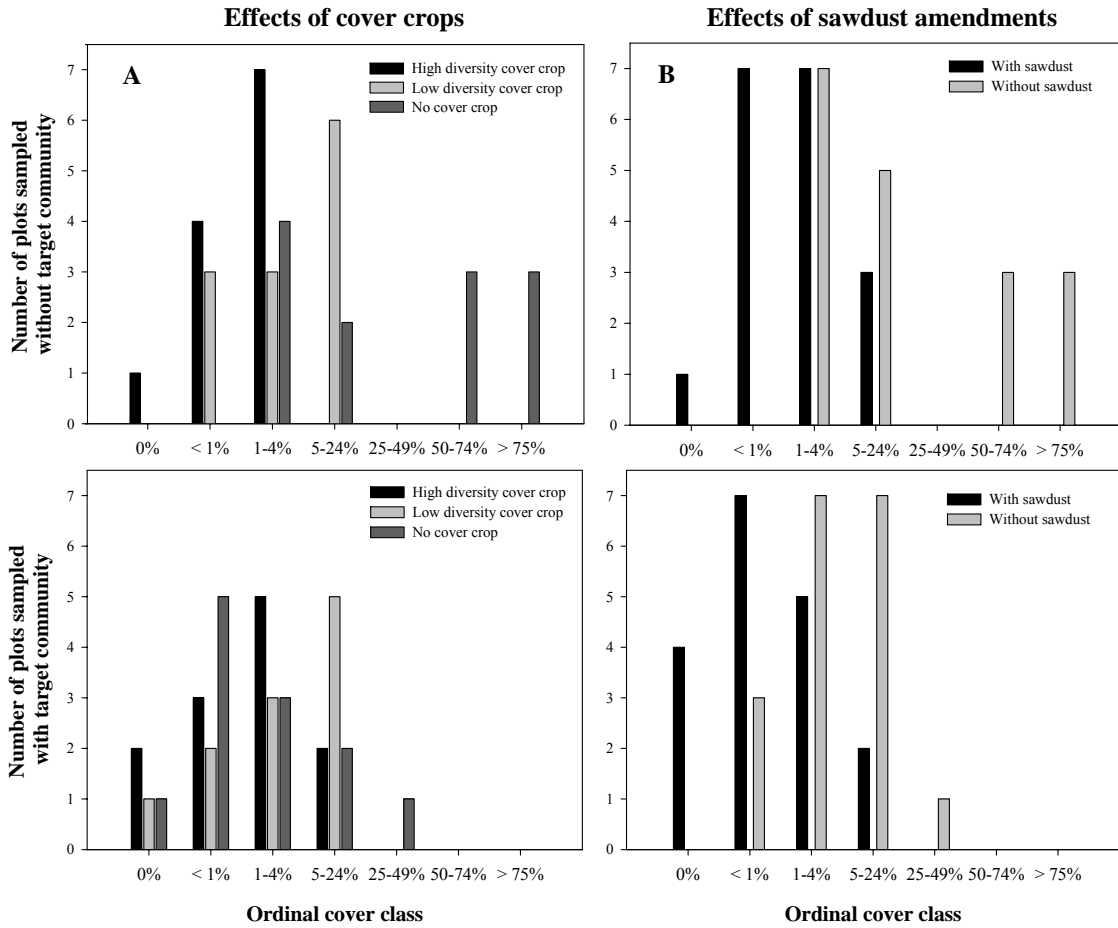


Figure 2. The effects cover crops (A) and sawdust amendments (B) on *Phalaris* growth in plots without and with target community. The values graphed are the number of plots sampled with that particular ordinal cover class. N = 72.

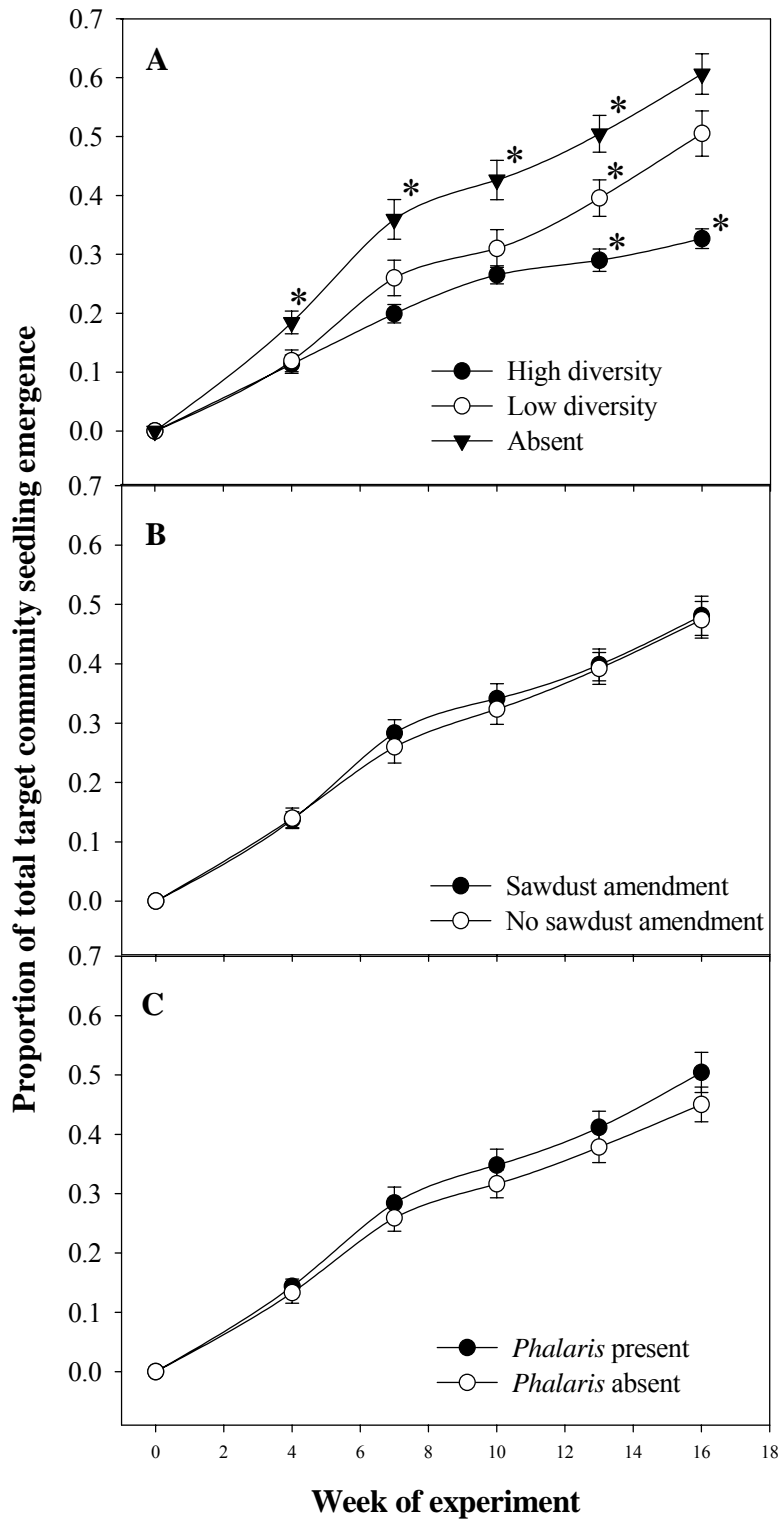


Figure 3. The effects of cover crops (A), sawdust amendments (B), and *Phalaris* (C) on the proportion of total target community seedling emergence. Data points with an (*) next to them are significantly different from the other data points at that particular week, based on $P < 0.05$.

CHAPTER 2

Evaluation of cover crops and sawdust amendments as *Phalaris arundinacea* control strategies in sedge meadow wetland restorations

Summary

1. Restorations sites are often resource-rich, making them prone to invasion by aggressive plants that prevent community recovery. One such species in sedge meadow restorations is *Phalaris arundinacea*. *Phalaris* establishment, however, is limited by light and nitrogen. Reducing these resources may prevent *Phalaris* invasion, allowing desired communities to reestablish.
2. To determine if reducing light with cover crops or reducing nitrogen with soil-sawdust amendments can prevent *Phalaris* invasions, a study was conducted in two wetland basins with controlled hydrology. A 10-species target community and *Phalaris* were seeded along with a high diversity, low diversity, or absent cover crop treatment in plots with or without sawdust. After two growing seasons, aboveground biomass was measured.
3. *Phalaris* establishment was reduced 68% and 38% by high diversity and low diversity cover crops, respectively. Sawdust, although only reducing nitrogen short-term, decreased *Phalaris* establishment by 56%. The target community, which reduced both light and nitrogen, decreased *Phalaris* establishment by 78% and 67% in plots with and without sawdust, respectively.
4. Target community establishment was reduced 73% by high diversity cover crops. Establishment of planted species in the Cyperaceae family doubled in sawdust-amended soils, increasing total graminoid biomass by 37%. In plots without high diversity cover crops, sawdust amendments reduced forb establishment by 26-32%.
5. When the target community and *Phalaris* were grown together, total community biomass was 44% *Phalaris* in plots with high diversity cover crops, 5-8% *Phalaris* and 19-33% unseeded species in sawdust-amended plots, and 48% planted forbs in plots without cover crops or sawdust.

6. ***Synthesis and applications:*** *Phalaris* control in restored sedge meadows should focus on establishing perennial species rather than reducing initial light or nitrogen levels. Cover crops should not be used since their use will likely result in a *Phalaris*-dominated community. Sawdust amendments may be impractical since they did not reduce *Phalaris* much beyond what the target community did. Reducing nitrogen, however, enhanced the target community's ability to suppress *Phalaris* and resulted in a community most similar to natural sedge meadows, suggesting nitrogen depletion deserves further research. Nonetheless, no treatment completely prevented *Phalaris* invasion, making follow-up *Phalaris* control necessary for community recovery.

Keywords: alternate community states, carbon amendments, community recovery, competition, invasion biology, resource availability and reduction, restoration ecology

Introduction

Invasive species can limit the recovery of restored ecosystems (Suding, Gross & Houseman, 2004; D'Antonio & Meyerson, 2002). Disturbed ecosystems which require restoration often have abundant resources and low plant cover (*e.g.* Adams & Galatowitsch, 2005; Orr & Stanley, 2006) making them prone to invasion (Johnstone, 1986; Hobbs & Huenneke, 1992; Baskin & Baskin, 1998; Davis, Grime & Thompson, 2000). Invasive species can change the trajectory of community development, resulting in undesirable, and possibly persistent, alternate community states (D'Antonio & Meyerson, 2002; Mulhouse & Galatowitsch, 2003; Orr & Stanley, 2006). Decreasing levels of abundant resources in restorations may help avoid this scenario, if desired species require less of these resources for establishment than invasive species do (*sensu* Tilman, 1982; Tilman *et al.*, 1999).

Phalaris arundinacea (hereafter *Phalaris*) is increasingly dominant in North American wetlands (Galatowitsch, Anderson & Ascher, 1999; Perkins & Wilson, 2004; Lavoie & Dufresne, 2005) and prevents the establishment of diverse plant communities in sedge meadow and forested 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 seedbanks are depleted and sources of propagules in the fragmented landscape are reduced (Galatowitsch and van der Valk, 1996; Kettenring, 2006). Therefore, when hydrology is restored, these moist non-vegetated, resource-rich areas (Adams & Galatowitsch, 2005) are quickly invaded by *Phalaris*, which forms persistent monotypes (Mulhouse & Galatowitsch, 2003). Even if *Phalaris* control and seeding of desired species occurs, *Phalaris* will dominate the system again after two years (Adams & Galatowitsch, 2006). Since *Phalaris* establishment is limited by light and nitrogen (N) (Lindig-Cisneros & Zedler, 2001; 2002a, b; Perry, Galatowitsch & Rosen, 2004), reducing these resources in restorations may create environmental conditions suitable for the reestablishment of a diverse plant community over persistent monotypes of *Phalaris*.

