

Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities

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Summary

1. Nutrient enrichment may adversely impact plant species richness in wetlands and enhance their susceptibility to colonization and dominance by invasive species. For North American prairie wetlands, enrichment by nitrate-N ($\text{NO}_3\text{-N}$) from agricultural runoff is thought to contribute to the increasing colonization and dominance of *Phalaris arundinacea* (reed canary grass), especially during restoration. If true, *P. arundinacea* might compromise the re-establishment of sedge meadow vegetation on sites reflooded with agricultural drainage water.

2. We tested this hypothesis using a fertilization experiment in wetlands with controlled hydrology. A community mixture comprising 11 species from native sedge meadow was seeded in mesocosms and grown under one of three $\text{NO}_3\text{-N}$ levels ($0 \text{ g m}^{-2} \text{ year}^{-1}$, $12 \text{ g m}^{-2} \text{ year}^{-1}$, $48 \text{ g m}^{-2} \text{ year}^{-1}$) with or without *P. arundinacea*. Above- and below-ground biomass were measured after two growing seasons to assess the response of vegetation to $\text{NO}_3\text{-N}$ and *P. arundinacea* treatments.

3. The total shoot biomass of the native community was suppressed in the presence of *P. arundinacea* at all $\text{NO}_3\text{-N}$ levels, but shoot suppression was significantly greater at the highest $\text{NO}_3\text{-N}$ dose level (48 g m^{-2}). Shoot growth of the native community was reduced by nearly one-half under these conditions.

4. The total root biomass of the community was also suppressed by *P. arundinacea* when no $\text{NO}_3\text{-N}$ was added.

5. As $\text{NO}_3\text{-N}$ increased, the relative abundance (shoot biomass) of native graminoids declined while native forbs increased in communities with and without *Phalaris*. The most common graminoid, *Glyceria grandis*, was suppressed by *P. arundinacea* at all levels, with suppression enhanced at the $48 \text{ g m}^{-2} \text{ NO}_3\text{-N}$ level. Three other species were suppressed at the highest $\text{NO}_3\text{-N}$ level, in the presence of *Phalaris*. The two most common forbs, *Asclepias incarnata* and *Sium suave*, exhibited a continual increase in growth with $\text{NO}_3\text{-N}$ additions along with overall suppression by *P. arundinacea*.

6. Community diversity and evenness declined with increasing $\text{NO}_3\text{-N}$ levels, whether or not *P. arundinacea* was present.

7. Our results demonstrate that if *P. arundinacea* is present, the restored sedge meadow community will not achieve levels of abundance that are possible when this species is absent, regardless of $\text{NO}_3\text{-N}$ enrichment conditions.

8. At the same time, the increased suppression by *P. arundinacea* at the $48 \text{ g m}^{-2} \text{ NO}_3\text{-N}$ dose level supports the hypothesis that the dominance of this species over the native sedge meadow community is enhanced by $\text{NO}_3\text{-N}$ inputs at levels that are common in agricultural landscapes.

9. Our results carry two implications for achieving biodiversity conservation in agricultural landscapes. First, reducing nitrate loads to wetland reserves is essential for minimizing declines in community diversity. Secondly, the use of *P. arundinacea* for soil conservation and other agri-environmental purposes should be curtailed because of the likelihood of off-site impacts to wetland biodiversity.

Key-words: agricultural impacts, ecological restoration, invasive species, prairie pothole wetland

Introduction

Wetlands are increasingly valued for ecosystem services, such as improving water quality through nutrient removal and filtration of sediments and chemicals, controlling and storing surface water, recharging groundwater, and providing wildlife habitat. In the prairie pothole region of North America thousands of wetlands have been restored in recent years, driven by the goal of improving or returning these ecosystem services to the landscape (Galatowitsch & van der Valk 1994). The prairie pothole region is an approximately 780 000 km² area in the central mid-continent where the vast majority of wetlands, once abundant landscape features, were drained for conversion to agricultural production (Kantard, Krapu & Swanson 1989; Dahl & Johnson 1991). Knowledge is conspicuously lacking on how to recreate successfully the ecological structure and function of natural wetlands (Galatowitsch & van der Valk 1994; Crumpton & Goldsborough 1998; Murkin 1998). Restored wetlands often fail to resemble extant wetlands in vegetative structure and composition, and in plant and animal diversity (Mack 1985; Delphay & Dinsmore 1993; Reinartz & Warne 1993; Galatowitsch & van der Valk 1996a,b). Moreover, restored wetlands in the prairie pothole region are often dominated by a small number of invasive plant species (Galatowitsch, Anderson & Ascher 1999). Dominance by fewer species can profoundly alter ecosystem processes and reduce biotic diversity on a landscape scale (Drake *et al.* 1989; D'Antonio & Vitousek 1992; Vitousek & Hooper 1993; Gordon 1998).

