



Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass

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Abstract

Despite the dramatic changes invasive plants cause to ecosystems and communities, factors that control dominance of invasive species after establishment in a community are poorly understood. Most active management relies on catastrophic disturbances of invasive-dominated communities to increase richness and diversity of plant communities. This study examines the importance of propagule dispersal and deer herbivory on continued dominance of *Phalaris arundinacea* after a non-catastrophic, short-term disturbance to monotypic stands of this invasive grass. The disturbance caused no change in *P. arundinacea* cover among treatments during any year of the study and, thus, simulates disturbance intensity more likely to be encountered in unmanaged settings. Despite the small disturbance, the combinations of disturbance + seeding and disturbance + seeding + deer exclusion caused greater species richness than controls even three years after disturbance. Increased invasion of *P. arundinacea* stands caused few effects on the dominant, as *P. arundinacea* biomass was unaffected after the first year. Selective herbivory by deer of species other than *P. arundinacea* increased the effects of disturbance and seeding, and aided in continued dominance of the grass. The tolerance of *P. arundinacea* for direct anthropogenic effects, including poor water quality and hydroperiod fluctuations, and indirect effects, such as increased herbivory by historically high deer populations, indicates the complexity of determining persistence of invasive species.

Introduction

The current rate of invasive species introduction is historically unprecedented and threatens ecosystems worldwide (Vitousek et al. 1996). Invasive plant species can have dramatic effects on ecosystems including changes in nutrient availability, water availability, trophic structure, and disturbance frequency (Vitousek 1990). Because invasives are often linked to declines in biodiversity (Lodge 1993; Vitousek et al. 1996; Schmitz and Simberloff 1997), ecologists have tried to determine the characteristics of successful

invaders (Lodge 1993; Kolar and Lodge 2001), invulnerable systems (Lodge 1993; Williamson 1996), and the effect of established non-indigenous species on subsequent invasions by other non-indigenous species (Simberloff and Von Holle 1999). There is also a large body of applied literature focusing on management and removal of invasive species. Despite interest in the causes of invasion and the removal of invaders, little research has focused on factors controlling the continued dominance of invasive plant species after invasion and establishment have occurred. In this study, we examine the effect of disturbance, herbivory,

and propagule dispersal on established communities of the invasive grass, *Phalaris arundinacea* (reed canarygrass).

Phalaris arundinacea is an invasive grass of inland marshes over much of North America (Galatowitsch et al. 1999; Kellogg and Bridgham 2002), and its spread may be linked to the decline of sedge meadows (Galatowitsch and van der Valk 1996). Varieties of *P. arundinacea* have been cultivated in northern temperate regions of the world since the early 19th century (Galatowitsch et al. 1999). Because of its long agricultural history, the grass is considered indigenous in temperate regions of all continents (Marten and Heath 1985), but its preagricultural distribution is uncertain. *P. arundinacea* spreads clonally (Boutin and Keddy 1993), is tolerant of a wide range of soil moisture (Zeiders and Sherwood 1985; Galatowitsch et al. 2000), and produces large numbers of seeds capable of germinating under a wide range of conditions (Baskin and Baskin 1998; Kellogg et al. 2003). Because of its long history as a forage grass, new genotypes have continually been introduced, increasing the probability of invasion success by *P. arundinacea* (Galatowitsch et al. 1999). After establishment, *P. arundinacea* is a competitive dominant in many freshwater marshes, especially in organic soils (Gaudet and Keddy 1995). Efficient use of nitrogen and phosphorous for stem and leaf production (McJannet et al. 1995) and abundant above-ground biomass (Lee et al. 1996) make *P. arundinacea* an excellent competitor for light. Additionally, the dense litter produced by *P. arundinacea* may inhibit (*sensu* Connell and Slatyer 1977) the germination and growth of other species (Bosy and Reader 1995).

Disturbance often increases invasibility of plant communities (Lodge 1993; Williamson 1996). This fact has been used in management of invasive plant monocultures, such as with *P. arundinacea*. By intensive disturbance of the invasive plants, opportunities for colonization of native species are enhanced. These disturbances are much more intense than would be encountered in natural settings and include complete manual removal of a species from an area (Ussery and Krannitz 1998), repeated mowing (Ussery and Krannitz 1998; Meyer and Schmid 1999; Brabec and Pysek 2000; Britton et al. 2000), intensive herbicide treatments that kill all vegetation (Duncan and McDaniel 1998; Paveglio and Kilbride 2000), intensive mechanical manipulations of the soil (Britton et al. 2000; Paveglio and Kilbride 2000), fire

(Clark and Wilson 2001), or combinations of several disturbances (Paveglio and Kilbride 2000). Although these disturbances often allow recruitment of native species, the high efficiency of removal in these experiments is unlikely to happen with any regularity in less managed settings. These types of studies, which predominate experiments involving *P. arundinacea*, give little indication of how communities dominated by invasive plants will respond to less intense disturbances more commonly encountered in unmanaged settings. Manipulative studies examining invasion success across differing disturbances found results ranging from both reduced or increased growth of cogongrass based on disturbance type (King and Grace 2000), to increased invasibility with greater disturbance intensity by a native seed mixture (Burke and Grime 1996). These differing results indicate the need for further study of non-catastrophic disturbances.