Researchers have suggested sowing native cover crops in wetland restorations to reduce light availability and prevent *Phalaris* invasions (Galatowitsch, Budelsky & Yetka, 1999; Lindig-Cisneros & Zedler, 2002a). This suggestion is reasonable given *Phalaris* germination is light-triggered (Lindig-Cisneros & Zedler, 2001) and intact wetland canopies limit *Phalaris* germination as well as clonal growth by blocking light (Lindig-Cisneros & Zedler, 2002a; b; Maurer & Zedler, 2002). Canopies that are more diverse possibly intensify this effect because they have greater structural complexity

(Lindig-Cisneros & Zedler, 2002a, b). Cover crops have been successful in reducing undesired species in agriculture and restorations (Ilnicki & Enache, 1992; Shebitz & Kimmerer, 2005). Studies of cover crop use in wetlands, however, suggest that they will limit the establishment of desired sedge meadow species, which have similar light requirements as *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 two 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.

Prairie pothole wetlands typically receive excess N when they are situated in agricultural landscapes (Neely & Baker, 1989; Brinson & Malvarz, 2002) possibly increasing the invasive ability of *Phalaris* (Green & Galatowitsch, 2002; Lavoie & Dufresne, 2005). Desired plant species may be able to outcompete *Phalaris* if this resource is limited. In a greenhouse study, Perry, Galatowitsch, and Rosen (2004) tested if *C. hystericina* could outcompete *Phalaris* when soil N was immobilized through a carbon (C) amendment in the form of pine sawdust. They found that when soil N availability was limited, *C. hystericina* competitively suppressed *Phalaris* because rates of *Phalaris* growth were greatly decreased. Carbon amendments, however, have produced mixed results when applied to restorations (Morghan & Seastedt, 1999; Blumenthal, Jordan & Russel, 2003; Huddleston & Young, 2005; Eschen, Müller-Schärer & Schaffner, 2006; Eschen *et al.*, 2007). In addition, the effects of C amendments on

competition between *Phalaris* and a typical restoration seed mix and the longevity of N-depletion caused by C amendments in wetlands are unknown.

Given that *Phalaris* establishment is reduced under low light and N conditions, cover crops and sawdust amendments may hinder *Phalaris* invasion and promote the establishment of sedge meadow communities. This study was conducted to evaluate the usefulness of these resource-limiting methods as possible restoration strategies in sedge meadow wetlands. This study had the following objectives: 1) determine if cover crops varying in structural complexity and C amendments will hinder *Phalaris* reestablishment, 2) determine if sedge meadow communities can establish in environmental conditions created by cover crops and C amendments, and 3) determine how treatment effects on light and soil N availability shaped experimental outcomes after two growing seasons.

Materials and Methods

EXPERIMENTAL OVERVIEW AND STUDY SITE

To determine if reducing light by sowing cover crops or reducing soil N with sawdust amendments will prevent *Phalaris* invasion while desired sedge meadow species establish, I designed a randomized complete block experiment with four factors.

Competition between seeds of a 10-species target community (absent or present; representing a restoration seed mix) and *Phalaris* (absent or present) was studied in plots with a high diversity (species varied structurally), low diversity, or absent cover crop treatment grown in soils with or without sawdust amendments. Cover crops that varied in structural complexity were used to create multiple below-canopy light levels (*sensu*

Lindig-Cisneros & Zedler, 2002a; b). After two growing seasons, aboveground biomass of all species was weighed to determine competitive outcomes.

This study was conducted in two experimental wetland basins that are located in Carver County, Minnesota at the University of Minnesota Horticultural Research Center, 44°51'45"N latitude, 93°36'00"W longitude. The site which was originally a drained wetland used for agriculture was later divided into four 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) (U.S. Department of Agriculture, 1968).

SEED MIX DESIGN AND PREPARATION

All cover crop and target community species selected for this study are native sedge meadow species common to central Minnesota. The cover crop species chosen were either annuals or short-lived perennials unlikely to be dominant in the community over the long-term. The high diversity cover crop was a mixture of *Beckmannia syzigachne* (Steud.) Fern., *Carex vulpinoidea* Michx., *Bidens cernua* L., *Polygonum lapathifolium* L., and *Epilobium glandulosum* Lehm. *Beckmannia syzigachne* was the only species in the low diversity cover crop treatment. Target community species were chosen from a seed mix approved for use on publicly funded restorations in Minnesota (Jacobson, 2003) and contained the following C₃ perennial graminoids and forbs: *Calamagrostis canadensis* (Michx.) P. Beauv., *Glyceria grandis* S. Wats., *Carex hystericina* Muhl., *Carex scoparia* Schk., *Scirpus atrovirens* Willd., *Mimulus ringens* L., *Vernonia fasciculata* Michx.,

Lobelia siphilitica L., *Pycnanthemum virginianum* L., and *Eupatorium maculatum* L.

Nomenclature followed Gleason and Cronquist (1991).

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

The cover crop sowing densities were based on State of Minnesota revegetation guidelines (Jacobson, 2003) and sowing densities of the target community and *Phalaris* were based on seedbank densities of natural and restored sedge meadows, respectively (Galatowitsch & Biederman, 1998; Adams & Galatowitsch, 2006). Cover crops were sown at 2100 viable seeds m⁻² and the target community was sown at 2250 viable seeds m⁻². *Phalaris* was sown at 60 viable seeds m⁻², a density typical of a remnant *Phalaris* seedbank after its removal from restored sedge meadows. The target community and high diversity cover crop seed mixes both contained their included species at equal proportions. Seed viability was determined by tetrazolium analysis of 200 seeds of each species (Grabe, 1970). After testing viability, seeds were stored at 4⁰C in moist steam-sterilized wetland soil for 4 months to break seed dormancy (i.e. cold-stratified; Baskin & Baskin, 1998; Kettenring, 2007) and mimic winter conditions.

EXPERIMENTAL SET UP AND SITE MAINTENCE

Preparation of the experimental basins began in fall of 2004. First, the western sides of both basins were surveyed and graded to achieve a uniform elevation relative to the

basin's lowest point. Basamid[®] soil fumigant (Dazomet; BASF Corporation, Mt Olive, NJ, USA) was used to deplete the existing seedbank. 24-one m² plots were then marked out at 1, 3, and 5 m from the water's edge in each basin, and weed fabric was laid between them to limit plant establishment in these areas. The 24 treatment combinations were randomly assigned to each row of plots resulting in six complete repetitions blocked on basin and distance from water. To avoid edge effects all samples and measurements were collected from the inner 0.8 m² of each plot.

Soil was amended with carbon during October 2004 using methods similar to Perry, Galatowitsch, and Rosen (2004). In the plots assigned C amendments, the upper 7 cm of soil was removed, replaced with cedar sawdust (*Thuja* sp.) (8.40 ± 0.13 kg dry weight plot⁻¹), and tilled to a depth of 20 cm (2:1 soil:sawdust ratio by volume). The sawdust was 49.9% C and 1.6% N with ammonium-N and nitrate-N concentrations of 141 and 15 mg kg⁻¹, respectively (Chapter 1). Sawdust was acquired from Ser-a-Dock, Inc (Victoria, MN).

The experiment began in spring 2005 after site set up was completed. To determine if soil freezing and thawing between fall 2004 and spring 2005 caused changes in plot elevation, each plot was resurveyed. After resurveying, fiberglass screen extending ≈ 15 cm above and below the soil surface was installed around the edge of all plots and reinforced with wood lathe to reduce seed loss and between-plot migration. Once plot set up was complete, 250 ml of water from a neighboring wetland was poured through a 106 μ m sieve onto each plot to promote recolonization of soil microbes. The sieve was used to prevent non-experimental propagules from entering the plots. Within each row of plots, two 50 cm deep wells were installed to monitor possible changes in the

water table. Seeds were sown on 4 and 5 May 2005 (week 1). After seeding, 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 (2 cm below lowest plot) to prevent early senescence due a dryer than average growing season (NOAA, 2006) Non-experimental species were weeded from all plots during the first 10 weeks of the study.

DATA COLLECTION AND ANALYSES

To determine the effects of sawdust and other treatments on N availability, nitrate-N and ammonium-N were measured three times during each growing season. One week prior to seeding, soil was collected from two random plots in each row (one of each sawdust treatment) to determine initial effects of sawdust amendments on various chemical parameters, including ammonium-N and nitrate-N (Chapter 1, Table 1). Three 1.5 cm diameter x 20 cm soil cores were collected from random points in all plots of four randomly selected rows (two per basin) during weeks 9 and 18 (middle and end) of the first growing season, and weeks 5, 9, and 14 (beginning, middle, and end) of the second growing season (i.e. time since 1 May 2006). Soil samples from the first growing season were analyzed using an AlpKem Rapid Flow Analyzer (Astoria-Pacific International, College Station, TX) at the University of Minnesota Research Analytical Laboratory (St. Paul, MN) (Chapter 1). Soil samples from the second growing season were analyzed using a Wescan N Analyzer (Wescan Instruments, Inc., Deerfield, IL; Carlson, 1986). Both analytical methods used a 2 M KCl solution to extract inorganic-N (Mulvaney, 1996), making results from both field seasons comparable. Nonetheless, 12 random

samples from the second growing season were sent to the University of Minnesota Research Analytical Laboratory to verify this assumption. Nitrate-N and ammonium-N levels were determined on moist soil samples and adjusted for percent soil moisture.

Throughout both growing seasons, the proportion of photosynthetically active radiation (PAR) blocked by plant canopies was measured in all plots to determine treatment effects on light availability. The average of two perpendicular ground-level PAR readings was divided by an above-canopy PAR reading and this value was subtracted from one. 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 LI-250A light meter (LiCOR[®] Biosciences, Lincoln, NE).

Establishment and growth was estimated by measuring aboveground dry-weight biomass of all experimental species, canopy heights, and percent cover. During the 15th week of the second growing season, plants were cut at 2 cm above the soil surface, separated by species, dried at 70°C for 48 hrs, and weighed. All unplanted species excluding *Solidago canadensis*, *Verbena hastata*, and unseeded *C. vulpinoidea* were weighed together. Unplanted species occurring in > 5% of the plots or that were listed as noxious in Minnesota (MNDNR, 2007) are listed in Table 1. Litter was also collected, dried, and weighed. Canopy height was estimated at the end of the first growing season and one week prior to biomass collection by taking the average of 10 measurements at random points in all plots. Percent cover of total plot vegetation was visually estimated to 5% increments during weeks 4, 7, 10, 13, and 16 of the first growing season and weeks 3, and 13 of the second growing season.

To further understand nitrogen competition, carbon:nitrogen (C:N) ratios were measured for plant tissue. The equivalent of 30 mg dry weight of leaf tissue was collected from the target community, *Phalaris*, and high and low diversity cover crop treatments. Tissue from all present target community and high diversity cover crop species were collected at equal proportions. Tissue was collected from all plots at weeks 9 and 18 of the first growing season and weeks 9 and 15 of the second growing season, dried at 70°C for 48 hrs, and then ground through a 1 mm screen. Percent N and C were measured on a 15 mg subsample using an Elementar Americas, Inc. Vario EL III CNS elemental analyzer (Elementar Americas, Inc., Mt. Laurel, NJ; Kirsten, 1983).

