

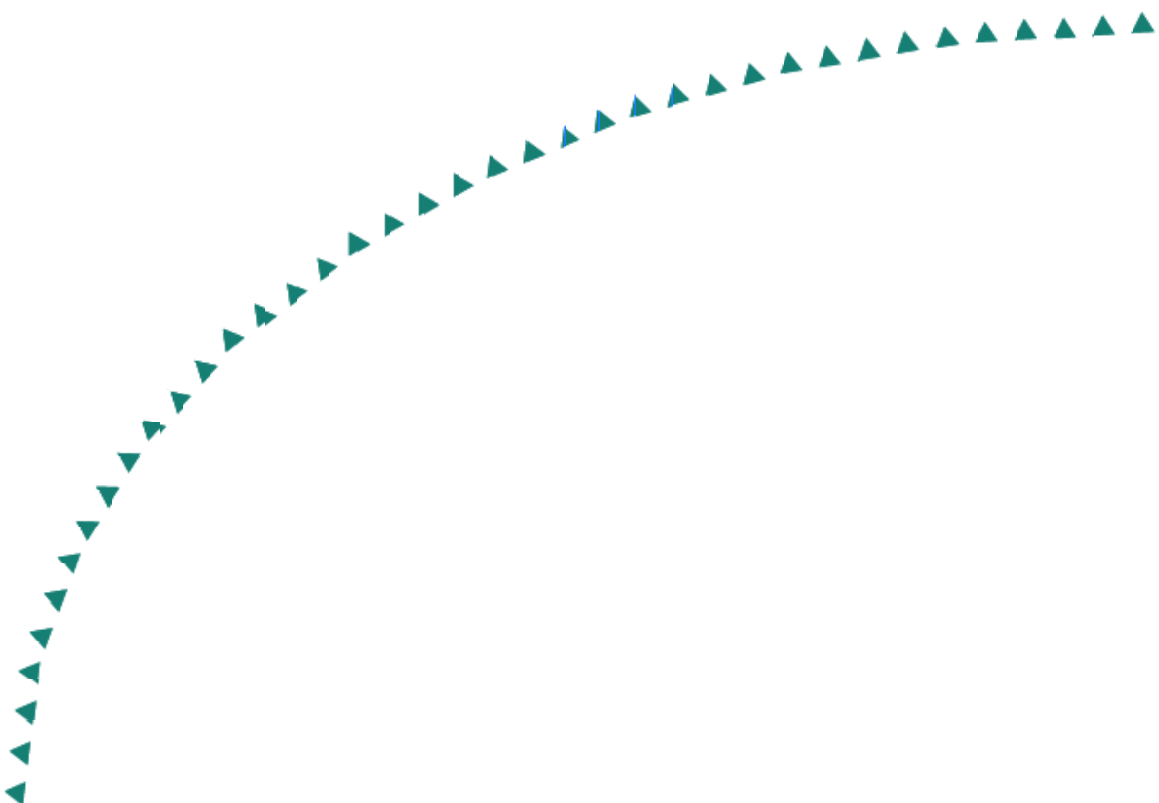
2004-36

Final Report

**Best Management Practices for the
Invasive *Phalaris arundinacea* L.
(Reed Canary Grass) in Wetland
Restorations**



Research



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Final Report

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STATEMENT OF TASKS

Task number	Description	Chapter in this document
1	Task 1: Complete detailed characterization of Arboretum site, including topographic survey and establish plots to be used for treatment trials, summarize characterization of North St. Paul site.	2
2	Task 2: For both sites, on a whole plot level, quantify seed bank, and existing vegetation by cover and above ground biomass.	2
3	Task 3: Select treatments for second season of study and finalize experimental design for the field experiment.	2
4	Task 4: Present preliminary findings at scientific and management meetings	6
5	Task 5: Compile manager survey into a written report.	2
6	Task 6: Conduct experiments on factors that require additional environmental control to be observable.	3, 4
7	Task 7: Analyze effects of control treatments on reed canary grass populations, natural vegetation, and seedbank.	2
8	Task 8: Monitor rhizome carbohydrate levels in reed canary grass rhizome tissues.	2
9	Task 9: Develop site preparation recommendations for North St. Paul sod farm site.	5
10	Task 10: Develop a fact sheet on reed canary grass site preparation for wetland restoration.	5

EXECUTIVE SUMMARY

Invasive species have major impacts on natural environments worldwide. The shift in persistence from many species to fewer species may profoundly alter ecosystem processes and reduce biotic diversity on a landscape scale (1-4). Ecosystem restorations are particularly susceptible to environmental weed invasion because disturbance associated with restoration favors invasive species by providing open sites for establishment (5-7). *Phalaris arundinacea* (reed canary grass), a fast-growing, rhizomatous perennial grass, is a major concern for wetland restorations in the northern US because establishment by *P. arundinacea* often precludes colonization by sedge meadow vegetation in restored prairie pothole wetlands (8-11). *P. arundinacea* also invades natural wetlands, forming monotypic stands and displacing native vegetation (12-14).

This research developed a predictive understanding of *P. arundinacea* dominance in prairie pothole wetland restorations. There were three objectives: 1) to investigate control techniques for reducing existing stands of *P. arundinacea* and the life history factors that contribute to treatment effectiveness, 2) to characterize unconstrained biomass production for an individual *P. arundinacea* plant and apply this knowledge to the understanding of the *P. arundinacea* invasion process, and 3) to determine how the *P. arundinacea* soil seed bank composition affects transition to the post-restoration community of native prairie pothole species. We designed a large-scale split-plot field experiment replicated at two research locations to examine the two most commonly used techniques to control *P. arundinacea* for their effects on *P. arundinacea* populations: 1) spring burning, and 2) glyphosate herbicide applications. Results from the field experiment led to additional greenhouse and mesocosm studies that address inherent species characteristics and how these relate to the invasion process and potential control avenues (Figure E-1).

Three major conclusions emerged from the field experiment. First, herbicide applications significantly reduced *P. arundinacea* biomass, and the effectiveness of the herbicide hinged on the timing of the herbicide application (Conclusion 1 from Figure E-1). Measurements eight months after treatment showed that the mid-May herbicide application reduced *P. arundinacea* to 25% of control levels, but both late August and late September herbicide applications were significantly more effective, and reduced *P. arundinacea* to 10% of control levels. To investigate the relationship between herbicide effectiveness and carbohydrate movement in *P. arundinacea*, we tracked *P. arundinacea* rhizome carbohydrate levels for 3 growing seasons. Carbohydrate content decreased in the spring (April to mid-July) and increased in the later season (mid-August and later), suggesting that the effectiveness of later season herbicide applications is likely due to enhanced translocation of glyphosate to rhizomes in the later season.

Also from the field experiment, we found that a spring burn does not reduce *P. arundinacea* biomass, nor does it enhance the effectiveness of subsequent herbicide applications (Conclusion 2 from Figure E-1). To investigate other ways burning and herbicide treatments might reduce *P. arundinacea* populations, we surveyed seed bank composition before and after the implementation of control techniques in the field experiment, and demonstrated that burning significantly reduces the *P. arundinacea* seed bank, most likely through germination of *P. arundinacea* and subsequent herbicide kill of the germinated seedlings. This reduction in propagule availability may limit recolonization of *P. arundinacea* following successful removal of large stands of *P. arundinacea*.

Although control techniques effectively reduced *P. arundinacea* in the field experiment, even after two rounds of control technique applications, *P. arundinacea* recolonized rapidly, preventing establishment of native species (Conclusion 3 from Figure E-1). To explore the transition between post-control bare ground and native species establishment, we designed a mesocosm experiment to investigate the influence of *P. arundinacea* propagule pressure on the establishment of native sedge meadow species in the context of a newly restored wetland. Results indicated that establishment from a high density of native seeds suppressed *P. arundinacea* growth, and the effect was more pronounced at high seed densities of *P. arundinacea* (>100 seeds m⁻²). However, higher densities of native seeding did not suppress recruitment of *P. arundinacea* from seed, even when *P. arundinacea* was present at 10 seeds m⁻² and native species were present at 15,000 seeds m⁻². Although native species in high propagule density can suppress early growth of *P. arundinacea*, they do not suppress recruitment of *P. arundinacea* individuals from seed.

To assess *P. arundinacea* growth potential and how it relates to mechanisms of invasion, we looked at unconstrained biomass production for *P. arundinacea* in a uniform planting study. We found that *P. arundinacea* grew rapidly compared to other wetland species, producing 132 g plant⁻¹ of aboveground biomass and 333 g plant⁻¹ of below ground biomass in just two growing seasons. Root:shoot ratios revealed that *P. arundinacea* produced proportionally more aboveground biomass during the first 2 months of establishment and proportionally more belowground biomass for the rest of the study. This morphologic plasticity may explain why *P. arundinacea* is so successful at first preempting establishment of other species and then spreading rapidly.

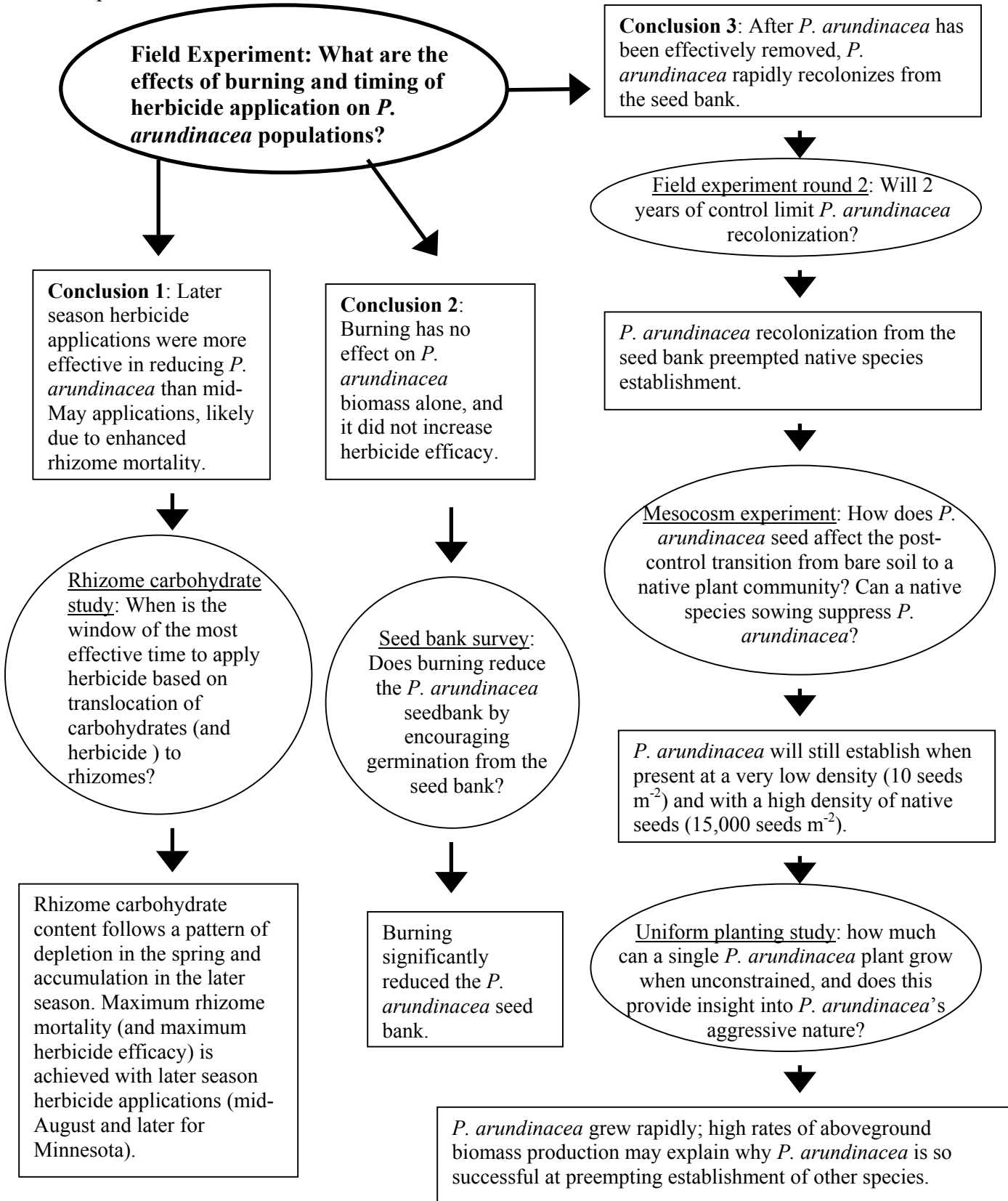
Conclusions and recommendations

Results from this research determined the most effective use of burning and glyphosate herbicide to control existing stands of *P. arundinacea* (burning to reduce the seed bank, and later season herbicide applications to maximize rhizome mortality). However, even 2 years of the most effective use of herbicide and burning are not sufficient to reduce *P. arundinacea* dominance to the point where native species can establish. Recolonization from seed (either on-site in the seed bank or off-site from dispersal) will complicate control techniques. *P. arundinacea* can establish from very low propagule densities (even when native species propagule densities are high), and once established, grows rapidly and in a way that facilitates preemption over other simultaneously establishing species. Long-term management of re-invading *P. arundinacea*, and limiting availability of *P. arundinacea* propagules in the landscape, will therefore be key to successful *P. arundinacea* control.

In summary, our research has demonstrated that the most effective way to control *P. arundinacea* is a combination of later season herbicide applications to maximize rhizome mortality, and burning to reduce the *P. arundinacea* seed bank density. Controlling *P. arundinacea* in the most efficient way is crucial to the establishment of native vegetation in wetland restorations. Reduction of *P. arundinacea* is a long-term process and one that is complicated by potential reinvasion of cleared sites, so control efforts must be as effective as possible. Moreover, *P. arundinacea* is still widely cultivated as a forage crop and planted as a conservation species (15, 16), and these populations may serve as sources of continuing propagule pressure, further complicating localized eradication efforts. The contribution of planted populations to the spread of *P. arundinacea* into natural areas is not well understood, however efforts to restore biodiversity may benefit from practices that reduce *P. arundinacea*

propagule pressure from planted sources (e.g. restricting use of *P. arundinacea* where non-aggressive species could be substituted, and preventing seed set from cultivated populations of *P. arundinacea*).

Figure E-1. A schematic diagram shows the development of the research from the original field experiment. Conclusions are depicted in squares/rectangles, and off-shoot experiments are depicted in circles/ovals.



CHAPTER 1

Introduction

Overview

This report summarizes the research performed at the University of Minnesota in conjunction with technical support from the Minnesota Department of Transportation (MnDOT), Minnesota Department of Natural Resources (DNR), and Ramsey Washington Metro Watershed District (RWMWD) on best management practices for the invasive grass *Phalaris arundinacea* L. (reed canary grass) in wetland restorations. This research was implemented from 1999 to 2004 by Carrie Reinhardt and Susan Galatowitsch. This document serves as the final technical document for the project.

Background of the research problem

More than two decades ago, Bradshaw (17) wrote that “the successful restoration of a disturbed ecosystem is the acid test of our understanding of that ecosystem.” Although he drew attention to the need for rigorous study of barriers to restoration, little research in restoration ecology has been designed to address biotic factors that affect the rate and direction of recovery.

There are several key barriers to ecological restoration. The most obvious barrier is physical site condition, e.g. hydrology and topography, which must be altered to resemble that of the target ecosystem. Although not perfectly understood, this barrier is perhaps the most researched and easily overcome for some ecosystems. Given the proper site conditions, the next most logical barrier to restorations is the establishment of native species that are present in the natural target ecosystem. For vegetation, colonization requires that refugial populations exist on site (e.g. the seed bank) or that colonization will result by dispersal from remote propagule sources. However, even if propagules are available for colonization, successful establishment of those target species faces another barrier: if weeds (or invasive species) are present at the restoration site, colonization of native target species becomes much less likely.

Weeds have historically had major impacts on agricultural systems and currently continue to reduce yields of agricultural crops, although to a lesser degree due to weed control efforts. Weed control research has addressed how to eliminate weeds from agricultural systems for well over a century. A need to achieve crop yields spurred the development of agricultural weed control research. Similarly, the conservation and restoration of natural areas has led to a need to understand the control of invasive species, or environmental weeds. Weed impacts in natural areas progress beyond loss of habitat and biodiversity to regional changes in landscape processes (2, 3, 18).

Experience with the control of agricultural weeds must be applied with caution to the control of environmental weeds (18). For instance, agricultural weed control strategies can often be applied yearly in conjunction with annual cropping practices. One of the challenges presented by environmental weeds is the need for more long-term control strategies, as the ultimate goal for natural and restored ecosystems is to minimize management intervention and create the most self-sustaining ecosystem possible. It follows that perennial environmental weeds are particularly problematic, as these species tend to be persistent. Control efforts are most successful if aspects of the biology of the invader suggest that control techniques employed might be effective (19).

Control of invaders has proven to be costly, emphasizing that effective control strategies must be researched. Mack et al. (19) point out that if we fail to implement effective strategies to

control the damaging impacts of environmental weeds, we risk impoverishing and homogenizing the ecosystems on which we rely to supply us with irreplaceable natural services.

In his review of a special feature on ecological invasions, Kareiva (20) noted that progress in developing a predictive ecology for invasions would speed up if field research on invasions adopts an experimental approach. This research addresses this need by presenting a series of experiments that contribute to the predictive understanding of perennial weeds in restored ecosystems. This research suggests the role of an invasive perennial grass in restored prairie pothole wetlands as a model system for understanding environmental weeds. The model environmental weed, *Phalaris arundinacea* (reed canary grass), is a cool season perennial grass which has been bred primarily for forage purposes throughout the temperate zone. This species preempts the establishment of target native species in prairie pothole restorations. Although some information on the biology and ecology of *P. arundinacea* has been addressed by agronomic breeding research, little attempt has been made to apply this knowledge to investigating possible control techniques and strategies for this species. Incorporating and supplementing this knowledge of the species and applying it to the search for effective control techniques suggests a route for identifying successful control techniques for other environmental weed species.

Ecology of restored wetland ecosystems

Less than half of the wetland area of the 1800s remains today in the US, with losses exceeding 90% in many agricultural regions (21). In an attempt to offset these losses and continued current losses, thousands of wetlands are restored each year.

Restoration ecology deals with management practices aiming at the re-establishment of plant species that are not present at the restoration site. For revegetation to occur, propagules must be available on site (in the soil seed bank), or propagules must disperse to the site by some vector, e.g. wind, water, animals (22). Target species may not effectively colonize (e.g. sedge meadow species in restored prairie pothole wetlands (9, 23, 24), and target grasses in restored species-rich grasslands (22)). Failure to colonize may be due to variable persistence in the seed bank. Some wetland plants (emergent perennials and mud flat annuals) produce abundant and long-lived seed that can persist as viable propagules in the soil for up to twenty years of drainage and cultivation (25). Other species may not survive drainage and cultivation, or may have naturally transient seed banks (26, 27). The natural limitations to dispersal may prevent the availability of propagules to the site, as the dispersal of propagules is essentially random, and there is no certainty that species capable of being established will do so (28). Also, as dispersal corridors are disrupted by anthropogenic barriers, dispersal might not be as reliable as it has been in the past (22, 28).

However even with proper site conditions and availability of propagules, the presence of environmental weeds may prevent natives from establishing. For instance, in North America, environmental weeds severely limit ecosystem recovery of restored wetlands with adequately restored hydrology (9, 29).

Invasion in restored wetlands

Since Elton's book, *The Ecology of Invasions by Animals and Plants* (1958), ecologists have struggled to understand what makes some invasions so damaging while other invasions have negligible effects. The past decade of research has focused on developing a predictive understanding for ecological invasions. Only relatively recently have ecologists focused on two

important questions: 1) what makes a community prone to weed invasion? and 2) what are the characteristics of a successful invader?

Life history characteristics of the invader undeniably play a crucial role in understanding the mechanisms of invasion. Several life history characteristics have emerged as typical of weed invaders. Perennial species may be more likely to be successful invaders because they tend to be more persistent (5, 6). Examples of problematic perennials abound in the literature. For example, Australian Northern Territory wetlands are threatened by several clonal perennial pasture grasses that escape from pastoral to conservation areas (18), and the inland wetlands of North America have been impacted by several perennial aggressive taxa (6).

There is abundant evidence for the assertion that disturbed communities (e.g. a newly regraded restored wetland) are more invasible than intact ecosystems (30-32). Disturbance creates many unoccupied physical or ecological niches that are “safe sites”, or opportunities, for invasion (33). Additionally, because wetlands (and restored wetlands) are high fertility and high moisture environments, they are more susceptible to weed invasion (34). These two factors combined suggest that the recovery of restored wetland ecosystems is particularly susceptible to limitations posed by invasion of environmental weed species. Indeed, dominance by invasive species, which prevents the establishment of target species, is listed as a common barrier to restoration success by many studies of multiple wetland restoration attempts (Kusler and Kentula 1990, McKinstry and Anderson 1993).

P. arundinacea life history and invasiveness

Phalaris arundinacea (reed canary grass) is an invasive perennial grass that is problematic to prairie pothole wetland restorations, particularly because many restoration sites are dominated by it prior to reflooding. Establishment by *P. arundinacea* often precludes colonization by sedge meadow vegetation in restored prairie pothole wetlands (6, 10, 11).

P. arundinacea is a tall, sod-forming, cool season perennial grass that ranges in height from 60 to 240 cm (16). *P. arundinacea* has been an important cultivated forage grass in northern temperate regions of the world for nearly two centuries and within North America since the 1830s (6). Early cultivation has made its pre-agricultural distribution uncertain, although *P. arundinacea* is considered indigenous to the temperate regions of all five continents (16).

Although the timing of phenologic events in perennial grasses varies with species, general growth dynamics are consistent across species. Perennial grasses typically form short shoots made up of unelongated internodes and leaves in the early spring. Inflorescence initiation occurs later in the spring when a young meristematic shoot apex begins to differentiate into a reproductive structure, and the bottom internode of the apical shoot begins to elongate to elevate the inflorescence above unelongated shoots. Then the inflorescence begins to emerge from the uppermost leaf collar (this is sometimes called the boot stage). In the early summer the inflorescence begins to flower, and the anthers of the floret are exposed and visible during certain periods of the day (anthesis). The embryos in the florets of the inflorescence mature into seeds during mid-summer (35).

Cool season perennial grasses produce numerous vegetative buds and rhizomes during late summer and early fall that live over winter. Only these overwintering rhizomes will produce shoots with inflorescences the next spring, and an overwintering requirement (cold temperatures or short day lengths or both) must be satisfied for shoot production to occur the following spring (36).

The phenology and morphologic development of *P. arundinacea* was described extensively by Evans and Ely (37), who studied stands in northern Ohio, USA (Lat. 42N). *P. arundinacea* was found to exhibit the general growth dynamics of a typical perennial cool season grass. They found that *P. arundinacea* growth begins in the early spring, initiating from shoots with growing points beneath the soil surface. These shoots have begun growth the previous fall from apices of underground rhizomes that turn upward, and require winter conditions to break dormancy. Stem elongation begins in April, and inflorescences begin to develop from growing points of shoots about mid-April. Flowering begins in early June, and seeds mature in June and early July. Evans and Ely (37) also noted that *P. arundinacea* rhizomes (which are short and fleshy) originate chiefly throughout May, June, July, and August. When these rhizomes begin to accumulate carbohydrates for storage is not clearly understood.

P. arundinacea thrives in areas with frequent and extreme fluctuations in water levels and is simultaneously more drought-resistant than many upland grasses (38-41). For this reason, *P. arundinacea* cultivars are widely planted for irrigated and non-irrigated forage systems and for land disposal of wastewater (42). *P. arundinacea* is also widely used as a forage crop.

Studies have highlighted characteristics that contribute to *P. arundinacea*'s dominance in wetland restorations. In addition to drought-tolerance and flood tolerance, *P. arundinacea* is winter hardy (16). This species has shown impressive environmental plasticity (6, 10), e.g. allocating more resources to seed production in unflooded conditions, and allocating more resources to below-ground vegetative production in flooded conditions (43). *P. arundinacea* is strongly clonal and sod-forming (38).

P. arundinacea forms dense seed banks that are believed to be persistent for at least one year and most likely more (44, 45). Even after *P. arundinacea* standing vegetation and vegetative propagules have been eliminated from the site, *P. arundinacea* may continue to dominate the site vegetation through recruitment from the seed bank (29). No studies have addressed the *P. arundinacea* seed bank density as it relates to competition between *P. arundinacea* and desirable wetland species.

Altered environmental conditions due to anthropogenic disturbance may be responsible for *P. arundinacea*'s increased dominance (6, 15). Several consequences of landscape modification create conditions that favor *P. arundinacea* over other species, including increased nitrogen availability (10, 46, 47), fluctuating water levels (40, 48, 49), and high light availability following disturbance (50, 51). Also, the aggressive growth of *P. arundinacea* in wetland restorations may be the result of a lack of competition in areas with bare soil, as *P. arundinacea* grows poorly in densely vegetated areas (14, 49). Although the theory behind *P. arundinacea* invasiveness is not yet clearly understood, the negative impacts of its dominance on the native wetland plant community are well-documented (6, 13, 44, 52).

P. arundinacea control

The starting condition for many wetland restorations is a basin dominated by *P. arundinacea*, and reestablishing wetland hydrology does not diminish its persistence (13). Even if *P. arundinacea* is only present in the seed bank (but not in the existing vegetation) prior to reflooding, it can germinate and rapidly spread as native vegetation is recolonizing and severely limit survival and growth of these species (29).

Mowing and grazing are ineffective at reducing *P. arundinacea* populations (13, 53). Some control success has been achieved with a combination of repeated controlled burns and herbicide treatments (glyphosate) (13, 45, 54, 55). No studies have been published that consider

the timing of various treatments relative to the growth dynamics of *P. arundinacea*. Additionally, treatments to reduce seed bank populations have not been reported.