Although there is agreement that greater propagule dispersal increases the likelihood of successful invasion (Lodge 1993; Williamson 1996), we found no studies on the effects of seeding on recruitment of native species into communities dominated by invasive species. However, Symstad's (2000) findings that lower richness of functional groups in a community allow greater invasion by seeded native prairie species, indicates that monotypic stands, often formed by *P. arundinacea*, may be more vulnerable to invasion. Additionally, vegetation communities in restored marshes were found to have little relationship to initial seed banks (Galatowitsch and van der Valk 1995; Brown 1998) and are primarily derived from colonization (Galatowitsch and van der Valk 1996a,b; Brown 1998). Reinartz and Warne (1993) found increased richness and suppression of invasives in seeded wetlands three years after restoration. Thus, increased propagule dispersal would be expected to affect the recovery of a monotypic community after disturbance.

Reduction in herbivory is thought to increase the chance of successful invasion by plants (Lodge 1993; Galatowitsch et al. 1999). Although this reduction in herbivory is typically thought to result from an exotic escaping its native herbivore assemblage, selective herbivory by mammals can favor increased dominance of indigenous unpalatable species (Augustine and McNaughton 1998). Despite its history as a forage grass, some *P. arundinacea* genotypes have reduced palatability due to high alkaloid content (Marten et al. 1976) and low digestibility (Frame and Morrison 1991). The grass also has a high tolerance for herbivory

and was only outcompeted by other grasses and sedges after being defoliated five times in one growing season in central Florida (Adjei and Pitman 1993). Thus, *P. arundinacea*'s resistance and tolerance of herbivory may result in herbivores having a more negative effect on other wetland plant species.

Our objective was to determine the effects of non-catastrophic disturbance, herbivory, and propagule dispersal on plant communities initially consisting of monotypic stands of *P. arundinacea*. We examined treatment effects of (1) an unmanipulated control, (2) enriched seed bank, (3) disturbance, (4) enriched seed bank + disturbance, and (5) enriched seed bank + disturbance + deer exclosures on biomass, richness, and diversity in three northern Indiana restored marshes. We hypothesized that monotypic *P. arundinacea* stands are not invasible without disturbance, due to a dense canopy and abundant litter. Our second hypothesis was that richness and diversity would increase in the order of the treatments mentioned above, due to increased numbers of propagules and opportunities for establishment. Our third hypothesis was that aboveground biomass of species other than *P. arundinacea* would show the same trend as richness and diversity.

Methods

Field manipulations

This study was conducted in three restored freshwater marshes in Potato Creek State Park in northern Indiana (41°14' N, 86°26' W). All sites were dominated by dense stands of near-monotypic *P. arundinacea* L., had similar surrounding vegetation, no distinct surface inlets, and were less than 1 ha in area. The wetlands' water regimes were restored in 1975, 1992, and 1994 by removal of drainage tiles, construction of earthen berms, and installation of water control structures. All restorations took place on previously drained wetlands that had been cultivated for greater than 100 years (Tim Cordell, Potato Creek State Park, pers. comm.) and received no planting or seeding. During the 3 years of the study, water depths in sample plots were 0–16 cm.

Each of the three replicate wetlands received five treatments: (1) disturbed (D); (2) disturbed + seeded (DS); (3) disturbed + seeded + deer exclosure (DSE); (4) undisturbed + seeded (S); and (5) control (C, no manipulation). We were limited in the number of exclosures we were allowed to install in the park,

so we chose to place them in combination with disturbance and seeding. We believed that this would give us the greatest insight into controls of invasive dominance, given the limitation on numbers of exclosures. In July 1996, locations of treatment areas in each wetland were randomly assigned with the exception that seeded treatments were kept adjacent to each other to minimize possibility of seeds entering non-seeded treatments. All treatment areas except the deer-exclosures plots were 25 m². Only the inner 16 m² of each treatment area was sampled during the study, providing a 0.5-m buffer on all sides to minimize edge effect.