To test for treatment effects on *Phalaris*, total forb, graminoid, and target community biomass, Analysis of Covariance (ANCOVA) was used. Nitrate-N, ammonium-N, PAR, and C:N ratios of target community and *Phalaris* leaf tissue were analyzed using random mixed-effects models. 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 identify effects of sawdust on canopy height, and biomass of litter, unseeded species, and planted grasses and members of the Cyperaceae family (i.e. *S. atrovirens*, *C. scoparia*, and *C. hystericina*). To test for a relationship between percent vegetative cover and proportion of PAR blocked, linear regression was used. Analysis of Variance (ANOVA) was used to test for differences in C:N ratios between target community, *Phalaris*, and high and low diversity cover crop leaf tissue at each sampling period. Four outliers were removed from ammonium-N analysis and one from nitrate-N analysis. The outliers either had values 8-20 times greater or 6-10 times smaller than the next closest value for that treatment combination at the time of sample

collection. All models contained plot elevation as a covariate, due to soil settling. Transformations and model terms for specific analyses are presented in appropriate tables. If a model term was significant ($P < 0.05$), differences in treatment levels were determined by Tukey's HSD tests ($\alpha = 0.05$). Significant model terms are not generally presented when a significant higher-order interaction explained results more clearly. Model test and linear regression analyses were done and in "R" (Ihaka & Gentleman, 1996) and pairwise comparisons, Wilcoxon rank-sums test, and t-test were conducted in JMP 6.0 (SAS Institute). All data were back-transformed for reporting and stated as mean \pm SE unless noted otherwise.

Results

PHALARIS AND TARGET COMMUNITY ESTABLISHMENT

Cover crops, sawdust amendments, and competition from the target community all reduced *Phalaris* biomass (Table 2a). The high diversity and low diversity cover crops reduced *Phalaris* biomass by 68% ($270 \pm 41 \text{ g m}^{-2}$) and 38% ($520 \pm 98 \text{ g m}^{-2}$), respectively, compared to plots without cover crops ($840 \pm 180 \text{ g m}^{-2}$). Plots amended with sawdust had 56% less *Phalaris* biomass ($330 \pm 74 \text{ g m}^{-2}$) than plots without sawdust amendments ($760 \pm 120 \text{ g m}^{-2}$) (Table 2a). Competition from the target community reduced *Phalaris* biomass as much as the high diversity cover crop and more than the low diversity cover crop (Fig. 1; Table 2a, cover crop x target community). In plots where the target community was seeded, *Phalaris* biomass was further reduced from 380 ± 82 to $120 \pm 32 \text{ g m}^{-2}$ (68%) by sawdust amendments ($t_{34} = -2.99$, $P = 0.003$).

Target community establishment and growth was reduced by the high diversity cover crop more than any other treatment. On average, total forb, graminoid, and target community biomass was reduced in plots with high diversity cover crops compared to plots with the low diversity or absent cover crop treatments (Tables 2b & 3). Plots with sawdust amendments had 37% higher graminoid biomass than plots without sawdust (Tables 2b & 3). Since sawdust amendments reduced the biomass of planted grasses by 62% ($X^2_1 = 15.102$, $P = 0.0001$), the observed increase in graminoids resulted from a doubling in biomass of planted species from the Cyperaceae family (Fig. 2) ($X^2_1 = 7.864$, $P = 0.005$). When soil was amended with sawdust, forb biomass decreased on average 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 2b & 3; cover crop x sawdust). Likewise, total target community biomass more than doubled in plots with the high diversity cover crop when soil was amended with sawdust. Regardless of these increases, forb and total target community biomass were still greatly reduced compared to plots with other cover crop treatments (Tables 2b & 3; cover crop x sawdust). Graminoid biomass decreased as plot elevation increased allowing forb biomass to increase slightly (Table 2b). These relationships, however, had no effect on the total target community biomass.

Besides affecting *Phalaris* and target community establishment and growth, experimental treatments also affected community composition. Seeded target community species, on average, comprised the highest percentage of the total established community in plots without cover crops (71-82%) (Fig. 3; Table 3). In contrast, seeded target community species only comprised 20-54% of the established community in plots with

the high diversity cover crops (Fig. 3; Table 3). In these plots, total plot biomass was also lower than it was in plots with other cover crop treatments (Table 3). Only two of the five cover crop species established during the second growing season, *C. vulpinoidea* and *E. glandulosum*, and their biomass was 23-55% of the established community (Fig. 3; Table 3). During the first growing season, all five cover crops species were present at covers ranging from 1-100%, with *B. cernua* dominating the treatment (modal cover $\geq 75\%$) (Chapter 1). In addition, when *Phalaris* was present in plots with high diversity cover crops it comprised 44% of the established community when soils were not amended with sawdust (Fig. 3; Table 3). Sawdust-amended plots had over 200% more biomass of unseeded species than non-amended plots (440 ± 63 and 190 ± 30 to g m^{-2} dry wt, respectively) ($X^2_1 = 11.038$, $P = 0.0009$), increasing the percentage of unseeded species in the community from 8-18% to 19-37% (Fig. 3; Table 3).

TREATMENT EFFECTS ON RESOURCE AVAILABILITY

Sawdust amendments affected soil-N in ways that were not anticipated. Ammonium-N and nitrate-N levels 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 nine weeks, however, the sawdust amendment increased ammonium-N levels from 3.9 ± 0.40 to 5.4 ± 0.40 mg kg^{-1} (28%) and did not affect nitrate-N levels (Table 4a). These trends persisted through the end of the study. Amending soils with sawdust did not appear to affect other soil parameters greatly (Chapter 1, Table 1).

Vegetation had a more persistent effect on soil-N than sawdust did. Early in the second growing season, plots with high diversity cover crops had slightly ($P = 0.06$)

higher ammonium-N levels (3.3 ± 0.5) than plots with low diversity or no cover crops (2.2 ± 0.2 and 2.3 ± 0.2 , respectively). Ammonium-N decreased from 5.9 ± 0.7 in plots with no vegetation to $3.9 \pm 0.4 \text{ mg kg}^{-1}$ (33%) in plots with the target community as long as *Phalaris* was not present (Table 4a; target community x *Phalaris*). Plots that had *Phalaris* growing alone or with the target community had ammonium-N levels equivalent to plots without vegetation (Table 4a; target community x *Phalaris*).

Vegetation had greater impacts on nitrate-N levels than ammonium-N levels. As expected, non-vegetated plots had higher nitrate-N levels than vegetated plots throughout the study (Tables 4a & 5; cover crop x target community x *Phalaris*). As with ammonium-N, early in the second growing season (week 5), plots with high diversity cover crops had greater nitrate-N levels than all other plots, excluding non-vegetated ones (Table 4a & 5; year x week x cover crop). The target community reduced nitrate-N levels when grown in plots without high diversity cover crops (Table 4a & 5; cover crop x target community). When grown alone, *Phalaris* was able to reduce nitrate-N levels as much as cover crops and the target community did (Table 4a & 5; cover crop x *Phalaris*; target community x *Phalaris*).

Light availability was strongly related to percent total vegetative cover throughout the study ($R^2 = 0.89$, $P = < 0.0001$). The high number of significant model terms reflects this relationship (Table 4). Throughout the study, the high diversity cover crop reduced light availability by an average of 75%, while the effects of the low diversity cover crop on light availability were slight and only detected during the first growing season when growing in plots without the target community (Fig. 4; Table 4b; year x week x cover crop x target community). The reduction in light availability caused by the high diversity

cover crop was not caused by increased structural complexity since *B. cernua* dominated the canopy during the first growing season (Chapter 1) and only two cover crop species established at high abundances during the second growing season (Table 3). Given that *B. syzigachne* establishment was greatly reduced in the second growing season compared to the first growing season (Iannone, University of Minnesota, unpublished data), decreased light levels in plots with the low diversity cover crop seeded alone were attributable to the establishment of non-experimental species (Fig. 4; Table 1). The target community was almost as effective at reducing light as the high diversity cover crop by the end of the first growing season and in the beginning of the second growing season reduced PAR more than the high diversity cover crop alone (Fig. 4; Table 4b; year x week x cover crop x target community). The effects of *Phalaris* on light availability were only detected when growing alone or in plots with low diversity cover crops (Fig. 4; Table 4a; cover crop x target community x *Phalaris*). Nonetheless, during the second growing season, *Phalaris* reduced PAR as much as the target community did (Fig. 4; Table 4b; year x week x target community x *Phalaris*).

Although the reduction in soil N by sawdust amendments was short-lived, this treatment reduced plant growth during the first growing season, indirectly increasing 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 (Fig. 4; Table 4). Sawdust-amended plots had less litter than plots without sawdust (100 ± 11 and 210 ± 16 g, respectively) ($X^2_1 = 22.89$, $P =$

<0.0001) resulting in 15% more light in sawdust-amended plots at the beginning of the second growing season (week 3) (Fig. 4; Table 4a; year x week x sawdust). Beyond week 3 of the second growing season, however, sawdust amendments did not affect light availability.

TISSUE C:N RATIOS

Experimental treatments had no effects on the 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 ($P < 0.0001$) (Fig. 5). 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* ($P < 0.05$) (Fig. 5). 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* ($P < 0.05$) (Fig. 5). During the second growing season, the C:N ratios of target community and high diversity cover crop leaf tissue were equivalent (Fig. 5). Carbon:nitrogen 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 (Fig. 5).

Discussion

Despite cover crops and sawdust amendments both reducing *Phalaris* invasion, cover crops will not be an effective restoration tool and using sawdust amendments may not be practical. First, 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). Second, sawdust amendments only reduced N short-term 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. However, another study comparing the effects of four different C amendments on N availability in sedge meadow soils confirmed that sawdust with higher C:N ratios than cedar sawdust will have longer-lasting effects on N depletion (Appendices A-C). Due to differences in the longevity of N reduction between sawdust species, practitioners using sawdust to reduce N need to pay careful attention to which species they incorporate.

When light or N was reduced with cover crops and sawdust amendments, respectively, the other resource increased, adversely affecting community invasibility. Reducing light by sowing a high diversity cover crop prevented target community establishment, resulting in a less productive community (i.e. less total biomass; Table 3). This less productive community had elevated soil nitrate-N and ammonium-N levels during the beginning of the second growing season (Table 5); likely the result of decreased plant uptake. Since *Phalaris* growth responds strongly to increased N (Green & Galatowitsch, 2002), this short period of elevated N potentially contributed to the high proportion of *Phalaris* in these plots (Fig. 3). Sawdust amendments reduced N in early summer of the first growing season. This period of N reduction occurred when C₃ plants are most 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 (Fig. 4), allowing more unseeded species, some invasive (MNDNR, 2007), to colonize. Since litter can prevent plant establishment (Carson & Peterson, 1990; Perry & Galatowitsch, 2003; Coleman & Levine, 2007), sawdust amendments may facilitate the colonization of other invasive species that occur in the surrounding area by decreasing litter accumulation. Interestingly, even with higher light levels, *Phalaris* establishment still was reduced in sawdust-amended plots, suggesting that N plays a more important role in *Phalaris* invasion than light in sedge meadows.

Even if N plays a more important role in *Phalaris* invasion than light, both resources control *Phalaris* germination and growth rates (Lindig-Cisneros & Zedler, 2001; Perry, Galatowitsch & Rosen 2004). Therefore, long-term prevention of *Phalaris* invasion will require reduction of both resources. Neither cover crops nor sawdust amendments consistently met this requirement, but once established the target community did (Fig. 4; Table 5). This resource reduction is likely the reason that the target community decreased *Phalaris* invasion as much as the high diversity cover crop; a surprising result given that *Phalaris* typically outcompetes desired 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 about four times higher than what is often used in restorations (Jacobson, 2003), and cold stratifying target community seeds prior to sowing. Seeding at higher densities and cold stratifying seeds likely minimized lag times to germination (Baskin & Baskin, 1998; Schutz & Rave, 1999; Kettenring, 2007; Sheley & Half, 2006), allowing the target community to sequester light and N faster than if these

actions were not taken. These results show the importance of establishing a perennial community quickly to achieve long-term reduction of resources and *Phalaris* invasion.