The causes for the vulnerability of restored prairie pothole wetlands to plant invasions have not been thoroughly investigated. In general, landscape disturbance is believed to enhance the susceptibility of a site to invasion (Burke & Grime 1996; Galatowitsch, Anderson & Ascher 1999; Symstad 2000). In addition, it appears that plant invasions are most successful where disturbance coincides with increased fertility (Hobbs & Atkins 1988; Burke & Grime 1996). Situated in landscapes of intensive agricultural row crop production, restored prairie pothole wetlands are subject to high levels of nutrient enrichment from surface runoff and subsurface drainage, particularly enrichment by nitrate-N (NO₃-N) (Baker & Johnson 1981; Davis *et al.* 1981; Neely & Baker 1989; de Molenaar 1990). A strong correlation has been demonstrated between increased nutrient loads and shifts in wetland species composition and species dominance in ombrotrophic and minerotrophic fens in the Netherlands (Verhoeven *et al.* 1983; Vermeer & Berendse 1983; Vermeer & Verhoeven 1987; Verhoeven, Koerselman & Beltman

1988). A similar shift, along with overall reduced species richness, has been demonstrated in eutrophied aquatic systems (Wentz 1976; Whigham, Simpson & Lee 1980; Dolan *et al.* 1981; Tilman *et al.* 2001).

In the prairie pothole region, one of the chief invasive species is *Phalaris arundinacea* L. (reed canary grass), a cool season, perennial grass, believed to be indigenous to the North American continent but improved by selection (Galatowitsch, Anderson & Ascher 1999). *Phalaris arundinacea* grows under a wide range of environmental conditions and has been observed to colonize preferentially post-disturbance moist devegetated sites and achieve rapid and near-total dominance over native wetland plant communities (Hodgeson 1968; Comes 1971; Morrison & Molofsky 1998; Galatowitsch, Anderson & Ascher 1999). In restored wetlands, *P. arundinacea* was shown to preclude the establishment of a common meadow graminoid, *Carex lacustris* (Budelsky & Galatowitsch 2000). *Phalaris arundinacea* has shown dramatic increases in biomass in response to nitrogen fertilizer inputs (Mason & Miltimore 1970; Niehaus 1971; Dubois 1994; Figiel, Collins & Wein 1995). In a controlled greenhouse experiment, Green & Galatowitsch (2001) found, however, that *P. arundinacea* could suppress the native community regardless of nitrate level (0–40 mg l⁻¹).

Improving control strategies for *P. arundinacea* requires greater understanding of its mechanisms for colonization and dominance over native species, including both innate biological characteristics and environmental factors. Furthermore, because restored wetlands in the prairie pothole landscape are frequently intended to achieve multiple ecological goals, in particular vegetative diversity and water quality improvement, it is critical to improve understanding of the potential interaction and/or conflict between these goals. The primary objective of this research was to test the hypothesis that NO₃-N enrichment of a restored prairie pothole community would be associated with greater dominance by *P. arundinacea* over the native sedge meadow plant community after the first two growing seasons. We conducted a controlled field experiment designed to observe an experimental plant community's responses to specific nitrogen input levels in the presence and absence of *P. arundinacea*, as well as to test for the interaction between the effects of these factors.

Methods

EXPERIMENTAL DESIGN OVERVIEW

Native communities were grown in controlled mesocosms in a field setting and subjected to six treatments consisting of three NO₃-N addition levels (0, 12 and 48 g m⁻² year⁻¹ NO₃-N) and two invasion conditions [native community mixture (non-weed); native community plus *P. arundinacea* addition] (all species nomenclature follows Gleason & Cronquist 1991). The

experimental design was a randomized incomplete block with each treatment replicated 10 times.

STUDY SITE AND PREPARATION

The experiment was conducted at the University of Minnesota Horticultural Research Center in Carver County, Minnesota, USA, 44°51'45"N latitude, 93°36'00"W longitude. Historically a depressional wetland, the research area was drained and planted with grain crops during the first half of the 20th century. In 1974, the area was cleared, an irrigation and drainage system was installed, and the site used for research on *Zizania aquatica* L. (wild rice). In 1994, it was dedicated to wetland restoration research. The area was cleared once again and the land surface graded to form four rectangular basins separated by earthen dikes. Each basin was approximately 0.20 ha, with an approximate 5% slope on all sides and a 1.0-m depth at the centre. Each basin had a water inlet and adjustable drainage tile to allow for precise control of water levels during the growing season. The experiment was conducted on the western sides of two basins. In October 1997, the experimental sides were regraded to create even soil elevation throughout, and treated with Basamid® soil fumigant (Dazomet; BASF Corporation, Mt Olive, NJ) to eliminate the seed bank. The soil was a Glencoe clay loam (Cumulic Endoaquoll). Soil tests conducted by the University of Minnesota Research Analytical Laboratory in spring 1998, prior to the start of the experiment, indicated surface soil (0–10 cm) macronutrient levels were as follows (all measurements in mg kg⁻¹): 0.4–0.8 NO₃-N; 409–627 total P; 3602–4163 Ca; 756–839 Mg; 128–180 K; 42–49 Na. NO₃-N in basin water was 0.01–0.02 mg kg⁻¹. The pH (KCl) of all water samples was between 6.4 and 6.8. Nitrate for all samples was extracted with 0.01 M CaCl and measured using cadmium reduction colorimetry on an Alpkem Rapid Flow Analyser (Astoria of Pacific International, Klackamas, Oregon, USA) at 520 nm. Total phosphorus was measured using a microwave digestion method (EPA 3052, US Environmental Protection Agency) and subsequent analysis of the digestate with inductively coupled argon plasma (ICP, Fisons Instruments Division, Waltham, Massachusetts, USA) analysis. The remaining nutrients were measured using a 1-N ammonium acetate extract with ICP analysis.