The DSE treatment areas were 100 m² in each wetland and 8 deer exclosures were installed in each area. Multiple exclosures in each wetland were used instead of one large exclosure to minimize visibility, at the request of the park naturalist. The exclosures were 2 m high, 4 m² in area, and had 900-cm² openings. This size allowed a 0.5-m buffer on each side and a sample plot size identical to all other treatment sample plots. Potato Creek State Park has high deer densities that have adverse effects on vegetation (Riemenschneider et al. 1995). During 1996–1998, the park had a mean density of 38 deer per km² (Tim Cordell, Potato Creek State Park, pers. comm.).

Areas receiving disturbance treatments were sprayed with herbicide (2% solution of glyphosphate, trade name Roundup) 3 times. The first application was in June 1996, after which the vegetation was allowed to die. The dead vegetation was cut and removed in July 1996 to expose any living vegetation and the plots were again sprayed. The plots were herbicided a third time in early June 1997. Although this clearly disturbed the vegetation, there were many living *P. arundinacea* shoots resprouting at the time of seeding. This herbicide has been noted to be far less effective on vegetation in standing water than on vegetation in dry areas in other applications in this park (Tim Cordell, Potato Creek State Park, pers. comm.). An application by us to a nearby dry area completely killed all *P. arundinacea* after one application and there was no resprouting. The litter layer was not removed from the plots.

Greater propagule dispersal of native marsh species was simulated by addition of a seed mixture of 28 wetland species (Table 1) on 25 July 1997. The plots were seeded with a constant weight of 16.35 g m⁻². These species were purchased from the native plant nursery of a local wetland restoration firm (J.F. New and Associates, Inc., Walkerton, Indiana) and were chosen

Table 1. Species list for seed mixture applied to all treatments receiving seeds.

<i>Acorus calamus</i> L. (0.2)	<i>Leersia oryzoides</i> (L.) Sw. (3)
<i>Agrostis gigantea</i> Roth (20)	<i>Liatris spicata</i> Willd. (2)
<i>Alisma plantago-aquatica</i> L. (3)	<i>Lobelia cardinalis</i> L. (3)
<u><i>Asclepias incarnata</i></u> L. (2)	<u><i>Lobelia siphilitica</i></u> L. (2)
<i>Aster novae-angliae</i> L. (2)	<u><i>Mimulus ringens</i></u> L. (2)
<i>Carex lupulina</i> Willd. (7)	<i>Panicum virgatum</i> L. (0.2)
<i>Carex vulpinoidea</i> Michaux (10)	<i>Scirpus atrovirens</i> Willd. (5)
<i>Cassia hebecarpa</i> Fern. (2)	<i>Scirpus cyperinus</i> (L.) Kunth (3)
<i>Eupatorium maculatum</i> L. (2)	<i>Scirpus validus</i> Vahl (3)
<i>Gentiana andrewsii</i> Griseb. (0.2)	<i>Spirea alba</i> Duroi (3)
<i>Glyceria striata</i> (Lam.) Hitchc. (1)	<u><i>Spartina pectinata</i></u> Link (16)
<i>Hibiscus moscheutos</i> L. (3)	<i>Verbena hastata</i> L. (2)
<i>Iris virginica</i> L. (3)	<i>Vernonia fasciculata</i> Michaux (2)
<i>Juncus effusus</i> L. (6)	<u><i>Zizia aurea</i></u> (L.) Koch (2)

Numbers in parentheses are percentage weight of each species in mix. Bold text indicates species occurring in seeded treatments. Underlined text indicates species occurring in non-seeded treatments.

to be capable of growing in the water depths present in the experimental plots. The seeds were stored for 12 months at 4 °C prior to seeding. The plots were seeded at approximately twice the density typically used by the consulting firm to ensure a large amount of viable seed. Prior to seeding, the seeds were soaked overnight in deionized water to increase the probability that seeds would sink and not float out of the plots.

Each replicate wetland was sampled for species percent cover and aboveground biomass annually during peak growing season (14 July–2 August) from 1998 to 2000. Each treatment area was subsampled in 4 1-m² plots (2 permanent and 2 randomly chosen each year) for percent cover. Randomly chosen plots were also destructively sampled for biomass, so were never sampled again. Permanent plots were compared to non-permanent plots to assure us that non-permanent plots were representative of annual changes within the treatment area. In one wetland, two exclosures were destroyed by tree fall, leaving only two DSE cover plots (the permanent plots) during the last study year. Cover was visually estimated (as a percentage) for all rooted plant species by two to three observers, and the observations were averaged for each species. Each observer was equipped with a guide representing 1% of the cover plot to aid in estimating cover. These data were used to determine plant species richness and Shannon's diversity index in each plot. Bare ground area was estimated during the first year to determine gaps for potential colonization. Cumulative species richness in each treatment was determined using a species list from all years of the study.

