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Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth

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Abstract *Phalaris arundinacea* (Poaceae) is aggressively invading wetlands across North America. We tested the hypotheses that open canopies and increased nutrients facilitate vegetative establishment in the field, using a phytometer (6 rhizome fragments/plot, 24 plots/wetland). In each of three wetlands, phytometers received three levels of an NPK fertilizer or served as controls. Emergence and survival differed among sites (P=0.0005), but not due to NPK addition. *P. arundinacea* survival was highest in a wet prairie with a late-developing canopy, but limited by prolonged flooding in one sedge meadow and by an early-growing, dense plant canopy in a second. These patterns were explained in greenhouse experiments, where both flooding (P<0.0001) and heavy shade (P=0.0002) decreased *P. arundinacea* aboveground biomass by up to 73% and 97%, respectively. Rhizome fragment survival was reduced by 30% under flooded conditions and 25% under heavy shade. We then tested the hypothesis that a clonal subsidy facilitates vegetative expansion into heavy shade. Established clones were allowed access to bare soil under four levels of shade and two levels of NPK fertilizer in a two-factor greenhouse experiment. Young ramets attached to parent clones readily grew into heavy shade, and the high nutrient treatment increased aboveground growth (P<0.0001) and distance of ramet spread (P=0.0051) by nearly 50%. Under low nutrient conditions, root biomass increased by 30% (P<0.0001). *P. arundinacea*'s rapid expansion into a variety of wetland types is likely a function of clonal subsidy, morphological plasticity, and nutrient availability: young ramets that emerge under shaded conditions are supported by parental subsidies; where nutrients are plentiful, *P. arundinacea* can maximize aboveground growth to capture more light; and where nutrients are scarce, it can increase belowground foraging.

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Introduction

It is widely accepted that invader attributes, community characteristics, and environmental conditions determine whether or not an exotic plant species can invade a new habitat (Groves 1986; Mooney and Drake 1986), but few studies test invader establishment in multiple communities under different growing conditions. The invader's genotype, mechanism of seed dispersal, germination requirements, reproductive capability, competitive ability, or climatic requirements might favor invasion (Baker 1965; Rejmanek and Richardson 1996; Molofsky et al. 1999), or the plant community's disturbance regime, native vegetation, or abiotic conditions, such as nitrogen (N) or phosphorus (P) availability might influence invasibility (Crawley 1987; Huenneke et al. 1990; Burke and Grime 1996; Lonsdale 1999). Recent experimental introductions have demonstrated that the invader, environment, and community interact to determine invasion (D'Antonio 1993; Robinson et al. 1995; Amsberry et al. 2000). Thus, the ability of an invasive species to invade should vary spatially and temporally, along with environmental conditions and plant community attributes (Davis et al. 2000).

Invaders that reproduce vegetatively (clonal species) generally have a greater ecological impact on native communities than non-clonal species (Pysek 1997), but the relationship between a clonal species' ability to establish and its ability to expand is rarely explored. Once established, some clonal species can persist and spread into conditions that are more stressful than those where it colonized (D'Antonio 1993). For example, *Phragmites australis* (Cav.) Trin. has few viable seeds, but ramets readily spread into saline soils if attached to parent clones (Amsberry et al. 2000). For clonal species, few studies have investigated invasion via vegetative fragments (stem or rhizome fragments),

and there remains a large gap in our knowledge of the conditions required for vegetative propagule establishment and spread (Pysek 1997). Advancing our understanding of the relationships among clonal invaders, community and environment is particularly important for communities that are commonly exposed to propagules (e.g., wetlands with inflowing water).

Wetlands surrounded by agriculture or urban development are often subject to increased surface runoff and eutrophication (Neely and Baker 1989). Elevated levels of N, P, or N+P enhance the spread of some clonal species (Aerts and Berendse 1988; Bobbink et al. 1988). Woo (2000) added 12.5 g N+1.4 g P+5.3 g K m^{-2} $year^{-1}$ in five applications to a sedge meadow invaded by *Typha×glauca* Godr., which doubled invader aboveground biomass and increased its rate of spread into the sedge meadow remnant.

Aggressive clonal invaders, such as *Phalaris arundinacea* (Reed canary grass, Poaceae), not only penetrate but also replace the native species (Apfelbaum and Sams 1987; Barnes 1999). Although native populations of *P. arundinacea* were present in North America at the time of European settlement, it is generally believed that the invasive form is a hybrid with exotic European genotypes (Galatowitsch et al. 1999). This rhizomatous grass has a broad distribution (Anderson 1961) and commonly invades freshwater wetlands in North America (Galatowitsch et al. 1999), where it rapidly dominates and reduces native species richness. For example, Spuhler (1994) found that stands of *P. arundinacea* had 1/3 to 1/4 of the species found in adjacent sedge meadows, and in two sites *P. arundinacea* had formed complete monotypes. Similarly, at Greene Prairie in the University of Wisconsin-Madison Arboretum, Werner (2001) showed that areas invaded by *P. arundinacea* had 9–11 fewer species per square meter than the adjacent wet prairie community. We selected *P. arundinacea* for study because it exhibits many of the characteristics of a model invader, such as rapid growth (Marten and Heath 1985), high reproductive capacity and tolerance to a wide range of environmental conditions (Coops et al. 1996).