In May 1998, 60 circular plots (1.13 m²) were established, 30 in each basin, in two rows per basin. Plot boundaries were formed with circles of 0.060 gauge plastic (0.61 m high, 1.2 m diameter), embedded in the soil to a depth of approximately 0.5 m, with a 1.0-m distance between every plot. Plot soil heights were surveyed before and after placement of plot boundaries and extensive effort was made to equalize soil height in every plot. Nevertheless, soil settling and microtopography resulted in some variance among plots. The range between the highest and lowest plot in the south basin was 4.6 cm (standard deviation = 0.99), while in

the north basin the range was 5.0 cm (standard deviation = 1.3). Additional survey measurements taken at the beginning of the second field season and at the end of both seasons verified that no additional soil settling occurred in the course of the research. Water levels in both basins were maintained constant throughout the experimental growing seasons at 2–3 cm below mean plot soil surface in each basin. Groundwater wells (2.54 cm diameter) were placed to a depth of 40 cm in each plot and between all plots to enable continual monitoring of water levels.

The native sedge meadow community mixture comprised 11 species that are abundant and widespread in prairie pothole wetlands in this region (Galatowitsch & van der Valk 1994) and that represent the two primary functional groups found in prairie wetlands: C₃ perennial graminoids and non-leguminous perennial forbs (see Table 2 for species list). All native community seeds were collected in 1996 or 1997 from wetlands in southern Minnesota or northern Iowa. *Phalaris arundinacea* seed from an open-pollinated population (i.e. not cultivars) was obtained through the University of Minnesota Department of Agronomy. Voucher specimens have been deposited at the University of Minnesota herbarium. Viability for each species' seed batch was estimated using a tetrazolium chloride test on a sample of 150–200 seeds per species (Grabe 1970).

The native community seed mixtures were created with equal viable densities of each species and a total native community viable seed density of 1500 seeds m⁻². The experimental density approximated actual densities found in wet meadow seed banks in prairie wetlands (van der Valk & Davis 1976, 1978; Weinhold & van der Valk 1989; Galatowitsch & Biederman 1998). Beginning in April 1998, the seed mixtures were placed in cold wet storage at 4 °C for 46 days to overcome seed dormancy. To prevent fungal infection during cold stratification, the mixtures were first soaked for 60 s in a 1 : 2 bleach and water solution and rinsed thoroughly.

EXPERIMENTAL TREATMENTS

Prior to cold stratification, *P. arundinacea* seed was added to 30 randomly chosen seed mixtures at a relative viable density equal to that of each individual species in the mixture, for a total viable seed density of 1636 m⁻² in *Phalaris*-addition plots.

Following the stratification period, the seed mixtures were sown with random assignments of treatments to plots within both basin and row blocks (15 plots per row in four row blocks, two rows per basin). Because the row blocks did not allow for three full replicates, the randomization process was as follows: two full replicates of the six treatment combinations plus three randomly selected treatments from a third replicate were assigned to one row block; the remaining three treatments from the incomplete replicate and another two full replicates were assigned to the second row block in the same basin. The process was repeated for the

second basin. Overall, the loss of statistical efficiency due to incomplete row blocks was minimized by the balancing of basin blocks.

NO₃-N treatment levels were as follows: control (0 g NO₃-N m⁻² year⁻¹), low (12 g NO₃-N m⁻² year⁻¹) and high (48 g NO₃-N m⁻² year⁻¹). The high NO₃-N level was chosen so that the resulting concentration would be comparable to above-average (but below maximum) values reported from tile drainage in the region (Davis *et al.* 1981; Neely & Baker 1989). Based on results from a greenhouse experiment (Green & Galatowitsch 2001) that showed greater treatment differences among low nitrate levels, the low NO₃-N level in this field study was selected to be 25% of the high level. Treatments consisted of calcium nitrate tetrahydrate [Ca(NO₃)₂·4H₂O] dissolved in water. Calcium nitrate was used for three reasons. First, this salt is very soluble in water so amenable to treatment application from stock solutions. Secondly, as the local soil is derived from highly calcareous glacial till, calcium is by far the dominant cation; use of this salt was less likely to change the ionic balance than other choices. Finally, nitrate is the predominant form of nitrogen that wetlands receive from tile runoff; ammonium is stable under anaerobic conditions so would not have readily nitrified. NO₃-N treatments were divided into two applications per field season, timed approximately 4 weeks and 9 weeks after plant emergence. Nitrogen solution was delivered to the plots using a fertilizer spreader with a manual control nozzle to minimize contact with plant tissue. Nitrogen applications were followed by 15 s of aerial water irrigation. Water from groundwater wells in each of the research plots was sampled, and nitrogen levels measured, 2 days and 4 weeks following NO₃-N treatment applications. Measurements were taken using a nitrate ion-selective electrode (HACH One Model 48680; HACH Company, Loveland, CO) in order to determine approximate range of NO₃-N levels experienced per treatment. During the first 6 weeks of the first field season, all plots were weeded weekly for all extraneous species, weeds consisting mainly of annual grasses. During the second field season, weeding was done only as needed to remove *P. arundinacea* from non-weed plots. Non-weed plots were carefully monitored throughout the field season for the presence of *P. arundinacea*, and weeding was required twice.