Aboveground biomass was destructively sampled each year in the randomly chosen, non-permanent cover plots by clipping all living vegetation to ground level in 2 random 400-cm² subplots in each plot. After clipping, *P. arundinacea* was separated from other vegetation, and all vegetation was dried at 65 °C for 48 h and weighed. Different biomass plots were used each year. Voucher specimens are on file at the University of Notre Dame Herbarium. Nomenclature follows Voss (1972, 1985, 1996).

Seed bank

We sampled the seed bank of each wetland in September 1998 to determine differences in potential germination among wetlands. We sampled at 20 random locations surrounding the treatment areas in each of 2 water depths per wetland: saturated (no standing water) and flooded (15 cm water). We used a PVC core 7.5 cm in diameter and 5 cm deep to sample all seeds that are capable of germinating under undisturbed conditions (Pierce and Cowling 1991). Samples from each wetland were composited (Galatowitsch and van der Valk 1994) and stored at 4 °C to maximize germination (Gross 1990).

Prior to germination, we sieved the samples to remove litter, roots, and tubers. Two 600-cm³ subsamples were spread 1 cm deep in pans on a layer of 600 cm³ of sterilized sand and germinated under two conditions (drawdown, consisting of saturated conditions, and flooded, consisting of 2 cm of standing water). Seeds were germinated in a greenhouse with supplemental lighting (14-h day length). Samples

were given six weeks to germinate (Galatowitsch and van der Valk 1994) starting in October 1998. We counted all seedlings every two weeks and identified species at the end of the germination period. Two control pans containing only sand were maintained under each germination hydrology to evaluate any colonization into the greenhouse.

Statistics

Plant species richness, Shannon's diversity (base 10), and aboveground biomass from the field experiment were analyzed using repeated measures ANOVA (rmANOVA) with plots averaged by treatment within each wetland. Significance of all factors was assessed at $P \leq 0.05$. There were no significant interaction terms or year effects for any rmANOVA, so ANOVA and Tukey *post-hoc* tests were performed on data (averaged by plot across years) to identify differences among treatments. rmANOVA results for plant species richness and Shannon's diversity were similar between permanent and annually chosen random plots, so both permanent and non-permanent plots in each treatment area were used during analysis. Bare ground percentage in the first year was compared among treatments by ANOVA and Tukey *post-hoc* tests. Total richness among treatments was analyzed by ANOVA and Tukey *post-hoc* test based on a cumulative species list from all plots within each wetland-treatment combination. Seed bank data were analyzed using ANOVA.

We assessed the dominance of *P. arundinacea* by comparing the percent of total cover and biomass in each plot accounted for by *P. arundinacea*. The results were analyzed using a Kruskal-Wallis test, due to deviations from normality. If differences were found, significant differences among years and treatment differences within years were determined using non-parametric multiple comparison tests (Zar 1999) with Dunn's (1964) modifications for uneven sample size. *P. arundinacea* cover was compared among years and treatments in the same manner as dominance. Significance of all factors was assessed at $P \leq 0.05$.

All treatments (S, D, DS, and DSE) were compared to C treatments to assess changes in invasion of *P. arundinacea* dominated-communities. Because our experimental design could not be fully crossed for seeding, disturbance, and herbivore exclusion, we could not explicitly examine the effect of herbivory exclusion in DSE treatments. Any differences between, for instance, D and DSE plots must therefore be attributed

to the interactive effects of seeding and herbivore exclusion, rather than a single factor.

Results

Field experiment

Plant species richness was different among treatments (rmANOVA, $P < 0.001$), but not among years. DS and DSE plots had greater richness than control plots (Tukey, $P < 0.001$), and DSE treatments were richer than D treatments (Tukey, $P = 0.002$) (Figure 1). All disturbance treatments were significantly richer than S plots. However, D and S plots had equivalent richness to controls (Figure 1).

The cumulative number of species (pooled over three years) at each site varied among treatments (ANOVA, $P < 0.001$). Mean richness per wetland was lowest in the S treatment ($2.7 \pm$ standard error 1.2), followed by C (6.3 ± 2.0), D (10 ± 1.0), DS (14.7 ± 1.9), and DSE (17.7 ± 1.9). DS and DSE plots had greater cumulative richness than control and S plots (Tukey, $P < 0.032$), and DSE treatments were richer than D treatments (Tukey, $P = 0.049$). D and S plots had equivalent richness to control plots. The control plots had approximately twice as many uncommon species as other treatments, with 67% of their species always occurring at cover $\leq 1\%$, while other treatments had from 25% to 36% uncommon species (Table 2). The D plots had a higher percentage