We address two general questions: what factors influence *P. arundinacea* rhizome fragment establishment (i.e., survival and growth) and how do shade and nutrient additions affect clonal expansion? In three southern Wisconsin wetlands, we employed a phytometer (standard planting of *P. arundinacea* rhizome fragments; Maurer 2001; Clements 1933 in Gaudet and Keddy 1995) to test the hypothesis that NPK addition (hereafter "nutrients") increases *P. arundinacea* establishment. After showing that establishment differed among wetland plant canopies, we designed greenhouse experiments to test the hypotheses that rhizome fragment survival and growth are reduced by heavy shade, flooding and soil type. Finally we tested the hypotheses that attachment to a parent clone (clonal subsidy) enhances invasion into heavy shade, especially where nutrients are added.

Materials and methods

Field sites

In May 2000, we selected three urban wetlands in the Yahara River Valley in Dane County, Wisconsin, with areas of native non-woody vegetation near existing stands of *P. arundinacea*. We avoided sites with flowing water that might bring propagules into treatment plots. Gardner Marsh (47°50′N 81°63′E), mean elevation 258 m, is a sedge meadow over a marl soil (Michaud 1994) surrounded by urbanization and exposed to increased surface water runoff and nutrient loading (Bedford et al. 1974). Large *P. arundinacea* clones extend from higher elevation shrub-covered areas into the wet meadow vegetation adjacent to the study site and small *P. arundinacea* clones grow throughout the meadow. Greene Prairie (46°54′N 80°60′E), mean elevation 285 m, is a 50-year-old restored wet mesic prairie with a Colwood Silty Loam soil type (Glocker and Patzer 1978). A 3-ha, nearly monotypic stand of *P. arundinacea* dominates lower Greene Prairie, which receives storm water runoff from a residential area to the northwest. Pheasant Branch Marsh (49°86′N 79°57′E), mean elevation 197 m, is a wet meadow historically surrounded by agriculture until the 1950s when urbanization became rapid (Bedford et al. 1974). The soil type is Houghton Muck (Glocker and Patzer 1978) above peat. Berms surrounding two storm water detention ponds adjacent to the marsh support clones of *P. arundinacea*.

Average monthly rainfall in May, June, July, and August in Dane County, Wisconsin is 8.0, 9.3, 8.6, and 10.3 cm, respectively (NWS data from 1961–1990, Dane County Regional Airport) (NOAA 2000). May and June 2000 were uncommonly wet, with 16.5 and 12.6 cm more precipitation than average. Estimated temperatures during the summer months ranged from a mean monthly low of 9.28°C in May to a high of 26.5°C in August (NOAA 2000).

Experimental design

In each of three study sites, four 7×12 m blocks were delimited near the *P. arundinacea* invasion front. The horizontal and vertical position of each plot was recorded with a high precision GPS unit (Leica 530) accurate to less than 5.0 cm horizontally and vertically. Each block contained six 1.5×2.0 m experimental units with a 2-m buffer between units to reduce the chance of contamination between treatments described below. Only the central 0.5×0.25 m area of each unit was used for data collection. This central area was divided into two 0.25 m^2 plots, one planted with *P. arundinacea* rhizome fragments and the other left unplanted. Plots planted with *P. arundinacea* were used to quantify the effects of nutrient addition on *P. arundinacea* establishment and growth. Unplanted plots were used to measure percent light transmission at ground level beneath the native canopy.

Three fertilizer treatments were randomly assigned to plots in four blocks for a total of eight replicates/treatment/site. A commonly available, granular lawn fertilizer (Ideal Lawn Food) with a 9 N:1 P:4 K ratio (elemental) was hand broadcast biweekly in five equal applications (4 in Pheasant Branch) at two of three sites (due to prolonged spring flooding, treatments were not applied in Gardner Marsh). Treatments were: control (C=no nutrient addition); low (L=15.65 g N+1.72 g P+6.54 g K $m^{-2}year^{-1}$); and high (H=78.25 g N+8.69 g P+33.02 g K $m^{-2}year^{-1}$). A portable 1.5×2.0-m quadrat frame was used to delineate the experimental unit during each application. The treatment concentrations and application rates were based on N+P responses (no mortality, increased invader growth and loss of native sedges) found by Woo (2000).

We used rhizome fragments rather than axillary buds to test invader establishment because rhizomes had higher rates of emergence in the greenhouse (Maurer 2001). All *P. arundinacea* rhizome fragments were collected from Wingra Fen at the University of Wisconsin-Madison Arboretum on 16 March 2000 and stored cold in peat until planted in the field on 6 and 7 May. Six rhizome

fragments with a sum weight of 11.0–12.0 g (each ~10 cm long with at least one bud and 2–6 fibrous roots) were planted vertically, 3.0 cm below the soil surface, in a circular grid in each plot. Where *P. arundinacea* tillers did not emerge within 2–3 weeks, one ramet from an adjacent plot was transplanted so that each plot had at least one visible tiller before the first fertilizer application on 24 May. Before fertilization application, plots were thinned to 2–3 ramets per plot as necessary to reduce intraspecific competition and make plots uniform in the number of *P. arundinacea* transplants. Because *P. arundinacea* survival and growth were unexpectedly low in all sites, light measurements in both unplanted and planted plots were used to assess light transmission below the native canopy.

For each *P. arundinacea* rhizome transplant that emerged, we measured survival and number of tillers/rhizome every 2 weeks. Harvest occurred on 31 July at Pheasant Branch (due to high *P. arundinacea* mortality, aboveground biomass was not assessed) and from 25–31 August 2000 at Greene Prairie. Flooding and poor survival precluded harvest in Gardner Marsh. Aboveground biomass of *P. arundinacea* and the native species were clipped to ground level and dried at 60°C to constant weight. *P. arundinacea* roots could not be separated from those of other species and were not collected.