Control techniques for *P. arundinacea* have been researched in the Pacific Northwest US, where the species establishes along irrigation canals, limiting channel capacity with vegetative growth by trapping silt (56-58). In one study addressing control along irrigation canals, *P. arundinacea* was effectively controlled for three months with amitrole-T, dalapon, and paraquat (58). In a field study in Prosser, Washington, USA, *P. arundinacea* seedlings were found to be effectively controlled with glyphosate at 5 to 10 weeks after seedling emergence (57). Control, however, in these studies lasted only for a few months, and then reapplications of herbicide were necessary. For wetland restoration, where the goal is to minimize management intervention, multiple continuous herbicide applications are not a feasible control technique.

More recently, several studies from Minnesota and Wisconsin in the northern US have documented *P. arundinacea* control attempts. From their study of a *P. arundinacea*-dominated wetland in Minnesota that had historically been cultivated, Preuninger and Umbanhowar (44) recommend periodic applications of glyphosate herbicide within one growing season, continued for multiple growing seasons, in order to control well-established *P. arundinacea* populations. In a degraded oak savannah in Wisconsin, efforts to control *P. arundinacea* were successful only when supplemented by hand weeding of newly germinating *P. arundinacea* over multiple growing seasons (55). A 5% solution of glyphosate provided 100% control of *P. arundinacea* in a small wetland in Minnesota, but control was not assessed beyond 3 weeks (45). In their review of *P. arundinacea* control methods, Apfelbaum and Sams (13) suggested that mechanical removal using heavy equipment did not provide long-term control, as *P. arundinacea* reestablished quickly from rhizomes and seeds remaining in the soil.

Control techniques investigated by this research

Because most managers who control *P. arundinacea* do not publish in the scientific literature, but do have valuable anecdotal information, a 1999 telephone survey of managers and consultants with experience controlling *P. arundinacea* identified potential successful avenues for *P. arundinacea* control. The manager survey revealed that 100% of managers had difficulty controlling *P. arundinacea*. The most common control method applied in the field was a controlled burn followed by a glyphosate herbicide application. The burn was designed to remove vegetation to facilitate herbicide application coverage, and herbicide was applied as soon as the *P. arundinacea* grew to a height of 8-12 inches.

The manager survey also revealed that prescribed burns and herbicide applications tend to be implemented in the spring and occasionally mid-summer, with little attempt to time treatments with respect to *P. arundinacea* phenology. Some managers reported short-term control success with the spring burn/spring-summer herbicide technique when treatment efficiency was evaluated several weeks after treatment, but no manager reported successful long-term control with this technique. Some managers suggested that incorrect herbicide coverage or application rate was the cause of control failure, and others cited "re-sprouting" as the cause of control failure, either as growth from rhizomes in the soil or as recruitment of seedlings from the seed bank.

The results from the survey suggested that glyphosate herbicide efficacy and spring burning were essential factors to investigate for their effects on *P. arundinacea*. Also, recruitment from the seed bank following control was highlighted as an important factor affecting long-term control success and also as a complicating factor in determining control

technique effectiveness. The role of the seed bank will likely be important in achieving control success and affecting the subsequent establishment of native species following control, and also warrants further investigation.

Glyphosate herbicide

Glyphosate (N-(phosphonomethyl)glycine, C₃H₈NO₅P) is overwhelmingly the most commonly used herbicide for restoration purposes (54), and in 1997 was the fourth most commonly used conventional pesticide in the United States (US EPA, 2000). Glyphosate is a post-emergent, non-selective, broad-spectrum herbicide that is effective on essentially all annual and perennial plants (Franz, 1985). These properties, as well as its relatively benign environmental behavior, contribute to make glyphosate a very widely used herbicide.

EPA lists glyphosate as toxicity class E, interpreted as “evidence of non-carcinogenicity for humans” (Occupational Health Services, Inc., 1988). Toxicity tests have established several LD₅₀s (lethal dosages) and LC₅₀s (lethal concentrations) for this chemical that place glyphosate in one of two FIFRA categories: least toxic and irritating, or practically non-toxic. Largely due to its low solubility in organics, glyphosate has no significant potential to accumulate in animal tissue (Malik et al., 1989). Occupational Health Services, Inc. (1988) found that glyphosate does not exhibit any common chemical toxicity mechanisms. Glyphosate has been described as moderately persistent in soil (Torstensson, 1985, Malik et al. 1992). Field studies have determined its half-life in soil to be 47 days (Wauchope, 1992, Ahrens, 1994), although some lab studies show half-lives that are less than 25 days (Ahrens, 1994). Comes et al. (1976) found that water entering dry irrigation canals from a crop that had been sprayed 23 weeks before with glyphosate contained 0.35 mg/L of this chemical. This runoff had a concentration significantly lower than the LC₅₀ for a daphnia (930 mg/L).

Glyphosate efficacy and rhizome carbohydrate content

Glyphosate is a systemic, or phloem-mobile, herbicide which is translocated with photosynthates to metabolic sites throughout the plant. Upon application, glyphosate is absorbed by leaf tissue. It then moves in the phloem with carbohydrates (photosynthates) and when metabolized, inhibits the production of amino acids and prevents secondary compound formation. Inhibition of chlorophyll synthesis results in chlorosis and then tissue death (59). For control of perennial weeds with glyphosate, it is essential that the herbicide translocate to rhizomes (60-64). If herbicide does not translocate to rhizomes, herbicide applications will affect the plant only partially, allowing rhizomes to persist (65-67).

If a seasonal pattern in rhizome carbohydrate fluctuation can be predicted for a perennial weed, it is possible to time herbicide applications to maximize translocation to rhizomes, thereby maximizing weed mortality. Carbohydrate levels in rhizomes of perennial weeds usually follow a trend of depletion during early season vegetative growth, until carbohydrate levels generally begin to accumulate during the later season. This pattern in seasonal carbohydrate movement has been confirmed for some perennial agricultural weed species, including *Apocynum cannabinum* L. (68), *Asclepias syriaca* L. (69), *Cirsium arvense* L. (70), and not for others (70).

Given the above-mentioned pattern in rhizome carbohydrate fluctuation, glyphosate applications during the later season (during rhizome carbohydrate storage) should be most effective (66). Several studies have found late season applications of phloem-mobile herbicides to be more effective than early season applications for controlling perennial weed species such as *Apocynum cannabinum* L. (71), *Euphorbia esula* L. (72), and *Sorghum halepense* L. (60).

Pairing results from these studies with carbohydrate fluctuation studies solidifies the dependence of glyphosate efficacy on season of application for these species, and suggests a mechanism behind that relationship.

Although techniques for tracking rhizome carbohydrate fluctuation and testing the efficacy of early vs. late season glyphosate applications are well established for agricultural weeds, these techniques have rarely been applied to environmental weeds. One environmental weed that invades wetlands across temperate North America, *Lythrum salicaria* L., has been investigated for glyphosate efficacy as it relates to rhizome carbohydrate levels. A field experiment in a randomized complete block design looked at differences in control achieved by early flower (mid-July) and late season (mid-September) glyphosate applications on established stands of *L. salicaria*. Control was estimated by a visual rating of observed mortality. Late season treatments of glyphosate at 0.84 kg/ha achieved 96% control while early flower (July 12) applications of 0.84 kg/ha achieved only 52% control (73).

A subsequent investigation of seasonal fluctuations in root carbohydrate levels for *L. salicaria* found that root carbohydrates do follow a seasonal pattern (74). In this study, *L. salicaria* rhizome samples were collected monthly from three wetland sites in Minnesota during the 1994 and 1995 growing seasons. Levels of carbohydrates in rhizome samples were determined using near infrared reflectance spectroscopy (NIRS). Rhizome carbohydrate levels were lowest during bud and early flowering stages of growth (May-July) and increased during flowering and plant senescence (August-November), suggesting that Becker et al.'s (73) more effective fall herbicide applications were linked to increased carbohydrate movement to rhizomes.

Prescribed burning

Prescribed burns, which may be used to mimic natural fire regimes, are a major part of many ecological restoration and vegetation management programs. In conjunction with herbicide applications, early season burning is often recommended as a method of removing any dead biomass from the previous growing season, thereby increasing herbicide access to live shoots as they emerge in the spring (53). Increased herbicide coverage of the live shoots should increase herbicide effectiveness. Indeed coverage is a critical factor in the efficient control of weeds for many situations (66). Translocated or systemic compounds (such as glyphosate), however, are less dependent upon this factor, and increasing coverage may not be necessary to ensure mortality (61).

Burning may actually reduce glyphosate effectiveness. Partial failure to control with glyphosate has occurred when perennial weeds have been cut or damaged shortly before glyphosate has been applied (65). Any factor, biotic or abiotic that reduces photoassimilation or disrupts phloem tissue, has been shown to reduce herbicide translocation to carbohydrate storage structures such as rhizomes (75). Little is known about the time necessary for photoassimilation to recover after the disruption, so the ultimate effect of burning on glyphosate efficacy is not known.

Research goals

The goals of this research were to develop a predictive understanding of *P. arundinacea* dominance in prairie pothole wetland restorations and suggest effective control strategies by addressing three objectives: 1) to investigate control techniques for reducing existing stands of *P. arundinacea* and the life history factors that contribute to effectiveness, 2) to characterize

unconstrained biomass production for an individual *P. arundinacea* plant and apply this knowledge to the understanding of the *P. arundinacea* invasion process, and 3) to determine how the *P. arundinacea* soil seed bank composition affects transition to the post-restoration community of native prairie pothole species. We addressed these objectives with several research questions and implemented related experiments:

1. Can timing and control techniques with respect to *P. arundinacea* growth more effectively reduce existing stands of *P. arundinacea* from wetland restoration sites? Experiment: In a replicated, control technique field experiment, *P. arundinacea* shoot density, biomass, and percent cover were measured in response to combinations of burning and glyphosate application timing.
2. Is the pattern in seasonal fluctuation in *P. arundinacea* rhizome carbohydrate content predictable, and how does it relate to glyphosate efficacy? Experiment: *P. arundinacea* rhizome carbohydrate content was measured every two weeks during the growing season for three growing seasons. The plot for this experiment was immediately adjacent to the plots used for the control techniques experiment, allowing translocation rates to be assigned to respective herbicide applications.
3. What is the effect of burning and timing of glyphosate application on remnant seed bank populations? Experiment: Effects of treatments applied in the control techniques field experiment were monitored through periodic seed bank assays of plots to which control treatments were applied.
4. Is there a level of *P. arundinacea* seed bank density in which *P. arundinacea* does not suppress native species establishing from seed? Experiment: In a mesocosm experiment, the competitive effects of different seed bank densities of *P. arundinacea* and different seeding densities of a mix of native sedge meadow species were assessed. Competitive performance of both natives and *P. arundinacea* was measured as aboveground biomass production over two growing seasons.
5. What is the unconstrained growth potential of *P. arundinacea* and does this provide insight into *P. arundinacea*'s aggressive nature? Experiment: A uniform planting study tracked the unconstrained growth of individual *P. arundinacea* plants over two growing seasons, measuring above and belowground biomass production.

Report organization

The above research questions are presented in Chapter 2 (questions 1, 2, and 3), Chapter 3 (research question 4), and Chapter 4 (research question 5) of this document. Chapter 5 uses conclusions from this research to construct a *P. arundinacea* control and management plan for a wetland restoration site. See “Statement of Tasks” in the front matter of this document for a list of tasks that the Technical Advisory Panel established as fundamental to answering these questions and how the results of the completed tasks are presented in this document.

CHAPTER 2

A large-scale field experiment tests control techniques for *Phalaris arundinacea* L. (reed canary grass) in wetland restorations

Summary

Controlled, replicated experiments of restoration practices are rare, yet the knowledge gained from such studies is crucial to the development of a predictive understanding for ecosystem restoration. Invasive species are a common barrier to the establishment of native communities in wetland restoration, and control of invasive species is often crucial to ecosystem recovery. *Phalaris arundinacea* L. (reed canary grass) is a perennial rhizomatous invasive grass that is problematic to wetland restoration across temperate North America. A combination of controlled burns and glyphosate herbicide applications are the most commonly employed control techniques, but no studies have addressed the relative effectiveness of either treatment with respect to *P. arundinacea* growth and life-history. We designed a large-scale field experiment to look at controlled burning and different herbicide application timings and their effect on *P. arundinacea* populations. We found that although burning does not reduce *P. arundinacea* in the long term, it does reduce the *P. arundinacea* seed bank, possibly limiting recolonization of *P. arundinacea* following successful removal of large stands of *P. arundinacea*. Herbicide applications were most effective when applied in late August or late September, as compared to mid-May, likely due to enhanced translocation of glyphosate to rhizomes. Implementing burning and herbicide applications for two consecutive growing seasons more effectively reduced *P. arundinacea*, but even after two rounds of control techniques, *P. arundinacea* recolonized rapidly from the seed bank, limiting establishment of native species. Recolonization from seed (either on-site in the seed bank or off-site from dispersal) will complicate control techniques, therefore efforts to limit the availability of propagules will be key to successful *P. arundinacea* control.

Introduction

Putting restoration practices to the test in controlled, replicated experiments is crucial to furthering the broader goal of ecosystem rehabilitation. Designing and implementing effective restoration practices requires the ability to predict the outcomes of specific management actions, and experiments contribute to greater predictability (76). Experiments in restoration are an important step beyond comparisons of natural and restored systems to determine feasible pathways to restoration goals (77).

Dominance by invasive species, which prevents the establishment of target native communities, is a common barrier to restoration success (11, 78, 79). It follows that invasive species control is often a large part of the early stages of restoration. For restoration projects, where time and resources are limited, optimal control strategies are crucial to subsequent establishment of native species and ultimately, ecosystem recovery. Particularly, more research is needed to develop safe and effective control measures, which has been suggested to be “the biggest challenge that conservation biologists will face in the next few decades” (80).

Phalaris arundinacea L. (reed canary grass), a perennial grass native to temperate North America, is an invasive species that forms a dense network of rhizomes and an abundant, persistent seed bank (81). In the northern US, this species is a major concern for wetland restorations because establishment by *P. arundinacea* often precludes colonization by sedge meadow vegetation in restored prairie pothole wetlands (6, 10, 11). The starting condition for many wetland restorations is a basin dominated by *P. arundinacea*, and reestablishing wetland hydrology does not diminish its persistence (13). Even if *P. arundinacea* is only present as seeds in the seed bank (but not in the existing vegetation) prior to reflooding, it can germinate and rapidly spread as native vegetation is recolonizing and severely limit survival and growth of these species (29).

P. arundinacea's aggressive spread and dominance in the northern US is likely tied to anthropogenic modification of the landscape (15). Several consequences of landscape modification create conditions that favor *P. arundinacea* over other species, including increased nitrogen availability (10, 46, 47), fluctuating water levels (40, 48, 49), and high light availability following disturbance (50, 51). Planting of *P. arundinacea* as a forage grass (most likely beginning in the 1830s) and for conservation purposes (most likely beginning in the 1930s) (15) may also contribute to increased availability of propagules in the landscape and subsequent spread into natural areas.

P. arundinacea is so prevalent in the landscape that for many wetland restorations, removal of *P. arundinacea* is necessary prior to establishing native vegetation. Mechanical methods alone (mowing and grazing) are ineffective at reducing *P. arundinacea* populations (13, 53, 82). Control success has been reported for combinations of burning or mowing and glyphosate herbicide application (13, 44, 54, 82). A recent survey confirmed that a spring burn followed by a spring herbicide application is the most commonly employed control technique, but evaluations of control success have been mixed (Chapter 1, this document). In longer-term assessments of glyphosate herbicide use, post-removal recolonization has been reported, both from resprouting rhizomes and germinating seeds (13, 55, 82).

Post-removal recolonization of *P. arundinacea* from resprouting rhizomes may be due to ineffective use of herbicide. For control of perennial weeds with glyphosate, it is essential that the herbicide applications be timed during translocation of carbohydrates to rhizomes, which generally occurs during the later-season (60-64). Prescribed spring burning, which is often recommended to remove dead biomass from the previous growing season to increase herbicide access to live shoots, may actually hinder herbicide effectiveness. Partial failure to control with glyphosate has occurred when perennial weeds have been cut or damaged shortly before glyphosate has been applied (65). Also, although coverage is a critical factor for efficient control for some herbicides (66), translocated or systemic compounds (such as glyphosate) are less dependent upon this factor, and increasing coverage may not be necessary to ensure mortality (61).

Post-removal recolonization of *P. arundinacea* from seed is likely a result of germination from a dense persistent seed bank (44, 45, 55). Little has been done to examine efforts to reduce the *P. arundinacea* seed bank, short of scraping the top 30 cm of soil off of the entire site (53), which is cost-prohibitive within the scope of typical project budgets. Altering site conditions to promote native species establishment over *P. arundinacea* establishment from seed has been studied (using cover crops (83) and lowering nitrogen availability (84)). However this line of research has not yielded a feasible approach.

The widespread nature of the problem of controlling *P. arundinacea* invasion, together with the consequence of *P. arundinacea* invasion to native vegetation communities, warrants that use of control techniques for *P. arundinacea* be applied in the most effective way. No studies have been published that consider the timing of burning and glyphosate herbicide applications relative to the growth dynamics of *P. arundinacea*. Additionally, treatments to reduce seed bank populations have not been reported, although this will be crucial to controlling *P. arundinacea*. We designed a large-scale field experiment to examine the two most commonly used techniques to control *P. arundinacea* (spring burning and glyphosate herbicide applications) for their effects on *P. arundinacea* populations. To investigate causal mechanisms for herbicide effectiveness, we tracked rhizome carbohydrate levels. To investigate potential reduction of the seed bank as a result of control techniques, we monitored changes in seed bank density with respect to control treatments.

Methods

Study site descriptions

The study sites were selected for their uniform topography and hydrology and their homogeneous cover of *P. arundinacea* (minimizing between plot variation in site characteristics). The first study site was a twenty-acre abandoned sod farm in North St. Paul, Minnesota, USA, 45°01'45"N latitude, 93°02'59" W longitude (Figure 2-1, hereafter referred to as the NSPSF site). The second study site was a historically wet area of University of Minnesota Landscape Arboretum in Chanhassen, Minnesota, USA, 44°51'45"N latitude, 93°36'00" W longitude (Figure 2-2, hereafter referred to as the Arboretum site). Both sites have been partially drained for several decades, and the *P. arundinacea* populations on site have been established for at least 25 years. Topographic surveys of established study plots at both sites revealed that sites were relatively flat, with elevation across study plots showing a total range in elevation of 1.1 m for the Arboretum site, and 0.7 m for the NSPSF site. Depth to water was not significantly different between sites (Table 2-1). Soil properties (samples analyzed by the University of Minnesota Soil Characterization Lab) did not range widely across each site, but did differ significantly between sites ($p < 0.001$, Table 2-1). Phosphorus content of the soil at the Arboretum site was almost double that of the NSPSF site (12 ppm vs 22 ppm), but total N at the NSPSF site was almost double that of the Arboretum site (2.8 % versus 1.6%). The Arboretum site had higher total organic carbon (20% versus 15% at NSPSF), and was less acidic (pH was 6.48 vs 5.45 at NSPSF).

Vegetation species composition prior to treatment was similar between both sites. *P. arundinacea* was the dominant cover in all plots at both sites, ranging in cover from 75-100%. *Urtica dioica*, a perennial forb, was the second most dominant at both sites, and was present at 0-25% cover. *P. arundinacea* biomass was similar across both sites (Arboretum = $838 \pm 67 \text{ g m}^{-2}$, NSPSF = $714 \pm 54 \text{ g m}^{-2}$), but the *P. arundinacea* seed bank density at the Arboretum site ($1165 \pm 146 \text{ seeds m}^{-2}$) was roughly double that of the NSPSF site ($667 \pm 159 \text{ seeds m}^{-2}$). This difference, as well as the aforementioned differences in soil characteristics, warranted statistical blocking of the experimental design across sites.

Rhizome carbohydrate content study

Every 2 weeks from ground thaw to ground freeze, at *P. arundinacea*-dominated plots adjacent to the field experiment at the NSPSF site, ten randomly located samples of rhizomes were taken with a 0.4-m² area corer to a depth of 10 cm and were analyzed for rhizome carbohydrate content. Samples were rinsed, dried at 70°C in a forced air oven to constant weight, and ground for analysis with Near Infra-Red Spectrophotometry. This study was implemented for the 2000, 2001, and 2002 growing seasons.

Rhizome samples were read with the near-infrared spectrophotometer (NIRS) in the University of Minnesota's Forage Quality Lab (74, 85). Lab analysis of 50 randomly selected samples calibrated the NIRS with an equation that identifies fructosans-specific wavelength spectra (fructosans are the primary storage carbohydrate in *P. arundinacea* (86, 87). Analytic determination of sample fructosan content was performed by employing para-hydroxybenzoic acid to hydrolyse sucrose, starch and fructosans, applying a colorimetric assay, and reading solution absorbance at $\lambda = 410$ nm in a spectrophotometer (Megazyme International Ireland Ltd, Wicklow, Ireland). From these fructosans determinations, NIRS readings for all samples were calibrated.

Control techniques field experiment

Twenty 12-m x 12-m treatment plots were established across the most homogenous area of each the site, for a total of 40 plots. The size of each plot was maximized to allow for adequate treatment opportunity, but was constrained by costs of conducting treatments and need for replication.

Experimental design

The experimental design for the large-scale control techniques field experiment was a complete block design, blocking on field site, as there were expected differences in response to treatments based on differences in site characteristics. The experiment had two factors: 1) burning and 2) herbicide application timing. The burning factor had two levels: control (no spring burn), and spring burn. The herbicide timing factor had four levels: control (no herbicide), spring application, late-season application, and later-season application. This experiment yields a 2 x 4 factorial structure with 8 treatment combinations. Replications were concentrated in the no burn treatment (n=12 whole plots) because the burn treatment (n=8 whole plots at each site) was anticipated to have little effect on *P. arundinacea* populations in the long term.

The randomization was based on a split-plot design (88, 89), with burning as the whole plot treatment, and herbicide application timing as the split plot treatment. Burn treatments (either burn or no burn) were randomized to whole plots (10-m x 10-m). Each whole plot was divided into four 5-m by 5-m split plots (yielding 160 split plots), to which the four herbicide treatments were randomized (Figure 2-3). This design logistically simplified the burn treatment by applying it to larger areas, but simultaneously allowed for 160 experimental units (80 at each site). For each of the 8 factor-level combinations (2 levels of burning x 4 levels of herbicide=8 factor level combinations), there were either 16 (for treatments including a burn) or 24 (for treatments not including a burn) replications.

Preliminary response data from the first year of the experiment suggested that a comparison of one round of burn/herbicide treatments vs. two rounds of burn/herbicide treatments was necessary. Therefore, statistical design was amended to include that factor. Half

of all whole plots at each site were randomly selected to receive two years of treatment, while the other half received only one year of treatment. This resulted in a 2 x 2 x 4 factorial design, with 16 treatment combinations.

Analysis of Variance (ANOVA) was used to assess treatment effects, with *P. arundinacea* biomass and *P. arundinacea* shoot density serving as response variables. Due to the unbalanced data, data were analyzed using the mixed model procedure (PROC MIXED) in SAS (SAS Institute Inc. Cary, NC). Tukey's honest significant difference test (HSD) was used to assess significance of differences between means using $\alpha=0.05$. Biomass and seed bank data were transformed to minimized heteroscedasticity, and appropriate transformations were determined using the Box-Cox technique in MacAnova (University of Minnesota, 1997).

Implementing control techniques

We implemented control techniques in an identical manner for each application. Burn treatments were coordinated with trained field burn crews (with North St. Paul Fire Company at the NSPSF site and with the assistance of the Arboretum burn crew at the Arboretum site) to ensure they were conducted safely. Climatologic conditions (wind speed and direction, relative humidity, air and soil temperature) were monitored before, during, and after each burn to ensure that safe conditions existed according to MN DNR specifications. Average burn temperature was measured in each plot with an infrared temperature gun, and maximum soil surface temperature was measured with crayons and slides.

Glyphosate (Monsanto's Roundup Ultra™, 41% glyphosate isopropylamine salt) was used for all herbicide applications. A 2% solution (20 ml of Roundup Ultra™ and 1080 ml of water) was applied at a rate of 187 L ha⁻¹ of the solution, which is consistent with label specifications for persistent perennial grasses (90). Climatologic conditions (wind speed and direction, relative humidity, air and soil temperature) were monitored before, during, and after each herbicide application to ensure that appropriate conditions existed for application according to label specifications (90). Herbicide was applied using a CO₂-powered hand-held sprayer (pressure=206 kPa, nozzle type = 8002). Drift retardant was mixed at 1 cm³ L⁻¹ to ensure that herbicide did not contaminate nearby plots.

The timing of burning and herbicide applications were affected by weather conditions. Therefore, timing differed from year to year and site to site, but all attempts were made to time treatments to equivalent points in growth based on the accumulation of growing degree days (base temperature used to calculate gdd = 32°F) (Table 2-2). During the first year of the experiment, the two later season herbicide applications were timed to test differences in pre and post frost effectiveness. When we found no significant treatment differences, we timed the treatments to include the period of rhizome carbohydrate accumulation and the period of rhizome carbohydrate stagnation, as dictated by 2000 carbohydrate data.

After treatments were implemented in a plot for either 1 or 2 growing seasons (as dictated by the statistical design), the plot was then seeded in early May with tall wet meadow grass and forb restoration mixes obtained from Prairie Restorations Inc. (Princeton, MN). The species included in the seed mix are listed in Table 2-3. The grass mixture was seeded at 6 kg ac⁻¹ pure live seed (PLS) (13 lbs ac⁻¹ PLS), and the forb mixture was seeded at 2 kg ac⁻¹ (4 lbs ac⁻¹ PLS). After burning the area, grass seed was sown and then raked into the soil, and then the forb seed was spread lightly onto the soil surface.