DATA COLLECTION

Plant material was harvested in late August 1999, 15 months after seeds were sown. Although an effort was made to time plant harvesting with the time of maximum standing crop for a majority of the species, it was impossible to correspond timing exactly for all species. Species that did not appear to be at maximum standing crop at the time of harvest were *Aster* spp., *Eleocharis palustris* and *Eupatorium purpureum*. Above-ground plant material was harvested from a 0.5-m² sampling area in each plot. Plant material was clipped

5 cm above the soil surface and sorted by species. After completion of above-ground harvest, below-ground plant material was taken from a 0.1-m² sampling area in plots of the south basin only. Below-ground plant material was removed with soil cores of 25 cm depth. The shallow depth to water table restricted roots to the top 25 cm of sediment.

The sampling areas for both above- and below-ground plant material were delineated by placing plastic hoops of the required size in the plot centre, equidistant from all edges, thereby avoiding edge growth in all plots. The below-ground material was rinsed thoroughly to remove soil, and sorted into groups of *P. arundinacea* and native community mixture. The 5-cm plant stem base was used to distinguish *P. arundinacea* and native community roots. Fine roots not attached to a plant stem base could not be reliably identified and were included in an 'unknown' group. All plant material was dried at 70 °C, for 48 h, and weighed.

STATISTICAL ANALYSES

Treatment effects on native community shoot, root and total biomass and total community evenness and diversity (Shannon's index) were analysed using the analysis of covariance (ANCOVA) procedures in MacAnova (University of Minnesota 1997). The model includes basin and row as fixed blocks and NO₃-N (0, 12 and 48 g m⁻² NO₃-N) and invasion condition (none and *Phalaris* addition) as fixed factors. The model assumes that row blocks may interact with factors whereas basin blocks do not. The difference in plot soil height from the basin-wide plot height mean was considered a covariate. The covariate did not contribute significantly to the observed variance of any dependent variable. Biomass data were logarithmically transformed in order to minimize heteroscedasticity (Sokal & Rohlf 1995). Means were compared using Tukey's honest significant difference (HSD) with $\alpha = 0.05$. In addition, ANCOVA procedures were used to analyse effects of NO₃-N treatments on the differences in shoot biomass for *P. arundinacea* and the non-weed native community. For all tests, differences were considered significant only if $P < 0.05$.

Results

NO₃-N levels declined from their application concentration to near 0 within 4 weeks following application (Table 1). Mean total community biomass increased with NO₃-N dose level ($F = 11.11$; d.f. = 2, 19; $P = 0.0006$). In the absence of *P. arundinacea*, mean total community biomass increased 27.8%, 3564.1 g m⁻²–4554.7 g m⁻², from 0 to 48 g m⁻² NO₃-N levels (Fig. 1). Mean total community biomass in *Phalaris*-addition plots was lower with no NO₃-N additions (3082.7 g m⁻²), but increased 53.2% to 4721.6 g m⁻² at the 48 g m⁻² level.

At all NO₃-N dose levels, total native community shoot biomass was significantly less in *Phalaris*-addition

Table 1. Changes in NO₃-N concentrations from time of application to 4 weeks following application. NO₃-N concentrations were measured from shallow wells within each research plot

Dose level	NO ₃ -N (mg l ⁻¹) post-application			
	Mean 2 days	SD 2 days	Mean 4 weeks	SD 4 weeks
0	0.3	0.6	0.03	0.1
12	5.9	6.0	0.05	0.1
48	28.8	21.0	0.5	1.2