Field conditions

Light transmission through the plant canopy above the litter layer was measured with a digital LUX meter (model INS DX-100) attached to a 50-cm rod and pushed under the canopy. Light measurements were taken on 24 May, 5 July and before harvest in the center of each plot at high noon on clear days.

On 18 May 2000, we collected two soil cores (2-cm diameter×20-cm depth) from each experimental unit. Soil cores from two experimental units in the same block were combined and homogenized as one sample for a total of 12 samples/site. Soil samples were dried at 60°C and analyzed for percent organic matter, pH, nitrate, ammonium, available P and K at the University of Wisconsin-Madison Soil Plant and Analysis Laboratory On 27 July 2000, soil redox potentials at 5- and 20-cm depths below the soil surface were measured following the methods of Faulkner et al. (1989) in a stratified random design (4 measurements/depth/block, 4 blocks/site) for a total of 16 measurements/depth/site.

Water-table depths relative to the soil surface were monitored approximately weekly with 15-cm diameter open wells (1–3/site). Wells were dug to a depth of approximately 50 cm with a post-hole digger (Carpenter 1990). Water-table depths relative to the soil surface were measured with a hollow metal cylinder fastened to a flexible measuring tape, which was lowered until contact with water.

Percent cover of native vegetation in Greene Prairie and Pheasant Branch was visually estimated in 0.25-m^2 plots before harvest with nine classes that followed a log-two scale (e.g. 0.5, 1, 2...32, 64, >64%). Gardner Marsh was not sampled due to prolonged flooding.

Statistical analysis

The SAS statistical program was used for all statistical analyses (SAS Institute 1996). A nested design was used in PROC MIXED to compare percent light transmission, soil type, redox potential, and *P. arundinacea* survival among sites (fixed effects). Light transmission in July was log transformed. Water-table depths among sites were compared qualitatively. A repeated measures analysis was used with a standard autoregressive order one error to test the effects of fertilization, time, and fertilization × time on mean number of *P. arundinacea* tillers/rhizome. The SLICE command was used to test for treatment effects on individual sampling dates. A general linear regression model (PROC GLM) was used to test for effects of block and nutrient addition on average *P. arundinacea* aboveground biomass/rhizome and mean native aboveground biomass/plot. Residual plots were used to assess the assumptions of normality and homogeneity of variance. Number of *P. arundinacea* tillers/rhizome was square root transformed and native aboveground biomass in Greene Prairie was log transformed. *P* values represent transformed data. Means and standard errors (SE) in the text and graphs represent untransformed data. *F* statistics were considered significant at α=0.05.

Greenhouse experiments

Unless otherwise indicated, rhizomes (1.0–3.0 g wet and 3–6 fibrous roots) were planted in Scott's Metro Mix. Experiments were conducted under natural light conditions and watered every other day with tap water to maintain a moist substrate. Roots were washed over a no. 10 mesh screen and biomass was dried to a constant weight at 60°C before weighing.

Effect of shading

The effects of shading on invader survival and growth were investigated with a complete randomized block design with four levels of continuous shading under black polypropylene shade cloth: 0, 47.5±0.4, 61.2±0.2, and 85.5±0.3%, respectively (n=10, ±1 SE). The 47% and 85% shade treatments were similar to mean percent light transmission measured 3 weeks after planting in Greene Prairie and Pheasant Branch, respectively. Each treatment had 8 replicates (4 replicates per block) for a total of 32 experimental units.

P. arundinacea ramets, 26 days old (started from rhizomes collected 16 March 2000), were pruned to 5.0 cm above- and 10 cm belowground and were transplanted on 4 July into 16-cm-diameter by 16-cm-deep pots. A shade tent (60 cm tall, 16 cm diameter) was erected around each pot. Plants were equally fertilized biweekly with Osmocote fertilizer (18 N:6 P:12 K). After 28 days, we recorded survival and harvested below- and aboveground biomass.

Effects of soil type and water depth

A complete randomized two-factor design was used to test the effects of soil type and water depth on *P. arundinacea* survival and growth. Soil types were: Marl (collected from Gardner Marsh), Colwood Silty Loam (Greene Prairie), and Houghton Muck (Pheasant Branch Marsh). Water-depth treatments were: moist (watered daily), surface (water depth maintained at the soil surface), and flooded (water depth maintained 6.5 cm above the soil surface). Nine treatments had 10 replicates each for a total of 90 experimental units.

Soils were collected from the top 30 cm in 4–6 randomly selected locations within each study site. Each soil type was homogenized and evenly distributed in 14-cm-diameter, 15-cm-deep pots. Ninety ramets of approximately the same age were pruned to the soil surface and transplanted into these pots on 7 July. Pots were placed in 3.8-l plastic containers with outlets at appropriate levels to maintain the water-level treatments. Average low and high water and soil temperatures were measured in 30 experimental units on 19 July (~coolest day) and 22 July (~warmest). *P. arundinacea* survival was recorded after 1 month when plants were harvested for above- and belowground biomass.