The difference in resources that limit target community and *Phalaris* establishment provided insights into *Phalaris*' ability to dominate restored sedge meadows. Target community establishment was reduced by high diversity cover crops but not by sawdust amendments (Table 3), suggesting that light limits the establishment of desired sedge meadow species. Although reduced by both cover crops and sawdust amendments, *Phalaris*' proportion in the community was decreased by sawdust-amendments, but not by high diversity cover crops (Fig. 3). These proportions suggest N limited *Phalaris* establishment and showed that *Phalaris* can outcompete target species in low-light but not low-N environments. Further, target community leaf tissue had higher C:N ratios than *Phalaris* leaf tissue (Fig. 5), suggesting target species require less N than *Phalaris*, making them better competitors for this resource (*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* in restored sedge meadows if N is reduced. Additionally, since sawdust only reduced N during the first part of the study, N reduction can likely be short-term if it coincides with seedling establishment. The difference between the resources that limited target community and *Phalaris* establishment (i.e. light and N, respectively) may also explain *Phalaris*' highly invasive nature in sedge meadows since a species will have greater invasive success the more its resource needs differ from the constituent species of the community it invades (Vitousek & Walker, 1989; Fargione, Brown & Tilman, 2003).

Phalaris growth responded more to changes in nitrate-N than 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, 2005). *Phalaris* establishment and proportion in the community decreased in sawdust-amended plots despite elevated ammonium-N levels. The target community also decreased *Phalaris* establishment and its relative abundance in the community. However, when grown with *Phalaris*, the target community reduced nitrate-N, but not ammonium-N. Furthermore, *Phalaris* reduced nitrate-N and not ammonium-N, suggesting its preferred form of N is nitrate. Alternatively, the inability of *Phalaris* to reduce ammonium-N may be a result of the strong affinity between negatively charged clay particles in the soil and positively charged ammonium molecules, which prevented ammonium uptake. Because *Phalaris* exhibits rapid growth and vegetative expansion (Adams & Galatowitsch, 2005), and responds more to increased nitrate than does desired sedge meadow species (Green & Galatowitsch, 2002), *Phalaris* can easily outcompete these species for light in nitrate-rich environments. This scenario likely explains *Phalaris*' dominance in the low-light environments of plots with high diversity cover crops since these plots had high nitrate-N levels in the first part of the second growing season. Further, since increased nutrient loads in wetlands can shift communities to states dominated by a few fast-growing species (Verhoeven *et al.*, 2006), *Phalaris* will likely continue to dominate restored sedge meadows and to invade natural ones within agricultural landscapes.

The resulting composition of established communities, which varied between treatment combinations (Fig. 3), may affect the floristic make-up of those communities in

the future. By preventing target community establishment, the high diversity cover crop mixture resulted in a community dominated by *Phalaris*, *C. vulpinoidea* and *E. glandulosum* in which *Phalaris* will likely become the most abundant species. In sawdust-amended plots, both the colonization of unseeded sedge meadow species and planted species in the Cyperaceae family increased, confirming that more diverse, graminoid-rich communities can establish at low N levels (Green & Galatowisch, 2002). Therefore, reducing N may help reestablish communities similar to natural sedge meadows (*sensu* Galatowitsch & van der Valk, 1996). Outcomes of natural colonization, however, depend on which species and propagules are present in the surrounding landscape. Plots without cover crops or sawdust amendments had low *Phalaris* invasion, but higher than typical forb abundance (Galatowitsch & van der Valk, 1996). The initial establishment of a forb-rich community in a successful sedge meadow restoration, however, suggests a period of high forb abundance may be typical in the early stages of sedge meadow development (Bohnen & Galatowitsch, 2005). If allowed, the forb-rich communities observed in this study will likely shift to graminoid-rich communities as established forbs reduce N availability.

In plots without cover crops or sawdust, the target community successfully established and *Phalaris* invasion was reduced (Fig. 3). These results suggest that efforts to control *Phalaris* in restored sedge meadows should focus on perennial establishment rather than reducing initial light or N levels. Reducing light by sowing cover crops resulted in a *Phalaris*-dominated community (Fig. 3), confirming that cover crops are ineffective as *Phalaris* control in restored sedge meadows. Cover crops, however, can control *Phalaris* in other ecosystems (Hovick & Reinartz, 2007). Since sawdust only

reduced N briefly, did not prevent *Phalaris* invasion much beyond what the target community did, and is difficult to incorporate, sawdust amendments may not be a practical N-limiting strategy. However, reducing N resulted in a community most similar to a natural sedge meadow by further reducing *Phalaris* invasion, and increasing both the colonization of unseeded species and the abundance of planted species in the Cyperaceae family. Given that the short-lived effects of sawdust on N reduction may have resulted from the sawdust species used (cedar), and that reducing N may benefit restored communities, N reduction needs further study. Long-term prevention of *Phalaris* invasions will require decreasing both light and N availability by establishing a perennial community. Seeding at higher densities and cold stratifying seeds may increase rates of perennial establishment and resource sequestering. Nonetheless, even after a perennial community establishes and reduces light and N availability, follow-up *Phalaris* control will still be required to assure the full recovery of the newly formed community.

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Table 1. Unplanted species occurring in greater than 5% of plots or listed as noxious in Minnesota (*). Only plots where *S. atrovirens*, *C. vulpinoidea*, and *G. grandis* were not sown were used to calculate their percentages.

| Non-seeded species | % of plots | Exotic |
|--------------------------------|------------|--------|
| <i>Solidago canadensis</i> | 38 | No |
| <i>Medicago lupulina</i> | 33 | Yes |
| <i>Lactuca serriola</i> | 33 | Yes |
| <i>Carex vulpinoidea</i> | 32 | No |
| <i>Poa palustris/pratensis</i> | 25 | No |
| <i>Verbena hastata</i> | 24 | No |
| <i>Taraxacum officinale</i> | 24 | Yes |
| <i>Erigeron annuus</i> | 17 | No |
| <i>Panicum capillare</i> | 17 | No |
| <i>Potentilla</i> sp. | 15 | ? |
| <i>Aster</i> sp. | 10 | ? |
| <i>Cerastium nutans</i> | 9 | No |
| <i>Rorippa palustris</i> | 8 | No |
| <i>Glyceria grandis</i> | 7 | No |
| <i>Trifolium repens</i> | 7 | Yes |
| <i>Trifolium pratense</i> | 7 | Yes |
| <i>Conyza canadensis</i> | 7 | No |
| <i>Scirpus cyperinus</i> | 7 | No |
| <i>Phleum pratense</i> | 7 | Yes |
| <i>Hordeum jubatum</i> | 7 | No |
| <i>Leersia oryzoides</i> | 6 | No |
| <i>Polygonum lapathifolium</i> | 6 | No |
| <i>Scirpus atrovirens</i> | 6 | No |
| <i>Solidago gigantea</i> | 6 | No |
| <i>Cirsium arvense</i> * | 6 | Yes |
| <i>Salix</i> sp. | 5 | ? |
| <i>Polygonum punctatum</i> | 5 | No |
| <i>Sonchus arvensis</i> * | <5 | Yes |
| <i>Melilotus officinale</i> * | <1 | Yes |
| <i>Hieracium aurantiacum</i> * | <1 | Yes |

Table 2. ANCOVA results (*P*-values) for *Phalaris* (a) and total graminoid, forb, and target community biomass (b). Models contained basin and distance from water as block-effects. Data was cube root-transformed prior to analyses ($X^{0.33}$).

| a. | Model term | d.f. | <i>Phalaris</i> | | |
|----|-------------------------------------|------|-----------------|--|--|
| | Basin | 1 | - | | |
| | Distance | 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 | d.f. | Total graminoid | Total forb | Total target community |
|----|--------------------------------------|------|-----------------|------------|------------------------|
| | Basin | 1 | - | - | - |
| | Distance | 2 | - | - | - |
| | Elevation | 1 | 0.0004 | 0.01 | - |
| | Cover crop | 2 | 0.01 | <0.0001 | <0.0001 |
| | <i>Phalaris</i> | 1 | - | - | - |
| | Sawdust | 1 | 0.03 | - | - |
| | Cover crop* <i>Phalaris</i> | 2 | - | - | - |
| | Cover crop*Sawdust | 2 | - | 0.02 | <0.0001 |
| | <i>Phalaris</i> *Sawdust | 1 | - | - | - |
| | Cover crop* <i>Phalaris</i> *Sawdust | 2 | - | - | - |

Table 3. Biomass composition of plots with target community present under different cover crop, sawdust, and *Phalaris* treatments. Data shown is Mean \pm SE. For total graminoids, forbs, target community, cover crops, unplanted species, and *Phalaris*, the percentage of total plot biomass is given in parentheses.