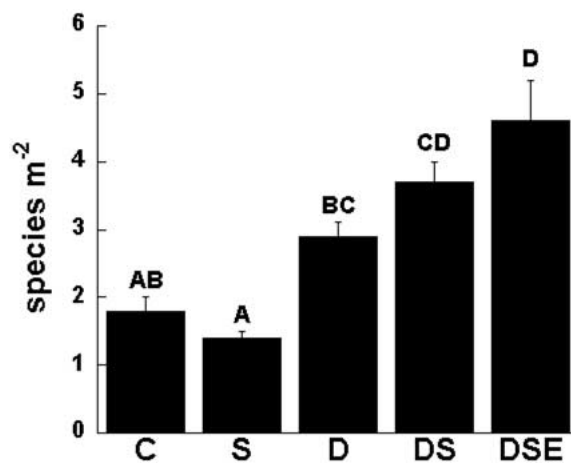


Figure 1. Mean richness per plot during all years of study. Letters indicate significant differences (Tukey, $P \leq 0.05$). Error bars are one SE. Abbreviations as in Table 2.

Table 2. Plant species, taxonomic authorities, and percent cover occurring in each treatment.

Species	Treatments				
	C	S	D	DS	DSE
<i>Agrostis perennans</i> (Walter) Tuckerman			1 (1) ^a		
<u>Alisma plantago-aquatica</u> L.			10 (8)	9 (8)	19 (11)
<i>Apios americana</i> Medicus		3 (5)	3 (8)	2 (2)	
<i>Asclepias amplexicaulis</i> Sm.			1 (1) ^a		1 (1) ^a
<u>Asclepias incarnata</u> L.	1 (2)		2 (5)	3 (10)	6 (12)
<i>Bidens comosus/connatus</i> (A. Gray) Wiegand/Willd.	12 (4)	19 (4)	9 (4)	6 (3)	12 (6)
<i>Bidens frondosus</i> L.			2 (1) ^a		4 (2) ^a
<u>Bromus commutatus</u> L.				1 (1) ^b	
<i>Carex bebbii</i> (Bailey) Fern.				1 (3)	1 (1)
<i>Carex grayi</i> Carey			1 (8)	1 (6)	2 (8)
<u>Carex lurida</u> Wahl.			10 (4) ^a	11 (4) ^a	8 (4) ^a
<u>Carex vulpinoidea</u> Michaux			2 (1) ^a	1 (2)	6 (6)
<i>Daucus carota</i> L.			1 (1) ^b	1 (2) ^b	1 (1) ^b
<i>Epilobium coloratum</i> Biehler	1 (1) ^b	1 (1) ^a		1 (1) ^a	1 (1) ^a
<i>Equisetum arvense</i> L.				3 (1) ^b	8 (6)
<i>Eupatorium serotinum</i> Michaux	1 (1) ^b		3 (1)	2 (4) ^a	3 (3) ^a
<i>Galium</i> spp.	6 (2) ^a			8 (4)	2 (1) ^a
<u>Glyceria striata</u> (Lam.) Hitch.					21 (3)
<u>Hibiscus moscheutos</u> L.				5 (1)	9 (7)
<i>Juncus acuminatus</i> Michaux			10 (1) ^a		
<u>Juncus effusus</u> L.			2 (1) ^a	1 (3)	1 (1) ^b
<u>Leersia oryzoides</u> (L.) Sw.		1 (1)	10 (2)	15 (5)	23 (9)
<u>Lobelia cardinalis</u> L.	1 (2) ^b			3 (4)	2 (3)
<i>Ludwigia palustris</i> (L.) Ell.	2 (3)	2 (2)			1 (1) ^b
<i>Lycopus americanus</i> W.P.C. Barton			1 (3)	1 (1) ^a	1 (1)
<i>Lysimachia terrestris</i> (L.) BSP.					2 (2) ^a
<i>Mentha arvensis</i> L.					2 (2) ^a
<u>Mimulus ringens</u> L.	1 (1) ^b			2 (13)	3 (8)
<u>Penthorum sedoides</u> L.			16 (8) ^a	17 (4) ^a	1 (4) ^a
<u>Phalaris arundinacea</u> L.	81 (36)	76 (36)	82 (34)	80 (33)	80 (32)
<i>Pilea pumila</i> (L.) A. Gray				1 (2) ^a	1 (1) ^a
<i>Polygonum hydropiperoides</i> Michaux				1 (1) ^b	1 (1) ^b
<i>Populus deltoides</i> (seedling) Marsh.	1 (3)		1 (2)		1 (1) ^a
<i>Rubus hispida</i> L.					2 (1) ^b
<i>Salix nigra</i> Marsh.			3 (4)	1 (1) ^b	9 (2) ^a
<u>Scirpus atrovirens</u> Willd.			1 (1)	1 (1) ^a	1 (1) ^a
<u>Scirpus cyperinus</u> (L.) Kunth	2 (1)			5 (5)	2 (2)
<u>Scirpus validus</u> Vahl				12 (3)	4 (5)
<u>Solanum carolinense</u> L.					1 (1)
<i>Solidago</i> spp.	1 (1)				1 (1) ^a
<i>Trifolium repens</i> L.	1 (1) ^b				
<i>Typha</i> spp.	9 (1) ^b		2 (3)	4 (2)	7 (4)
<i>Vitis riparia</i> Michaux			2 (1)		
Unknown seedling	1 (5)		1 (2)	1 (2)	1 (1) ^a