Effects of shading and nutrients on clonal expansion

To examine the effects of shade and nutrient availability on clone growth and expansion, we used a complete randomized two-factor block design with four shade levels: 0, 47.5±0.4, 65.5±0.6, and 85.5±0.3% (n=10,±1 SE) and two nutrient additions (9 N:1 P:4 K), applied three times, biweekly: low (no nutrient addition) and high (46.95 g N+5.15 g P+19.6 g K m^{-2} $year^{-1}$, same application rate as in the field experiment). "Parent" clones, approximately 3.5 months old, were blocked by plant age (1-week difference in emergence of first tiller) and transplanted into Conetainers (6.4 cm

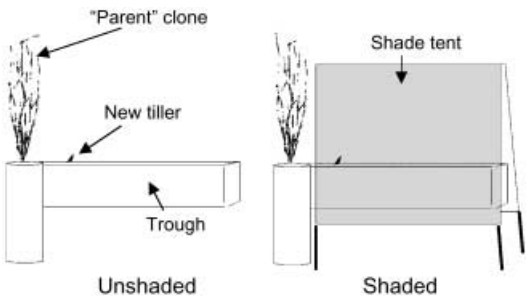

Fig. 1 Experimental unit of the clonal expansion experiment. Conetainers with "parent" clones were attached to troughs filled with substrate. New tillers were allowed to spread laterally into the troughs. Troughs were shaded with shade tents and fertilized with high- or low-nutrient treatments. Parent clones were not shaded

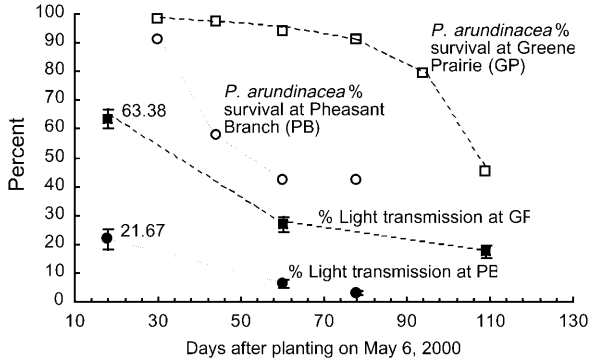

Fig. 2 Survival of *Phalaris arundinacea* rhizomes with at least one tiller in Greene Prairie (–□–) and Pheasant Branch (–○–) (n=24) and mean % light transmission at ground level in Greene Prairie(–■–) and Pheasant Branch (–●–) (n=48, *error bars*=±1 SE)

diameter×25 cm deep) attached to plastic-lined, aluminum troughs (40 cm long×6.0 cm wide×10.0 cm deep) (Fig. 1). Troughs were filled with Metro Mix and functioned as vacant spaces for the spread of new ramets. Troughs were completely shaded by shade tents (45 cm long×30 cm above the trough). The parent clone was not shaded. Nutrient treatments were applied to moist soil, the first application was applied 4 days after clones were transplanted. Eight treatments were replicated 4 times for a total of 32 experimental units.

Seven weeks after planting we measured the number of tillers inside the troughs, distance of the farthest tiller from the parent clone, total number of tillers and total stem length (with tallest leaf extended) per clone. On 20 November, we collected biomass from inside the trough and separated it into shoots (tillers+rhizomes) and roots. Starting biomass of clones could not be measured non-destructively, so increases in total stem length and total tiller number were used to estimate the growth of each clone. Average high and low soil temperatures were measured 5 cm below the soil surface before watering on 19 October and 8 November (n=32).

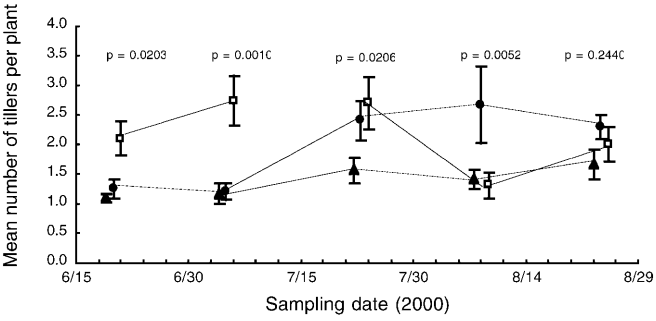

Fig. 3 Mean number of tillers per plant in high (□), low (●) and control (▲) treatments in Greene Prairie (n=8, *error bars*=±1 SE). ANOVAs for each sampling date (P values shown at the top) were used to compare treatment means on each date

Statistical analysis

The SAS statistical program was used for all analyses (SAS 1996). With a general linear model, type I error was used to determine the significance of covariables and type III error was used to test for main effects and interactions. Where appropriate, least significant difference (LSD) was used to compare treatment means. Residual plots were examined to assess the assumptions of homogeneity of variance and normality. The F statistic was considered significant at α=0.05. Although some data were transformed to meet the assumptions of statistical analysis, text and figures represent untransformed means and standard errors. For analysis of the soil type by water level experiment, total biomass was log transformed and aboveground biomass was log(y+1) transformed. Aboveground and total biomass in the shade experiment were log transformed. In the clonal expansion experiment, total stem length, change in tiller number and number of tillers that spread into each trough (tillers/trough/clone) were square root transformed; root biomass and the root:shoot ratio were log transformed.