| Species | High diversity | | | | | | Low diversity | | | | | | Absent | | | | | |
|---------------------------------|--------------------|--------------------|--------------------|-------------------|-------------------|---------------------|--------------------|---------------------|---------------------|---------------------|---------------------|--------------------|---------------------|-------------|---|---------|--------|---|
| | With | | | Without | | | With | | | Without | | | With | | | Without | | |
| | Present | Absent | % | Present | Absent | % | Present | Absent | % | Present | Absent | % | Present | Absent | % | Present | Absent | % |
| Cover crop: | | | | | | | | | | | | | | | | | | |
| Sawdust: | | | | | | | | | | | | | | | | | | |
| <i>Phalaris</i> : | | | | | | | | | | | | | | | | | | |
| <i>Calamagrostis canadensis</i> | 4.1 \pm 2.4 | 2.4 \pm 1.5 | 2.4 \pm 1.5 | 13 \pm 4.1 | 19 \pm 9.0 | 0.81 \pm 0.38 | 2.1 \pm 0.78 | 6.6 \pm 2.1 | 11 \pm 2.5 | 4.0 \pm 1.8 | 1.6 \pm 0.61 | 4.0 \pm 1.8 | 65 \pm 25 | 70 \pm 32 | | | | |
| <i>Glyceria grandis</i> | 3.0 \pm 1.4 | 4.5 \pm 2.5 | 4.5 \pm 2.5 | 40 \pm 22 | 42 \pm 22 | 21 \pm 10 | 13 \pm 6.2 | 35 \pm 25 | 44 \pm 15 | 21 \pm 16 | 33 \pm 22 | 61 \pm 26 | 59 \pm 12 | | | | | |
| <i>Carex hystericina</i> | 7.6 \pm 4.9 | 34 \pm 17 | 34 \pm 17 | 11 \pm 2.0 | 5.5 \pm 2.0 | 34 \pm 4.7 | 49 \pm 15 | 15 \pm 9.1 | 20 \pm 5.5 | 62 \pm 27 | 26 \pm 12 | 20 \pm 7.2 | 44 \pm 16 | | | | | |
| <i>Carex scoparia</i> | 31 \pm 6.9 | 74 \pm 19 | 74 \pm 19 | 33 \pm 4.8 | 28 \pm 10 | 72 \pm 25 | 190 \pm 44 | 86 \pm 29 | 77 \pm 21 | 170 \pm 49 | 150 \pm 24 | 140 \pm 54 | 120 \pm 38 | | | | | |
| <i>Scirpus atrovirens</i> | 2.10 \pm 1.20 | 3.10 \pm 1.40 | 3.10 \pm 1.40 | 21 \pm 14 | 37 \pm 10 | 250 \pm 200 | 150 \pm 100 | 77 \pm 34 | 110 \pm 49 | 310 \pm 120 | 250 \pm 140 | 150 \pm 55 | 140 \pm 50 | | | | | |
| Total graminoids | 280 \pm 130 (25) | 470 \pm 160 (37) | 470 \pm 160 (37) | 120 \pm 38 (14) | 130 \pm 21 (16) | 380 \pm 210 (22) | 400 \pm 94 (30) | 220 \pm 72 (15) | 270 \pm 67 (17) | 470 \pm 150 (27) | 570 \pm 130 (35) | 440 \pm 120 (24) | 440 \pm 100 (26) | | | | | |
| <i>Minutulus ringens</i> | 2.7 \pm 1.6 | 18 \pm 4.2 | 18 \pm 4.2 | 4.0 \pm 2.6 | 3.0 \pm 1.4 | 23 \pm 7.7 | 90 \pm 33 | 24 \pm 7.9 | 75 \pm 26 | 61 \pm 26 | 59 \pm 28 | 110 \pm 39 | 86 \pm 20 | | | | | |
| <i>Vernonia fasciculata</i> | 170 \pm 78 | 140 \pm 61 | 140 \pm 61 | 44 \pm 14 | 90 \pm 23 | 700 \pm 210 | 430 \pm 220 | 750 \pm 180 | 970 \pm 100 | 470 \pm 180 | 910 \pm 310 | 870 \pm 72 | 950 \pm 320 | | | | | |
| <i>Pycnanthemum virginianum</i> | 2.2 \pm 1.4 | 4.5 \pm 2.8 | 4.5 \pm 2.8 | 0.70 \pm 0.22 | 0.45 \pm 0.41 | 8.6 \pm 3.1 | 21 \pm 10 | 6.0 \pm 23.4 | 14 \pm 4.8 | 12 \pm 6.2 | 7.7 \pm 5.6 | 2.7 \pm 1.1 | 28 \pm 12 | | | | | |
| <i>Lobelia siphilitica</i> | 0.41 \pm 0.24 | 0.09 \pm 0.09 | 0.09 \pm 0.09 | 0.03 \pm 0.02 | 0.44 \pm 0.24 | 0.09 \pm 0.05 | 1.1 \pm 0.68 | 0.35 \pm 0.30 | 2.8 \pm 1.4 | 0 \pm 0 | 0 \pm 0 | 0.03 \pm 0.03 | 0.55 \pm 0.26 | | | | | |
| <i>Eupatorium maculatum</i> | 22 \pm 20 | 13 \pm 7.8 | 13 \pm 7.8 | 5.1 \pm 4.8 | 16 \pm 15 | 19 \pm 9.8 | 41 \pm 13 | 41 \pm 13 | 69 \pm 33 | 50 \pm 38 | 46 \pm 41 | 32 \pm 16 | 97 \pm 45 | | | | | |
| Total forbs | 190 \pm 95 (18) | 180 \pm 63 (17) | 180 \pm 63 (17) | 50 \pm 13 (6) | 110 \pm 35 (11) | 750 \pm 210 (36) | 580 \pm 210 (33) | 820 \pm 170 (48) | 1100 \pm 140 (70) | 600 \pm 180 (35) | 1000 \pm 290 (48) | 1000 \pm 39 (56) | 1200 \pm 300 (56) | | | | | |
| Total target community | 480 \pm 100 (43) | 650 \pm 100 (54) | 650 \pm 100 (54) | 170 \pm 33 (20) | 240 \pm 29 (27) | 1100 \pm 190 (59) | 980 \pm 190 (63) | 1000 \pm 140 (62) | 1400 \pm 120 (88) | 1500 \pm 220 (75) | 1200 \pm 120 (71) | 1500 \pm 91 (81) | 1600 \pm 240 (82) | | | | | |
| <i>Baccharis sylvatica</i> | 0.23 \pm 0.16 | 0 \pm 0 | 0 \pm 0 | 0.08 \pm 0.08 | 0.24 \pm 0.24 | 0 \pm 0 | 1.3 \pm 1.3 | 0.01 \pm 0.01 | 0 \pm 0 | NA | NA | NA | NA | | | | | |
| <i>Bidens cernua</i> | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | NA | NA | NA | NA | NA | NA | NA | NA | | | | | |
| <i>Polygonum lapathifolium</i> | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | NA | NA | NA | NA | NA | NA | NA | NA | | | | | |
| <i>Carex vulpinoidea</i> | 64 \pm 28 | 79 \pm 59 | 79 \pm 59 | 69 \pm 15 | 110 \pm 42 | NA | NA | NA | NA | NA | NA | NA | NA | | | | | |
| <i>Epilobium glandulosum</i> | 210 \pm 57 | 210 \pm 59 | 210 \pm 59 | 180 \pm 72 | 390 \pm 81 | NA | NA | NA | NA | NA | NA | NA | NA | | | | | |
| Total cover crops | 280 \pm 31 (28) | 260 \pm 60 (23) | 260 \pm 60 (23) | 250 \pm 65 (27) | 500 \pm 78 (55) | 0 \pm 0 (0) | 1.3 \pm 1.3 (0) | 0 \pm 0 (0) | 0 \pm 0 (0) | NA | NA | NA | NA | | | | | |
| <i>Solidago canadensis</i> | 77 \pm 45 | 150 \pm 92 | 150 \pm 92 | 44 \pm 21 | 110 \pm 33 | 210 \pm 96 | 350 \pm 210 | 33 \pm 29 | 11 \pm 11 | 210 \pm 73 | 220 \pm 47 | 19 \pm 12 | 24 \pm 17 | | | | | |
| <i>Verbena hastata</i> | 67 \pm 62 | 66 \pm 46 | 66 \pm 46 | 1.1 \pm 1.1 | 1.5 \pm 1.3 | 170 \pm 130 | 140 \pm 120 | 22 \pm 14 | 45 \pm 30 | 200 \pm 190 | 91 \pm 68 | 23 \pm 23 | 61 \pm 60 | | | | | |
| unplanted <i>C. vulpinoidea</i> | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 0 \pm 0 | 100 \pm 63 | 120 \pm 40 | 84 \pm 37 | 140 \pm 57 | 75 \pm 23 | 39 \pm 15 | 53 \pm 24 | 210 \pm 64 | | | | | |
| others species | 81 \pm 40 | 19 \pm 5.2 | 19 \pm 5.2 | 26 \pm 22 | 61 \pm 45 | 135 \pm 65 | 44 \pm 23 | 29 \pm 18 | 19 \pm 8.1 | 78 \pm 40 | 21 \pm 15 | 39 \pm 30 | 59 \pm 44 | | | | | |
| Total unplanted species | 230 \pm 94 (20) | 230 \pm 84 (20) | 230 \pm 84 (20) | 71 \pm 36 (9) | 180 \pm 66 (18) | 600 \pm 160 (33) | 650 \pm 200 (37) | 170 \pm 60 (11) | 210 \pm 67 (12) | 370 \pm 79 (19) | 560 \pm 210 (29) | 130 \pm 53 (8) | 360 \pm 110 (18) | | | | | |
| <i>Phalaris</i> | 84 \pm 21 (8) | NA | NA | 400 \pm 64 (44) | NA | 180 \pm 84 (8) | NA | 500 \pm 190 (27) | NA | 95 \pm 44 (5) | NA | 240 \pm 150 (12) | NA | | | | | |
| Total plot biomass | 1100 \pm 93 | 1200 \pm 79 | 1200 \pm 79 | 890 \pm 85 | 920 \pm 110 | 1900 \pm 240 | 1600 \pm 240 | 1700 \pm 210 | 1600 \pm 160 | 1900 \pm 200 | 1700 \pm 160 | 1800 \pm 100 | 2000 \pm 250 | | | | | |

Table 4. Results of random mixed-effects model analyses of nitrate-N, ammonium-N, and percent of PAR blocked. Models contained basin, distance from water, and plot as random-effects, and year and week as continuous variables. Results are presented in two parts. The first part (a) are results of test for treatment effects across the entire experiment and the second part (b) shows results of test for changes in treatment effects over the course of the experiment. Ammonium-N and nitrate-N were Box-Cox transformed.

| a. Model term | d.f. | NH ₄ -N | NO ₃ -N | % PAR Blocked |
|---|------|---|--------------------|-----------------|
| | | Transformation: [(x ^{-0.4}) - 1] * -1 | log (x + 1) | arcsinesqrt (x) |
| | | P-value | P-value | P-value |
| Elevation | 1 | - | - | - |
| Cover crop | 2 | - | - | <0.0001 |
| Target community | 1 | 0.002 | <0.0001 | <0.0001 |
| <i>Phalaris</i> | 1 | - | 0.001 | <0.0001 |
| Sawdust | 1 | <0.0001 | - | - |
| Cover crop x Target community | 2 | - | <0.0001 | <0.0001 |
| Cover crop x <i>Phalaris</i> | 2 | - | 0.0003 | <0.0001 |
| Cover crop x Sawdust | 2 | - | - | 0.002 |
| Target community x <i>Phalaris</i> | 1 | 0.04 | 0.0008 | <0.0001 |
| Target community x Sawdust | 1 | - | - | - |
| <i>Phalaris</i> x Sawdust | 1 | - | - | <0.0001 |
| Cover crop x Target community x <i>Phalaris</i> | 2 | - | 0.01 | <0.0001 |
| Cover crop x Target community x Sawdust | 2 | - | - | - |
| Cover crop x <i>Phalaris</i> x Sawdust | 2 | - | - | 0.0009 |
| Target community x <i>Phalaris</i> x Sawdust | 1 | - | - | 0.005 |

| b. Model term | d.f. | NH ₄ -N | NO ₃ -N | % PAR Blocked |
|---|------|---|--------------------|-----------------|
| | | Transformation: [(x ^{-0.4}) - 1] * -1 | log (x + 1) | arcsinesqrt (x) |
| | | P-value | P-value | P-value |
| Year | 1 | 0.008 | <0.0001 | <0.0001 |
| Year x Week | 1 | 0.001 | <0.0001 | <0.0001 |
| Year x Week x Elevation | 2 | - | - | - |
| Year x Week x Cover crop | 1 | - | 0.006 | 0.003 |
| Year x Week x Target community | 1 | - | - | 0.03 |
| Year x Week x <i>Phalaris</i> | 1 | - | - | 0.02 |
| Year x Week x Sawdust | 1 | - | - | 0.03 |
| Year x Week x Cover crop x Target community | 2 | - | - | 0.007 |
| Year x Week x Cover crop x <i>Phalaris</i> | 2 | - | - | - |
| Year x Week x Cover crop x Sawdust | 2 | - | - | 0.002 |
| Year x Week x Target community x <i>Phalaris</i> | 1 | - | - | 0.03 |
| Year x Week x Target community x Sawdust | 1 | - | - | - |
| Year x Week x <i>Phalaris</i> x Sawdust | 1 | - | - | - |
| Year x Week x Cover Crop x Target community x <i>Phalaris</i> | 2 | - | - | - |
| Year x Week x Cover crop x Target community x Sawdust | 2 | - | - | - |
| Year x Week x Cover crop x <i>Phalaris</i> x Sawdust | 2 | - | - | - |
| Year x Week x Target community x <i>Phalaris</i> x Sawdust | 1 | - | - | - |

Table 5. Effects of different vegetative treatment combinations on nitrate-N levels throughout the the course of the study. Values presented are Mean \pm SE.