Cover is mean value of all plots containing species during all years of study. Numbers of plots species occurred in are in parentheses. Species in bold were included in seed mix. Underlined species were found in seed bank at start of study. C = control, S = seeded only, D = disturbed, DS = disturbed + seeded, and DSE = disturbed + seeded + exclosure.

^aSpecies occurred in first year of study only.

^bSpecies occurred in last year of study only.

of species that occurred in only one plot during the 3 years of the study (46%), when compared to the other disturbance treatments (30–38%) (Table 2). Of the species in the seed mix, 12 species (46%) were

present in plots receiving seed, and 8 of these species were present in non-seeded plots (Table 1). However, of the 8-seeded species present in non-seeded plots, 1 was present in the seed bank, 4 occurred in only 1 plot

during the study, and another species had less than 1% cover when present in non-seeded plots (Table 2), indicating that introduced seeds stayed primarily in the seeded treatments. Shannon's diversity (0.15 ± 0.02) and aboveground biomass ($852 \pm 119 \text{ g m}^{-2}$) did not vary among years or treatments. Percentage of ground that was bare in the first year ($40 \pm 6\%$) did not vary among treatments.

The fraction of vegetation cover composed of *P. arundinacea* varied among years (Kruskal–Wallis, $P < 0.0001$), although it averaged $\geq 65\%$ in all treatments and $\geq 97\%$ in control plots. *P. arundinacea* occupied a significantly greater fraction of total cover in 2000 than either 1998 or 1999 (Table 3). There were no significant differences between 1998 and 1999. In 1998 and 1999, *P. arundinacea* occupied a smaller fraction of total cover in D, DS, and DSE treatments than either control or S plots (Table 3). The differences among treatments were smaller in 2000, with only the DSE treatment different than control plots. Any differences in fraction of vegetation cover composed of *P. arundinacea* was due to increased presence of other species, as all treatments had equivalent cover of *P. arundinacea* to control plots in all years (Table 2).

The fraction of aboveground biomass composed of *P. arundinacea* varied among years (Kruskal–Wallis, $P = 0.013$). Because there were no differences in total aboveground biomass, these fractional differences represent differences in biomass of *P. arundinacea* among treatments. *P. arundinacea* occupied a significantly greater fraction of total aboveground biomass in 2000 than in 1998, while 1999 was not significantly different from either year (Table 3). In 1998, DS treatments had a lower fraction of *P. arundinacea* biomass than either control or S treatments (Table 3). The DSE

treatments were not significantly different than control or S treatments ($P = 0.066$), but indicated a trend similar to the DS treatments. There were no differences among treatments for 1999 or 2000.

Seed banks

The seed banks were not different among sites based on number of germinating seeds or richness. There were also no differences based on germination hydrology or water depth sampled at the sites. The sites (pans from each site pooled) had a mean of 10 ± 0.8 species and 2624 ± 758 germinable seeds per m^2 (top 5 cm of soil) in the seed bank. *P. arundinacea* was present in the seed bank of all wetlands. The only species shared between the seed bank and the seed mixture added to treatments were *Alisma plantago-aquatica* and *Juncus effusus*. A total of seven species from the seed bank were present in sampled plots during the study (Table 2).

Discussion

These results show that a relatively small, transient disturbance can set the stage for major community differences in stands of established invasive plant species. Although there are many management studies that examine the effect of catastrophic disturbances on dominance by established invasive plants, fewer show the effects of smaller disturbances. Our study imposed a transient disturbance that was undetectable in the cover of *P. arundinacea* at the end of the first growing season, and only moderately affected aboveground biomass in the first year after disturbance. Our disturbance treatment also had no effect on bare ground in the plots, so the only expected effect was an increase

Table 3. Percent *Phalaris arundinacea* total cover and biomass in each treatment \pm one standard error.