Results

Rhizome fragment establishment differed among wetlands

P. arundinacea planted in Gardner Marsh had the highest emergence (38%) 20 days after planting, but only 9 of the plants that emerged survived to the end of July. *P. arundinacea* emergence was 57% greater in Greene Prairie than in Pheasant Branch by the end of July (Table 1). Of the individuals that emerged at Greene Prairie, 91% survived for 78 days, more than twice the rate at Pheasant Branch and Gardner Marsh (P=0.0005) (Fig. 2). The effect of nutrient addition on number of *P. arundinacea* tillers/plant in Greene Prairie was marginally significant (P=0.075). Repeated measures analysis showed that there was a significant treatment by time interaction (P=0.0005) and a significant effect of time (P=0.006) on number of tillers/plant. Mean number of tillers/plant in the high nutrient treatment was significantly greater than that in the control in June and July, but not August (Fig. 3). Nutrient addition did not affect *P. arundinacea* aboveground biomass/plant [control (C)=0.21±0.02 g, low (L)=0.28±0.04 g, high (H)=0.27±0.05 g, P=0.17] or native plant aboveground biomass/plot at Greene Prairie (C=143.0±9.9 g, L=156.9±9.1 g, H=153.4±16.7 g, P=0.86) or Pheasant Branch (C=144.9±6.6 g, L=185.5±16.9 g, H=157.5±14.7 g, P=0.067). We observed many torn leaves and severed tillers, possibly due to herbivory, and few shoots grew above the native canopy.

Table 1 Number of *Phalaris arundinacea* rhizome fragments in each of three wetland study sites that produced at least one tiller

Study site	Rhizomes planted	Number of rhizome fragments with at least 1 tillen[a]			
		5/26	6/6	6/23	Total
Greene Prairie	143	45	66	71	79
Pheasant Branch	143	31	32	33	34
Gardner Marsh	144	55	Flooded	Flooded	55

[a] Sum of rhizome fragments with at least one living tiller observed up until the date indicated. The total number of plants that emerged was recorded on 24 July 2000

Table 2 Analysis of variance (ANOVA) of differences in mean soil parameters among three study sites (n=12) (site means±1 SE)

	Greene Prairie	Gardner Marsh	Pheasant Branch	*F* statistic	*P* value
pH	7.03±0.03	7.78±0.10	7.39±0.05	10.56	0.0044
Percent organic matter	6.25±0.28	6.29±0.11	4.88±0.17	6.15	0.0208
N as nitrate (ppm)	4.26±0.30	9.01±0.50	4.06±0.54	24.68	0.0002
N as ammonium (ppm)	9.17±1.13	5.54±0.53	13.49±0.54	44.85	<0.0001
Available P (ppm)	2.00±0.00	2.00±0.00	33.17±1.58	143.01	<0.0001
Available K (ppm)	62.25±1.30	11.92±1.19	69.67±2.93	88.98	<0.0001

Native plant canopies affected light conditions

The Greene Prairie canopy had 60% greater average light transmission on 24 May (P<0.0001) and 5 July (P=0.0004) than that at Pheasant Branch. *P. arundinacea* survival was lower in Pheasant Branch and tended to decline in both sites as light transmission declined (Fig. 2). Light was measured in Gardner Marsh only on 24 May when percent transmission averaged 63.61±4.5%. Thereafter, water levels were greater than 25 cm above the soil surface, precluding light measurements at ground level.

At the time of planting, the native plant canopy in Pheasant Branch was taller (~20 cm taller) and had greater cover than that in Gardner Marsh or Greene Prairie. The most common species found in Pheasant Branch (*Aster puniceus* L., *Carex stipata* Muhl., *C. stricta* Lam., *Impatiens capensis* Meerb., *Rumex orbiculatus* A. Gray., and *Eupatorium maculatum* L.) were early- and mid-successional, fast growing species that emerged early in the growing season. Species that were common in Greene Prairie (*Silphium terebinthinaceum* Jacq., *Rudbeckia subtomentosa* Pursh., *Andropogon gerardii* Vitman, and *Schizachyrium scoparium* (Michx.) Nash.) emerged later in the growing season.

Soil characteristics and water-table depth differed among wetlands

Soil characteristics (Table 2) and redox potential (P<0.0001) differed among sites. Gardner Marsh soil, which had been inundated for 55 consecutive days (Fig. 4), had the lowest mean redox potential at 5-cm (127.6±32.4 mv) and 20-cm depth (55.8±38.7 mv). Greene Prairie had the highest mean redox potential (5-cm depth=590.4±12.8 mv and 20-cm depth=560.7±23.0 mv), and had the lowest water-table depth (Fig. 4).

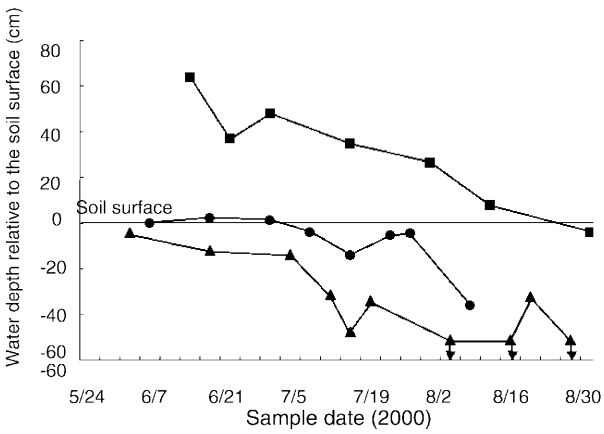

Fig. 4 Mean depth of water table relative to the soil surface in Gardner Marsh (–■–), Pheasant Branch (–●–), and Greene Prairie (–▲–). *Arrow*=dry well

Pheasant Branch mean redox potentials at 5-cm and 20-cm depths were 470.5±39.8 mv and 418.4±29.7 mv, respectively.