| Vegetation in plot | Mean NO ₃ -N (mg kg ⁻¹) | | | | | | |
|---|--|----------------|----------------|-----------------|-----------------|---------|---------|
| | Year: 2005 | | | 2006 | | | |
| | Week 9 | Week 18 | Week 5 | Week 9 | Week 14 | Week 18 | Week 23 |
| High diversity, Target community, <i>Phalaris</i> | 6.7 \pm 0.68 | 12 \pm 1.3 | 4.8 \pm 0.73 | 0.92 \pm 0.21 | 0.14 \pm 0.09 | | |
| High diversity, Target community | 6.5 \pm 0.71 | 10 \pm 1.4 | 5.4 \pm 0.82 | 0.61 \pm 0.14 | 0.07 \pm 0.04 | | |
| High diversity, <i>Phalaris</i> | 6.1 \pm 0.60 | 9.3 \pm 0.81 | 4.4 \pm 0.84 | 0.80 \pm 0.10 | 0.14 \pm 0.09 | | |
| High diversity | 6.6 \pm 0.86 | 9.6 \pm 1.0 | 4.7 \pm 0.67 | 0.86 \pm 0.18 | 0.04 \pm 0.03 | | |
| Low diversity, Target community, <i>Phalaris</i> | 6.7 \pm 1.4 | 8.6 \pm 1.6 | 2.3 \pm 0.47 | 0.66 \pm 0.13 | 0.19 \pm 0.14 | | |
| Low diversity, Target community | 6.1 \pm 0.72 | 9.6 \pm 1.0 | 2.5 \pm 0.39 | 0.60 \pm 0.09 | 0.05 \pm 0.05 | | |
| Low diversity, <i>Phalaris</i> | 6.1 \pm 0.79 | 12 \pm 1.8 | 2.8 \pm 0.48 | 0.62 \pm 0.11 | 0.41 \pm 0.25 | | |
| Low diversity | 9.4 \pm 1.8 | 15 \pm 2.2 | 2.9 \pm 0.66 | 0.93 \pm 0.14 | 1.0 \pm 0.45 | | |
| Target community, <i>Phalaris</i> | 7.7 \pm 2.0 | 8.3 \pm 1.4 | 1.8 \pm 0.35 | 0.38 \pm 0.10 | 0.12 \pm 0.11 | | |
| Target community | 8.4 \pm 1.1 | 9.7 \pm 2.0 | 2.1 \pm 0.50 | 0.48 \pm 0.09 | 0.06 \pm 0.04 | | |
| <i>Phalaris</i> | 5.3 \pm 0.80 | 16 \pm 2.9 | 2.9 \pm 0.70 | 0.44 \pm 0.09 | 0.16 \pm 0.09 | | |
| No vegetation | 7.7 \pm 1.8 | 21 \pm 3.3 | 10 \pm 2.0 | 4.8 \pm 1.2 | 7.1 \pm 2.5 | | |
| Weekly experimental mean \pm SE | 6.9 \pm 0.35 | 12 \pm 0.63 | 3.9 \pm 0.32 | 1.0 \pm 0.16 | 0.80 \pm 0.28 | | |

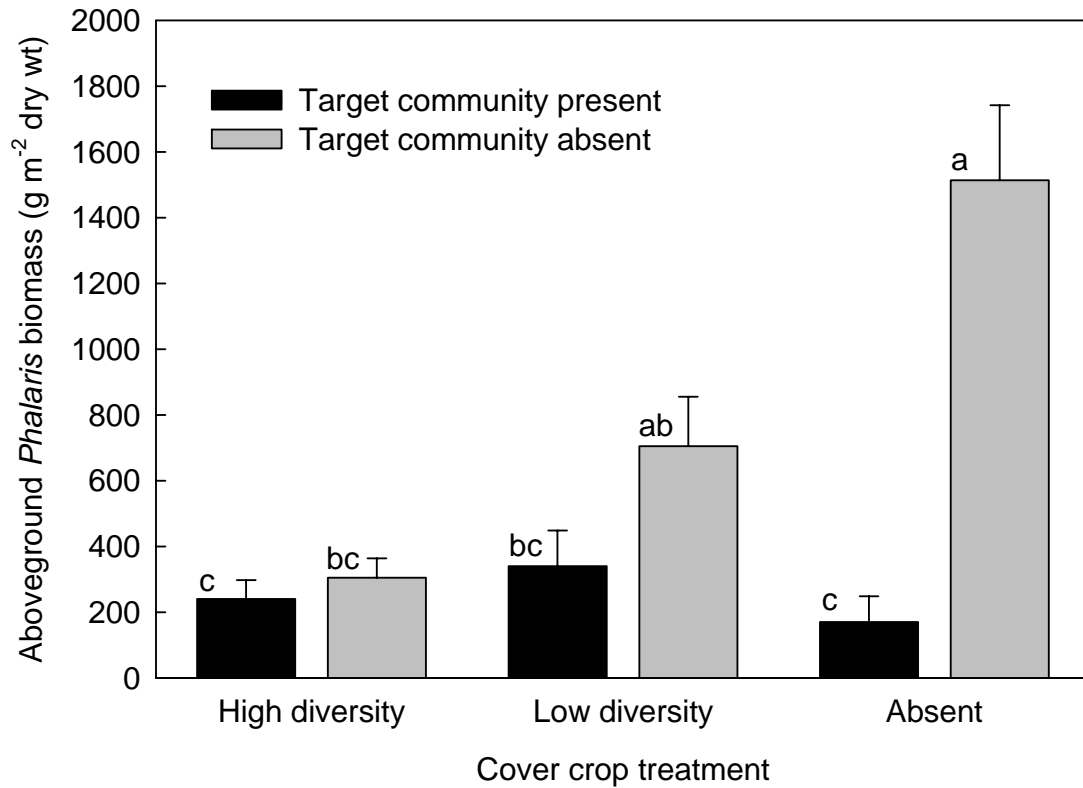


Fig. 1. The effects of cover crops and target community on aboveground biomass of *Phalaris*. Bars with different letters are significantly different based on $P < 0.05$.

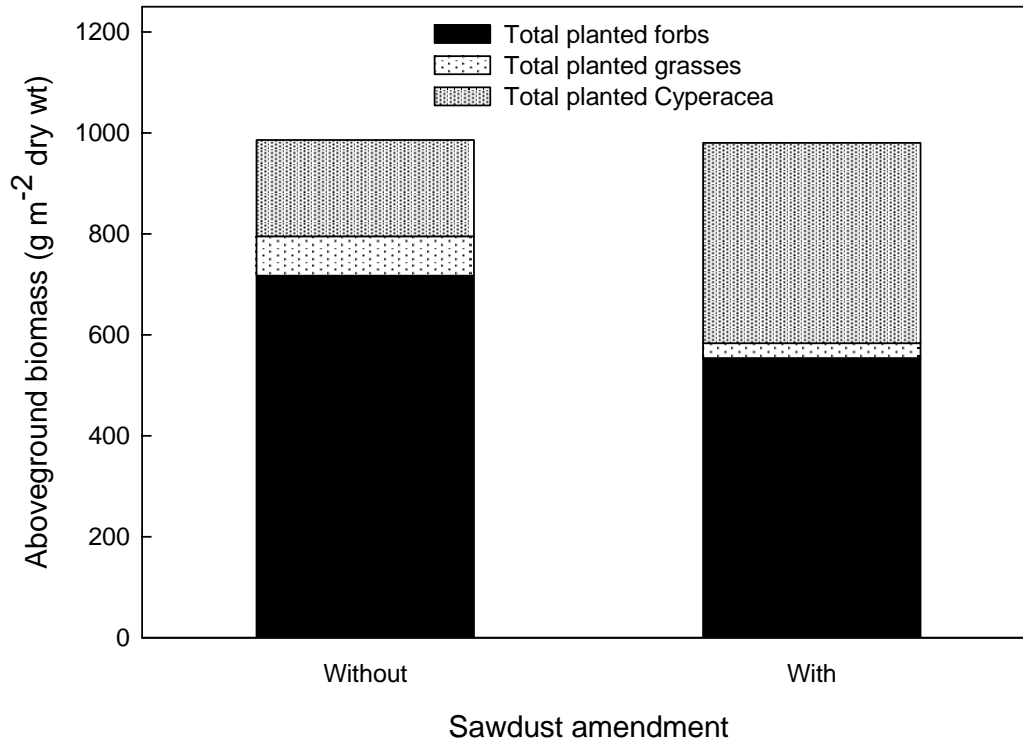


Fig. 2. The effects of sawdust amendments on biomass of grasses, forbs, and planted species of the Cyperaceae family in the target community. Only changes in biomass of grasses and of the Cyperaceae family were significant ($P < 0.05$).

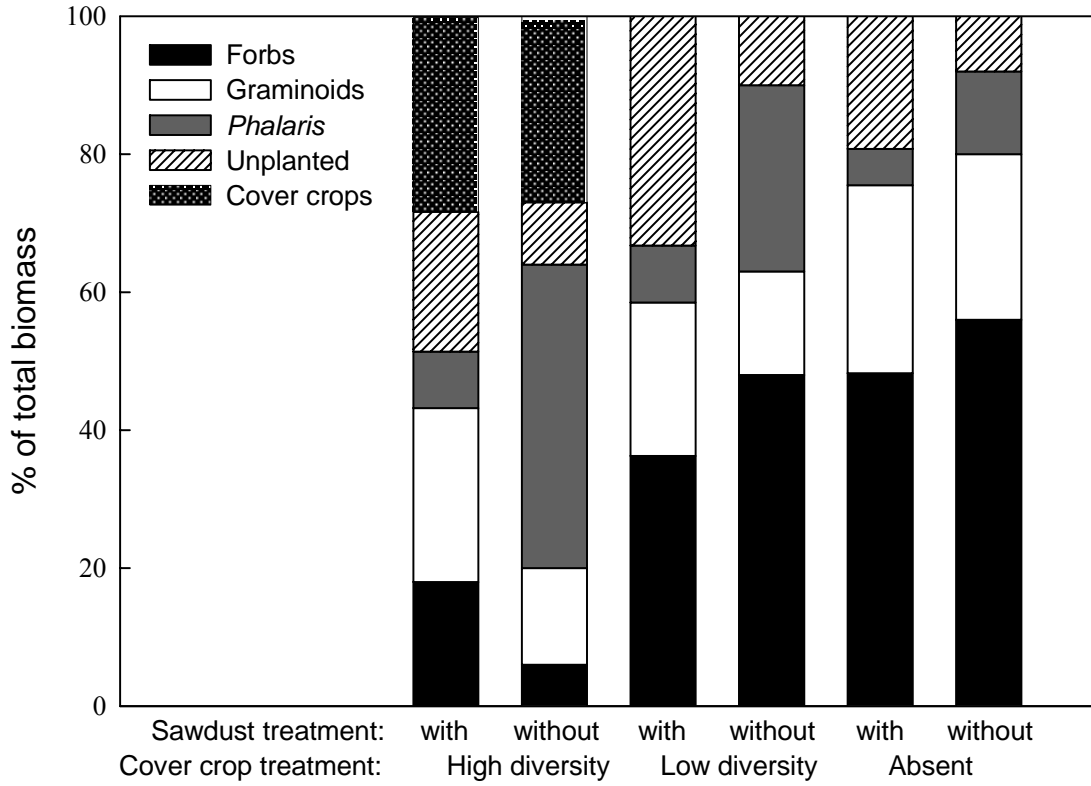


Fig. 3. Final community composition in plots with both the target community and *Phalaris* growing under different sawdust and cover crop treatment combinations.