All plots at the NSPSF site received burning and herbicide treatments during the 2000 growing season. In May 2001, half of all plots were seeded with a restoration mix, and were

monitored during 2001 and 2002. The other half of the plots received a second round of burning and herbicide treatments in 2001, were seeded with a restoration mix in May 2002, and were monitored during the 2002 and 2003 growing season. The same treatment/monitoring schedule was implemented at the arboretum site, staggered one year later.

Data Collection

P. arundinacea populations were monitored for one year following completion of control treatments. Four times during each growing season (in April before any treatments are implemented, in July before seed set, in September before late fall herbicide applications, and in October before senescence) *P. arundinacea* shoot density was measured. The number of live *P. arundinacea* shoots within a 0.5 m²-area hoop was determined at permanently established repeated measures plots (the use of repeated measures plots will reduce any noise associated with spatial variability). Shoot density has been shown to be positively correlated with above-ground biomass production (91), but is a non-destructive sampling technique, allowing for repeated measures in the same location.

In late August of each year, aboveground biomass and percent vegetation cover were assessed for *P. arundinacea* and non-target species (available plot size allowed for destructive sampling once each growing season). For above ground biomass collection, new randomly located points were established for each data collection period. Hoops with an area of 0.5 m² were centered around randomly located points, and all above ground biomass was cut at the soil surface, separated by species, and placed into paper bags, dried at 70°C in a forced air oven to constant weight, and weighed. For percent cover data collection, total cover for each species found was estimated using a seven-point cover scale (92). This scale uses the following categories: 1 individual with insignificant cover, more than 1 individual with insignificant cover, 1-4% cover, 5-24% cover, 25-49% cover, 50-74% cover, 75-100% cover. For analyses of cover data the midpoint percentage cover for each of these categories was used.

To keep track of weather that might affect vegetation response, climatic variability was assessed with well readings and soil and air temperature data collection throughout the experiment. Local climate data was also used to get context for the conditions during the years of the experiment. Optic Stowaway thermistors (Onset, Pocasset, MA) measured air and soil temperature for the entirety of the experiment. Slotted PVC piezometer monitoring wells (built to NRCS specifications) were used to measure depth to the water table (93).

The portion of the field experiment located in at the Arboretum was used to assess remnant seed bank response to the burning and herbicide treatments. Plots at this site were sampled for seed bank composition in October 2000 (before implementing burning/herbicide treatments), October 2001 (after one year of treatments), and October 2002 (after 2 years of treatments). To collect samples, in each plot a 7.5 cm-diameter corer was used to take 3 seed bank samples per plot to the depth of 10 cm. The samples for each plot were then homogenized and sieved to remove litter, roots and tubers, and stored in a cold room at 4°C until January of each year. A 250 ml-subsample was taken from the homogenized sample and spread into plastic trays (19.5 cm x 19.5 cm x 6 cm) that had been filled with sterilized universal potting soil. Samples were grown in the greenhouse under a 14-hr day (24 C), 10 hr night (17 C) light cycle, (with supplemental day-time lighting provided by high intensity discharge lamps), under saturated soil conditions, for 6 months (90% of temperate wetland seedlings germinate within the first three months (94)). Seedlings were counted and removed as soon as they could be identified. Seedlings that could not be identified without flowering parts were removed from

trays and grown until flowering and subsequently identified; seedlings that did not flower were identified to genus if possible, or were recorded as unknown. Seed bank data from the initial survey (October 2000) showed that the *P. arundinacea* seed bank density did not differ between plots prior to treatment.

Results

Climate variability

Climate data show that accumulation of growing day degrees was similar between years (0). First hard frost (32F for 3 or more hours) occurred on September 23 in 2000 and 2002, and on September 17, 2001. Monthly temperature and precipitation did not depart from normal average temperatures or precipitation by more than 25% of normal range (Dave Weirstad, North St. Paul Weather Observatory, unpublished data).

Changes in rhizome carbohydrate content

Rhizome carbohydrate data show a pattern of a decrease in the early season, followed by an increase in the later season across all three study years (Figure 2-5). The period of maximum rate of accumulation begins in late July for all three growing seasons, and continues to accumulate until the end of the growing season for both 2001 and 2002. For the 2000 growing season, rhizome carbohydrate content increases until mid September, and then stays constant for the remainder of the growing season.

Carbohydrates began to accumulate in rhizomes at roughly the same calendar date every year (July 20, 2000, July 19 2001, and July 26, 2002). Rhizome carbohydrate content increased up to the end of the sampling period during 2001 and 2002 (mid-November), but in 2000, did not increase after August 29. The rate of carbohydrate storage varied for each year. During 2000, accumulation occurred from July 20 to August 29 at a rate of $0.46 \text{ g g}^{-1} \text{ day}^{-1}$, and then remained constant for the rest of the growing season. Rates of storage for 2001 and 2002 were much slower ($0.15 \text{ g g}^{-1} \text{ day}^{-1}$ and $0.12 \text{ g g}^{-1} \text{ day}^{-1}$, respectively). Early-season depletion of carbohydrate reserves is suggested by the few data points prior to accumulation in 2000 and 2001. For 2002, the only year in which early season carbohydrate content was extensively measured, rhizome carbohydrate content decreased from April 19 to July 26 at a rate of $0.11 \text{ g g}^{-1} \text{ day}^{-1}$.

P. arundinacea response to control techniques

P. arundinacea existing stand response to burning

Burning resulted in an initial increase in shoot density immediately after burning. Shoot counts taken 4 weeks after burning indicated that *P. arundinacea* shoot density was doubled in burned plots compared to the control ($F= 11.49$, $p<0.01$, Figure 2-6). However, when evaluated 12 weeks after burning, *P. arundinacea* biomass was similar in burned and unburned plots (ANOVA mean comparison burn=1/2 at herb=1 $F=,1.67$ $p=0.10$). Burning did not change the effect of the herbicide: the burn-herbicide interaction was insignificant for both biomass (ANOVA for burn at time=1 $F=0.08$, $p=0.39$) and shoot density responses ($F=2.45$, $p=0.07$).

Plots which were burned for 2 years in a row had similar *P. arundinacea* biomass compared to plots that had received no treatment, and 2 years of burning plots that also received herbicide did not affect *P. arundinacea* biomass.

P. arundinacea existing stand response to herbicide

Herbicide applications significantly reduced *P. arundinacea* biomass (ANOVA for herb at time=1 $F=131.34$, $p<0.01$), and the timing of the herbicide application was significant. While the mid-May herbicide application reduced *P. arundinacea* to 25% of control levels, both late August and late September herbicide applications were significantly more effective, and reduced *P. arundinacea* to 10% of control levels.

In the early spring (April 25) following the year of treatment, *P. arundinacea* shoot density prior to seeding was very low in mid-May herbicide plots (141 shoots m^{-2} , 5% of the control shoot density). Late August and late September herbicide plots, however, had extremely low shoot densities (2-3 shoots m^{-2}). After 2 rounds of treatment, late August and late September herbicide plots had a mean shoot density of 0-1 shoots m^{-2} , and mid-May plots had a mean shoot density of 26 shoots m^{-2} (3% of control levels), but these treatments were not significantly different from one another. Shoots observed in late August and late September herbicide plots were entirely of seedling origin, whereas shoots observed in mid-May plots were of mostly of rhizome origin, with a few shoots of seedling origin (Figure 2-7).

P. arundinacea recolonized in all plots one year after seeding with native species, regardless of the burning/herbicide treatment implemented in that plot (Figure 2-8). *P. arundinacea* biomass quadrupled in mid-May herbicide plots, and increased by a factor of 10 in late August and late September herbicide plots, bringing the *P. arundinacea* biomass to roughly equivalent levels in all plots that had received herbicide treatment. However, plots which received herbicide treatments still had 50% less *P. arundinacea* biomass than the control plots. *P. arundinacea* recolonized differently with respect to herbicide application at each site ($F=4.53$, $p<0.01$). At the Arboretum site, *P. arundinacea* biomass was reduced in herbicided plots compared to the control, but was similar across mid-May, late August and late September treatments. At the NSPSF site, the mid-May treatments were not significantly different than the control, but both late August and late September treatments had significantly less biomass than the control.

When herbicide treatments were applied for 2 growing seasons before seeding, treatment effects were slightly different. When evaluated 3 months after seeding, all herbicide treatments had reduced *P. arundinacea* biomass compared to control densities, but no herbicide treatment was significantly better than any other. In a comparison of one or two rounds of control, if measured 3 mos after seeding, one round of treatments did not reduce *P. arundinacea* as much as 2 rounds of treatment ($F=6.73$, $p=0.01$, Figure 2-9).

One year post-seeding, *P. arundinacea* had recolonized significantly more biomass in mid-May herbicide plots (478 g m^{-2}) than in late and later season herbicide plots (246 and 218, respectively, Figure 2-10). Comparing one versus two years of control, measured one year after seeding, *P. arundinacea* biomass is not significantly different in plots that received one round of treatment or two rounds of treatment (ANOVA time $F=0.5$, $p=0.49$, Figure 2-11).

P. arundinacea seed bank density response to burning and herbicide

Burning reduced seed bank density; burned plots had a mean density of 75 ± 52 seeds m^{-2} , and unburned plots had a mean density of 283 ± 97 seeds m^{-2} ($F=6.3$, $p=0.03$,). There was no significant change in *P. arundinacea* seed bank density with respect to the application of herbicide treatments after one round of treatments ($F=1.17$, $p=0.34$). After two years of burning/herbicide treatments, burned plots still had a significantly lower seed bank density ($75 \pm$

40 seeds m⁻²) as compared to unburned plots (175 ± 42 seeds m⁻²) (F=4.78, p=0.03, Figure 2-12). Also, plots which received herbicide had a significantly lower seed bank density (60-120 seeds m⁻²) than plots which had not received herbicide (280 seeds m⁻²) when two rounds of herbicide had been applied (F=4.01, p=0.01), but mid-May, late August, and late September seed bank densities did not differ from each other.

Post-removal vegetation recolonization

NSPSF site

Establishment from the 28 species in the native species restoration seed mix was low (when evaluated 3 months after seeding and one year after seeding): only 10 out of the 26 species planted were detected by the biomass data collection (Table 2-4, Table 2-5), and these species accounted for less than 7% of the mean total non-*P. arundinacea* biomass in any plot. An exception was *Eupatorium perfoliatum* establishment in later season herbicide plots one year after one round of treatments (up to 50% of non-*P. arundinacea* biomass in some plots, Figure 2-13). None of the seeded species were detected by the biomass survey in the control plots or the plots that had received mid-May herbicide application. Although they were not detected in the biomass survey, several other planted species were detected by the cover survey, but these species were only detected in 1-4 replications (out of a possible 120, Table 2-6, Table 2-7). Non-planted species accounted for the majority of the total non-*P. arundinacea* biomass that recolonized in plots following control (Figure 2-13). Several wetland species colonized including those present at the site prior to application of control techniques (e. g. *Verbena hastata*, *Urtica dioica*, *Mimulus ringens*) and those present in refugial native patches along the ditch of the wetland (*Rudbeckia hirta*, *Solidago* sp.).

Arboretum site

Establishment from planted species was low at the Arboretum site as well. Only 7 of the 28 planted species were detected by the biomass data collection (Table 2-8, Table 2-9), and these species accounted for less than 5% of the mean total non-*P. arundinacea* biomass in any plot (Figure 2-14). Four planted species that were not detected in the biomass survey were detected in cover estimates (Table 2-10, Table 2-11). For the arboretum site as well, the non-*P. arundinacea* recolonizing community was dominated by non-planted species (Figure 2-14). Of the wetland species that colonized, several were present on site prior to control treatments, including *Elytrigia repens*, *Urtica dioica*, and *Impatiens capensis*.

Discussion

Our results demonstrated that the timing of the glyphosate herbicide application significantly influenced the effectiveness of that application, and that later season herbicide applications (late August and late September) were more effective in reducing *P. arundinacea* biomass than were mid-May herbicide applications. The lack of rhizome-based shoots observed in the early spring in later season herbicide plots suggests that this timing of herbicide application resulted in greater rhizome mortality than the mid-May applications. Several studies have found late season applications of phloem-mobile herbicides to be more effective than early season applications for controlling perennial weed species (60, 71, 95). Later season flux of

carbohydrates to rhizomes has been linked to herbicide effectiveness in several studies (66, 68, 74).

Given the carbohydrate pattern determined for *P. arundinacea* in this study, it is highly likely that increased rhizome mortality with the later season herbicide applications is due to enhanced translocation of the herbicide to rhizomes. *P. arundinacea* rhizome carbohydrate content followed a trend of depletion during early season vegetative growth, until carbohydrate levels generally begin to accumulate during the later season. This is similar to patterns of seasonal carbohydrate fluctuation found in other perennial species in temperate climates, including *Apocynum cannabinum* L. (68), *Asclepias syriaca* L. (69), and *Cirsium arvense* L. (70). Other species may exhibit a more random pattern in rhizome carbohydrate content (70).

Although our results suggest that the period of timing for maximum efficacy with herbicide applications begins in late August, the duration of this period was not consistent across years. Rhizome carbohydrate content continued to accumulate up to November in 2001 and 2002, but the lack of increase in rhizome carbohydrate content for the 2000 growing season after September suggests that the window of maximum herbicide efficacy may not be as predictable as we had hoped. Extreme variations in day degree accumulation during the growing season could be responsible for year-to-year differences in carbohydrate pattern, but overall accumulation was relatively similar for all three years of this study period. Disruption of carbohydrate accumulation patterns have been demonstrated with respect to differences in hydrology, where carbohydrate accumulation in *Lythrum salicaria* halted earlier in seasonally flooded wetlands than in semi-permanently flooded wetlands (74). However plot-to-plot and year-to-year differences in hydrology were minimal for this study. *P. arundinacea* carbohydrate storage has been demonstrated to be disrupted by stress due to massive leaf defoliation or cutting (96), but no damage was observed in the stands of *P. arundinacea* designated for carbohydrate sampling. Other studies have concluded that atypical halt in carbohydrate content may actually be the result of investment in new root growth, which is not measured by variations in carbohydrate content analyzed on a dry weight basis (70). Our data provide evidence for late season storage of carbohydrates into rhizomes for *P. arundinacea*, which indicates a physiological basis for the increased effectiveness of later season herbicide applications in the field experiment. But the differential accumulation pattern observed in the 2000 data and the potential effect of seasonal variation on prediction of effective herbicide timing merits further investigation into year-to-year in *P. arundinacea* carbohydrate storage patterns.

The spring burn did not reduce existing stands of *P. arundinacea*, nor did it enhance the effectiveness of subsequent herbicide applications. Results from the seed bank surveys demonstrated that burning reduced the density of the *P. arundinacea* seed bank. This study was not designed to investigate the mechanism by which burning reduces the seed bank, however some inference can be made from the data collected. Average burn temperature in this experiment (range: 90-130°C) was comparable to a high intensity grassland fire, and created conditions that have increased seed germination or induced seed mortality in other species (97, 98). Heat-induced seed mortality may have been a factor, but we have no data to assess the importance of this factor to the reduction in seed bank density. The observed germination of *P. arundinacea* seedlings immediately following the spring burn suggests that burning provided a high light environment which is optimal for *P. arundinacea* germination (50), and germinating seedlings resulted in depletion of the seed bank density. Repeated cycles of encouraging germination and subsequent treatment with herbicides is a often-employed strategy for reducing

the weed seed bank for restoration purposes in degraded sites, where non-target species typically emerge from the seed bank following vegetation removal (22, 54).

Reducing the *P. arundinacea* seed bank is likely central to successful control for this species, as our results suggest that the seed bank plays an important role in the reinvasion of *P. arundinacea* following the clearing of existing stands. Subsequent recolonization of *P. arundinacea* is not surprising; seed bank surveys have shown that *P. arundinacea* seed bank is dense and persistent (13, 53), and other studies have observed similar reinvasion of *P. arundinacea* from the seed bank (44, 55). Also, conclusions about *P. arundinacea*'s colonizing habit from Lindig-Cisneros and Zedler (17,18) suggest that this species will readily establish seedlings after canopy disturbance (e.g. removal of vegetation).

Even 2 years of burning and herbicide applications did not reduce *P. arundinacea* populations to the point where native species could establish. Low recruitment from the restoration seed mix is likely a result of competition with both newly germinating *P. arundinacea* seedlings and the establishment of other species from the existing seed bank. Conclusions from tests of light availability on *P. arundinacea* establishment led to the recommendation that a dense, native canopy could prevent *P. arundinacea* establishment and growth (14, 99). As demonstrated in this study, *P. arundinacea* will establish from seed despite the presence of native seed. Given *P. arundinacea*'s establishment habit and ability to preempt other native species, it is likely that *P. arundinacea* management will be necessary during the establishment of the native species canopy, and during other times in which gaps in the native species canopy occur (e. g. during hydrologic drawdowns, in the early spring before native species begin growth).

In addition to the seed bank, for sites with nearby populations of *P. arundinacea*, dispersal of propagules from off-site sources will also contribute to *P. arundinacea* establishment. Ever-present sources of *P. arundinacea* propagules may mean that *P. arundinacea* control is necessary for long-term protection of native vegetation. In a full-scale wetland restoration demonstration, *P. arundinacea* control effort was substantial at first (175 and 70 hours acre⁻¹ yr⁻¹ for the first and second year of restoration, respectively), and then decreased over time to less than 7 hours acre⁻¹ yr⁻¹ for the seventh year of the restoration (Galatowitsch and Bohnen, in preparation). Similarly for *Mimosa pigra* outbreaks, recolonization from the persistent seed bank necessitated 7 or more years of sustained control (100). Our data support the assertion that environmental weed management strategies for *P. arundinacea* are like those for other persistent invasive species in that they will be most successful if implemented in the long-term (19, 101, 102).

Our experiment demonstrated the most effective ways to use burning and herbicide applications to achieve *P. arundinacea* control in wetland restorations. Efficiency in restoration practices is important because it frees up resources for more restoration (103). Our research also raised several questions that will be crucial to determining the most effective strategy for managing *P. arundinacea* invasions to allow native species establishment. Identifying the primary source of *P. arundinacea* seeds following vegetation removal will be important; what is the relative importance of the seed bank, on-site annual seed production, and off-site dispersal for the reinvasion of cleared sites? *P. arundinacea* removal and follow up management is necessary for at least 2 years prior to native species establishment, but at what point can restoration efforts safely shift focus from *P. arundinacea* control to native species establishment?

In summary, our results indicated that implementing control treatments with respect to *P. arundinacea* growth characteristics improved the effectiveness of control treatments.

Specifically, we demonstrated that later season herbicide applications are more effective in controlling *P. arundinacea*, and burning (in conjunction with subsequent herbicide applications) reduces the density of the *P. arundinacea* seed bank, limiting *P. arundinacea*'s ability to recolonize from seed. Controlling *P. arundinacea* in the most efficient way is crucial to the establishment of native vegetation in wetland restorations. Reduction of *P. arundinacea* is a long-term process and one that is complicated by potential reinvasion of cleared sites, so control efforts must be as effective as possible. Moreover, *P. arundinacea* is still widely cultivated as a forage crop and planted as a conservation species (15, 16), and these populations may serve as sources of continuing propagule pressure, further complicating localized eradication efforts. The contribution of planted populations to the spread of *P. arundinacea* into natural areas is not well understood, however efforts to restore biodiversity may benefit from practices that reduce *P. arundinacea* propagule pressure from planted sources (e.g. restricting use of *P. arundinacea* where non-aggressive species could be substituted, and preventing seed set from cultivated populations of *P. arundinacea*).

Table 2-1. Soil characteristics vary significantly between sites ($p < 0.01$ for all characteristics) but do not differ significantly within each site ($p > 0.05$ for all characteristics). Depth to water was similar for each site, as was range in elevation. Means are presented ± 1 SE, and range is shown below.

Site	Elevation (m)	Depth to water (cm)	Soil Characteristics			
			Olsen-P (ppm)	Total N (%N)	Total Organic Carbon (%C)	pH (0.01 M CaCl ₂)
NSPSF site	934.9 \pm 0.06	40.04 \pm 1.72	12.26 \pm 0.32	2.75 \pm 0.06	15.04 \pm 0.72	5.48 \pm 0.02
	934.5-935.2	31.8-45.5	10-17	2.1-3.3	5.5-21.1	5.2-5.9
Arboretum site	976.8 \pm 0.06	45.05 \pm 6.66	22.50 \pm 0.92	1.60 \pm 0.05	20.17 \pm 0.59	6.46 \pm 0.04
	976.2-977.3	13.0-84.0	17-29	1.3-1.8	16.6-24.6	6.2-6.9

Table 2-2. Timing of burning and herbicide applications varied from year to year, but attempts were made to time treatments at similar growing degree days (gdd).

treatment	NSPSF site				Arboretum site				average	
	round 1		round 2		round 1		round 2			
	date	gdd	date	gdd	date	gdd	date	gdd	date	gdd
burn	4/29/2000	711	5/7/2001	504	5/14/2001	874	5/14/2002	731	5/10	721
spring herbicide	5/9/2000	1058	5/18/2001	785	5/24/2001	1215	6/5/2002	1311	5/21	1137
late season herbicide	9/12/2000	5458	8/16/2001	4378	8/16/2001	4378	8/25/2002	4541	8/16	4460
later season herbicide	9/24/2000	5769	9/24/2001	5625	9/24/2001	5625	9/25/2002	5643	9/24	5634

Table 2-3. Grass and forb species were included in the restoration mix of native species. The percent of the mixture made up by each species in terms of the weight of pure live seed (PLS) is given below. The grass mixture was applied at a rate of 6 kg ac⁻¹ pure live seed (PLS) (13 lbs ac⁻¹ PLS), and the forb mixture was seeded at 2 kg ac⁻¹ (4 lbs ac⁻¹ PLS).

Grasses	PLS % by weight	Forbs	PLS % by weight
<i>Andropogon gerardii</i>	53.42	<i>Eupatorium maculatum</i>	23.01
<i>Elymus canadensis</i>	13.89	<i>Heliopsis helianthoides</i>	12.56
<i>Panicum virgatum</i>	12.22	<i>Alisma subcordatum</i>	12.46
<i>Sorghastrum nutans</i>	7.52	<i>Eupatorium perfoliatum</i>	11.33
<i>Calamagrostis canadensis</i>	6.36	<i>Aster puniceus</i>	6.91
<i>Spartina pectinata</i>	2.24	<i>Acorus calamus</i>	6.15
<i>Elymus</i> sp.	2.22	<i>Agastache foeniculu.</i>	5.87
<i>Sparganium eurycarpum.</i>	1.10	<i>Helianthus giganteus</i>	4.77
<i>Scirpus cyperinus</i>	0.73	<i>Aster lanceolatus</i>	3.99
<i>Scirpus atrovirens</i>	0.42	<i>Helenium autumnale</i>	3.33
		<i>Asclepias incarnata</i>	3.01
		<i>Aster umbellatus.</i>	2.35
		<i>Desmodium canadense</i>	2.89
		<i>Pycnanthemum virginianum</i>	2.01
		<i>Monarda fistulosa</i>	1.01
		<i>Aster novae-angilae</i>	0.88
		<i>Dalea candida</i>	0.56
		<i>Euthamia graminifolia</i>	0.47

Table 2-4. Biomass data for the NSPSF site, for plots that received one year of burning/herbicide applications. Mean biomass estimated from replications where each species was detected.

Three months post-seeding			One year post-seeding		
	no. of plots	mean biomass (g m ⁻²)		no. of plots	mean biomass (g m ⁻²)
Planted species					
<i>Eupatorium perfoliatum</i>	35	57.52	<i>Eupatorium perfoliatum</i>	20	380.36
<i>Eupatorium maculatum</i>	11	22.80	<i>Helianthus giganteus</i>	8	85.10
<i>Desmodium canadense</i>	3	1.66	<i>Asclepias incarnata</i>	1	40.12
<i>Asclepias incarnata</i>	2	26.40	<i>Calamagrostis canadensis</i>	1	1.04
<i>Aster sp.</i>	1	10.39			
Non-planted perennial species					
<i>Phalaris arundinacea</i>	97	215.67	<i>Phalaris arundinacea</i>	121	420.79
<i>Urtica dioica</i>	24	101.31	<i>Urtica dioica</i>	35	317.14
<i>Verbena hastata</i>	18	98.19	<i>Verbena hastata</i>	7	108.13
<i>Rudbeckia hirta</i>	14	17.90	<i>Mentha arvensis</i>	7	51.73
<i>Cirsium vulgare</i>	10	41.68	<i>Nepeta cataria</i>	6	150.40
<i>Mentha arvensis</i>	9	57.61	<i>Mimulus ringens</i>	5	60.26
<i>Lycopus americanus</i>	5	19.96	<i>Medicago sativa</i>	4	14.86
<i>Nepeta cataria</i>	4	79.44	<i>Cirsium vulgare</i>	2	536.80
<i>Mimulus ringens</i>	2	2.29	<i>Lycopus americanus</i>	2	21.05
<i>Solidago sp.</i>	1	43.34	<i>Cirsium arvense</i>	1	101.45
<i>Cirsium arvense</i>	1	9.56	<i>Solidago sp.</i>	1	14.34
<i>Taraxcum officinale</i>	1	8.73	<i>Rudbeckia hirta</i>	1	8.21
			<i>Epilobium coloratum</i>	1	0.83
Non-planted annual species					
<i>Erechtites hieracifolia</i>	29	361.55	<i>Impatiens capensis</i>	23	78.90
<i>Rorippa palustris</i>	10	39.55	<i>Polygonum sagittatum</i>	4	29.34
<i>Hypericum sp.</i>	10	7.63	<i>Polygonum lapathifolium</i>	3	48.26
<i>Impatiens capensis</i>	9	83.90	<i>Potentilla norvegica</i>	2	24.32
<i>Potentilla norvegica</i>	4	15.49	<i>Chenopodium album</i>	1	8.83
<i>Galium aparine</i>	2	5.77	<i>Erechtites hieracifolia</i>	1	0.52
<i>Solanum nigrum</i>	1	37.31	<i>Solanum nigrum</i>	1	0.21
Woody species					
<i>Populus deltoides</i>	10	7.71	<i>Salix sp.</i>	1	691.20
<i>Salix sp.</i>	2	4.52			
<i>Acer negundo</i>	1	0.62			
Unknown species					
<i>unknown forb</i>	24	16.61			
<i>unknown grass</i>	8	4.61			

Table 2-5. Biomass data for the NSPSF site, for plots that received two years of burning/herbicide applications. Mean biomass was estimated from plots where each species was detected.