Heavy shade limited rhizome fragment survival and growth in the greenhouse

After 28 days, survival was 1/4 less in the 85% shade treatment than that in the other treatments with 100% survival; 1/2 of the plants that survived the 85% shade treatment were yellowing with dead tissue after 4 weeks. Shading decreased *P. arundinacea* aboveground biomass and total biomass per plant (P<0.0001). Mean aboveground biomass/plant in the 85% shade treatment was approximately 1/40 that of the 0% shade treatment and showed a near linear relationship with shade level (Fig. 5). A similar pattern was found for total biomass;

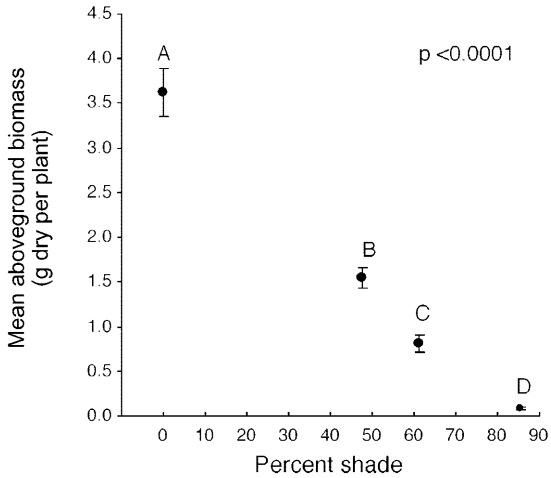

Fig. 5 Mean aboveground biomass produced under four shade levels; 0, 47.5, 61.2 and 85.5% 4 weeks after planting (*n*=8) (*error bars*=±1 SE). Means with the same letter are not significantly different (LSD=0.355). Shade accounted for 67.0% of the variability

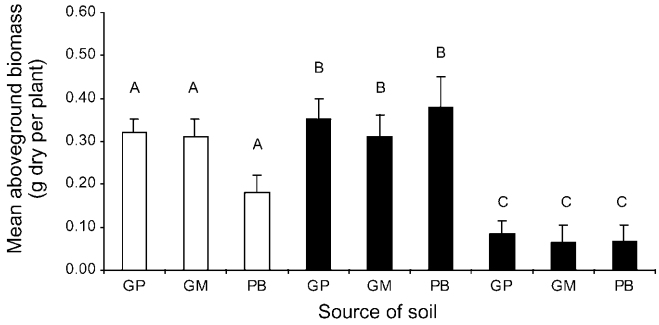

Fig. 6 Mean aboveground biomass of plants in three water depths and three soil types (*n*=30). Water treatments were: moist (*white bars*), surface (*gray*), and flooded (*black*). Soil types were from: Greene Prairie (GP), Gardner Marsh (GM), and Pheasant Branch (PB) (*n*=10) (*error bars*=±1 SE). Water-depth treatments with the same letter are not significantly different

mean total biomass/plant was 4.82±0.39 g, 1.99±0.14 g, 1.20±0.12 g, and 0.41±0.05 g for the 0, 47, 61, and 85% treatments, respectively. Two covariables, stem length before clipping and starting tiller number, were positively related to *P. arundinacea* total and aboveground biomass growth.

Flooding reduced survival and growth in the greenhouse

As hypothesized, flooding decreased *P. arundinacea* survival and growth, but soils with significantly different properties did not affect establishment. In a two-factor experiment, *P. arundinacea* mortality was 20% in the flooded, 3.3% in the moist and 0% in the surface-water treatments. Mean aboveground biomass/plant was 1/5 to 1/3 as high in the flooded treatment as in the surface and moist treatments (Fig. 6). Mean total biomass in the flooded treatment was 0.35±0.03 g, significantly less (P<0.0001) than the surface (0.89±0.06 g) and moist (0.85±0.06 g) treatments. There was no effect of soil type on aboveground biomass (Fig. 6) or total biomass (P>0.1), and there were no significant interactions (P>0.10). Average water temperatures were 17.8°C±0.09 (low) and 29.9°C±0.22 (high); soil temperatures were 18.0°C±0.08 (low) and 29.9°C±0.17 (high).

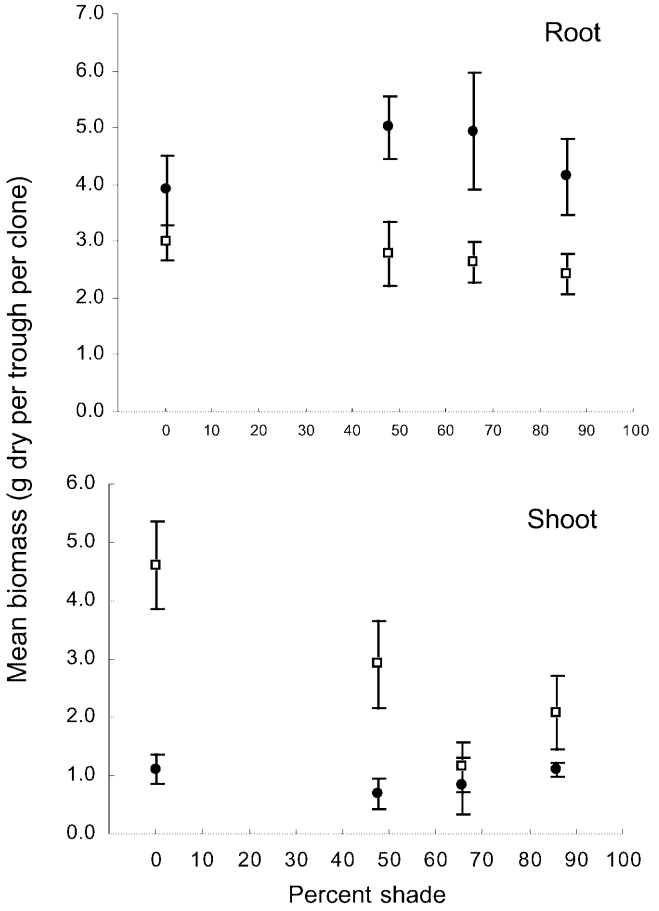

Fig. 7 Mean root biomass (*top*) and shoot biomass (*tillers+rhizomes*) (bottom) in high (□) and low (●) nutrient treatments among four shade treatments (*n*=4) (*error bars*=±1 SE)