	Treatments				
	C	S	D	DS	DSE
Percent <i>P. arundinacea</i> of total plant cover					
1998, 1999 ^a	97 \pm 1 ^A	95 \pm 2 ^{AB}	71 \pm 9 ^{BC}	74 \pm 6 ^C	65 \pm 8 ^C
2000	98 \pm 1 ^{AB}	100 \pm 0 ^A	97 \pm 1 ^{ABC}	94 \pm 3 ^{BC}	86 \pm 7 ^C
Percent <i>P. arundinacea</i> of total aboveground biomass					
1998	100 \pm 0 ^A	100 \pm 0 ^A	83 \pm 13 ^{AB}	57 \pm 19 ^B	59 \pm 19 ^{AB}
1999 ^b	No treatment effect, 92 \pm 4				
2000	No treatment effect, 97 \pm 2				

Bold superscript letters indicate significant differences (non-parametric multiple comparison test, $P \leq 0.05$) within each row. Abbreviations as in Table 2.

^aYears not significantly different.

^bNot significantly different from 1998 or 2000.

in light at the soil surface for less than one growing season. This small, short-term disturbance was sufficient to assist invasion by native species into plots previously dominated by *P. arundinacea*. Although disturbance or seeding alone did not affect richness or *P. arundinacea*'s dominance of the plant community, these treatments had important interactive effects when combined, and when added to herbivore exclusion. Even three years after disturbance, DS and DSE treatments were significantly richer than control plots.

Under much more intense disturbance regimes, invasibility of *P. arundinacea* (Paveglio and Kilbride 2000) and *Phragmites australis* (Farnsworth and Meyerson 1999) stands increased in richness and diversity due to disturbance alone. Similarly, Burke and Grime (1996) found that invasibility of native grasslands increased with increasing disturbance, as measured by availability of bare ground. Although some have found colonization to be limited by litter and unaffected by living aboveground biomass (Tilman 1993; McIntyre et al. 1995), aboveground biomass is a good indicator of litter production in these systems. As our results show, smaller disturbances can be important in allowing native plants to reinvade established stands of invasive species. Invasion of native species in our study was not affected by bare ground, as there were no differences among treatments. Litter was left in place in all plots, and biomass differences were minimal in the first year, so it seems unlikely that litter affected recruitment of native species. That disturbance alone increased cover of species other than *P. arundinacea* indicates the increased light from canopy removal allowed increased germination and growth of other species.

Disturbed *P. arundinacea* plots exhibit recruitment limitation. Both disturbance and seeding were required to increase richness over controls, although diversity was unchanged. Only seven species from the seed bank were found in the vegetation, supporting a small relationship between vegetation communities and initial seed banks (Galatowitsch and van der Valk 1995; Brown 1998). The majority of species found in the DS treatments were not in the seed bank or seed mix, emphasizing the importance of colonization in structuring wetland vegetation communities (Galatowitsch and van der Valk 1996a, b; Brown 1998). However, most colonizing species were present at low abundance and in few plots, showing the strong effect of numbers of propagules dispersed on plant communities (Tilman 1997). Species that benefited from seeding included *Asclepias incarnata*, *Glyceria striata*, *Hibiscus*

moscheutos, *Leersia oryzoides*, *Lobelia cardinalis*, *Mimulus ringens*, *Scirpus cyperinus*, and *Scirpus validus*. Although some of these species occurred in non-seeded plots, they were either uncommon, or occurred in the last year of the study and may have been dispersed from reproduction in seeded plots. These species are, generally, more tolerant of longer periods of standing water than many of the species that did not establish. Additionally, the year of seed storage may have reduced viability of some species, such as *Carex* spp. (van der Valk et al. 1999).

The interactive effects of disturbance, seeding, and deer exclusion had the greatest impact on invasibility of *P. arundinacea*. Despite the limitations to interpretation by not fully crossing herbivore exclusions with other factors, we believe this study indicates that deer herbivory plays an important interactive role in reducing invasibility of *P. arundinacea* stands. There are five lines of evidence that support our conclusion. DSE treatments had (1) the only increases in plant cover of species other than *P. arundinacea* during the third year relative to controls, (2) higher richness than D plots, while DS did not, (3) five species that occurred in more plots than other treatments, (4) two species that increased in cover over other treatments, and (5) nearly twice the number of species during the first year compared to D or DS treatments. Furthermore, greater variability in DSE treatments may have masked differences between DS and DSE treatments in richness and cover of other plant species that greater replication would have made clear. Species that occurred in more plots as a result of herbivore exclusion were *Carex vulpinoidea*, *Equisetum arvense*, *G. striata*, *H. moscheutos*, and *L. oryzoides*. *A. plantago-aquatica* and *Typha* spp. had increased cover in exclusions, although they occurred in a similar number of plots among treatments. Any effect of deer herbivory on dominance of *P. arundinacea* must be due to selective herbivory of the native plants, due to the lack of difference in aboveground biomass of *P. arundinacea* between C and DSE plots. Evidence of selective browsing of native wetland plants, such as *A. plantago-aquatica*, is often noted for wetlands in this area (C.H. Kellogg, pers. observ.). Altered species composition of plant communities by selective herbivory has been commonly noted (Augustine and McNaughton 1998). Through selective grazing, white-tailed deer can locally remove more palatable woodland forbs, while increasing the prevalence of unpalatable species (Anderson 1994; Balgooyen and Waller 1995; Rooney 1997;