Three months post-seeding			One year post-seeding		
Planted species	no. of plots	mean biomass (g m ⁻²)	Planted species	no. of plots	mean biomass (g m ⁻²)
<i>Eupatorium perfoliatum</i>	12	17.89	<i>Eupatorium maculatum</i>	4	13.86
<i>Aster sp.</i>	2	80.93	<i>Calamagrostis canadensis</i>	3	7.91
<i>Desmodium canadense</i>	1	1.04	<i>Helenium autumnale</i>	3	3.18
<i>Panicum virginicum</i>	1	0.73	<i>Elymus canadensis</i>	1	7.90
			<i>Eupatorium perfoliatum</i>	1	1.01
Non-planted perennial species					
<i>Phalaris arundinacea</i>	68	288.39	<i>Phalaris arundinacea</i>	99	430.92
<i>Urtica dioica</i>	42	118.72	<i>Urtica dioica</i>	39	94.85
<i>Nepeta cataria</i>	12	248.84	<i>Epilobium coloratum</i>	16	23.44
<i>Rudbeckia hirta</i>	11	6.25	<i>Nepeta cataria</i>	10	29.22
<i>Verbena hastata</i>	8	71.60	<i>Verbena hastata</i>	9	136.66
<i>Epilobium coloratum</i>	5	56.31	<i>Polygonum persicaria</i>	8	64.15
<i>Mentha arvensis</i>	4	15.18	<i>Lycopus americanus</i>	4	223.48
<i>Mimulus ringens</i>	3	5.37	<i>Mentha arvensis</i>	4	22.72
<i>Achillea millefolium</i>	3	2.29	<i>Carex sp.</i>	4	2.53
<i>Mentha spicata</i>	2	180.44	<i>Solidago sp.</i>	1	1.56
<i>Solidago sp.</i>	2	3.95	<i>Carex scoparia</i>	1	1.46
<i>Carex sp.</i>	2	0.21	<i>Rudbeckia hirta</i>	1	0.54
<i>Cirsium vulgare</i>	1	225.65			
<i>Rumex crispus</i>	1	10.60			
<i>Cirsium arvense</i>	1	7.80			
<i>Glyceria grandis</i>	1	2.49			
<i>Cyperus strigosus</i>	1	1.56			
Non-planted annual species					
<i>Erechtites hieracifolia</i>	51	168.64	<i>Impatiens capensis</i>	54	57.14
<i>Impatiens capensis</i>	35	216.36	<i>Polygonum sagittatum</i>	25	178.73
<i>Polygonum lapathifolium</i>	9	140.52	<i>Polygonum hydropiper</i>	19	84.13
<i>Polygonum hydropiper</i>	3	170.84	<i>Polygonum lapathifolium</i>	5	166.22
<i>Polygonum sagittatum</i>	3	38.42	<i>Erechtites hieracifolia</i>	5	23.49
<i>Rorippa palustris</i>	3	35.86	<i>Ludwigia palustris</i>	3	35.39
<i>Potentilla norvegica</i>	3	31.18	<i>Hypericum sp.</i>	2	5.92
<i>Ludwigia palustris</i>	3	15.18	<i>Bidens cernua</i>	1	136.79
<i>Hypericum sp.</i>	3	3.26			
<i>Solanum nigrum</i>	3	2.98			
<i>Lindernia dubia</i>	2	2.70			
<i>Setaria faberi</i>	1	417.94			
<i>Galium aparine</i>	1	1.97			
Woody species					
<i>Sambucus canadensis</i>	2	32.27	<i>Rhamnus cathartica</i>	2	1.82
<i>Populus deltoides</i>	2	2.39	<i>Sambucus canadensis</i>	1	70.81
<i>Salix sp.</i>	2	2.08	<i>Acer negundo</i>	1	1.77
Unknown species					
			<i>unknown forb</i>	5	2.59
			<i>Polygonum sp.</i>	3	126.71

Table 2-6. Cover data for the NSPSF site, for plots that received one year of burning/herbicide applications. Mean % cover was estimated from plots where each species was detected (maximum of 44 plots) (continued next page).

Three months post-seeding			One year post-seeding		
Planted species	no. of plots	mean cover (%)		no. of plots	mean cover (%)
<i>Eupatorium perfoliatum</i>	27	11.62	<i>Eupatorium perfoliatum</i>	32	20.32
<i>Helianthus giganteus</i>	11	0.50	<i>Helenium autumnale</i>	19	6.68
<i>Asclepias incarnata</i>	9	1.08	<i>Heleanthus gigantea</i>	13	6.01
<i>Aster sp.</i>	11	1.08	<i>Aster sp.</i>	3	0.23
<i>Eupatorium maculatum</i>	7	2.46	<i>Agastache foeniculum</i>	2	1.50
<i>Panicum virgatum</i>	5	0.42	<i>Eupatorium maculatum</i>	2	0.10
<i>Andropogon gerardii</i>	3	0.23			
<i>Sorghastrum nutans</i>	2	0.30			
<i>Desmodium canadense</i>	1	0.50			
<i>Elymus canadensis</i>	1	0.50			
<i>Helenium autumnale</i>	1	0.10			
<i>Pycnanthemum virginianum</i>	1	0.50			
<i>Spartina pectinata</i>	1	0.10			
Non-planted perennial species					
<i>Phalaris arundinacea</i>	43	53.78	<i>Phalaris arundinacea</i>	43	67.79
<i>Urtica dioica</i>	25	10.32	<i>Urtica dioica</i>	33	23.20
<i>Verbena hastata</i>	23	5.36	<i>Verbena hastata</i>	28	5.37
<i>Rudbeckia hirta</i>	20	1.36	<i>Asclepias syriaca</i>	21	5.02
<i>Mentha arvensis</i>	11	1.55	<i>Cirsium vulgare</i>	15	2.97
<i>Polygonum persicaria</i>	10	3.36	<i>Nepeta cataria</i>	12	4.49
<i>Lycopus americanus</i>	7	1.30	<i>Mondarda fistulosa</i>	11	2.15
<i>Nepeta cataria</i>	6	3.92	<i>Mentha arvensis</i>	8	1.45
<i>Cyperus strigosus</i>	2	0.30	<i>Rudbeckia hirta</i>	6	0.63
<i>Rumex crispus</i>	1	0.50	<i>Epilobium purpurea</i>	4	0.90
<i>Oxalis stricta</i>	1	0.10	<i>Cirsium arvense</i>	4	0.80
			<i>Solidago sp.</i>	3	0.23
			<i>Carex sp.</i>	1	2.50
			<i>Lycopus americanus</i>	1	0.10
			<i>Rumex crispus</i>	1	0.10

Table 2-6 (continued)

Three months post-seeding			One year post-seeding		
Non-planted annual species	no. of plots	mean cover (%)		no. of plots	mean cover (%)
<i>Erechtites hieracifolia</i>	41	28.78	<i>Impatiens capensis</i>	36	7.11
<i>Impatiens capensis</i>	24	6.49	<i>Polygonum sagittatum</i>	12	5.29
<i>Polygonum lapathifolium</i>	13	4.12	<i>Erechtites hieracifolia</i>	6	0.77
<i>Cirsium arvense</i>	12	1.60	<i>Potentilla norvegica</i>	5	0.34
<i>Solanum nigrum</i>	11	4.37	<i>Polygonum hydropiper</i>	3	6.00
<i>Polygonum hydropiper</i>	11	2.84	<i>Senecio vulgaris</i>	1	0.10
<i>Bidens cernua</i>	8	0.85			
<i>Cirsium vulgare</i>	7	1.30			
<i>Hypericum sp.</i>	7	0.50			
<i>Rorrippa palustris</i>	7	0.33			
<i>Setaria faberi</i>	7	0.21			
<i>Polygonum sagittatum</i>	6	3.18			
<i>Potentilla norvegica</i>	5	0.26			
<i>Galium aparine</i>	3	0.37			
<i>Echinochloa crusgalli</i>	1	0.00			
Non-planted woody species					
<i>Populus deltoides</i>	10	0.50	<i>Sambucus canadensis</i>	3	1.03
<i>Salix sp.</i>	4	0.40	<i>Salix nigra</i>	2	1.30
<i>Sambucus canadensis</i>	2	0.30	<i>Acer negundo</i>	1	0.10
<i>Acer negundo</i>	1	0.50	<i>Populus deltoides</i>	1	0.10
Unknown species					
<i>unknown forb</i>	3	1.83	<i>Polygonum sp.</i>	10	2.91
<i>unknown grass</i>	5	0.50	<i>unknown grass</i>	1	0.10
<i>Cyperaceae</i>	1	0.50			

Table 2-7. Cover data for the NSPSF site, for plots that received two years of burning/herbicide applications. Mean % cover was estimated from plots where each species was detected (maximum of 36 plots) (continued on next page).

Three months post-seeding			One year post-seeding		
Planted species	no. of plots	mean cover (%)		no. of plots	mean cover (%)
<i>Eupatorium perfoliatum</i>	17	4.14	<i>Eupatorium perfoliatum</i>	9	8.73
<i>Panicum virgatum</i>	4	0.30	<i>Asclepias incarnata</i>	6	1.70
<i>Helenium autumnale</i>	3	5.07	<i>Elymus canadensis</i>	6	0.63
			<i>Eupatorium maculatum</i>	4	0.30
			<i>Scirpus atrovirens</i>	4	0.40
			<i>Calamagrostis canadensis</i>	2	1.50
			<i>Aster sp.</i>	1	0.10
			<i>Helenium autumnale</i>	1	2.50
Non-planted perennial species					
<i>Phalaris arundinacea</i>	36	35.78	<i>Phalaris arundinacea</i>	35	63.43
<i>Urtica dioica</i>	26	19.52	<i>Urtica dioica</i>	26	20.45
<i>Verbena hastata</i>	16	4.75	<i>Polygonum persicaria</i>	16	5.00
<i>Nepeta cataria</i>	14	15.82	<i>Epilobium coloratum</i>	14	9.61
<i>Rudbeckia hirta</i>	7	1.01	<i>Verbena hastata</i>	12	5.80
<i>Cirsium vulgare</i>	7	0.16	<i>Nepeta cataria</i>	11	4.05
<i>Epilobium purpurea</i>	6	4.18	<i>Mimulus ringens</i>	8	4.58
<i>Lycopus americanus</i>	5	3.64	<i>Rudbeckia hirta</i>	8	0.95
<i>Asclepias syriaca</i>	4	0.40	<i>Mentha arvensis</i>	7	1.01
<i>Mentha arvensis</i>	3	6.00	<i>Lycopus americana</i>	6	5.60
<i>Cirsium arvense</i>	2	2.50	<i>Carex scoparia</i>	5	1.14
<i>Cyperus strigosus</i>	2	0.50	<i>Carex sp.</i>	3	6.00
<i>Rumex crispus</i>	2	0.10	<i>Penthorum sedoides</i>	2	1.30
<i>Achillea millefolium</i>	1	0.50	<i>Rumex crispus</i>	2	1.30
<i>Mimulus ringens</i>	1	0.50	<i>Glyceria grandis</i>	2	0.10
<i>Solidago sp.</i>	1	0.10	<i>Lythrum salicaria</i>	1	15.00
<i>Lythrum salicaria</i>	1	0.10	<i>Ludwigia palustris</i>	1	2.50
			<i>Achillea millefolium</i>	1	0.50
			<i>Monarda fistulosa</i>	1	0.50

Table 2-7 (continued)

Three months post-seeding			One year post-seeding		
Non-planted annual species	no. of plots	mean cover (%)		no. of plots	mean cover (%)
<i>Impatiens capensis</i>	34	17.09	<i>Impatiens capensis</i>	35	22.03
<i>Erechtites hieracifolia</i>	29	26.40	<i>Polygonum sagittatum</i>	29	28.33
<i>Polygonum sagittatum</i>	22	14.98	<i>Polygonum hydropiper</i>	14	10.82
<i>Polygonum hydropiper</i>	13	13.00	<i>Polygonum lapathifolium</i>	14	5.90
<i>Solanum nigrum</i>	7	3.37	<i>Potentilla norvegica</i>	8	1.15
<i>Potentilla norvegica</i>	5	0.34	<i>Polygonum pennsylvanicum</i>	7	1.93
<i>Ludwigia palustris</i>	4	7.75	<i>Erechtites hieracifolia</i>	4	1.40
<i>Ambrosia artemisiifolia</i>	4	5.13	<i>Ambrosia artemisiifolia</i>	3	0.37
<i>Echinochloa crusgalli</i>	4	0.40	<i>Bidens cernua</i>	2	7.75
<i>Senecio vulgaris</i>	3	0.10			
<i>Galium aparine</i>	2	0.50			
<i>Setaria faberi</i>	1	15.00			
<i>Bidens cernua</i>	1	2.50			
<i>Hypericum sp.</i>	1	0.50			
<i>Rorippa palustris</i>	1	0.10			
<i>Amaranthus retroflexus</i>	1	0.10			
<i>Chenopodium album</i>	1	0.10			
Non-planted woody species					
<i>Populus deltoides</i>	3	5.87	<i>Sambucus canadensis</i>	3	10.83
<i>Sambucus canadensis</i>	3	5.20	<i>Rhamnus cathartica</i>	3	0.50
<i>Acer negundo</i>	1	0.10	<i>Acer negundo</i>	3	0.10
			<i>Populus tremuloides</i>	1	0.10
			<i>Salix sp.</i>	1	0.10
Unknown species					
<i>Polygonum sp.</i>	24	12.07	<i>Erigeron sp.</i>	1	0.10
			<i>Ranunculus sp.</i>	1	0.50

Table 2-8. Biomass data for the Arboretum site, for plots that received one year of burning/herbicide applications. Biomass was estimated from plots where each species was detected.

Three months post-seeding			One year post-seeding		
Planted species	no. of plots	mean biomass (g m ⁻²)	Planted species	no. of plots	mean biomass (g m ⁻²)
<i>Panicum virgatum</i>	2	9.77	<i>Calamagrostis canadensis</i>	6	2.82
<i>Heliopsis helianthoides</i>	1	17.25	<i>Panicum virginicum</i>	5	0.91
<i>Calamagrostis canadensis</i>	1	5.2	<i>Asclepias incarnata</i>	3	4.90
			<i>Sorghastrum nutans</i>	1	45.68
			<i>Helenium autumnale</i>	1	4.89
Non-planted perennial species					
<i>Cyperus strigosus</i>	97	239.28	<i>Cyperus strigosus</i>	98	59.57
<i>Phalaris arundinacea</i>	68	449.41	<i>Phalaris arundinacea</i>	93	766.94
<i>Urtica dioica</i>	17	38.73	<i>Polygonum persicaria</i>	67	96.44
<i>Taraxcum officinale</i>	16	17.01	<i>Urtica dioica</i>	25	43.22
<i>Cirsium arvense</i>	9	118.05	<i>Oxalis stricta</i>	9	2.10
<i>Rudbeckia hirta</i>	9	13.69	<i>Rumex crispus</i>	6	56.08
<i>Rumex crispus</i>	5	409.05	<i>Asclepias syriaca</i>	5	66.44
<i>Silene latifolia</i>	5	30.91	<i>Verbena hastata</i>	4	2.21
<i>Oxalis stricta</i>	3	21.58	<i>Rudbeckia hirta</i>	3	0.70
<i>Achillea millefolium</i>	3	2.6	<i>Monarda fistulosa</i>	2	0.91
<i>Elytrigia repens</i>	1	48.33	<i>Zizia aurea</i>	2	0.67
<i>Asclepias syriaca</i>	1	43.76	<i>Leersia oryzoides</i>	1	107.58
<i>Polygonum persicaria</i>	1	29.83	<i>Cirsium vulgare</i>	1	46.05
<i>Leersia oryzoides</i>	1	0.83	<i>Elytrigia repens</i>	1	10.39
			<i>Cirsium arvense</i>	1	1.35
			<i>Thalictrum sp.</i>	1	0.46
Non-planted annual species					
<i>Portulaca oleracea</i>	24	30.43	<i>Setaria glauca</i>	37	98.19
<i>Thalapsi arvense</i>	20	17.44	<i>Setaria faberi</i>	37	34.80
<i>Potentilla norvegica</i>	19	100.26	<i>Polygonum pensylvanicum</i>	33	139.15
<i>Rorippa palustris</i>	14	17.25	<i>Acalypha rhomboidea</i>	28	34.46
<i>Setaria glauca</i>	10	275.62	<i>Potentilla norvegica</i>	23	5.10
<i>Setaria faberi</i>	7	495.57	<i>Polygonum lapathifolium</i>	13	175.31
<i>Polygonum lapathifolium</i>	7	365.94	<i>Echinochloa crusgalii</i>	10	7.94
<i>Chenopodium album</i>	7	112.8	<i>Rorippa palustris</i>	6	4.92
<i>Amaranthus sp</i>	5	72.07	<i>Thalspi arvense</i>	4	8.93
<i>Polygonum convovulvus</i>	3	55.05	<i>Chenopodium album</i>	3	9.27
<i>Acalypha rhomboidea</i>	3	11.88	<i>Lindernia dubia</i>	2	297.87
<i>Echinochloa crusgalii</i>	1	10.29	<i>Erechtites hieracifola</i>	2	27.39
			<i>Hypericum sp.</i>	1	0.62
Non-planted woody species					
<i>Vitis sp</i>	1	33.99	<i>Salix sp.</i>	1	1.35
<i>Salix sp</i>	1	1.14			
Unknown species					
<i>Polygonum sp</i>	8	184.12			

Table 2-9. Biomass data for the Arboretum site, for plots that received two years of burning/herbicide applications, taken three months post-seeding. Mean biomass was estimated from plots where each species was detected.

Planted species	no. of plots	mean biomass (g m ⁻²)
<i>Panicum virginicum</i>	39	54.04267
<i>Calamagrostis canadensis</i>	15	6.200367
<i>Helenium autumnale</i>	8	0.679508
<i>Aster novae-angilae</i>	3	1.365079
<i>Asclepias incarnata</i>	2	84.65913
<i>Dalea candida</i>	1	19.27048
Non-planted perennial species		
<i>Cyperus strigosus</i>	91	132.0086
<i>Polygonum persicaria</i>	56	131.0516
<i>Phalaris arundinacea</i>	49	717.51
<i>Urtica dioica</i>	29	14.97955
<i>Rudbeckia hirta</i>	22	6.758462
<i>Rumex crispus</i>	18	38.75749
<i>Monarda fistulosa</i>	11	1.467727
<i>Oxalis stricta</i>	10	14.63995
<i>Portulaca oleracea</i>	9	0.540488
<i>Verbena hastata</i>	7	2.797471
<i>Amaranthus retroflexus</i>	6	72.7632
<i>Taraxcum officinale</i>	4	0.366388
<i>Epilobium coloratum</i>	3	15.58754
<i>Silene latifolia</i>	3	2.830633
<i>Asclepias syriaca</i>	2	13.40826
<i>Cirsium arvense</i>	1	54.69323
<i>Leersia oryzoidea</i>	1	28.99926
<i>Medicago sativa</i>	1	0.737974
<i>Cirsium vulgare</i>	1	0.654822
Non-planted annual species		
<i>Rorippa palustris</i>	45	16.44331
<i>Setaria glauca</i>	44	235.8876
<i>Setaria faberi</i>	35	238.4689
<i>Potentilla norvegica</i>	35	8.812033
<i>Polygonum pensylvanicum</i>	32	264.1736
<i>Polygonum lapathifolium</i>	30	354.8664
<i>Echinochloa crusgalli</i>	25	144.5365
<i>Lindernia dubia</i>	25	3.264548
<i>Acalypha rhomboidea</i>	14	68.29823
<i>Thalspi arvense</i>	4	14.2138
<i>Chenopodium album</i>	4	7.946213
<i>Erechtites hieracifolia</i>	3	49.97782
<i>Sonchus oleraceus</i>	1	84.60716
Non-planted woody species		
<i>Salix sp.</i>	3	0.689469
<i>Fraxinus sp.</i>	2	317.1833
<i>Populus deltoides</i>	2	1.008218

Table 2-10. Cover data for the Arboretum site, for plots that received one year of burning/herbicide applications. Mean % cover was estimated from plots where each species was detected (maximum of 40 plots) (continued on next page).

Three months post-seeding			One year post-seeding		
	no. of plots	mean biomass (g m ⁻²)	x	no. of plots	mean biomass (g m ⁻²)
Planted species					
<i>Panicum virgatum</i>	11	0.83	<i>Asclepias incarnata</i>	8	0.85
<i>Asclepias incarnata</i>	7	0.21	<i>Panicum virgatum</i>	3	0.50
<i>Helianthus giganteus</i>	2	0.30	<i>Helenium autumnale</i>	2	0.30
<i>Heliopsis helianthoides</i>	1	0.50	<i>Elymus candensis</i>	1	0.10
<i>Eupatorium perfoliatum</i>	1	0.10	<i>Eupatorium maculatum</i>	1	0.10
Non-planted perennial species					
<i>Cyperus strigosus</i>	37	49.64	<i>Phalaris arundinacea</i>	39	66.73
<i>Phalaris arundinacea</i>	34	32.15	<i>Polygonum persicaria</i>	35	9.96
<i>Urtica dioica</i>	25	7.42	<i>Urtica dioica</i>	30	4.86
<i>Cirsium vulgare</i>	18	11.49	<i>Cyperus strigosus</i>	27	13.67
<i>Rumex crispis</i>	15	5.16	<i>Rumex crispis</i>	16	4.22
<i>Rudbeckia hirta</i>	15	0.71	<i>Asclepias syriaca</i>	9	1.02
<i>Asclepias syriaca</i>	11	4.85	<i>Oxalis stricta</i>	7	0.39
<i>Cirsium arvense</i>	7	1.30	<i>Polygonum amphibium</i>	4	1.00
<i>Oxalis stricta</i>	4	0.80	<i>Verbena hastata</i>	3	1.83
<i>Verbena hastata</i>	3	0.37	<i>Cirsium vulgare</i>	3	0.23
<i>Solidago sp.</i>	1	0.10	<i>Taraxcum officinale</i>	3	0.23
<i>Scutellaria lateriflora</i>	1	0.10	<i>Rudbeckia hirta</i>	2	1.50
<i>Bromus sp.</i>	1	0.10	<i>Vernonia fasciculata</i>	2	0.30
			<i>Medicago sativa</i>	2	0.10
			<i>Lycopus americanus</i>	1	2.50
			<i>Bromus inermis</i>	1	2.50
			<i>Aster ericoides</i>	1	0.10
			<i>Carex sp.</i>	1	0.10
			<i>Zizia aurea</i>	1	0.10
			<i>Cirsium arvense</i>	1	0.10
			<i>Epilobium coloratum</i>	1	0.00

Table 2-10 (continued)

Three months post-seeding			One year post-seeding		
	no. of plots	mean biomass (g m ⁻²)	x	no. of plots	mean biomass (g m ⁻²)
Non-planted annual species					
<i>Setaria glauca</i>	33	14.97	<i>Polygonum pensylvanicum</i>	34	13.34
<i>Polygonum pensylvanicum</i>	30	21.52	<i>Setaria faberi</i>	29	11.81
<i>Setaria faberi</i>	27	12.55	<i>Polygonum lapathifolium</i>	28	9.97
<i>Potentilla norvegica</i>	25	10.09	<i>Setaria glauca</i>	28	9.10
<i>Rorripa palustris</i>	25	1.64	<i>Potentilla norvegica</i>	21	1.13
<i>Amaranthus</i>	22	2.88	<i>Rorripa palustris</i>	15	1.25
<i>Thapsi arvense</i>	20	0.70	<i>Acalypha rhomboidea</i>	14	10.68
<i>Chenopodium album</i>	18	4.82	<i>Echinochloa crusgalli</i>	7	12.93
<i>Portulaca oleracea</i>	17	3.41	<i>Conyza canadensis</i>	6	0.30
<i>Acalypha rhomboidea</i>	13	1.36	<i>Chenopodium album</i>	5	0.34
<i>Erechtites hieracifolia</i>	10	1.99	<i>Polygonum convovulus</i>	5	0.18
<i>Polygonum convovulus</i>	8	0.70	<i>Impatiens capensis</i>	5	0.10
<i>Polygonum lapathifolium</i>	7	14.64	<i>Erechtites hieracifolia</i>	4	0.30
<i>Echinochloa crusgalli</i>	5	0.82	<i>Amaranthus retroflexus</i>	2	0.50
<i>Ambrosia artemisiifolia</i>	5	0.26	<i>Ambrosia artemisiifolia</i>	2	0.10
<i>Lactuca canadensis</i>	4	1.40	<i>Hypericum sp.</i>	1	0.10
<i>Solanum nigrum</i>	2	0.30	<i>Thapsi arvense</i>	1	0.10
<i>Lindernia dubia</i>	2	0.10			
<i>Senecio vulgaris</i>	1	0.10			
Non-planted woody species					
<i>Vitis sp.</i>	1	0.10	<i>Acer negundo</i>	1	0.10

Table 2-11. Cover data for the Arboretum site for plots that received two years of burning/herbicide applications, three months post-seeding. Mean % cover was estimated from plots where each species was detected (maximum of 40 plots) (continued next page).