Nutrient addition enhanced clone expansion into heavy shade

Nutrient addition had a significant positive effect on clone growth in this two-factor experiment. The average increase in total stem length/clone with high nutrient addition was 1,509.6±96.1 cm compared to 849.9±59.6 cm without nutrient addition. Additionally, mean increase in number of tillers/clone in the low nutrient treatment was approximately 1/2 (12±1.4 tillers) that of clones in the high nutrient treatment (21±1.5 tillers). Increases in total stem length and number of tillers were not affected by shade (P=0.159 and P=0.177, respectively).

Nutrients significantly affected the root:shoot ratio of new tillers that spread into each trough; root: shoot ratios

were 3–15 times greater in the low than the high nutrient treatment ($P<0.0001$). Mean tiller root biomass/trough was greater in the low than the high nutrient condition ($P=0.0001$), but shading had no effect ($P=0.762$) (Fig. 7). Nutrient addition ($P<0.0001$) increased mean tiller shoot biomass/trough by nearly 3 times that of unfertilized clones (Fig. 7). Conversely, shading significantly decreased mean tiller shoot biomass/trough ($P=0.0063$) compared to the 0% shade treatment. Nutrient addition did not affect the mean total biomass of tillers/trough ($P=0.1245$). The mean number of tillers that spread into each trough was greatest under the 0% shade treatment (5.1±1.4 tillers), but LSD showed that 47% (4.1±0.9 tillers) and 85% (3.8±0.9 tillers) shade treatments were not significantly different. Nutrient addition more than doubled the mean number of tillers that spread into the troughs (5.7±0.7 compared to 2.1±0.2 tillers) ($P<0.0001$) and maximum distance of spread increased by 50% with nutrient addition (8.05±1.08 cm vs 3.94±1.05 cm) ($P=0.0051$). Shade did not significantly affect tiller expansion ($P=0.0832$). Mean greenhouse temperatures were 18.12±0.33°C (low) and 27.87±0.88°C (high); mean soil temperatures were 16.3±0.14°C (low) and 31.5±0.33°C (high).

Discussion

What causes differential invasion by *P. arundinacea*?

Our findings are consistent with the conclusion that establishment of rhizome fragments was limited by flooding in Gardner Marsh (16% survival) and by the dense canopy of Pheasant Branch Marsh (42% survival). At the end of July, Greene Prairie had the highest survival (91%), and half of those plants survived to late August (Fig. 2). Even though the soils of the three wetlands differed in several parameters, *P. arundinacea* grew equally well in all three soil types in the greenhouse. Since neither soils nor nutrient addition explained differences, we attributed the higher establishment of *P. arundinacea* in Greene Prairie to drier conditions and later canopy development. Differential establishment of vegetative propagules is related to differential shading and flooding.

For rhizomes that survived, nutrient addition substantially increased tillering; the high treatment producing nearly twice as many tillers as the control plots in late June and July at Greene Prairie (Fig. 3); similarly, tiller production of clones in the greenhouse was increased by high nutrient additions. In many clonal plants, meristem production is positively related to resource availability (Watson et al. 1997). Elevated levels of nitrogen have been shown to activate lateral bud growth and cause tiller and ramet formation in many clonal species (McIntyre 1967; Hutchings and Mogie 1990). Likewise, greenhouse and other studies (Wetzel and Van der Valk 1998; Green and Galatowitsch 2001) have shown that nutrient addition increases the growth and spread of young *P. arundinacea* clones. In our study, *P. arundinacea* produced more tillers in the high nutrient treatment in the greenhouse, but not in the field experiment. At least two factors might have made detection of an aboveground response difficult in the field. Herbivory and physical damage on young ramets reduced sample size and removed tissue that could not be accounted for in harvests. The drop in tiller number in high nutrient plots on 8 August may be the result of preferential herbivory by deer or small rodents. Also, *P. arundinacea* may have allocated more resources to below- than aboveground growth when less light was available, as in Morrison and Molofsky (1998). Late in the season, low light transmission through the Greene Prairie canopy may have been more limiting to growth than nutrients.

The negative effect of heavy shade was supported by our greenhouse experiment, where survival was 25% lower and aboveground biomass 20% lower than that of plants in moderate shade. Similarly, Morrison and Molofsky (1998) found that *P. arundinacea* above- and belowground biomass and average tiller number were significantly reduced in field plots of high vegetative cover. Light availability at the soil surface is largely determined by canopy characteristics, which are in turn influenced by physical disturbance, which is often linked to invasions in established native vegetation (Fox and Fox 1986; Hobbs and Atkins 1988; Burke and Grime 1996). The composition and canopy characteristics of native vegetation contribute to invasibility (Crawley 1987). Lindig-Cisneros (2001) showed that species-rich canopies, particularly those with broad-leaved forbs, reduce light availability in a Wisconsin fen. The early-growing sedges and broad-leaved species of our Pheasant Branch study site developed a complex canopy before *P. arundinacea* transplants emerged, while the grasses and forbs in Greene Prairie emerged later in the growing season. Because plant height is associated with competitive ability for light (Givnish 1982; Gaudet and Keddy 1988), tall native species likely interfered with light capture by *P. arundinacea* propagules. Our data suggest that a dense, closed canopy composed of early emergent, fast-growing species can reduce invasibility.