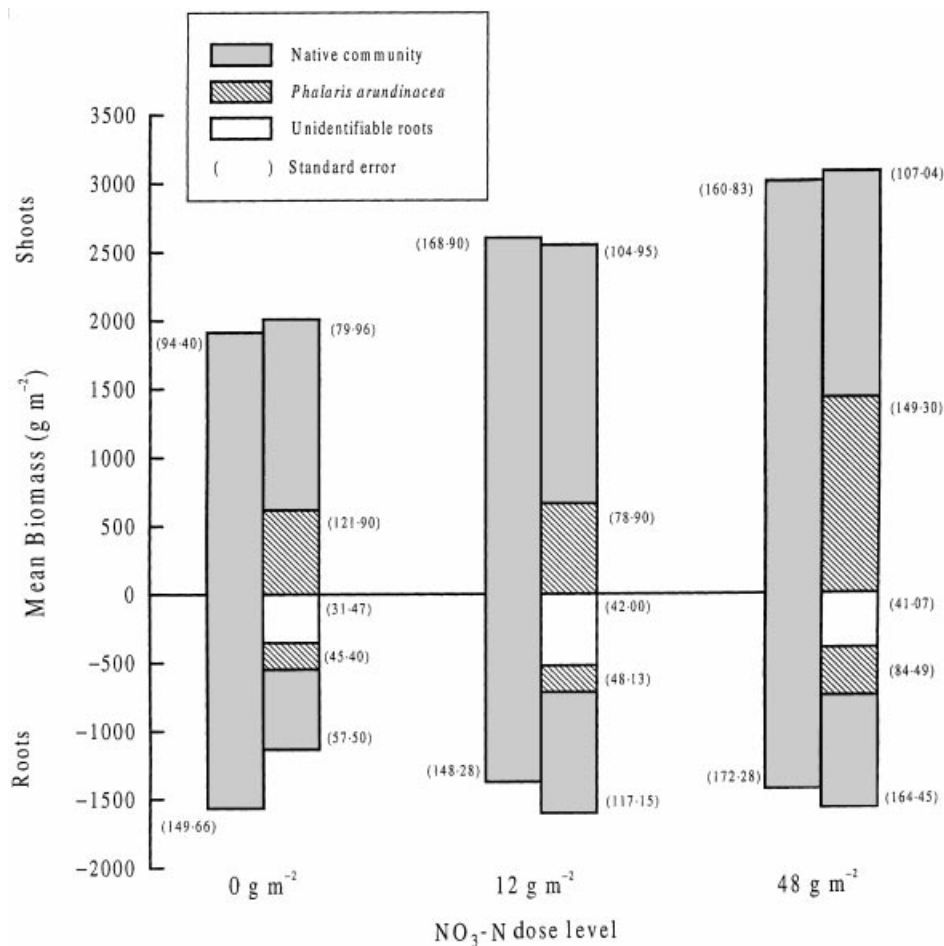


Fig. 1. Mean shoot and root biomass response of the native community and *Phalaris arundinacea* to NO₃-N treatments (0, 12 and 48 g m⁻²). Values are means $\pm$ 1 SE.

plots than in non-*Phalaris* plots ($F = 5.72$; d.f. = 1, 19; $P = 0.027$; Fig. 1). The analysis of covariance on total native community shoot biomass showed the NO₃-N-invasive interaction was significant ($F = 6.80$; d.f. = 2, 41; $P = 0.003$). In non-*Phalaris* plots the native shoot response to NO₃-N addition was a continuous increase in mean biomass from 1915.3 g m⁻² to 3010.0 g m⁻² in 0–48 g m⁻² NO₃-N-treated plots, respectively. In contrast, in *Phalaris*-treated plots native shoot biomass increased from 1392.2 g m⁻² to 1891.4 g m⁻² in 0–12 g m⁻² NO₃-N treatments, but then decreased to 1653.2 g m⁻² in 48 g m⁻² NO₃-N treatments.

NO₃-N additions enhanced shoot growth of *P. arundinacea* ($F = 16.82$; d.f. = 2, 17; $P < 0.0001$), its biomass more than doubling from 618.8 g m⁻² to

1426.0 g m⁻² over the range of NO₃-N treatments. The growth increase response occurred between 12 and 48 g m⁻² NO₃-N treatments, while there was no difference between 0 and 12 g m⁻² treatments (Fig. 1). At the highest NO₃-N dose level, the quantity of *P. arundinacea* shoot biomass (1426.0 g m⁻²) was similar ($t = 1.11$; $P = 0.15$) to that of the aggregate 11 species in the total native community (1653.2 g m⁻²).

Because the fraction of unknown roots was high (> 30% in all treatments) and not constant across NO₃-N treatment levels, characterizing differences in root growth between *P. arundinacea* and the native community was not possible. Comparing total root biomass between communities with and without *Phalaris* was informative. *Phalaris arundinacea* had a suppressing

Table 2. Shoot biomass response to NO₃-N treatments (0, 12 and 48 g m⁻²) for individual species in the seed mix. All species were planted at the same density: 9.1% of seed mix for plots without *Phalaris arundinacea* and 8.3% for plots with *P. arundinacea*. Percentages shown are based on total community biomass (+ < 1%)

NO ₃ -N treatments (g m ⁻²)	Shoot biomass (g m ⁻²) – plots without <i>Phalaris</i>									Shoot biomass (g m ⁻²) – plots with <i>Phalaris</i>								
	0			12			48			0			12			48		
	Mean	SE	%	Mean	SE	%	Mean	SE	%	Mean	SE	%	Mean	SE	%	Mean	SE	%
Native graminoids (total)	1251.6	72.8	65.3	1040.9	10.9	40.0	984.0	141.6	32.7	907.8	103.7	45.1	942.8	113.6	36.9	366.4	57.7	11.9
<i>Glyceria grandis</i> S. Wats.	509.1	117.1	26.6	416.9	64.3	16.0	681.1	164.0	22.6	323.0	65.0	16.1	355.8	50.4	13.9	248.0	48.9	8.1
<i>Scirpus atrovirens</i> Willd.	478.0	114.9	25.0	383.6	70.5	14.7	98.1	39.2	3.2	342.2	67.7	17.0	369.6	84.8	14.5	51.8	11.6	1.7
<i>Carex hystericina</i> F. Boott.	157.8	44.0	8.2	130.9	43.8	5.0	89.4	30.4	3.0	170.3	38.6	8.5	120.8	33.7	4.7	28.5	15.2	+
<i>Carex stricta</i> Lam.	82.0	25.8	4.3	67.9	19.4	2.6	88.9	26.1	2.9	55.4	16.9	2.8	73.0	18.5	2.9	25.7	10.5	+
<i>Calamagrostis canadensis</i> Michx.	18.2	3.5	+	39.4	9.5	1.5	25.7	6.7	+	16.0	6.85	+	22.0	3.4	+	11.3	6.0	+
<i>Eleocharis palustris</i> L.	6.5	2.4	+	2.4	1.2	+	0.9	0.5	+	1.0	0.3	+	1.8	0.9	+	1.0	0.8	+
Native forbs (total)	478.4	48.8	25.0	1372.1	183.3	52.7	1931.7	197.5	64.2	385.5	64.0	19.2	812.0	67.9	31.8	1169.7	112.7	38.0
<i>Asclepias incarnata</i> L.	140.8	23.3	7.4	627.3	106.1	24.1	1264.7	164.1	42.0	123.4	21.0	6.1	373.3	39.5	14.6	843.5	93.4	27.4
<i>Sium suave</i> Walter	107.5	31.5	5.6	233.7	54.5	9.9	394.3	71.7	13.1	111.7	44.9	5.6	166.6	33.2	6.5	222.8	35.5	7.2
<i>Aster</i> spp.	190.7	47.9	10.0	496.2	70.8	19.1	261.9	71.2	8.7	130.7	17.9	6.5	262.1	38.9	10.3	99.0	33.9	3.2
<i>Sagittaria latifolia</i> Willd.	39.0	21.7	2.0	13.9	5.2	+	4.3	2.1	+	19.3	12.0	+	9.7	5.7	+	4.3	3.2	+
<i>Eupatorium purpureum</i> L.	0.5	0.2	+	0.9	0.5	+	6.5	5.2	+	0.4	0.2	+	0.3	0.2	+	0.1	0.1	+
<i>Phalaris arundinacea</i> L.	–	–	–	–	–	–	–	–	–	618.8	121.9	30.8	663.0	78.9	26.0	1426.0	149.3	46.3
Unknown/other	185.2	42.8	9.7	191.4	40.2	7.3	94.4	33.7	3.1	98.93	24.97	4.9	136.6	18.6	5.3	117.12	28.62	3.8
Total community	1915.3	94.4		2604.5	168.9		3010.0	160.8		2011.0	117.0		2554.3	101.0		3079.2	159.1	