Planted species	no. of plots	mean biomass (g m ⁻²)
<i>Panicum virgatum</i>	22	5.31
<i>Asclepias incarnata</i>	4	0.20
<i>Aster novae-angillae</i>	1	0.10
<i>Desmodium canadense</i>	1	0.10
<i>Heliopsis helianthoides</i>	1	0.10
Non-planted perennial species		
<i>Polygonum persicaria</i>	33	9.30
<i>Cyperus strigosus</i>	29	28.78
<i>Urtica dioica</i>	25	2.46
<i>Phalaris arundinacea</i>	24	37.67
<i>Rumex crispus</i>	19	7.62
<i>Rudbeckia hirta</i>	12	2.14
<i>Oxalis stricta</i>	8	1.25
<i>Asclepias syriaca</i>	6	0.63
<i>Cirsium vulgare</i>	5	0.82
<i>Epilobium coloratum</i>	5	0.34
<i>Scutellaria lateriflora</i>	4	0.20
<i>Monarda fistulosa</i>	3	0.10
<i>Verbena hastata</i>	3	0.10
<i>Leersia oryzoides</i>	1	2.50
<i>Lycopus americanus</i>	1	0.50
<i>Zizia aurea</i>	1	0.10
<i>Silene latifolia</i>	1	0.10
<i>Taraxcum officinale</i>	1	0.10

Table 2-11 (continued)

Non-planted annual species	no. of plots	mean biomass (g m ⁻²)
<i>Polygonum lapathifolium</i>	38	21.63
<i>Polygonum pensylvanicum</i>	33	16.54
<i>Setaria faberi</i>	29	19.90
<i>Setaria glauca</i>	26	20.35
<i>Rorripa palustris</i>	26	2.76
<i>Echinochloa crusgalli</i>	23	7.22
<i>Acalypha rhomboidea</i>	17	9.33
<i>Potentilla norvegica</i>	16	3.59
<i>Chenopodium album</i>	11	0.32
<i>Lindernia dubia</i>	10	0.81
<i>Amaranthus retroflexus</i>	9	0.54
<i>Erechtites hiracifolia</i>	9	0.37
<i>Conyza canadensis</i>	6	6.53
<i>Ambrosia artemisiifolia</i>	6	1.43
<i>Thapsi arvense</i>	3	0.50
<i>Portulaca oleraceae</i>	3	0.23
<i>Polygonum convovulus</i>	3	0.23
<i>Impatiens capensis</i>	3	0.10
<i>Hypericum sp.</i>	1	0.10
<i>Veronica peregrina</i>	1	0.10
<i>Sonchus oleraceus</i>	1	0.10
Non-planted woody species		
<i>Acer negundo</i>	2	0.10
<i>Fraxinus nigra</i>	2	0.10
<i>Populus deltoides</i>	2	0.10

Figure 2-1. Field experiment study area at the NSPSF site in North St. Paul, MN, USA.

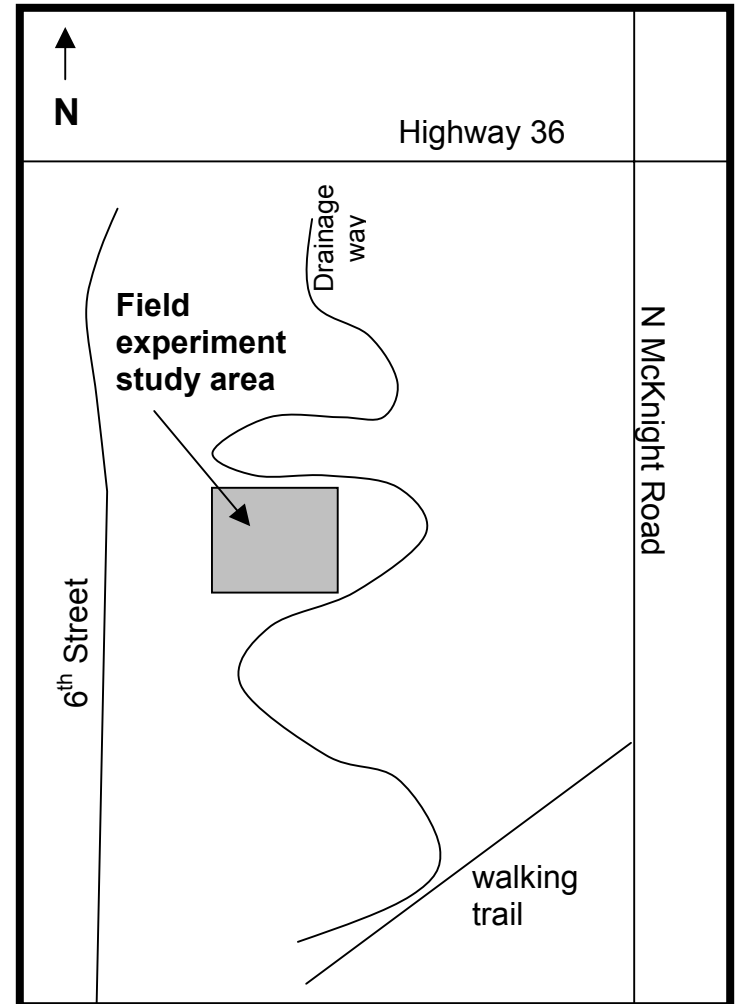


Figure 2-2. Field experiment study area at the Arboretum site in Chanhassen, MN, USA.

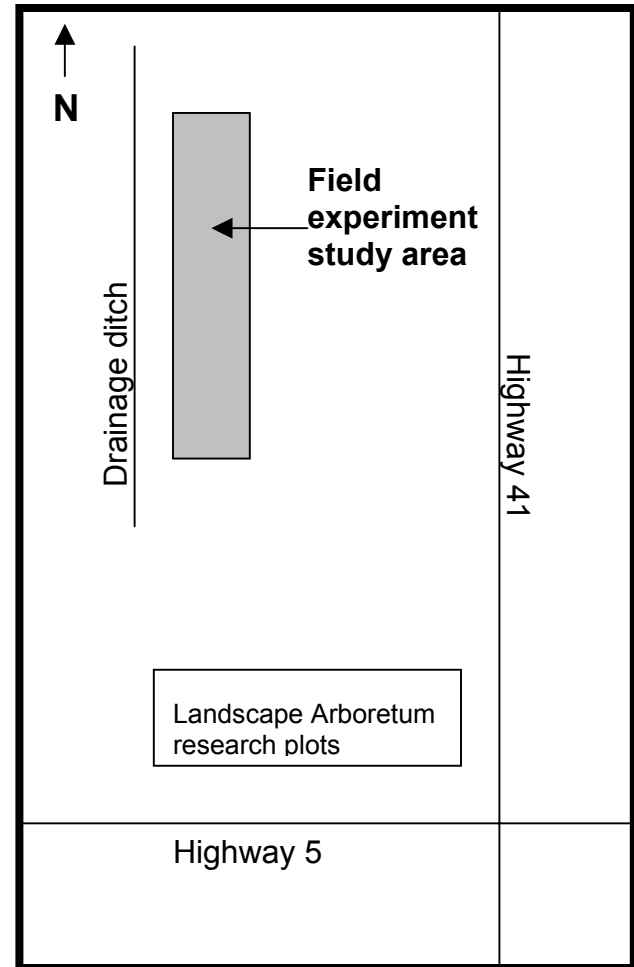


Figure 2-3. Schematic of treatment randomization for the large-scale control techniques field experiment for a single site. Each site had 20 whole plots. Burn treatments were randomized to whole plots (10 m x 10 m in area). Whole plots were divided into split plots (5 m x 5 m in area), and herbicide applications were randomized to split plots. In this schematic, the gray area represents the black poly edging that separated plots to minimize treatment contamination between plots.

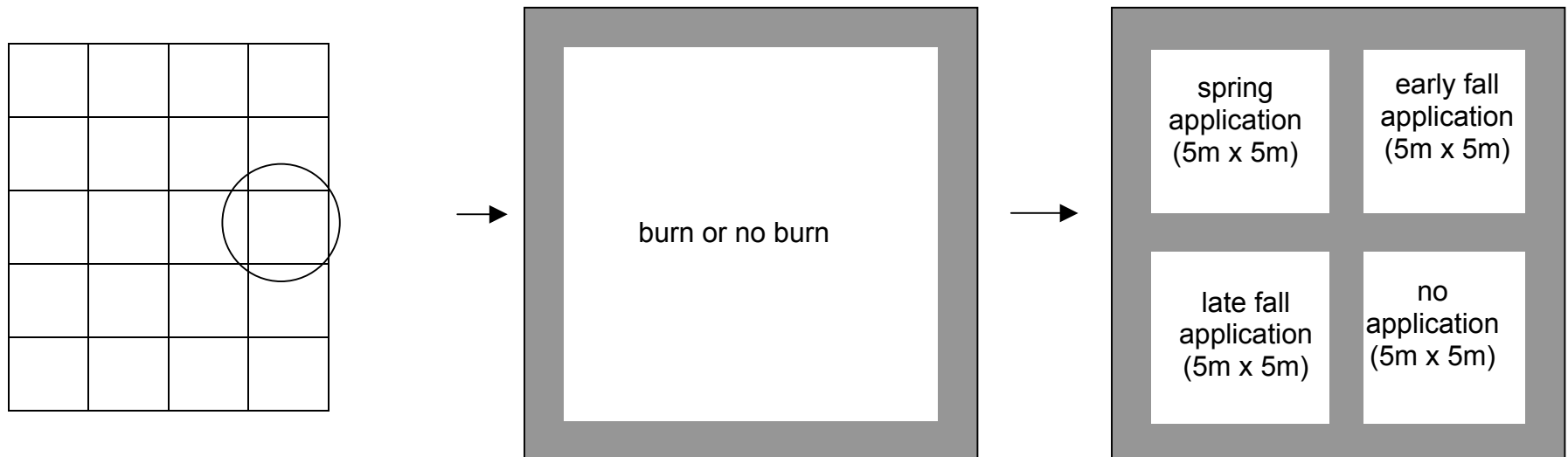


Figure 2-4. Accumulation of growing degree days was similar for all three years.

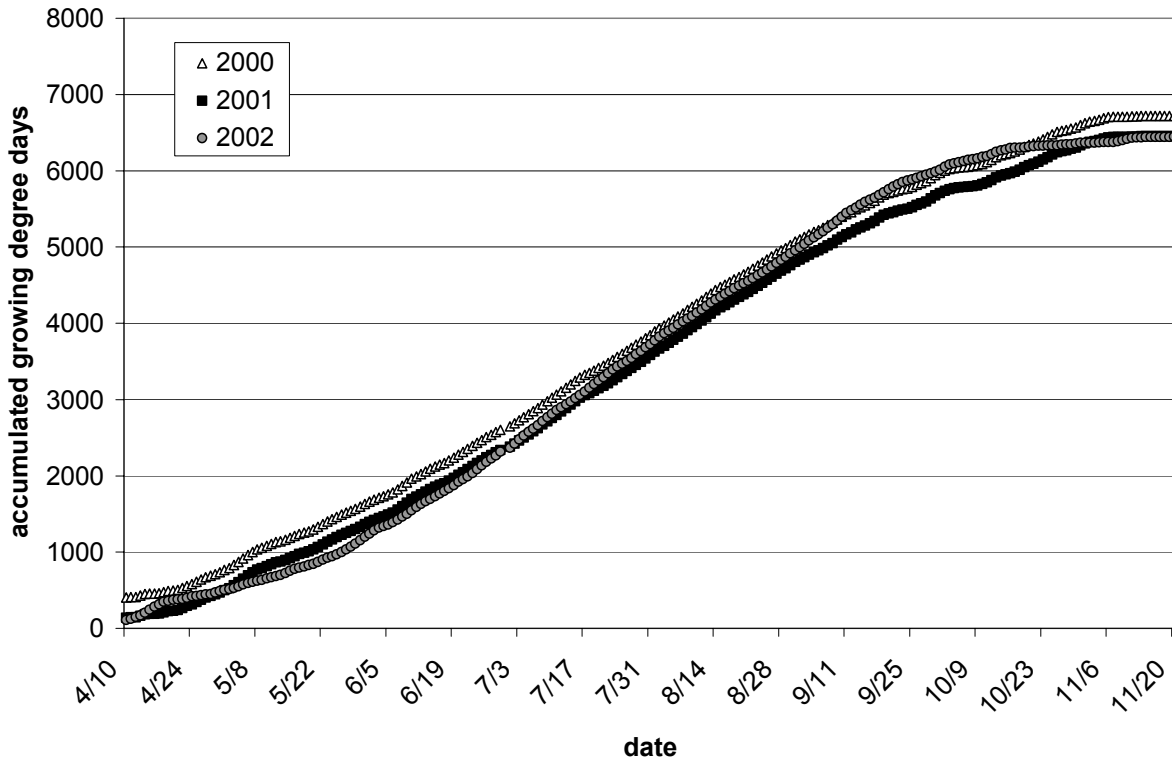


Figure 2-5. Rhizome carbohydrate concentration followed a similar pattern across the three growing seasons. The dotted line represents the date at which rhizome carbohydrate content increased, regardless of year.

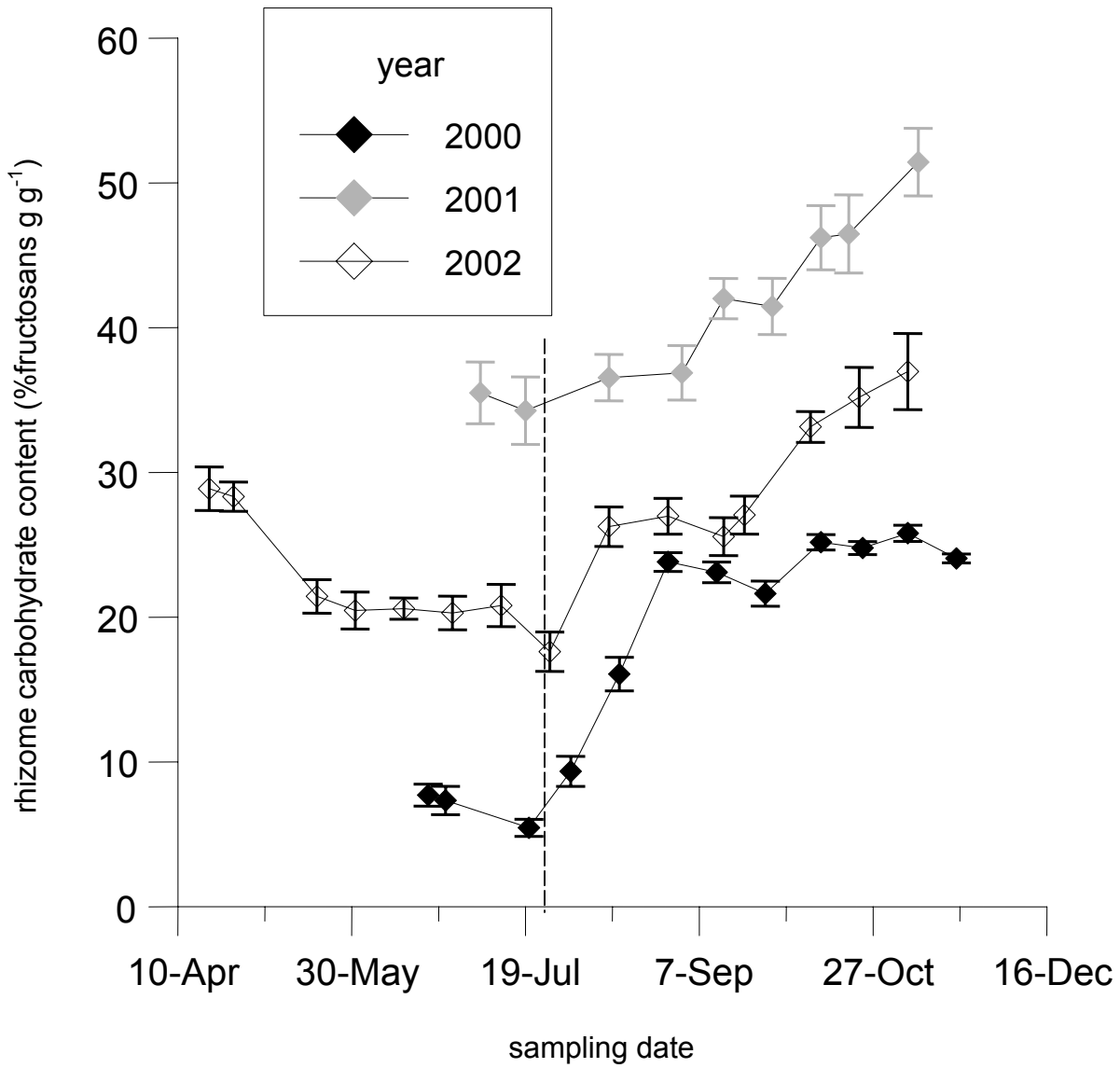


Figure 2-6. Burning increased *P. arundinacea* shoot density when measured four weeks after burning, but ultimately had no significant effect on *P. arundinacea* biomass when measured three months after burning.

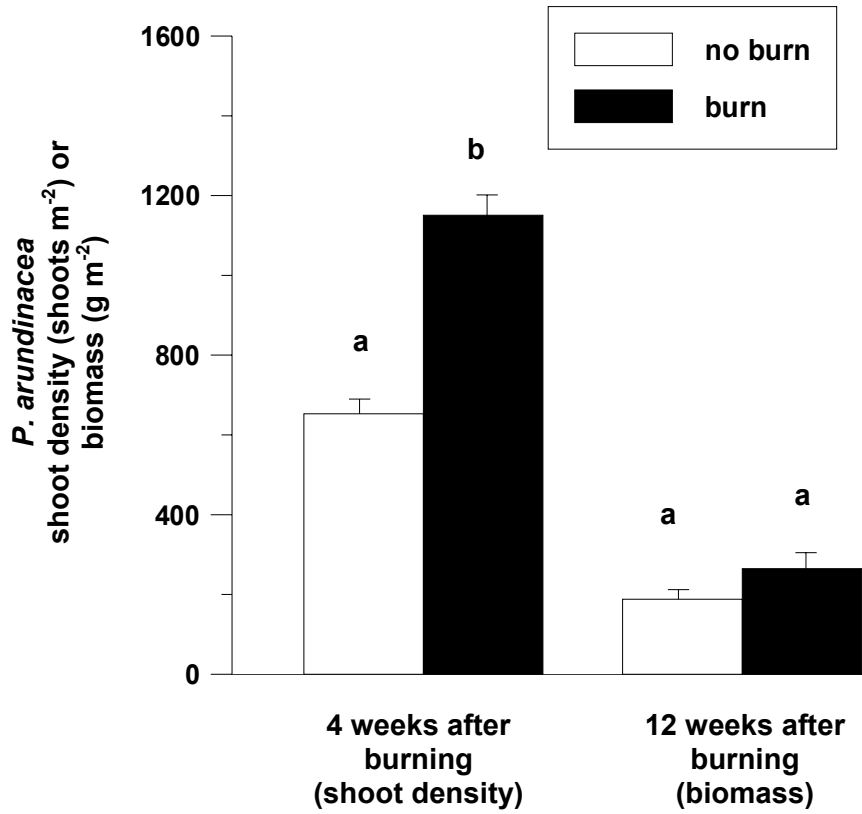


Figure 2-7. When assessed 8 months after treatment, regrowth from rhizomes was apparent in mid-May herbicide plots, but not in late August and late September plots.

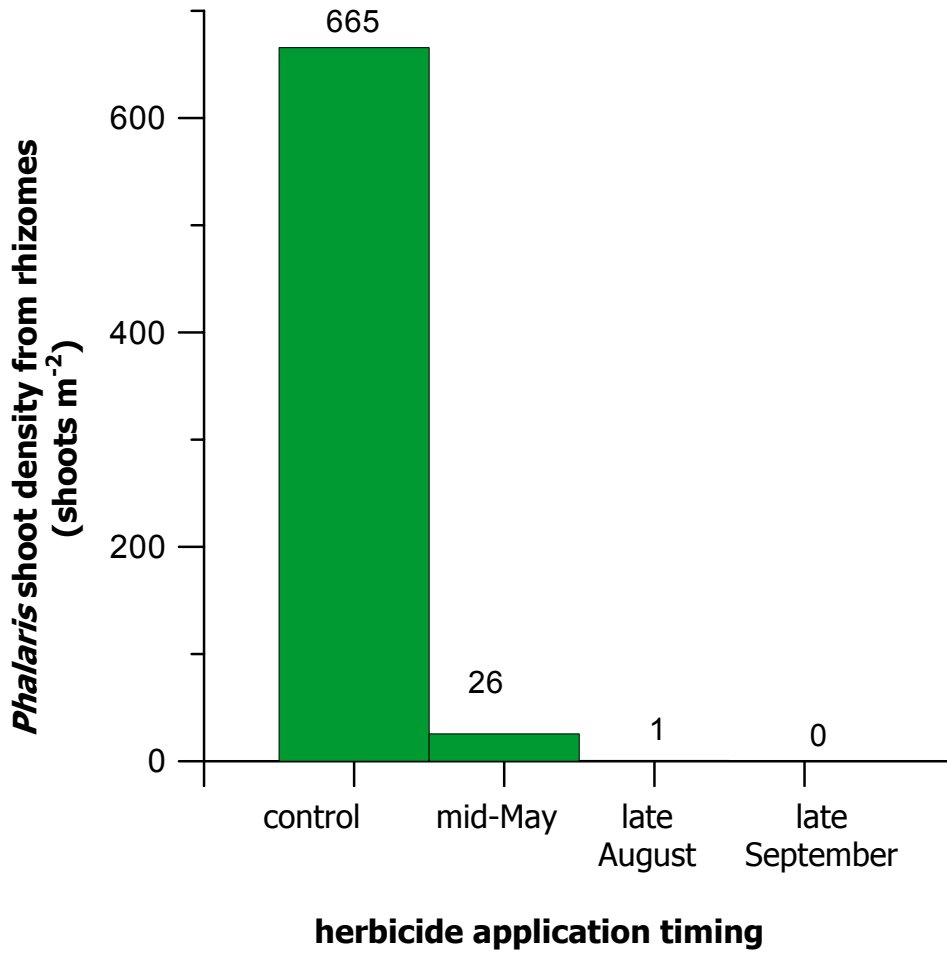


Figure 2-8. For plots that received one round of treatments, *P. arundinacea* recolonized rapidly during the year following seeding.

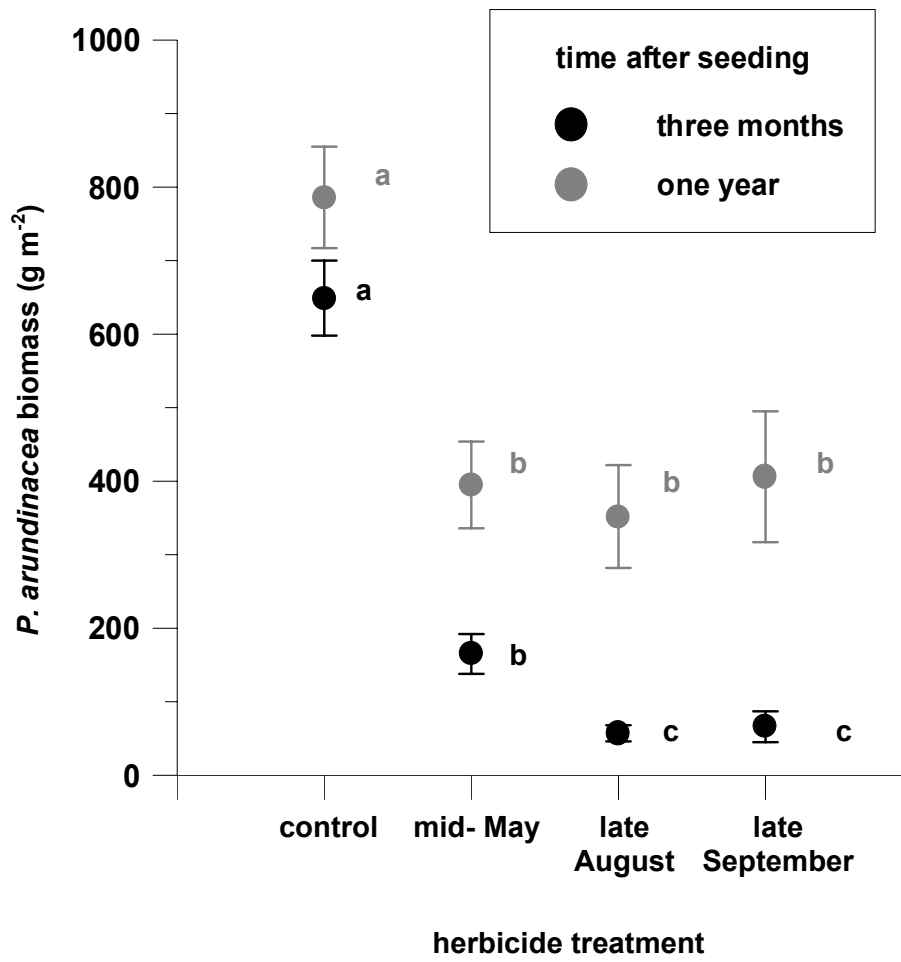


Figure 2-9. One round of treatments did not reduce *P. arundinacea* as effectively as 2 rounds of treatments. Means shown are for biomass data collected 3 months post-seeding.