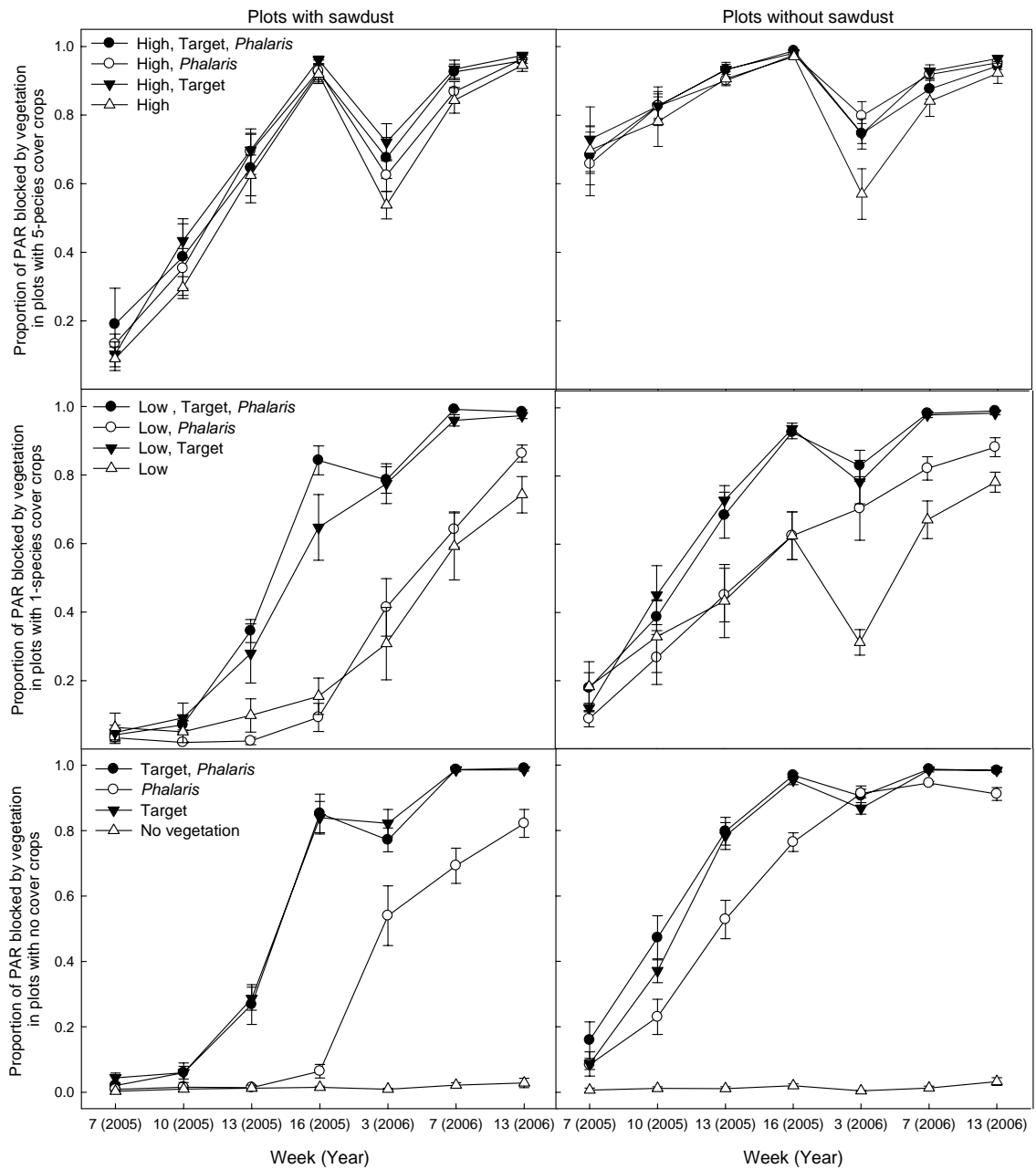


Fig. 4. Effects of vegetation on the proportion of PAR blocked throughout the experiment in plots with and without sawdust amendments. High refers to the high diversity cover crop treatment. Target refers to the target community. Low refers to the low diversity cover crop treatment.

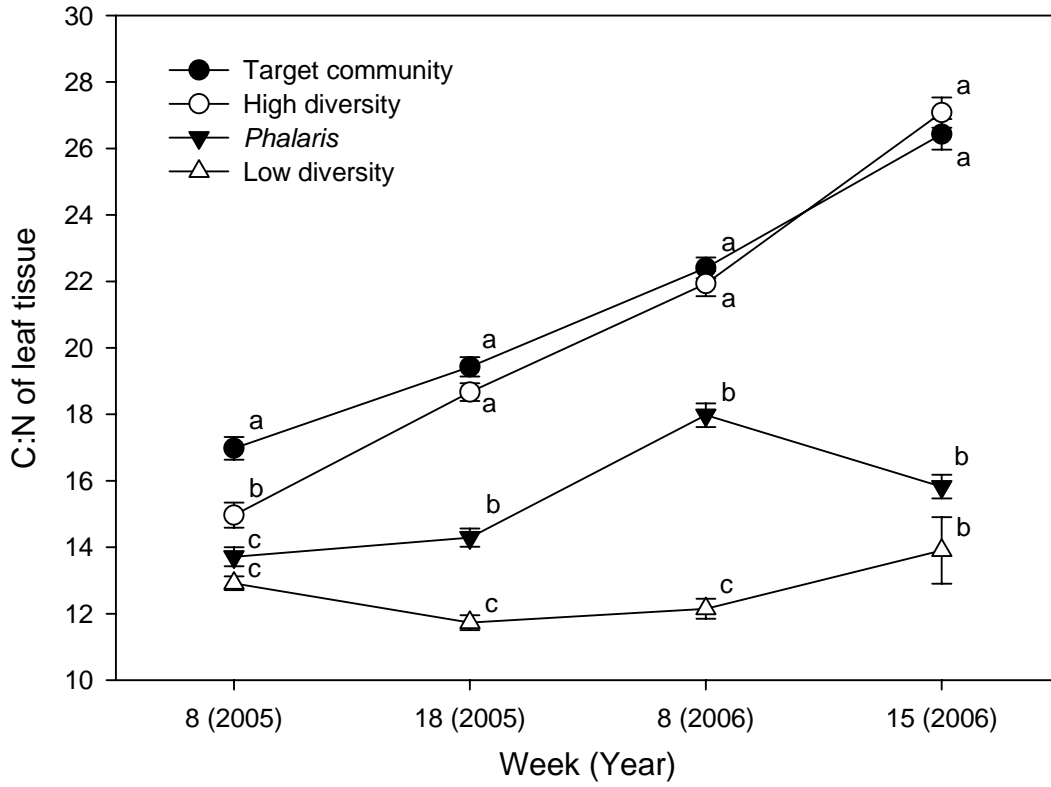


Fig. 5. C:N ratios of target community, *Phalaris*, and low and high diversity cover crop leaf tissue. Data points at each individual sampling period that have different letters next to them are significantly different ($P < 0.05$).

GENERAL CONCLUSIONS

This study showed that implementing strategies to reduce initial light and nitrogen (N) levels was less important to preventing *Phalaris* invasion in restored sedge meadows than quickly establishing a perennial community. The target community was able to establish while reducing *Phalaris* invasion in plots without cover crops or sawdust amendments (Chapter 2). Sowing a high diversity cover crop resulted in a less productive perennial community dominated by *Phalaris*, confirming that cover crops do not work as *Phalaris* control in sedge meadows (Perry & Galatowitsch 2003; 2004). The low diversity cover crop was also ineffective as *Phalaris* control because it did not reduce *Phalaris* biomass as much as the target community did (Chapter 2) and it delayed target community seedling emergence (Chapter 1). In addition, cedar sawdust amendments only reduced N levels for part of the first growing season, and did not reduce *Phalaris* invasion much beyond what the target community did (Chapters 1 & 2). Short-lived N reduction, however, may have resulted from the sawdust species used (Appendices A-C). Decreasing N levels, however, did further reduce *Phalaris* invasion and resulted in a community that resembled a natural sedge meadow (sensu Galatowitsch & van der Valk 1996) by increasing both the establishment of seeded species in the Cyperaceae family and the colonization of unseeded wetland species (Chapter 2).

Within the period of this study, some treatments that caused delays in seedling emergence had lasting effects on competitive outcomes and community composition. *Phalaris* seedling emergence was delayed in plots with either sawdust amendments or the target community, possibly facilitating the establishment of the latter (Chapter 1). Reduced nitrate-N levels in these treatments may help explain the delay in *Phalaris*

emergence since many ruderal species require nitrate for germination (Fenner 1985; Pons 1989; Lambers et. al. 1998). The high diversity cover crop greatly decreased target community seedling emergence by reducing light availability (Chapter 1). Regardless of the mechanisms that caused the delays in *Phalaris* and target community seedling emergence, these delays led to reduced *Phalaris* and target community establishment for the remainder of the study (Chapter 2), confirming that factors affecting seedling establishment will influence later community composition (Grubb 1977; Schupp 1995; Eriksson 2002). Therefore, these factors need strong consideration in seeded restorations, especially when invasive propagules are present.

Considering the factors that allowed *Phalaris* to outcompete the target community in plots with high diversity cover crops can help explain why reducing light availability will not prevent *Phalaris* invasion or facilitate community reestablishment. First, since *Phalaris* germination requires shorter photoperiods than sedge meadow species (Lindig-Cisneros & Zedler 2001; Kettenring 2006), the rate at which the high diversity cover crop established likely prevented seedling emergence of the target community but not *Phalaris* (Chapter 1). Second, plots with high diversity cover crops had elevated N levels early in the second growing season possibly from reduced biomass and plant uptake (Chapter 1 & 2). Elevated N in these plots likely triggered a stronger response in *Phalaris* growth than target community growth (Green & Galatowitsch 2002), resulting in a *Phalaris*-dominated community (Chapter 2). In plots with high diversity cover crops, both the decreased target community seedling emergence (Chapter 1) and *Phalaris* dominance (Chapter 2) suggested that light is more limiting to sedge meadow species than to *Phalaris*. When a species is a superior competitor for a particular resource, reducing that

resource should give that species a competitive advantage over other species (sensu Tilman et al. 1999). Therefore, reducing light should favor *Phalaris* over desired species, especially if high N levels increase *Phalaris* growth (Green & Galatowitsch 2002).

Acquiring the amount of sawdust needed to deplete N, transporting it, and incorporating it into moist soil will be difficult and possibly impractical given sawdust did not reduce *Phalaris* invasion much beyond what the target community did (Chapters 1 & 2). Still, reducing initial N levels may benefit restorations. Higher C:N ratios in target community leaf tissue than *Phalaris* leaf tissue (Chapter 2), suggest that sedge meadow species are superior competitors for N (sensu Tilman et al. 1999). Being a better competitor for N can explain the target community's ability to suppress *Phalaris* in sawdust-amended soils (Chapter 2). These results confirmed that sedge meadow species can outcompete *Phalaris* if N is reduced (Perry et al. 2004). Increased establishment of species from the Cyperaceae family in sawdust-amended plots (Chapter 2) suggests that reducing N may help speed up the transition from a forb-dominated community observed in non-amended soils (Chapter 2) to a graminoid-dominated community resembling natural sedge meadows (sensu Galatowitsch & van der Valk 1996). Colonization of unseeded species also increased in sawdust-amended plots (Chapter 2). Increased colonization may enhance community diversity if restoration sites are near propagule sources of desired species, but increased colonization may also hinder restoration efforts if sites are near invasive plant populations. Regardless of the invasion risk, reducing N may potentially benefit restored communities. Additionally, using sawdust species with higher C:N ratios may prolong N reduction (Appendices A-C). Given the possible

benefits of N reduction and the uncertainty of how other C amendments may affect restorations, N-reducing techniques deserve further investigation.

From this study, perhaps the most important finding to the practice of sedge meadow restorations was the reduction in *Phalaris* invasion caused by the target community (Chapter 2). Several hypotheses may explain this surprising outcome. First, once established the target community reduced both light and N levels possibly limiting *Phalaris* expansion (sensu Maurer & Zedler 2002; Perry et al. 2004). In addition, cold stratifying the target community seed mix and seeding target species at high densities likely decreased the amount of time required for germination and increased the amount of seedlings that established (Baskin & Baskin 1998; Kettenring 2007; Sheley & Half 2006), possibly allowing the target community to sequester resources faster than if these actions were not taken. Lastly, high establishment of the broad-leaf forb *Vernonia fasciculata* across all treatments (Chapter 1) likely increased the proportion of light the target community canopy blocked. These results suggest that both accelerating seedling establishment and seeding competitive species can help decrease resource levels, therefore reducing the impacts of invasive species on restorations.