Table 3. Community diversity and evenness for NO₃-N and *Phalaris*-addition treatment combinations ($n = 10$ for each). Both evenness and diversity differed among NO₃-N treatment levels ($*P < 0.0001$) but not between *Phalaris*-addition and non-*Phalaris* plots ($P > 0.05$). Tukey HSD tests showed the high NO₃-N treatment level (b) differs from low and no NO₃-N levels (a) for both evenness and diversity ($P = 0.05$)

Nitrate treatments	Plots without <i>Phalaris</i>			Plots with <i>Phalaris</i>		
	Mean	SE	Range	Mean	SE	Range
Community diversity						
0 g m ⁻² *a	1.584	0.087	1.118–1.923	1.719	0.054	1.422–1.911
12 g m ⁻² *a	1.717	0.041	1.385–1.821	1.822	0.064	1.374–2.105
48 g m ⁻² *b	1.416	0.087	0.833–1.839	1.350	0.066	0.957–1.684
Community evenness						
0 g m ⁻² *a	0.700	0.031	0.538–0.826	0.721	0.019	0.618–0.797
12 g m ⁻² *a	0.755	0.017	0.666–0.818	0.769	0.025	0.597–0.878
48 g m ⁻² *b	0.637	0.036	0.379–0.798	0.605	0.026	0.436–0.702

effect on total community root growth when NO₃-N was not added, but not at 12 and 48 g m⁻² doses ($F = 18.06$; d.f. = 1,19; $P = 0.0004$). With no NO₃-N addition, total root biomass was 27.6% lower in invasive plots (1135.22 g m⁻²) than in those without the invader (1567.82 g m⁻²). With NO₃-N addition, the total root biomass of plots with *Phalaris* was slightly higher (1572.61 and 1606.14 g m⁻², for 48 and 12 g m⁻² levels) than in the absence of *Phalaris* (1374.70 and 1430.10 g m⁻² for 12 and 48 g m⁻² levels). NO₃-N treatments had no effect on native total community root growth and there were no significant differences among treatment group means at any NO₃-N dose level.

The native community in the absence of *Phalaris* exhibited a significant decrease in proportional allocation to below-ground biomass in response to NO₃-N levels between 0 and 12 g m⁻² (Fig. 1). Root : shoot ratios for the non-weed native community ranged from 0.82 at 0 g m⁻² NO₃-N to 0.48 at 48 g m⁻² NO₃-N, with no significant difference between ratios at 12 and 48 g m⁻² dose levels (Fig. 1). In contrast, the root : shoot ratio of plots with *P. arundinacea* was similar across all NO₃-N levels, from 0.51 to 0.63.

General shifts in floristic composition, between graminoids and forbs, in response to NO₃-N levels were similar in plots with and without *Phalaris*. As NO₃-N levels increased, the relative abundance (shoot biomass) of native graminoids declined while native forbs increased (Table 2). Three of six graminoids, *Carex stricta*, *Calamagrostis canadensis* and *Eleocharis palustris*, and two of five forbs, *Sagittaria latifolia* and *Eupatorium purpureum*, were of minor importance (< 2% of community biomass) in all treatment combinations.

Growth patterns and responses to experimental treatments by the other six individual species in the native community, however, differed substantially. The most abundant graminoid, *Glyceria grandis*, was suppressed by *P. arundinacea* at all levels, with suppression enhanced at the 48 g m⁻² NO₃-N level, the growth trend that strongly coincided with that of the overall native community. The two most common forbs, *Asclepias incarnata* and *Sium suave*, exhibited a continual

increase in growth (absolute and relative) with NO₃-N additions along with overall suppression by *P. arundinacea* (Table 2). The remaining three species, *Aster* spp., *Carex hystericina* and *Scirpus atrovirens* had diminished abundance at the 48 g m⁻² NO₃-N dose level in the presence of *P. arundinacea*. *Aster* spp. had a peak biomass at 12 g m⁻² NO₃-N in plots with and without *Phalaris*.