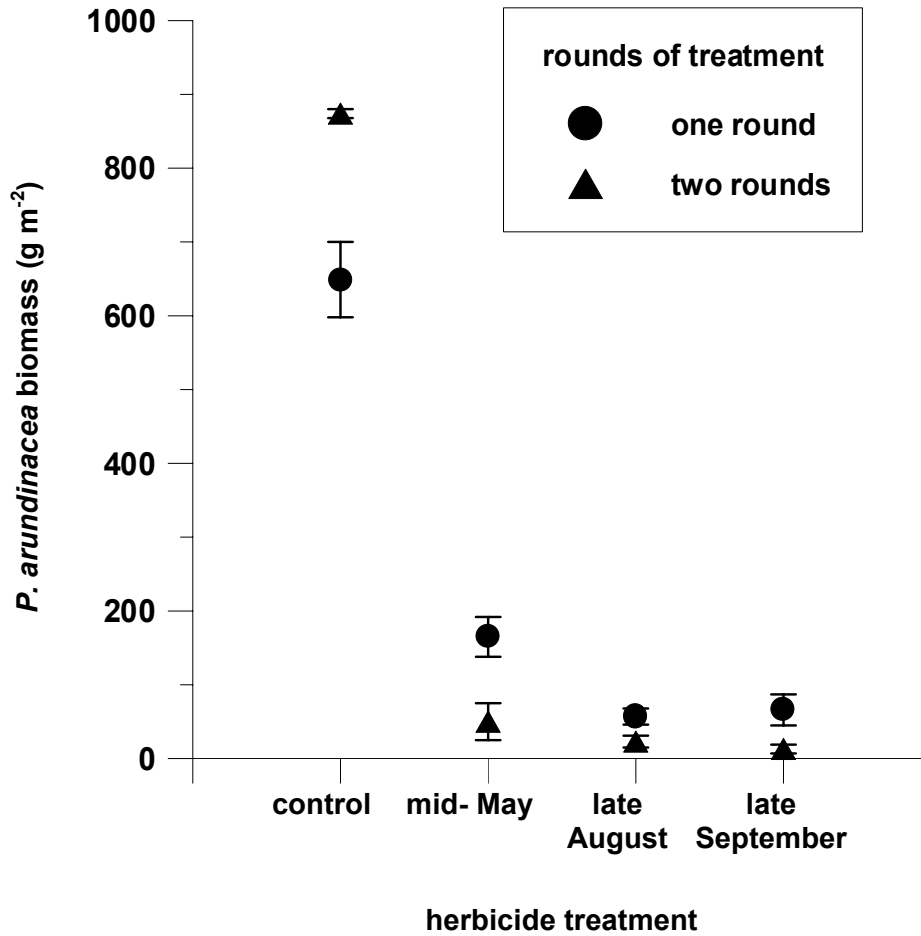


Figure 2-10. *P. arundinacea* also rapidly recolonized during the year following seeding after 2 rounds of treatment. After one year, only plots which received herbicide during late-August and late-September are significantly different from the control. Means shown are from NSPSF site only, as the data were not collected from the Arboretum site.

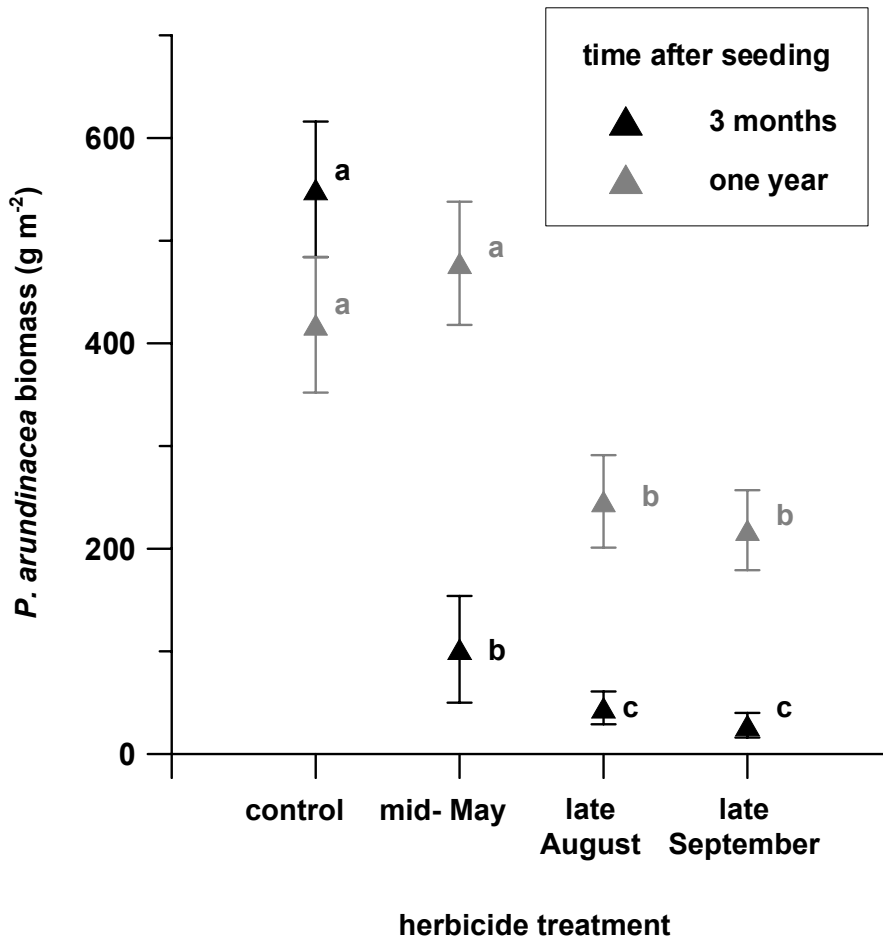


Figure 2-11. *P. arundinacea* biomass one year after treatment was similar in plots that had received one or two rounds of treatment, regardless of herbicide application timing. Means shown are from the NSPSF site, as these data were not collected from the Arboretum site.

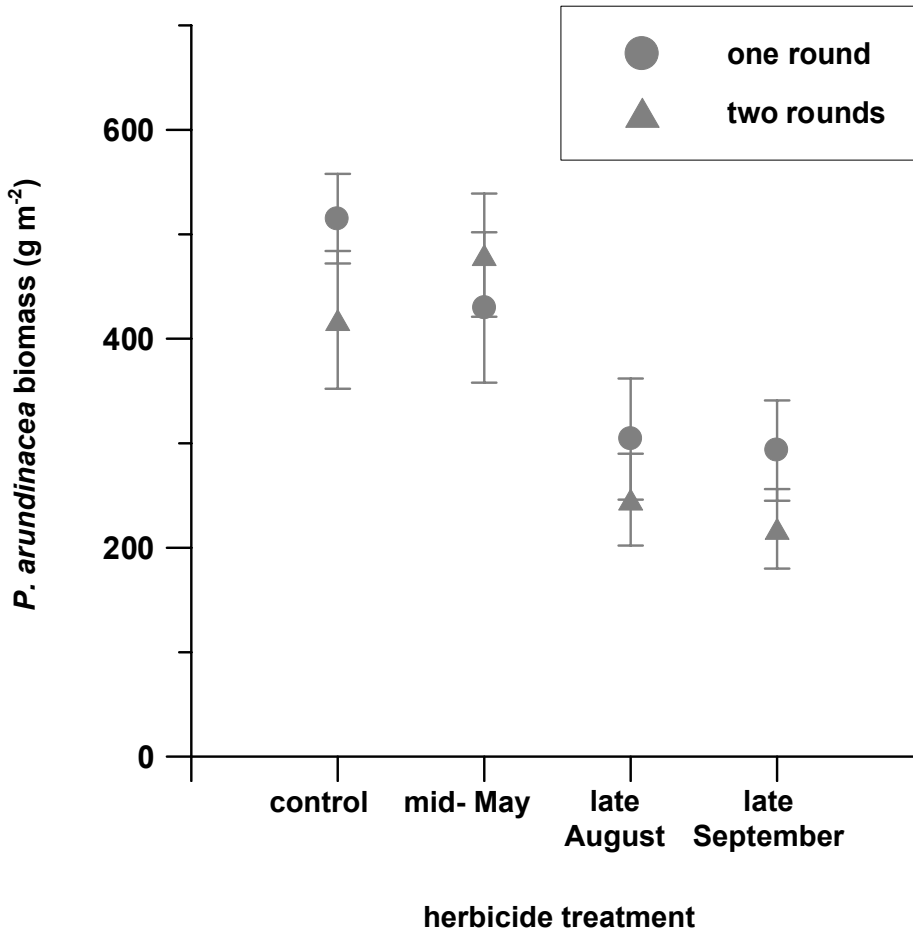


Figure 2-12. The spring burn was effective in reducing the density of the *P. arundinacea* seed bank (for 1 round of treatment $F=6.3$, $p=0.03$, for 2 rounds of treatment $F=1.17$, $p=0.34$).

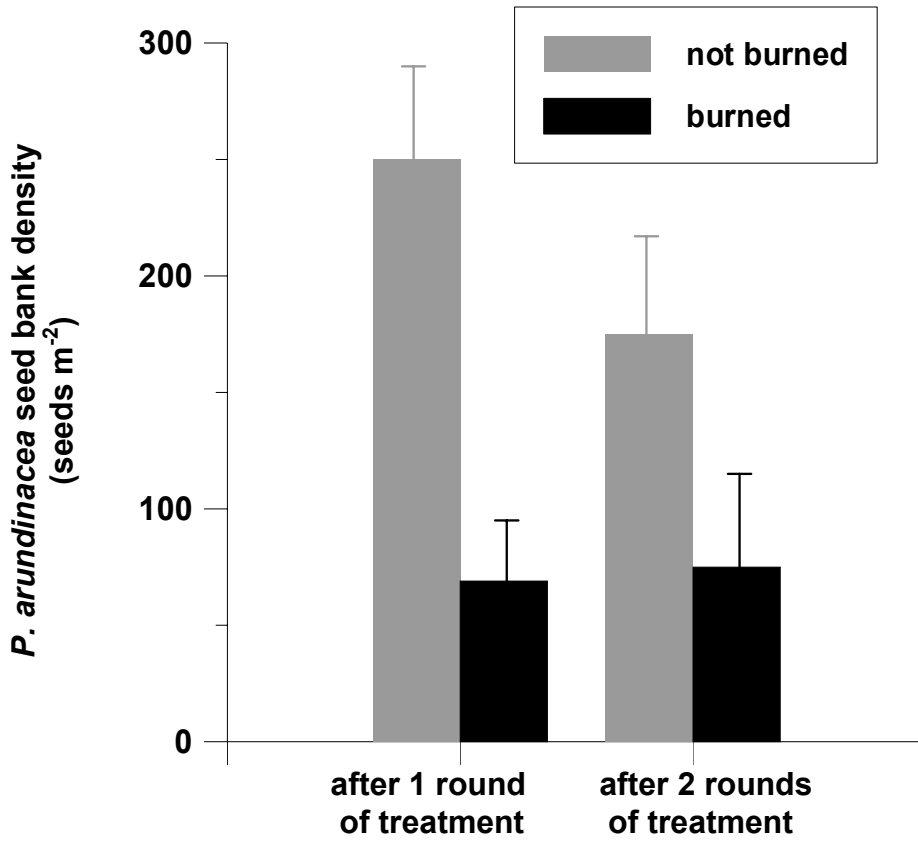


Figure 2-13. Planted species (species from the restoration seed mix) established little biomass at the NSPSF site, and unplanted species established the majority of the biomass. Both planted and unplanted species colonized significantly more biomass in plots that received herbicide applications.

NSPSF site

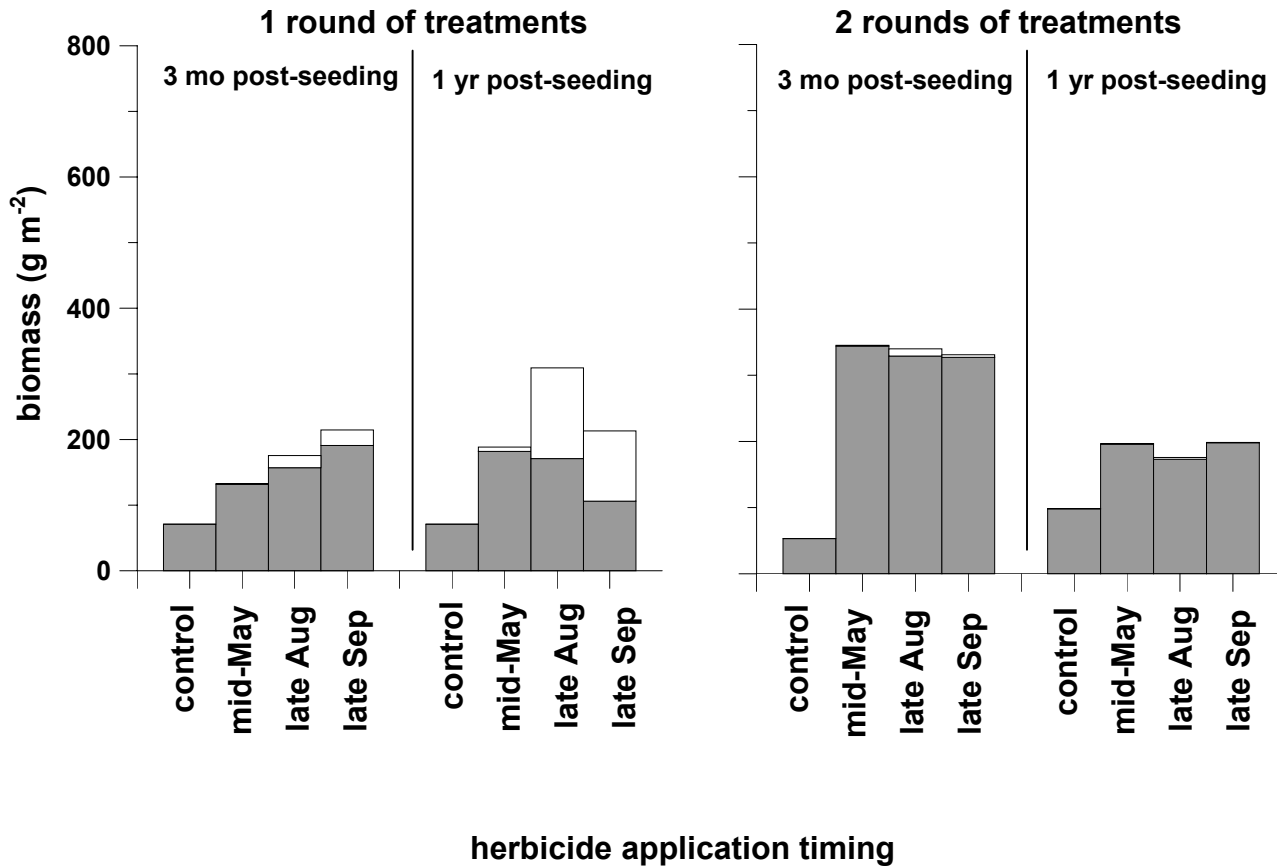
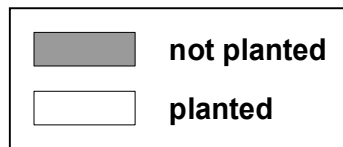
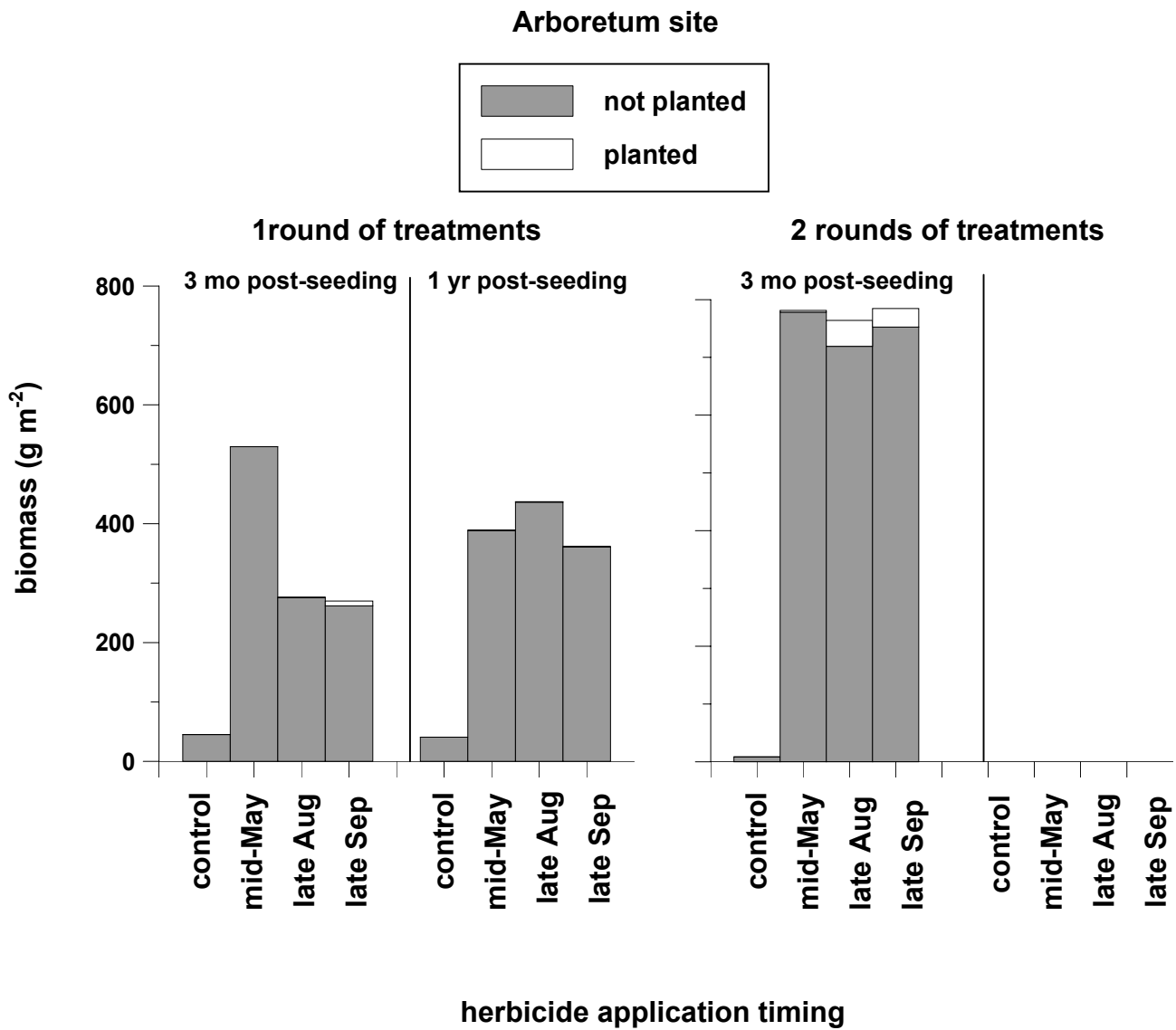


Figure 2-14. Planted species (species from the restoration seed mix) established little biomass at the Arboretum site, and unplanted species established the majority of the biomass. Both planted and unplanted species colonized significantly more biomass in plots that received herbicide applications.



CHAPTER 3

The transition from invasive species control to native species establishment: *Phalaris arundinacea* L. (reed canary grass) in wetland restorations

Summary

Invasive species often complicate restoration efforts by inhibiting the establishment of native species; therefore large-scale clearing of invasive species is a common first step in restoration. Despite widespread application of invasive species removal, little is known about the post-control transition to establishment of native plant species. Control of *Phalaris arundinacea* L. (reed canary grass) and subsequent native revegetation in northern US sedge meadow restorations presents a model system for investigating the post-control transition to native species establishment. To explore the transition between post-control bare ground and native species establishment, we designed a mesocosm experiment to investigate the influence of *P. arundinacea* propagule pressure on the establishment of native sedge meadow species in the context of a newly restored wetland. Two key questions were asked: (1) Is the transition from bare ground to a native species community different when different densities of *P. arundinacea* seed are present? (2) Is it possible to manage the transition to the native species-dominated system state by manipulating sowing density of the native community? Results indicated that the high-density native seeding suppressed *P. arundinacea* growth, and the effect was more pronounced at high seed densities of *P. arundinacea* (>100 seeds m^{-2}), but that higher densities of native seeding did not suppress recruitment of *P. arundinacea* from seed. At densities greater than 100 seeds m^{-2} of *P. arundinacea*, *P. arundinacea* suppression of native species was enhanced. In the context of a state-and-transition model, these results suggest that a threshold exists based on *P. arundinacea* propagule pressure, beyond which transition to a native community is less likely. This research represents an attempt to identify the nature of transitions between states, allowing for a predictive understanding of initial colonization dynamics.

Introduction

Dominance by invasive species, which prevents the establishment of target native communities, is a common barrier to restoration success (11, 78, 79). It follows that invasive species control is often a major part of the early stages of restoration: large scale invasive species clearing programs are increasingly common, e.g. removal of *Tamarix* sp. (saltcedar) from floodplains in the southwestern US (104), mass eradication of alien woody species from riparian areas in South Africa (105), and biocontrol of *Lythrum salicaria* (purple loosestrife) throughout the northern US (106). Commonly large-scale restoration efforts do not plan for active revegetation, with the assumption that once the barrier of the invasive species is removed, efficient revegetation will occur through natural recolonization (107). It has been suggested that natural recolonization is the best strategy for revegetation following initial restoration (108), however several studies have shown that failure to plant will result in depauperate communities for long periods because of barriers to establishment for native species (9, 109, 110).

Despite the widespread application of clearing programs and the debate on active revegetation, little is known about the transition from post-control bare ground to the establishment of native species (111), save that initial dynamics during this establishment phase are expected to have long term effects on plant community composition (112). Studies of

vegetation development following *Pteridium aquilinum* control in British heathlands have shown that the direction and rate of vegetation community establishment can be highly variable (113, 114), and that vegetation development after control can be slow and rarely results in establishment of the target community (115). Similarly, Morrison (116) observed that removal of *Lythrum salicaria* in lowland meadows in the northeastern US resulted in various outcomes in species composition, including an increase in other non-native species. Given the economic investment in invasive species clearing (the United States and South Africa together spend 326 million US dollars annually for this purpose (117)) and the degree to which it is increasingly implemented, efficient techniques for post-clearing vegetation establishment based on sound scientific knowledge are needed. Considering the difficulties associated with large-scale restoration experiments (lack of replication and controls), conceptual models and limited-scale experiments are a more feasible way to develop a predictive understanding of the processes that occur as part of restoration (76).

State and transition models can be used to interpret plant community dynamics. For these models, a given number of stable states exist for any ecosystem, and transitions between states may be caused by disturbances or management actions, or both (118). The system crosses a threshold for a transition to occur from one state to another, such that the system is not stable halfway through a transition (119). Only recently have rangeland ecologists focused on the evaluation of vegetation dynamics between states and the application of the threshold concept to transitions. Stringham et al. (120) defined transitions as either 1) reversible: reversal of the trajectory of change requires the elimination of the stress or stresses responsible for triggering the transition, or 2) irreversible: a trajectory of change occurs after a threshold has been breached, and the system can no longer self-repair even with the removal of the stressor(s). In a management context, irreversible transitions may become reversible given “accelerating practices” such as seeding or follow-up invasive control (121).

The state and transition model is suitable for exploring the transition from post-control bare ground to native species establishment and how that transition is affected by the presence of invasive species. High light, low competition environments, such as those created by elimination of vast stands of invasive species during restoration, are themselves more invadable than intact ecosystems (30-32). It follows that propagule pressure from invasive species is a stressor that has a major influence on native species establishment following invasive species clearing. Invader propagule-pressure based thresholds may govern whether or not the transition to a native-dominated state occurs, or an irreversible transition to an invader-dominated state occurs. Knowledge of a propagule-pressure based threshold that dictates the species composition of a newly established plant community may identify accelerating practices that manipulate the transition to favor native species establishment.

Control of *Phalaris arundinacea* L. (reed canary grass) and subsequent native revegetation in northern US sedge meadow restorations presents a model system for investigating the post-control transition to native species establishment. *P. arundinacea* is a perennial, invasive grass that forms a dense network of rhizomes and an abundant, persistent seed bank. In the northern US, this species is a major concern for wetland restorations because establishment by *P. arundinacea* often precludes colonization by sedge meadow vegetation in restored prairie pothole wetlands (6, 10, 11).

To explore the transition between post-control bare ground and native species establishment, we designed a mesocosm experiment to investigate the influence of *P. arundinacea* propagule pressure on native sedge meadow species establishment in the context of a newly restored wetland. Two key questions were asked: (1) Is the transition from bare ground to a native species community different when different densities of *P. arundinacea* seed are

present? (2) Is it possible to manage the transition to the native species-dominated state by manipulating sowing density of the native community?

Methods

Study site

The thirty mesocosms used for this experiment are located alongside an experimental wetland basin at the University of Minnesota's Landscape Arboretum in Chanhassen, Minnesota, USA (41°51'45"N, 93°36'00"W). The wetland basin is equipped with extensive tile networks that allow optimum hydrologic conditions for the experiment. The mesocosms were 1.13 m² and consisted of 1-m diameter circles that were contained with 0.63-cm thick plastic extending to 50 cm below the soil surface. All mesocosms were surveyed and graded to ensure that the soil surface is at an equivalent elevation (range between highest and lowest plot was 2.5 cm). Mesocosms were filled with wetland soil (Glencoe clay loam, Cumulic Endoaquoll) that was sterilized *in situ* using dazomet granular soil fumigant (Basamid[®], Hopkins Agricultural Chemical Company, Madison, WI). Water level in the adjacent basin was maintained throughout the experiment at 2-3 cm below mean soil elevation.