Hydrological conditions strongly affect wetland plant communities (Keddy 2000). Not surprisingly, *P. arundinacea* establishment probably was limited by prolonged flooding in Gardner Marsh, which was continuously inundated from late May to late July. In the greenhouse, continuous inundation for 28 days reduced propagule growth, and plants that could not grow above the water died. Likewise, Klimesova (1994) found that submerged *P. arundinacea* seedlings had lower total and aboveground biomass compared to seedlings that grew above the water table before flooding, and Rice and Pinkerton (1993) showed that plant height and tiller production were reduced when *P. arundinacea* plants were submerged. Hence, flooding can influence *P. arundinacea* invasion.

How do nutrient addition and shading affect clonal spread?

Morphologically plastic species are capable of "foraging behavior;" the modification of belowground stems, aerial shoots, or roots to increase resource acquisition in response to changes in environmental conditions (Grime 1979; Sutherland and Stillman 1988; De Kroon and Hutchings 1995). Our finding that *P. arundinacea* clones exhibit morphological plasticity in root: shoot ratios and lateral expansion rates adds to earlier data on shoot height plasticity (Marten and Heath 1985) and recent work by Green and Galatowitsch (2001). Our clones allocated approximately 30% more resources to root than shoot growth in low nutrient conditions, but nearly 75% more resources to rhizome and tiller growth than roots in high nutrient treatments, an indication that *P. arundinacea* responds to spatial variability of resources through opportunistic growth. The strategy of spread that a clonal species uses to invade a new area varies with environmental conditions (Hutchings and Mogie 1990). *P. arundinacea* exhibited a "guerilla" strategy (sensu Lovett Doust 1981a) under our high nutrient condition, i.e., *P. arundinacea* spread nearly 50% farther and produced twice as many tillers, and a "phalanx" strategy under our low nutrient condition (fewer tillers closer to the parent clone). In a review of clonal strategies, De Kroon and Schieving (1990) hypothesized that clonal species capable of dominating vegetation year after year in very dense stands combine phalanx and guerilla strategies (a "consolidation strategy") to maintain their position. By producing many tillers next to the parent, *P. arundinacea* may fill and retain space, but the lateral growth of some rhizomes in high nutrient conditions expands the area invaded. The morphological plasticity of clonal growth facilitates invasiveness.

Can clonal subsidies facilitate spread into heavy shade?

In the greenhouse, we found that tillers readily grew into heavy shade when connected to an unshaded parent clone, and that nutrient additions further enhanced vegetative expansion. Physiological integration, the import of carbon, nutrients or water from one tiller to another is common among clonal plants (Pitelka and Ashmun 1985; De Kroon and van Groenendael 1990) and is known to exist in many grass species (Forde 1966b; Ong and Marshall 1974), and possibly *P. arundinacea* (Mittra and Wright 1966). At least in the early stages of new growth, *P. arundinacea* tillers exposed to shaded conditions might have increased survival if attached to a parent clone, as has been demonstrated in understory herbs (Alpert and Mooney 1986), a native tundra sedge (Jonsdottier and Callaghan 1989), and an invasive wetland reed (Amsberry et al. 2000). Support from a parent clone also may decrease the effects of neighbor competition and herbivory on young tillers (Hartnett and Bazzaz 1985; Welker et al. 1985), and might reduce intra-ramet competition (Pitelka and Ashmun 1985). We postulate that *P. arundinacea* maintains vascular connections between parent and daughter tillers, at least in the short term, and that this connection facilitates the support of new tiller growth in heavy shade. It is likely that both the resource subsidy from parent clones and resource foraging plasticity contribute to this invader's ability to spread rapidly into native vegetation.

How can vegetative expansion be managed?

Evaluating the dynamic interactions between model invaders and specific environmental conditions may increase the accuracy of our predictions and improve management in habitats with similar attributes and environmental conditions (D' Antonio 1993). Prevention of *P. arundinacea* invasion and eradication of existing clones is challenging, given that multiple environmental conditions enhance growth and spread, and both the composition and complexity of native plant canopies contribute to invasibility. However, three strategies might slow the establishment of clonal species similar to *P. arundinacea* and reduce clonal expansion.

First, managers should plant or encourage the growth of native species that emerge early in the growing season and rapidly develop dense canopies. In Midwestern wetlands of the United States, such species might include: *Aster puniceus*, *Carex stipata*, *C. stricta*, *Eupatorium maculatum*, and *Impatiens capensis*. Second, one should reduce and/or eliminate the flow of nutrient-rich waters into wetlands to reduce the spread of *P. arundinacea* monotypes and other clonal invaders, such as *T.* × *glauca*. Third, managers should act quickly to eradicate new clones before they spread. The ability of *P. arundinacea* to vary its allocation to root and shoot tissues and their support of new tiller growth into shaded microsites likely increases chances of spread into sub-optimal and variable sites. A modest invasion could expand aggressively with a pulse of nutrients in stormwater. Frequent monitoring and immediate removal of new clones is essential to prevent spread. Hence, continual management is needed to conserve and maintain wetlands that are rich in native plant species.

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