Both total community diversity ($F = 19.72$; d.f. = 2,42; $P < 0.0001$) and evenness ($F = 17.33$; d.f. = 2,42; $P < 0.0001$) were lower in high NO₃-N plots than in low or no NO₃-N plots (Table 3). In contrast, *Phalaris* addition did not significantly affect either diversity or evenness. In plots with no NO₃-N addition, two species (*Glyceria grandis* and *Scirpus atrovirens*) comprised 52% of the community biomass together in plots without *Phalaris*; individually each had a relative biomass (26.6% and 25%, respectively) comparable to *Phalaris* (30.8%) in plots where NO₃-N was added. At 12 g m⁻² NO₃-N levels, *Phalaris* was 26% of the total biomass, similar to *Asclepias incarnata* (24.1%), the most abundant species in plots where *Phalaris* was not added. Where NO₃-N levels were highest (48 g m⁻²), two species combined for approximately two-thirds of the overall biomass, regardless of *Phalaris* addition. *Asclepias incarnata* (42%) and *Glyceria grandis* (22.6%) dominated plots without *Phalaris*, whereas *Phalaris* (46.3%) and *Asclepias* (27.4%) did so in plots where it was added.

Discussion

Our results illustrate the dominance of *P. arundinacea* over the restored native sedge meadow community across the range of NO₃-N inputs used here. At the same time, the significance of the NO₃-N–competition interaction and the enhanced suppression of native community shoot biomass in *Phalaris*-treated plots at the 48 g m⁻² NO₃-N dose levels supports the hypothesis that an increase in NO₃-N inputs further enhances the competitive ability and dominance of *P. arundinacea* over the native community. The greater suppression of

community root growth by *P. arundinacea* at the 0 g m^{-2} $\text{NO}_3\text{-N}$ dose level shifts to greater suppression of shoots at the 48 g m^{-2} $\text{NO}_3\text{-N}$ level. Although diversity and evenness declined with increasing $\text{NO}_3\text{-N}$ levels, this was not observed for *Phalaris* additions. *Phalaris arundinacea* essentially replaced one to two native species that dominated at each $\text{NO}_3\text{-N}$ level.

The extraordinary capacity of *P. arundinacea* to use $\text{NO}_3\text{-N}$ inputs for growth is illustrated in its doubling of shoot biomass in response to an $\text{NO}_3\text{-N}$ dose level between 12 and 48 g m^{-2} . In comparison, the native sedge meadow community in non-weed plots demonstrated a steady increase in growth in response to $\text{NO}_3\text{-N}$ inputs, with an overall proportional biomass increase of 1.6 over the range of treatments. None the less, the apparent equivalency of *P. arundinacea* shoot biomass and the total aggregate shoot biomass of 11 species at the $48 \text{ g m}^{-2} \text{ year}^{-1}$ $\text{NO}_3\text{-N}$ dose level suggests an obvious advantage of the former in resource capture. Perry (2001) observed that the nitrogen-use efficiency of *P. arundinacea* increased with inorganic N concentrations while that of *Carex hystericina* declined, suggesting *Carex* is less likely to benefit from high N availability when competing with *Phalaris*.

We suspect that the extent of productivity increase we observed on the part of *P. arundinacea* may not be unusual in the North American prairie pothole region. Measurements of the range of $\text{NO}_3\text{-N}$ conditions experienced just before and several weeks after treatment applications in this experiment coincide approximately with actual $\text{NO}_3\text{-N}$ levels that have been measured in prairie wetlands or in agricultural drainage water entering wetlands. For example, data collected from 1976 to 1979 on influent waters at Eagle Lake Marsh in north-central Iowa showed a flow-weighted average of 13.0 mg l^{-1} $\text{NO}_3\text{-N}$ (Davis *et al.* 1981). In a review of literature from 1970 to 1979, Neely & Baker (1989) reported $\text{NO}_3\text{-N}$ concentrations found in subsurface drainage associated with corn and soybean cropping systems to range from 5.8 to 61.2 mg l^{-1} , with a mean of 21.0 mg l^{-1} .

The overall suppression of native community growth across the range of $\text{NO}_3\text{-N}$ treatments suggests that *P. arundinacea* must be controlled in restorations where an abundant native sedge meadow community is desired, regardless of $\text{NO}_3\text{-N}$ input levels. At the same time, our results suggest that the abundance of the native community will be even further reduced in the presence of *P. arundinacea* given an increase in $\text{NO}_3\text{-N}$ dose levels from 12 to 48 g m^{-2} . In both the enhanced suppression of the native community by *P. arundinacea* over a range of $\text{NO}_3\text{-N}$ levels, and the significance of the $\text{NO}_3\text{-N}$ -invasive interaction in explaining variance in native community biomass, our results concur with those of Wetzel & van der Valk (1998). They found that *P. arundinacea* suppressed growth of *Carex stricta* and *Typha latifolia* at both low and high levels of a combined N, P and K nutrient treatment and that the interaction of competition and

nutrient input factors contributed to the reduction in *Carex stricta* productivity.