Experimental Design

Mesocosms were seeded with one of five *P. arundinacea* seed densities (0, 10, 50, 100, and 500 seeds m⁻²) and one of two native species mixture densities (3,000 and 15,000 seeds m⁻²) in a 2 x 5 factorial, randomized complete block design (10 mesocosms per block, 3 blocks). Each of the 10 treatment combinations was replicated 3 times.

Seed mixtures and densities

The native species seed mixture for this experiment was chosen to reflect a variety of forbs and grasses found in wetlands in the region (all species nomenclature follows Gleason and Cronquist 1999, Table 3-1). Two levels of restoration mix seed density were seeded: low (3000 seeds m⁻²), and high (15,000 seeds m⁻²). The low density was chosen to reflect what is typically found in wet meadows (range is 450-6000 seeds m⁻² (122)). Each species within the native mixture was sown in equal proportion, such that individual seeding rate for the twelve species was 250 seeds m⁻² (low-density seeding) and 1250 seeds m⁻² (high-density seeding).

P. arundinacea seed (open-pollinated, no cultivars) was obtained from Premium Seed Company, Inc. in Shakopee, Minnesota. Five levels of *P. arundinacea* seed density were tested: 10 seeds m⁻², 50 seeds m⁻², 100 seeds m⁻², 500 seeds m⁻² and 0 seeds m⁻². Densities of *P. arundinacea* were chosen to be lower than densities found in the field.

Seed was obtained from Ion Exchange, Harpers Ferry, Iowa, and Prairie Moon Nursery, Winona, Minnesota. All native species seed was collected from locations within 350 km of the study site. Species were tested for viability using tetrazolium to estimate pure live seeding rates (123). Seeds were weighed to determine densities, and were sown in a dormant seeding in November 2001, affording natural stratification over winter.

Data Collection

Mesocosms were observed for *P. arundinacea* establishment (number of individuals in each mesocosm) and *P. arundinacea* shoot production on July 23 2003, just prior to the end-of-experiment harvest. *P. arundinacea* and native species biomass were harvested in late July 2003,

at the time of maximum standing crop. Within a 0.5-m² circle within the mesocosm, aboveground plant material was clipped at the base and sorted by species. Aboveground biomass was placed in paper bags, dried at 70°C in a forced air oven for 48 hours, and weighed.

Soils

During biomass harvest, soil samples for nitrogen content determination were collected to a depth of 10 cm. Total nitrogen was determined by the Kjeldahl method. Dried samples were ground, digested in sulfuric acid, diluted with water, and total nitrogen was measured using a Wescan N Analyzer (124). To measure soil inorganic nitrogen concentrations (nitrate and ammonium) samples were corrected for soil moisture. Eight grams of wet soil were placed in 25 ml of 2 N KCl, shaken horizontally with a reciprocal shaker, filtered and analyzed for NH₄-N and NO₃-N using a two channel Wescan N Analyzer (124). Soil analyses were performed by the University of Minnesota Research Analytical Lab.

Total nitrogen outside the mesocosms was 0.45% ± 0.01% and inside the mesocosms was 0.35% ± 0.01%. The containers created a closed system, preventing further input of nutrients into the mesocosm over the course of the experiment.

Statistical Analyses

Treatment effects on native species and *P. arundinacea* biomass were analyzed using the analysis of variance (ANOVA) procedure in SAS (SAS Institute Inc. Cary, NC). The model included *P. arundinacea* seeding density and native species seeding density as fixed factors, and blocking on north to south plot location. Means were compared using Tukey's honest significant difference with $\alpha=0.05$. For all statistical analyses, differences were considered significant at p-values less than 0.05.

Results

Native species biomass

The native communities in the mesocosms were graminoid-dominated with forbs making up only 3-5% of the native community biomass (Figure 3-1, Table 3-2). The three most dominant graminoids, *Carex hystericina*, *Glyceria grandis* and *Calamagrostis canadensis* together comprised 75% of the total native community biomass on average. Of the twelve native species planted, two species, *Eleocharis palustris* and *Vernonia fasciculata*, did not germinate in any mesocosm.

Total native community biomass was greater at the high-density native seeding than the low-density native seeding (high density seeding = 326.8 g m⁻², SE = 21.76, and low density seeding = 239.5, SE = 23.13, ANOVA F=8.40 df=1, p<0.01). Although the high-density seeding (15,000 seeds m⁻²) was 5 times greater than the low-density seeding (3,000 seeds m⁻²), total native community mean biomass only increased by 28% with the increase in seeding density.

Total native species biomass did not differ significantly with *P. arundinacea* seed density (Figure 3-2). However, biomass of one native species, *Glyceria grandis* declined significantly in response to increased *P. arundinacea* seed density (Figure 3-3). This response differed at high and low densities of native seed. At the low-density native seeding, *G. grandis* produced similar biomass with 0, 10 and 50 seeds m⁻² of *P. arundinacea*, and produced significantly less biomass with 100 and 500 seeds m⁻² of *P. arundinacea*. At the high-density native seeding, *G. grandis* produced significantly less biomass only when 500 seeds m⁻² of *P. arundinacea* were present.

P. arundinacea response to native seeding density

As expected, *P. arundinacea* produced significantly more biomass (ANOVA $F=21.98$, $p<0.01$), higher number of individuals (ANOVA $F=87.11$, $p<0.01$), and greater shoot density (ANOVA $F=39.57$, $p<0.01$) with increasing *P. arundinacea* seed density. *P. arundinacea* established in all mesocosms in which it was planted (including when seeded at 10 seeds m^{-2}).

P. arundinacea biomass was suppressed by the high-density native seeding (ANOVA $F=6.74$, $p=0.02$) (Figure 3-4). This suppression of biomass production was most pronounced when *P. arundinacea* was present at 500 seeds m^{-2} ; at this density *P. arundinacea* biomass was halved from 158 g m^{-2} with the low-density native seeding to 78 g m^{-2} with the high-density native seeding.

Although *P. arundinacea* produced significantly less biomass with the high-density native seeding, the same number of *P. arundinacea* individuals established under both the high and low native seeding density (ANOVA $F=1.21$, $p=0.28$) (Figure 3-5). Similarly, *P. arundinacea* shoot density did not differ with native seeding density (ANOVA $F=0.04$, $p=0.84$). These data demonstrate that both *P. arundinacea* recruitment from seed and shoot production were not suppressed by the high-density native seeding.

P. arundinacea produced more biomass than would be expected given the proportion of seeds present and the proportion of total biomass produced (Figure 3-6). At lower proportions of the seeds present, *P. arundinacea* was equally or more successful under the high-density seeding, but at higher proportions of the seeding mixture, *P. arundinacea* was more successful under the low-density seeding. Also, it should be noted that when *P. arundinacea* was present as 0.3% of total seed, it still managed to establish 4% of total community biomass at the low-density native seeding and 7% at the high-density native seeding, after just two growing seasons.

Discussion

P. arundinacea produced less biomass with the high-density native seeding than with the low-density native seeding, suggesting that in the establishment phase of a restored wetland, *P. arundinacea* will be suppressed by a high-density native seeding. Suppression was most pronounced at the highest density of *P. arundinacea* seed (500 seeds m^{-2}), demonstrating that the effect of the native seeding density will be most important when *P. arundinacea* propagule pressure is highest. Also, when *P. arundinacea* was present as a larger proportion of seed present, the high-density native seeding more effectively suppressed *P. arundinacea* biomass production. Studies in other systems have found that quick establishment of desirable vegetation can limit recolonization from invasive species following control. For instance, the regeneration of native heathland vegetation following effective initial control of *Pteridium aquilinum* was found to limit *Pteridium aquilinum* recovery (125). Other studies have found substantial invasion problems despite native seeding. Planted *Calluna* spp. establishment following bracken control was too slow to suppress the invasion of two weed species in heathlands (113). Indeed, even short term suppression of the invasive species by planted native species is not likely to provide long-term control of the invader.

Despite the suppression of growth by *P. arundinacea* by the high-density native seeding in this experiment, our results show that recruitment from the *P. arundinacea* seed bank was similar with both low and high-density native seedings in this experiment. Even when native seed was present at 15,000 seeds m^{-2} , recruitment was not prevented from as little as 10 seeds m^{-2} of *P. arundinacea*. Mesocosm, fen and restoration experiments with *P. arundinacea* have demonstrated that already-established native species canopies can inhibit *P. arundinacea* establishment from seed (51). This has led to the recommendation that planting species that will

rapidly provide high canopy cover will reduce the chance of *P. arundinacea* establishment (14, 51). Results from this experiment, however, suggest that even minimal propagule pressure during the native species establishment phase is likely to ensure *P. arundinacea* recruitment and establishment, and that it is unlikely that a high-density native seeding will altogether prevent *P. arundinacea* recruitment from seed. In the context of a newly restored wetland, the development of a native canopy (from which considerable resistance to *P. arundinacea* invasion will eventually result) will face propagule pressure from *P. arundinacea* during establishment, likely necessitating *P. arundinacea* removal during this stage.

The response of native species biomass production to *P. arundinacea* establishment was minimal. Similarly, early recolonization of *Pteridium aquilinum* does not appear to affect the growth of newly established native vegetation, but it is well known that the species will eventually replace native vegetation if left to recover unchecked by control methods (115). The exception to the lack of native species response to *P. arundinacea* in this experiment was *Glyceria grandis*, a species commonly found in sedge meadow wetlands, and a typical component of native seed mixes for restoration purposes. At the low native seeding density, *G. grandis* biomass declined significantly when *P. arundinacea* occurred at 100 and 500 seeds m⁻². At the high-density native seeding, *G. grandis* biomass was only suppressed when *P. arundinacea* occurred at 500 seeds m⁻². From the response of this species to *P. arundinacea* propagule pressure, we conclude that native species will be suppressed by *P. arundinacea*, but may withstand a greater density of *P. arundinacea* seed if they are themselves seeded at a higher density.

The relationships between *P. arundinacea* establishment and native species establishment were seed density-dependent, suggesting that if the native seeding density and *P. arundinacea* seed density are known, propagule pressure-based thresholds exist that can be used to predict the vegetation community. For higher density native seedings, these results suggest that *P. arundinacea* propagule pressure is not likely to suppress native species growth unless *P. arundinacea* is present at 500 seeds m⁻² and greater. For lower density native seedings, 100 seeds m⁻² *P. arundinacea* may be enough to suppress native species growth. Given *P. arundinacea*'s persistence, it is likely that *P. arundinacea* dominance is irreversible on a practical time scale without management. Intervention in the form of *P. arundinacea* selective removal may reverse this transition, allowing the system to return to a native-dominated state.

The threshold levels of *P. arundinacea* seed density determined by this experiment have direct application to management of *P. arundinacea* in wetland restorations. Unfortunately, little is known about *P. arundinacea* propagule pressure in the landscape. *P. arundinacea* densities in the seed bank have often been observed to be responsible for rapid recolonization following control (13, 45, 53, 55), but no experiment has quantitatively linked an estimate of *P. arundinacea* seed density in the seed bank to *P. arundinacea* recolonization. Two recent assays of seed banks under stands of *P. arundinacea* that have been established for more than 20 years determined that seed banks had 1163 and 663 seeds m⁻² of *P. arundinacea* (Chapter 2, this document). At both sites, *P. arundinacea* continued to dominate despite 2 years of effective control (no recolonization from rhizomes) and a typical native species seeding. This result, taken with the successful establishment and growth of *P. arundinacea* at lower seed densities in this experiment (500 seeds m⁻² and less), suggest that *P. arundinacea* seed densities commonly encountered following effective control will require management, beyond seeding with native species, for a native community to establish.

The response of *P. arundinacea* to native species seed density in this experiment has implications for wetland restorations that are exposed to *P. arundinacea* propagule pressure. Our results indicate that for restoration sites that experience high *P. arundinacea* propagule pressure,

competition from natives species (via the native species seed bank or a native species seeding) may not substantially limit *P. arundinacea* growth. Increased density of native seeds, although it will not likely prevent *P. arundinacea* recruitment from the seed bank, may limit *P. arundinacea* growth during initial establishment.

Varying site conditions may influence the threshold density of *P. arundinacea* that would allow for native species establishment following *P. arundinacea* control. A number of factors besides *P. arundinacea* seed density and native species seeding density may influence this transition, including hydrology. Hydrology was held at a constant level throughout this experiment, but *P. arundinacea* is known to have a competitive advantage in fluctuating water regimes (48) so the threshold level of *P. arundinacea* propagule pressure that could be withstood by the newly establishing native species may be lower under these conditions. Alternatively, *P. arundinacea* does not germinate under flooded conditions (14), so a native species seeding might be able to withstand significantly higher *P. arundinacea* propagule pressure under flooded conditions. Fertility is also known to alter competitive dynamics for this species (47, 83, 126). In sites with higher nitrogen soil content than those in this experiment, *P. arundinacea* is likely to exert more of a suppressive effect on native species than our results suggest. Hydrology and nutrients, like native seeding density, are factors that present opportunities for management intervention to manipulate the post-control transition towards a native-dominated state. The thresholds determined in this experiment are important benchmarks from which to determine target conditions for manipulation. Thresholds will vary with site conditions, but quantifying propagule pressure thresholds is key to a predictive understanding of the process of transition from post-control bare ground to native species establishment.

Results from this experiment suggest that clearing efforts for *P. arundinacea*, even when accompanied by native species seeding, may not result in long-term native species establishment, because *P. arundinacea* propagule pressure from the seed bank and dispersal will facilitate recolonization of this invader following control efforts, despite planting with native species. Because the transition from post-control bare ground to native species establishment is poorly understood (for *P. arundinacea* and other invasive species), it is not safe to assume that revegetation will occur following removal of the invader. Therefore it is risky to uncouple large scale clearing efforts and planning for native revegetation. In many cases, particularly where barriers to native species propagule dispersal exist, clearing efforts should be accompanied by equally extensive native revegetation programs. Otherwise, we risk failure to establish native species even after expensive invasive species removal efforts, or worse yet, we facilitate the further invasion of problematic species. Knowledge of propagule pressure based thresholds will help formulate the extent to which 1) post-control follow-up removal of the invader is necessary and 2) active native revegetation strategies are necessary, and in turn, will protect our large-scale alien removal investments against further invasion.

Table 3-1. Grasses and forb species were included in the native species seeding. Purity and germination rates were determined and accounted for in the calculation of seeding rate density. Each species was seeded at 250 seeds m⁻² for the low density treatment, and at 1250 seeds m⁻² for the high density treatment.

Grasses	Forbs
<i>Calamagrostis canadensis</i> Michx.	<i>Asclepias incarnata</i> L.
<i>Carex hystericina</i> F. Boott.	<i>Eupatorium maculatum</i> L.
<i>Carex stricta</i> Lam.	<i>Helenium autumnale</i> L.
<i>Carex vulpinoidea</i> Michx.	<i>Sium suave</i> Walter
<i>Glyceria grandis</i> S. Wats.	<i>Verbena hastata</i> L.
<i>Eleocharis palustris</i> L.	<i>Vernonia fasciculata</i> Michx.

Table 3-2. Biomass for individual species in the native species seeding are shown. Means shown are for mesocosms in which *P. arundinacea* was not seeded. All native species were planted at the same density: 283 seeds m⁻² for the low-density native seeding, and 1413 seeds m⁻² for the high-density native seeding. Percentages shown are based on total community biomass.

	Low native species density			High native species density		
	Mean	SE	%	Mean	SE	%
Native graminoids (total)	130.6	7.1	97.0	190.3	13.7	78.7
<i>Carex hystericina</i>	57.4	10.2	42.7	70.4	6.9	29.1
<i>Glyceria grandis</i>	38.0	3.5	28.2	55.6	11.9	23.0
<i>Calamagrostis canadensis</i>	21.0	5.0	15.6	41.9	6.2	17.3
<i>Carex vulpinoidea</i>	14.1	3.7	10.5	21.4	3.0	8.8
<i>Carex stipata</i>	0.1	0.0	0.1	1.1	0.7	0.4
Native forbs (total)	6.7	2.4	5.0	7.5	2.5	3.1
<i>Asclepias incarnata</i>	5.2	1.3	3.9	1.9	0.9	0.8
<i>Verbena hastata</i>	1.3	1.3	0.9	5.1	1.6	2.1
<i>Helenium autumnale</i>	0.2	0.1	0.2	0.2	0.1	0.1
<i>Sium suave</i>	0.1	0.0	0.1	0.3	0.2	0.1
<i>Eupatorium maculatum</i>	0.0	0.0	0.0	0.0	0.0	0.0
Total community	134.6	50.1	100.0	241.8	8.6	100.0

Figure 3-1. Mean *P. arundinacea*, native forb, and native grass biomass produced at both low and high-density native seeding, across *P. arundinacea* seed densities.

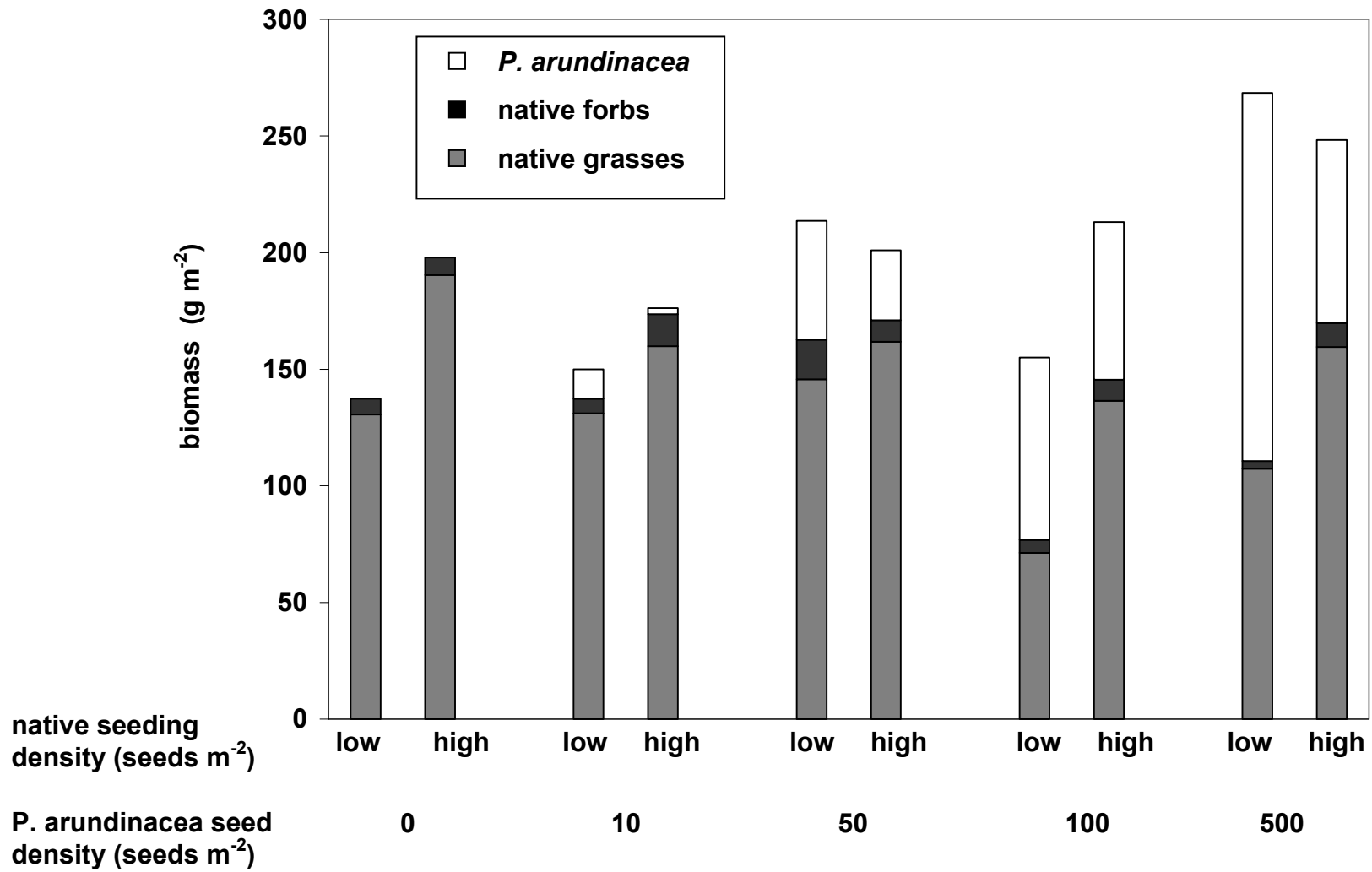


Figure 3-2. Native species biomass was not significantly different across *P. arundinacea* seed densities (ANOVA $F = 1.17$, $p = 0.35$).

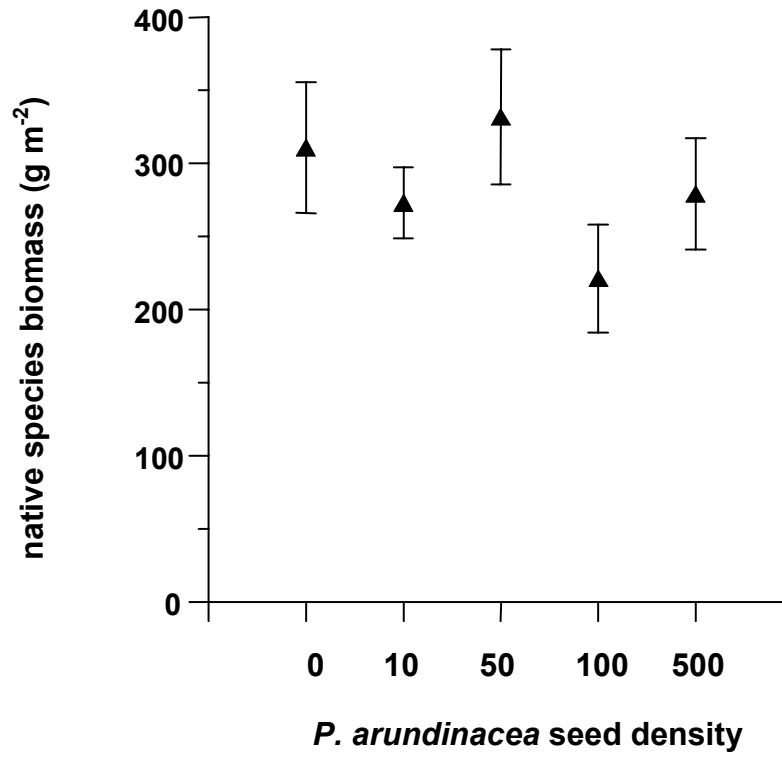


Figure 3-3. *Glyceria grandis* was suppressed by higher densities of *P. arundinacea*, but this response varied with native seeding density (ANOVA native seeding density $F = 3.82$ $p = 0.02$, *P. arundinacea* seed density $F = 4.07$, $p = 0.01$).

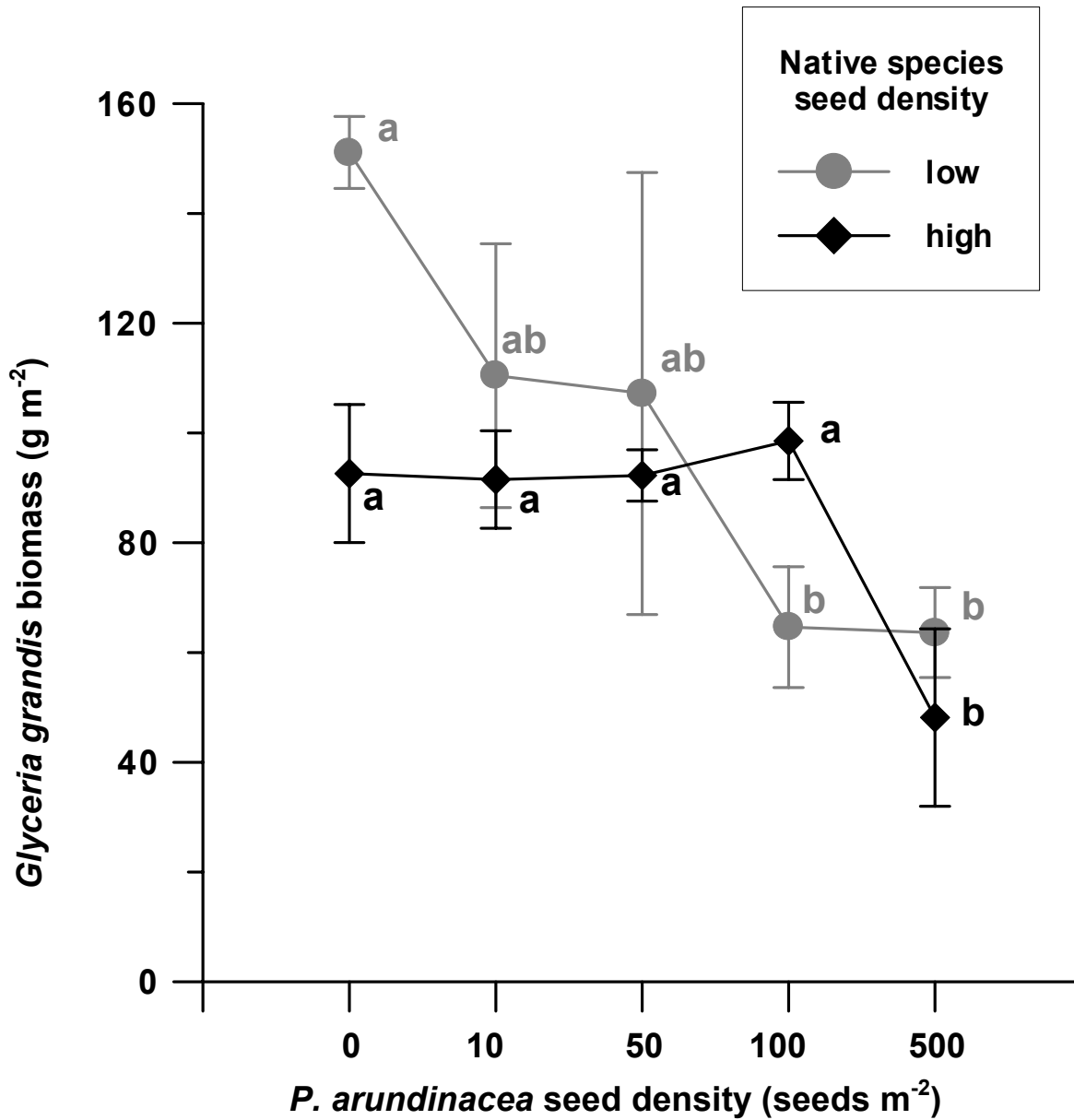


Figure 3-4. *P. arundinacea* biomass production was suppressed by the high-density native seeding, especially at 500 seeds m^{-2} of *P. arundinacea*. (ANOVA native seeding density $F = 5.52$, $p = 0.02$, *P. arundinacea* seed density $F = 18.01$, $p < 0.01$).