Sowing a target community and incorporating sawdust amendments pushed community development further along a trajectory towards a restored sedge meadow and further away from a *Phalaris*-dominated state than sowing cover crops did. However, this shift was not complete. Because *Phalaris* can outcompete sedge meadow species in low light environments, sowing cover crops only delayed the shift to a *Phalaris*-dominated state (Chapter 2). Seeding the target community at high densities and cold stratifying target community seed prior to sowing likely prevented a rapid shift to a *Phalaris*-

dominated state by allowing the target community to quickly reduce light and N. Plots with both the target community and sawdust amendments may have been furthest along the trajectory towards a restored community since these plots had the least amount of *Phalaris* establishment (Chapter 2). However, no treatment completely prevented *Phalaris* invasion. Because *Phalaris* grows rapidly (Adams & Galatowitsch 2005) and can vegetatively expand into existing canopies (Maurer & Zedler 2002), even a small amount of *Phalaris* establishment can cause a community to transition back to a persistently invaded monotype. Therefore, follow-up *Phalaris* control will be required regardless of what initial pre-seeding treatments are used. Ensuring rapid perennial establishment, however, may greatly reduce the amount of follow-up *Phalaris* control needed, facilitating the transition to a restored sedge meadow. Additionally, since reducing N availability may push a community further along the trajectory towards a restored state, N reduction deserves more research.

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APPENDIX

Introduction

My thesis research used cedar (*Thuja* sp.) sawdust as a carbon amendment to immobilize nitrogen (N) (Chapters 1 & 2). Analysis of total carbon (C) and total N on cedar sawdust, however, revealed that this species had a much lower C:N ratio than the pine sawdust used in Perry et al.'s (2004) greenhouse study (Chapter 1). Further, studies investigating C amendments as restoration tools have used sucrose instead of sawdust (e.g. Vinton & Giergen 2006; Prober et al. 2005). Both sawdust with varying C:N ratios as well as different sources of C (i.e. sawdust vs. sucrose) may affect soil N availability differently. In addition, different types of C amendments have not been tested in wetland soils.

To determine how different C amendment will affect N availability in sedge meadow wetlands, I conducted a randomized block experiment. This side study was conducted in an experimental wetland basin at the same location as my main study (Chapters 1 & 2). This basin had an irrigation line and tile drainage system to control hydrology as well as the same soil type as the basins used in my main study (Glencoe clay loam soil; Cumulic Endoaquoll; U.S. Department of Agriculture 1968). In addition, prior to experimental set up, standing vegetation was removed and the seedbank was depleted (See methods in Chapters 1 & 2) to mimic conditions of a recently reflooded wetland (Adams & Galatowitsch 2005; 2006).

This side study was set up 30 May 2006 and lasted for 24 weeks. A row of 20 one-m² plots was laid out 3 m from the edge of the water in the basin. The plots were divided into four blocks of five plots. One of five C treatments was randomly assigned to each plot within a block. The C treatments were white pine (*Pinus strobus* L.), cedar, and

red oak (*Quercus rubra* L.) sawdust, as well as sucrose (white granulated cane sugar), and a control (no C). Cedar sawdust was acquired from Ser-a-Dock, Inc (Victoria, MN, USA). Other sawdust species were acquired from Larson's Sawmill (Mora, MN). Sawdust was hand-tilled into plots to a depth of 20 cm using the same methods in Chapters 1 & 2 (for dry wt see Appendix A). Plots assigned a control or sucrose were also hand-tilled to a depth of 20 cm. Sucrose was broadcasted over plots at a rate of 0.5 kg m⁻². The water level in the basin was kept constant at 5 cm below the lowest plot.

Nitrate-N, ammonium-N, and C:N ratios for the different C amendments are listed in Appendix A. To determine these C:N ratios, total C and N were measured on a 15 mg subsample of each C amendment using an Elementar Americas, Inc. Vario EL III CNS elemental analyzer (Elementar Americas, Inc., Mt. Laurel, NJ; Kirsten, 1983). Inorganic-N was extracted from the C amendments and measured by the same analytical methods used to determine the nitrate-N and ammonium-N levels of cedar sawdust in Chapter 1.

To determine the effects of the different C amendments on soil N availability, nitrate-N and ammonium-N were measured over a 24-week period. Five 1.5-cm x 20-cm soil cores were collected from random points in each plot. These samples were collected at weeks 0, 2, 4, 8, 12, 16, 20, and 24. Nitrate-N and ammonium-N levels were measured using the same methods used to determine nitrate-N and ammonium-N levels on my second-year soil samples from my main study (Chapter 2). To determine treatment effects, nitrate-N and ammonium-N values were analyzed using a random mixed-effects model. The analysis was conducted in "R" (Ihaka & Gentleman 1996). For model terms, transformations, and results of statistical analyses see Appendix B. The results of this study are summarized in Appendix C.

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Appendix A. Ammonium-N and nitrate-N concentrations and carbon:nitrogen ratios of four different carbon sources. Carbon in the form of sawdust was added at a soil:sawdust ratio of 2:1 (by volume) and sucrose was added at 0.5 kg m⁻² to plots in a sedge meadow wetland. The approximate dry weight at which each carbon source was added to each plot is provided in the last column

| Carbon source | NH ₄ -N (mg kg ⁻¹) | NO ₃ -N (mg kg ⁻¹) | C:N | Dry wt/ plot (kg m ⁻²) |
|---------------|---|---|------|------------------------------------|
| Cedar | 161 | 4.5 | 34 | 8.4 ± 0.1 |
| White pine | 29 | 2.9 | 222 | 8.4 ± 0.1 |
| Red Oak | 36 | 1.8 | 320 | 13.7 ± 0.1 |
| Sucrose | 13 | 3.2 | 7714 | 0.5 ± 0 |

Appendix B. Results of mixed-model analyses of nitrate-N and ammonium-N (*P* -values) in soils of experiment mentioned in Appendix A. Measurements were made over a 24 week period. Experiment was blocked on repetition so repetition was included in the model as a random-effect. Elevation was included in the model as a covariate since plot elevation relative to the basin bottom varied. Week was included as a continuous variable and carbon treatment was included as a fixed-effect. N = 160

| Model term | d.f. | <u>NO₃-N</u> | <u>NH₄-N</u> |
|-------------------------|------|---|---|
| | | Transformation: Log (NO ₃ -N + 1) <i>P</i> -value | (NH ₄ -N ^{-0.5}) x -1 <i>P</i> -value |
| Elevation | 1 | - | - |
| Carbon treatment | 4 | < 0.0001 | < 0.0001 |
| Week | 1 | 0.0003 | 0.0025 |
| Week x Elevation | 1 | - | - |
| Week x Carbon treatment | 4 | < 0.0001 | 0.0001 |

Appendix C. Effects of carbon amendments on soil nitrate-N (a) and ammonium-N (b) levels over a 24-week period in soils of a sedge meadow wetland. Values within the same column (i.e. week) having different lettered superscripts are significantly different based on results of a Tukey HSD test ($P < 0.05$). Weekly experimental (grand) mean is provided on the last row of each table.

| a. Carbon treatment | $\text{NO}_3\text{-N (mg kg}^{-1}\text{)}$ | | | | | | | | | |
|--------------------------|--|--------------------------|--------------------------|--------------------------|--------------------------|-------------------------|------------------------|--------------------------|--|--|
| | Week 0 | Week 2 | Week 4 | Week 8 | Week 12 | Week 16 | Week 20 | Week 24 | | |
| Control (no C) | 6.7 ± 1.0 ^{ab} | 5.8 ± 0.6 ^{ab} | 12.2 ± 5.1 ^a | 15.7 ± 3.7 ^a | 23.6 ± 3.4 ^a | 0.7 ± 0.2 ^{ab} | 6.1 ± 1.4 ^a | 9.1 ± 1.0 ^a | | |
| Cedar | 14.0 ± 2.5 ^a | 12.3 ± 3.3 ^a | 6.9 ± 1.9 ^{ab} | 8.3 ± 3.3 ^{ab} | 3.4 ± 1.6 ^b | 0.0 ± 0.0 ^b | 1.5 ± 0.6 ^b | 5.8 ± 2.2 ^{ab} | | |
| Red Oak | 4.9 ± 1.3 ^b | 2.5 ± 0.5 ^{b,c} | 0.7 ± 0.1 ^c | 0.5 ± 0.2 ^c | 0.1 ± 0.0 ^c | 0.0 ± 0.0 ^b | 0.5 ± 0.1 ^b | 0.6 ± 0.0 ^c | | |
| Sucrose | 0.4 ± 0.1 ^c | 1.9 ± 0.6 ^c | 2.3 ± 0.6 ^{b,c} | 13.9 ± 3.7 ^a | 6.5 ± 1.7 ^b | 1.3 ± 0.7 ^a | 5.3 ± 0.9 ^a | 6.3 ± 2.1 ^{ab} | | |
| White Pine | 0.9 ± 0.3 ^c | 1.1 ± 0.3 ^c | 0.9 ± 0.2 ^c | 2.0 ± 0.6 ^{b,c} | 1.3 ± 0.2 ^{b,c} | 0.1 ± 0.1 ^{ab} | 1.1 ± 0.3 ^b | 2.7 ± 0.3 ^{b,c} | | |
| Weekly experimental mean | 5.4 ± 1.2 | 4.7 ± 1.1 | 4.6 ± 1.4 | 8.1 ± 1.8 | 7.0 ± 2.0 | 0.4 ± 0.1 | 2.9 ± 0.6 | 4.9 ± 0.9 | | |

| b. Carbon treatment | $\text{NH}_4\text{-N (mg kg}^{-1}\text{)}$ | | | | | | | | | |
|--------------------------|--|------------------------|------------------------|-------------------------|------------------------|------------------------|------------------------|-------------------------|--|--|
| | Week 0 | Week 2 | Week 4 | Week 8 | Week 12 | Week 16 | Week 20 | Week 24 | | |
| Control (No C) | 2.6 ± 0.4 ^b | 3.0 ± 0.3 ^b | 3.5 ± 0.7 ^a | 5.4 ± 0.8 ^a | 7.3 ± 3.7 ^a | 4.9 ± 0.8 ^a | 3.0 ± 0.3 ^a | 2.6 ± 0.2 ^{ab} | | |
| Cedar | 18.0 ± 5.4 ^a | 9.8 ± 0.8 ^a | 4.8 ± 0.6 ^a | 14.0 ± 7.3 ^a | 3.9 ± 0.8 ^a | 9.8 ± 0.9 ^a | 5.6 ± 0.8 ^a | 4.1 ± 0.7 ^a | | |
| Red Oak | 2.1 ± 0.3 ^b | 2.4 ± 0.2 ^b | 2.6 ± 0.3 ^a | 5.6 ± 1.2 ^a | 3.0 ± 0.4 ^a | 6.1 ± 0.8 ^a | 3.1 ± 0.7 ^a | 2.2 ± 0.2 ^b | | |
| Sucrose | 1.2 ± 0.1 ^b | 1.8 ± 0.0 ^b | 3.0 ± 1.0 ^a | 8.1 ± 1.7 ^a | 4.3 ± 0.6 ^a | 5.9 ± 1.0 ^a | 3.8 ± 0.3 ^a | 3.8 ± 0.4 ^a | | |
| White Pine | 4.6 ± 3.0 ^b | 3.4 ± 1.2 ^b | 2.5 ± 0.3 ^a | 7.2 ± 2.1 ^a | 4.6 ± 1.0 ^a | 7.9 ± 1.4 ^a | 4.9 ± 0.7 ^a | 3.7 ± 0.2 ^a | | |
| Weekly experimental mean | 5.7 ± 1.8 | 4.1 ± 0.7 | 3.2 ± 0.3 | 8.1 ± 1.6 | 4.6 ± 0.8 | 6.8 ± 0.5 | 4.1 ± 0.3 | 3.3 ± 0.2 | | |