This experiment was not designed to investigate the nature nor the mechanisms of competition between *P. arundinacea* and the native community. Nevertheless, the decline of root : shoot ratios with nitrogen addition suggests that, with reduced nitrogen limitation, competition for light was greater. How and why *Phalaris* addition resulted in greater nutrient limitation for the native community with increasing $\text{NO}_3\text{-N}$ is less clear. With no nitrate addition, the native community produced less root biomass per shoot biomass in the presence of *Phalaris*. At the highest $\text{NO}_3\text{-N}$ level, the native community produced more root biomass per shoot biomass with *Phalaris* addition. *Phalaris* can cause a light limitation for its competitors by growing much faster after seedling emergence (Perry 2001). If *Asclepias incarnata* and *Sium suave* grew even faster than *Phalaris* with $\text{NO}_3\text{-N}$ addition, light would have been more limiting in the absence of *Phalaris*.

Our results suggest that the floristic composition of restored wetlands is primarily affected by nitrate additions rather than *P. arundinacea*, at least in the short term. Our findings are consistent with mounting evidence correlating eutrophication and species richness reductions (Willis 1963; Golley & Gentry 1966; Thurston 1969; Al Mufti *et al.* 1977; van den Bergh 1979; Willems 1980; Tilman 1982; Wilson & Keddy 1988; Wisheu *et al.* 1991). In our study, nitrate additions decreased diversity and evenness and favoured native forbs over native graminoids, whether or not *Phalaris* was part of the community. Like *Phalaris*, *Asclepias incarnata* and *Sium suave* both have a high capacity to increase production in response to $\text{NO}_3\text{-N}$ additions. *Asclepias* exhibited nine- and sevenfold increases, with and without *Phalaris* additions, respectively; *Sium suave* had four- and threefold increases. In the absence of *Phalaris*, the community shifted from being dominated by two graminoids, *Glyceria grandis* and *Scirpus atrovirens*, to being dominated by a forb (*Asclepias incarnata*) and a graminoid (*Glyceria grandis*) at the 48 g m^{-2} $\text{NO}_3\text{-N}$ additions. Plots with *Phalaris* additions were likewise dominated by one to two species across the nutrient gradient: *Phalaris* dominated at no to low $\text{NO}_3\text{-N}$ additions, while *Asclepias* co-dominated at the highest $\text{NO}_3\text{-N}$ inputs. Diversity and evenness decrease with and without *Phalaris* additions because the proportion of the biomass contributed by the most abundant one to three species increases from approximately one-half to nearly three-fourths across the nitrate gradient. The combination of high nitrate levels and the presence of *Phalaris*, however, differentially suppressed four of the six common species (three graminoids and one forb) in this experiment. At least four of six planted native graminoids had relative biomass greater than 1% in all but the 48 g m^{-2} $\text{NO}_3\text{-N}$ level treatment with *Phalaris*. Only two graminoids achieved this abundance under the treatment combination of high nitrates with *Phalaris*.

Limitations in the experimental time period preclude determining whether forbs, such as *Asclepias incarnata*, that capitalize on nitrate inputs can coexist in the long term with *Phalaris*. Observations from wetland restorations within the region (Mulhouse & Galatowitsch 2001) lead us to hypothesize that presence of *P. arundinacea* in a restored prairie pothole wetland may lead to a reduction in diversity over the long-term. The overall productivity of this species in N-enriched conditions and the suppressive effect on the native community suggests an increase in plant-induced stress upon its competitors that is likely to have a positive feedback effect further enhancing the resource capture and growth potential of the dominant species (*sensu* Grime 1979). Positive correlations have been demonstrated between increases in herbaceous plant community biomass and shifts in species composition, and the composition shifts have been further correlated with a decrease in species richness at the community scale (Willis 1963; Grime 1973, 1978, 1979; Al Mufti *et al.* 1977; Wheeler & Giller 1982). Long-term research (e.g. greater than 3 years) is critical for understanding plant community dynamics, and the outcomes of interspecific competition may in fact be substantially different over varying time frames (Tilman 1986; Wilson 1988).

Our results have several implications for developing strategies to maintain biodiversity within agricultural landscapes; restoration of natural habitats is often an essential component of these schemes (Ostermann 1998; Ovenden, Swash & Smallshire 1998). First, substantially reducing nitrogen losses into wetland reserves is critical for minimizing losses of community diversity. The experimental communities we assembled for this study exhibited a significant loss of diversity within their first growing season. Unfortunately, schemes that rely on wetlands to achieve water quality improvement by intercepting agricultural drainage (Dubois 1994; Bernard & Lauve 1995) cannot assume coincidental biodiversity benefits. Within an agricultural landscape, some wetlands need to be restored that are not fed by enriched runoff, if diversity is a primary goal. Secondly, our results demonstrate that if the species *P. arundinacea* is present, wetland reserves will not achieve levels of biodiversity that are possible when the invader is absent. Moreover, if $\text{NO}_3\text{-N}$ enrichment occurs to the extent that has been recorded in agricultural landscapes, the native community will be even further suppressed. Because *P. arundinacea* is widely used for pastures and soil-erosion prevention, this species is often considered part of sustainable agriculture (i.e. agri-environmental management) within the northern US. A belated recognition of the invasive potential that this species presents poses a special resource management problem: agencies primarily responsible for soil conservation include *Phalaris* on the list of recommended plants, while those concerned with wildlife habitat and species conservation prohibit its use and encourage eradication. Because native seed

banks are typically depauperate in newly restored wetlands in agricultural landscapes (Galatowitsch & van der Valk 1996b), the relative abundance of *Phalaris* seed dispersed from nearby sources could result in restored assemblages even more skewed to the invader than observed here.

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