Augustine and Frelich 1998). Exotic pigs in Hawaii selectively eat some native plants (Stone 1985), and an introduced deer facilitates invasion of woodland understory by selective herbivory of native plants in Ireland (Cross 1981). In this study site, the negative effect of deer on native wetland plants may be greater than other sites, due to high densities of deer caused by removal of their historic predators and limited hunting (Reimenschneider et al. 1995).

P. arundinacea appears to be minimally affected by the increased presence of subdominant species. Cover of *P. arundinacea* was not different among treatments, and the small effect on *P. arundinacea* aboveground biomass only occurred during the first year of our study. Despite the limited effect of treatments on *P. arundinacea* cover and biomass, invasibility was increased, as shown by richness and cover of species other than *P. arundinacea*. Although recent vegetation surveys have found that sites with higher richness have more invasive species (Kalkhan and Stohlgren 2000; Stadler et al. 2000), manipulative experiments have found that increased community richness makes communities less invasible (Tilman 1997; Levine 2000). This may indicate that near-monotypic stands of invasive species will be vulnerable to invasion, but these studies do not predict the effect of invasion on the previous occupants of communities. Our results indicate that invasion of a community need not affect the success of previously established aggressive plant species.

Although invasion of *P. arundinacea* has often been directly linked to human disturbance, the indirect effects of humans on *P. arundinacea*'s dominance have not been fully appreciated. Human cultivation as a forage grass is responsible for much of this grass' spread (Marten and Heath 1985). Repeated introductions of different genotypes increase the phenotypic plasticity of *P. arundinacea* populations through differences in root:shoot allocations (Morrison and Molofsky 1999) and differences in growth and reproduction strategies in response to duration of flooding (Conchou and Pautou 1987). These differences favor its establishment following devegetation caused by large variations in water depth and poor water quality (Galatowitsch et al. 2000), which are often anthropogenically induced. In contrast to these well-known, direct effects, this study indicates an indirect positive effect on *P. arundinacea* populations, through human-induced increases in deer populations. Many marshes that are invaded by *P. arundinacea* after anthropogenic disturbances are in areas that have

deer populations much higher than historic levels. Thus, efforts to enrich plant communities in degraded wetlands may require a comprehensive approach that extends beyond the plant communities, and includes the role of selective herbivory of non-invasive plants.

Our study emphasizes that prediction of invasive species persistence in a community is complex. In freshwater marshes, disturbance, herbivory, and propagule dispersal interact to control invasibility of established communities of *P. arundinacea*. Lack of invasion in S treatments show that *P. arundinacea* is not invasible without disturbance, confirming our first hypothesis. Our second hypothesis, that richness and diversity would increase from C to DSE plots, was disproved by the complexity of interactions among the three factors of our study. Although richness generally increased in the manner expected, diversity was unaffected by the treatments. Lack of differences in aboveground biomass among treatments refuted the expectations of our third hypothesis. Differences between our expectations and results, for diversity and biomass, are due to the lack of effect of increasing richness on *P. arundinacea*. Although *P. arundinacea* was unaffected by our treatments, other native wetland plants benefited from the combination of disturbance, increased propagule dispersal, and reduction in herbivory. Three years after disturbance, the increased richness of DSE treatments appears unchanged, although increasing abundance of *P. arundinacea* as a percent of total cover may signal that some species will be excluded in the near future. Because of the beneficial impacts of humans on *P. arundinacea*, and the ability of this invasive grass to withstand invasion, it is unlikely that any disturbances, other than catastrophic manipulations typical of active management, will affect the long-term abundance of *P. arundinacea* in freshwater marshes. However, our results show that even without a measurable effect on dominant, invasive plants, small disturbances can positively affect the abundance of native wetland species. Thus, our results indicate that seeding and reduction of herbivory can be useful additions to disturbance in active management of *P. arundinacea*, and may be generally applicable to invasive plant species.

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