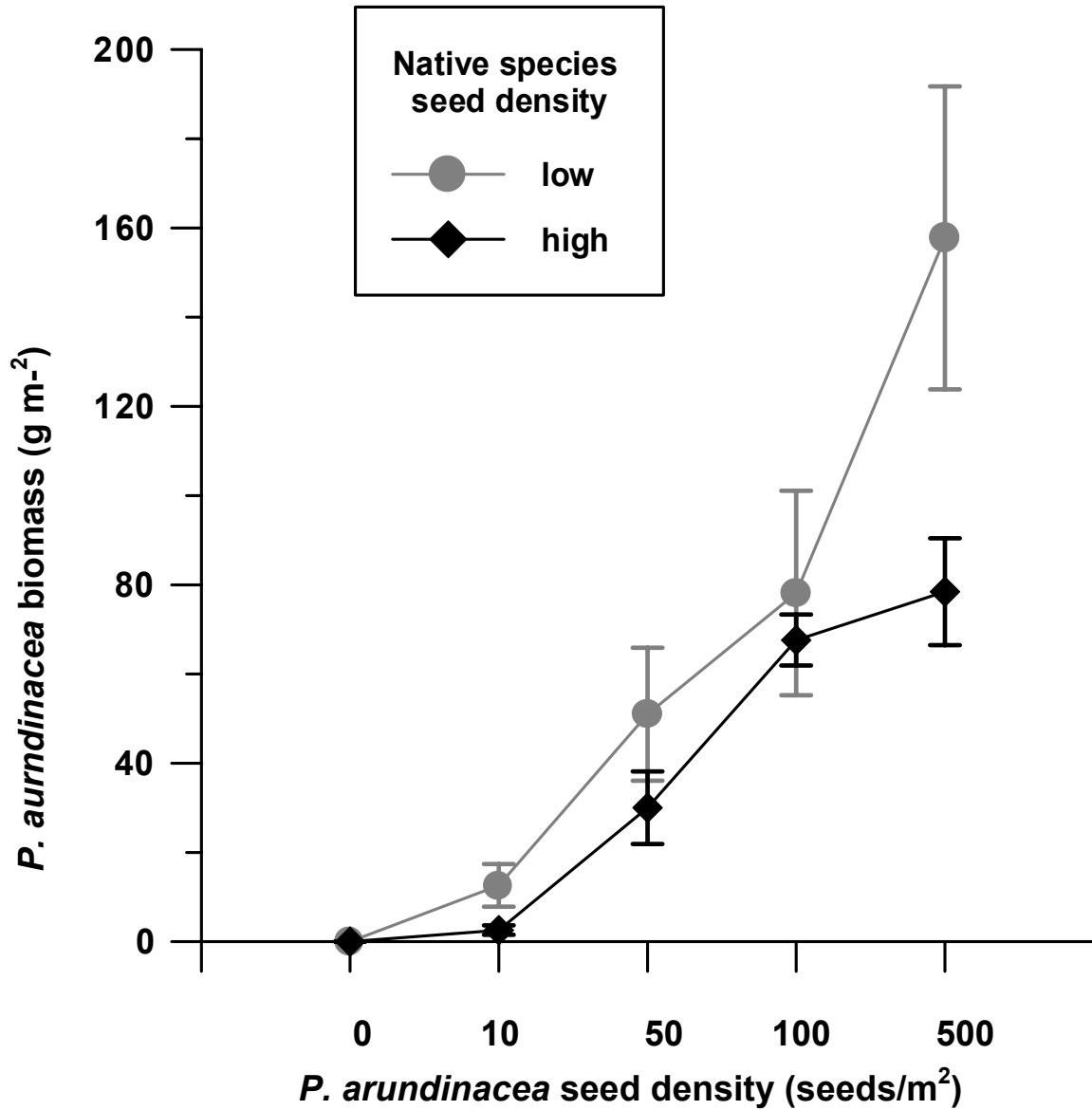


Figure 3-5. When present at a density 500 seeds m^{-2} , *P. arundinacea* biomass is suppressed by the high-density native seeding. *P. arundinacea* number of individuals and shoot density, however, do not differ with native seeding density.

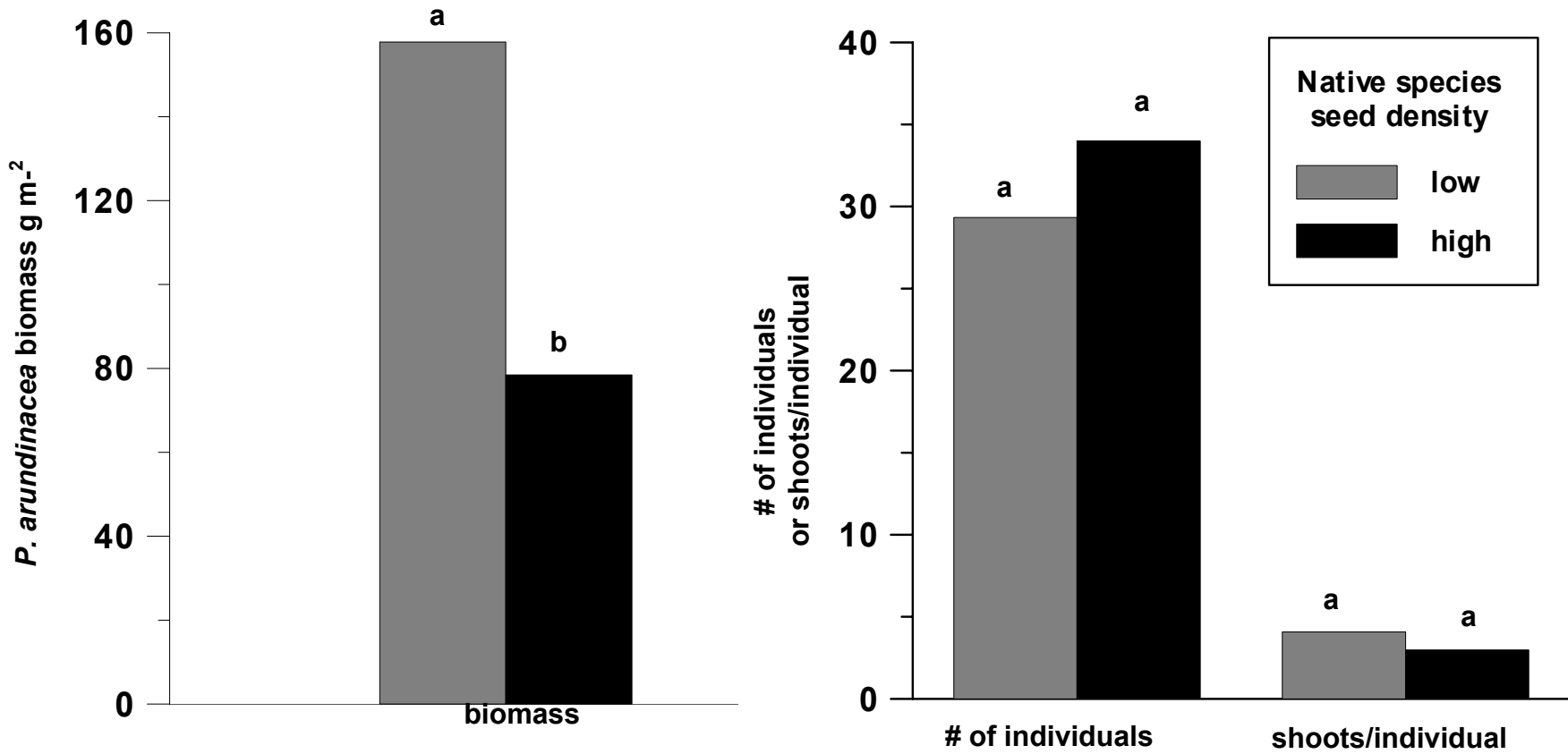
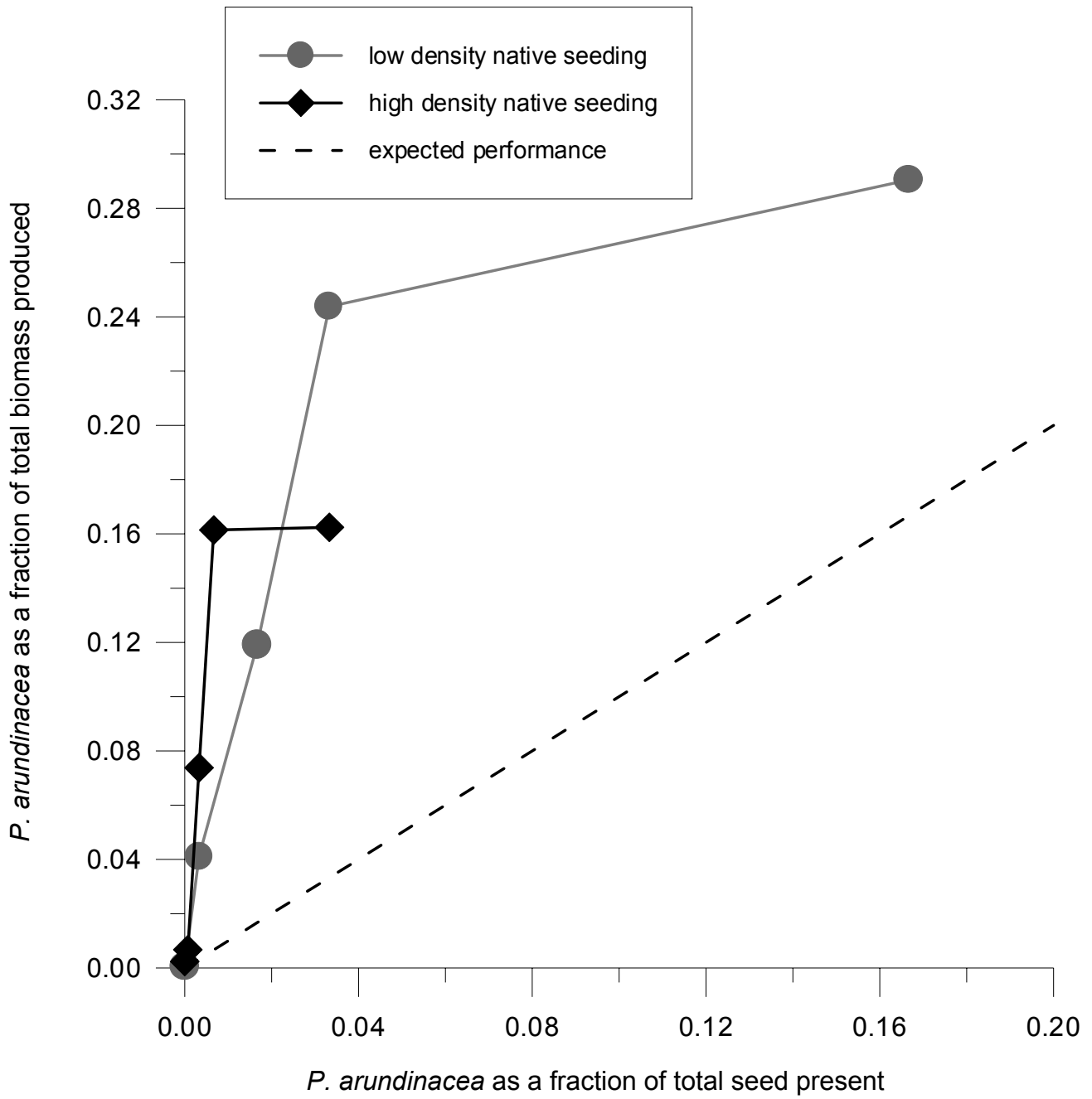


Figure 3-6. *P. arundinacea* expressed as a fraction of the seed density present and as a fraction of the resulting biomass at the time of harvest.



CHAPTER 4

The biology and growth potential of *Phalaris arundinacea* L. (reed canary grass)

Summary

Knowledge of the life history of an invasive species can contribute to understanding invasion mechanisms for that species. *Phalaris arundinacea* L. (reed canary grass) is an invasive perennial grass that is problematic across temperate North America. This species has been reported to have substantial rates of biomass production and be morphologically plastic in response to environmental conditions. In order to determine above and belowground biomass production potential for *P. arundinacea*, we conducted a uniform planting study to observe biomass production of *P. arundinacea* over two growing seasons. The objectives for this study were: 1) to characterize biomass production, shoot production, and spread for an individual *P. arundinacea* plant, and 2) to apply this knowledge to the understanding of the *P. arundinacea* invasion process. *P. arundinacea* produced a peak of 132 g plant⁻¹ of aboveground biomass and 333 g plant⁻¹ of below ground biomass in just two growing seasons. *P. arundinacea* belowground biomass grew to the edges of the 1.2-m diameter container after one growing season. Root:shoot ratios revealed that *P. arundinacea* produced proportionally more aboveground biomass production during establishment, and more belowground biomass production during the second growing season. Our data indicate that *P. arundinacea* has a multi-stage growth pattern, producing more aboveground investment during establishment and producing more belowground investment after establishment. This growth pattern may explain why *P. arundinacea* is so successful at preempting establishment of other species.

Introduction

Increasingly, many wetlands are becoming dominated by a few invasive species (6). The loss in biodiversity that occurs as a result of invasion urges a need to understand how species characteristics contribute to the invasion process. Life history strategies and plant biomass allocation patterns largely influence plant community dynamics (127, 128). It follows that knowledge of the life history and growth patterns of an invasive species can contribute to a predictive understanding of mechanisms of invasion and rates of spread (7, 19).

Clonal, perennial invaders are generally recognized to have a greater ecological impact on native communities than non-clonal species (129). Many clonal species such as *Lythrum salicaria* L., *Typha x glauca* Godr., and *Phragmites australis* (Cav.) have been identified as problematic in wetlands in temperate North America (6). Spreading vegetatively gives clonal species an advantage by allowing them to expand into areas that are more stressful than where the plant originally colonized (130, 131). For *Phalaris arundinacea* L. (reed canary grass), an invasive wetland clonal grass, little is known about the unconstrained growth potential of populations that have invaded natural areas. This species is circumboreal in distribution (16, 81). The aggressive spread of *P. arundinacea* into wetlands may be a result of anthropogenic modification of the landscape. Conventional selection of this species as a forage may also be a factor; for two centuries this species was selected for aggressive vegetative growth, abundant seed production, and a wide tolerance of hydrologic regimes (6). In the northern US, this fast-growing, rhizomatous species is a major concern for wetland restorations because establishment by *P. arundinacea* often precludes colonization by sedge meadow vegetation in restored prairie

pothole wetlands (8-11). *P. arundinacea* also invades natural wetlands, forming monotypic stands and displacing native vegetation (12-14).

Observations of *P. arundinacea*'s rapid growth potential led to agronomic studies that investigated *P. arundinacea* for use as forage, biofuel, or wastewater treatment. Forage crop studies have demonstrated favorable *P. arundinacea* shoot growth response to cutting, mowing, and fertilization (16, 96, 132). When compared with other common forage species, *Bromus inermis*, *Phleum pratense*, and *Dactylis glomerata*, produced only 40-70% of the aboveground biomass yield from *P. arundinacea* (39). *P. arundinacea* belowground biomass production has also been reported to be substantial: in an investigation into the use of *P. arundinacea* as biofuel crop, *P. arundinacea* was found to produce 1kg m⁻² of belowground biomass in a monotypic unfertilized field (133). *P. arundinacea*'s rate of biomass production likely contributes to its competitive ability. In a mesocosm study, when *P. arundinacea* was seeded (along with 10 other native species) at 9% of the total seed density, it produced 50% of the total biomass of the community 15 months after seeds were sown (47).

P. arundinacea is well adapted to a range of hydrologic regimes even during early establishment, giving it a competitive edge over species whose growth and survival is affected by hydrology (134, 135). It typically is found in wet habitats, and has been reported to survive 8 weeks of flooding (136) but is also drought-tolerant (16, 36, 137). *P. arundinacea* is also productive in environments with fluctuating water levels such as sites that receive stormwater runoff (40, 46, 48, 49). Manipulating biomass allocation patterns is likely the strategy that allows *P. arundinacea* to be productive with variable hydrology. Conchou and Fustec (1988) found that the flood pulse cycle is responsible for the patterns of biomass production in *P. arundinacea* on the Garonne River in France. There, biomass production was bimodal, with the first generation of *P. arundinacea* individuals emerging during the early flood (when nutrient stocks decline in rhizomes and aboveground biomass is produced) and the second generation of *P. arundinacea* individuals emerging during the exposure period (when below ground biomass accumulates, and aerated conditions allow nutrient uptake by roots). The strategy of two successive generations of plants ensures two periods of nutrient storage by aboveground parts of the plant. This study demonstrated the ecological plasticity of *P. arundinacea*, and its strategy of making use of a wide range of hydrologic conditions to maximize nutrient uptake. In another study of *P. arundinacea* in submergent flood regimes, Klimesova found that the survival of young seedlings was not affected by spring or autumn flooding, but that summer flooding reduced tillering as compared to plants not flooded during the summer. They concluded that *P. arundinacea* is most strongly suppressed by flooding at the start of rhizome growth and tillering (in spring for mature plants (as found by Conchou and Fustec), and in early summer for seedlings), but is considerably less vulnerable at other points in the life cycle (135).

P. arundinacea is also morphologically plastic in response to nutrient conditions, another trait of highly competitive plants. In high nutrient conditions, *P. arundinacea* spread 50% farther, but produced just a few tillers close to the parent clone under low nutrient conditions (14). This strategy allows *P. arundinacea* to both fill and retain space when low nutrient conditions exist, and then expand into new areas under high nutrient conditions. Other authors have also found that *P. arundinacea* varies its root:shoot ratio in response to nutrient limitations (47, 134). This adaptation, as well as the ability to support new tiller growth into low nutrient conditions, increases the chance of this plant spreading into sub-optimal and variable sites, creating the potential for a small invasion to expand rapidly with a pulse of nutrients, e.g. a flood (99).

P. arundinacea life history, which further contributes to its ability to grow rapidly upon emergence, is similar to that of other species that typically dominate temperate wetlands, e.g. Typha (138), and Phragmites (139). This growth pattern includes the development of shoots in autumn that overwinter as small shoots about the soil surface that emerge quickly in spring (132, 140). Rapid early growth is one mechanism by which *P. arundinacea* precludes the establishment of other slower growing species (11, 84).

P. arundinacea root:shoot ratios respond to changes in environmental conditions, but how does the root:shoot ratio change during establishment when environmental conditions are held constant? A number of studies suggest that *P. arundinacea* growth rate contributes to its competitive ability; how much can a single plant grow when unconstrained? To answer these questions, we designed a uniform planting study that tracked the growth of *P. arundinacea* individual plants over two growing seasons. The objectives for this study were: 1) to characterize biomass production, shoot production, and spread for an individual *P. arundinacea* plant, and 2) to apply this knowledge to the understanding of the *P. arundinacea* invasion process.

Methods

On June 12, 2002, 90 *P. arundinacea* seedlings were taken from the greenhouse and planted one per container, into 90 1.2-m diameter, 30-cm deep containers filled with steam-sterilized wetland soil (Glencoe clay loam, Cumulic Endoaquoll). Container size was chosen such that containers would not be likely to limit belowground growth for two growing seasons. The containers with the individually planted seedlings were arranged in 3 rows of 30 containers each, and the individual seedlings were left to grow unconstrained for two growing seasons. Throughout the study, containers were kept moist through twice daily drip irrigation. Irrigation was interrupted for winter following senescence of plants and freezing of the upper soil layer (November 30, 2002), and resumed as soon as thaw occurred in early spring (March 30, 2003).

For response data collection, 7 plants were randomly selected for harvest at regular intervals once every 3-5 weeks from June 2002 to November 2002, and April 2003 to November 2003. Upon harvest, each plant was observed for mean height, height of apical shoot, number of shoots (number of live stems), number of seed heads and crown size. Aboveground spread was measured as the distance from the outermost shoot to the center of the plant. Aboveground biomass was clipped for each plant and separated into live and dead shoots. Belowground biomass was entirely rinsed of soil, and for the first season of the study, separated into roots and rhizomes. Root and rhizome fractions were found to follow a similar pattern of growth over the entire growing season. Therefore, root and rhizome fractions are combined into belowground biomass for all analyses in this paper. Above and belowground biomass was placed into paper bags, dried in a forced air oven at 70°C for 48 hours, and then weighed.

The seedlings of *P. arundinacea* used for this study were germinated from seeds collected from a wetland at the University of Minnesota's Landscape Arboretum in Chanhassen, Minnesota, USA (41°51'45"N, 93°36'00"W), and grown in wetland soil in the greenhouse for 6 months (January-June 2002). Before planting, each seedling was observed for the number of shoots, length of each shoot, and total rhizome length. Also at the beginning of the study, several seedlings were separated into above and belowground biomass, and dried in a forced air oven at 70C for 48 hours, then weighed. Initial measurements taken just prior to planting showed that *P. arundinacea* seedlings had a mean of 7.33 shoots per plant (SE=0.55), and mean shoot height was 12.57 cm (SE=1.72). The seedlings had an initial mean aboveground biomass weight of 0.18 g (SE = 0.05) and a mean belowground biomass weight of 0.16 g (SE = 0.06).

Climate data for the duration of the study were provided by the University of Minnesota's Climatology Working Group, which observes daily temperature data at a field station less than 1 km away from the study area. From these data, the 2002 and 2003 growing seasons were determined to be similar in temperature (987 and 879 cooling degree days, respectively). Year-to-year differences in growth patterns for the two growing seasons of the study can therefore be attributed to differences in establishment phase, as differences in season are not confounded with that factor.

Results

Belowground growth

In the first five months of the study, mean *P. arundinacea* belowground biomass increased roughly 1000-fold from 0.16 g plant⁻¹ to 113.37 g plant⁻¹. At the conclusion of the two growing seasons of the study, mean belowground biomass was 333.08 g plant⁻¹ (Table 4-1, Figure 4-1).

The average rate of belowground biomass production was higher in the second growing season, when belowground biomass was accumulated at a mean of 1.15 g plant⁻¹ day⁻¹, as compared to 0.92 g plant⁻¹ day⁻¹ during the first growing season. Belowground biomass increased throughout the entire study, and the peak growth rate for belowground biomass occurred during July of the second growing season, when production was 2.7 g plant⁻¹ day⁻¹. Surprisingly, belowground growth reached the edges of the 1.2-m diameter container at the end of the first growing season (Figure 4-2, Figure 4-3). Belowground spread was therefore limited by the container during the second growing season.

During initial establishment (June through August of the first growing season), root:shoot ratios were greater than 2 (Table 4-1). For the remainder of the study, root:shoot ratio was less than 1 (ranging from 0.94 to 0.02), with the lowest root:shoot ratios occurring during senescence in the late fall (November of the second growing season).

Aboveground growth

Aboveground biomass increased from 0.18 g plant⁻¹ at the start of the study to a peak of 58.16 g plant⁻¹ before senescing during the first growing season and to a peak of 132.26 g plant⁻¹ before senescing during the second growing season (Table 4-1, Figure 4-1). The average rate of aboveground biomass production during the second growing was only slightly higher than that of the first growing season (0.59 g plant⁻¹ day⁻¹ and 0.41 g plant⁻¹ day⁻¹, respectively), and slower than the rate of belowground biomass production. The peak growth rate for aboveground biomass occurred during July of the second growing season, and was 2.04 g plant⁻¹ day⁻¹. In contrast to belowground biomass, which accumulated throughout the study, aboveground biomass did not increase after early October of each growing season.

In the first year of the study, the number of shoots per plant increased until mid-August, when plants reached a mean of 157 shoots plant⁻¹, after which there was no significant increase in shoots (Figure 4-4). In the second year, shoots emerged from overwintering buds in the early spring, and plants began the second growing season with a mean of 137 shoots plant⁻¹. This increased to 197 shoots plant⁻¹ in mid-September, after which there was no significant increase in the number of shoots.

The mean shoot weight (mean biomass of an individual shoot) varied significantly throughout both growing seasons (Figure 4-5). Shoot weight increased until early October in the

first growing season, and until early August in the second growing season. Shoot weight decreased in the end of both growing seasons, when plants exhibited many (~200) shoots plant⁻¹, 5 to 15 cm tall, accounting for a low average shoot weight at that harvest period.

As plants grew from an initial 4-cm diameter loose crown, shoots amassed into a dense crown; aboveground spread of the crown increased to a diameter of 25 cm during the first growing season, but only increased 3 cm more to a diameter of 28 cm during the second growing season. Spatial distribution of shoot growth varied over time. Plants began to produce shoots that emerged from the soil surface more than 15 cm from the outer edge of the crown in May of the second growing season. The proportion of shoots that occurred outside of the crown increased through the second growing season from 5% in May to 21% in November (Figure 4-6).

Only 3% of plants flowered and set seed during the first growing season, but 100% of plants flowered and set seed during the second growing season. Flowering occurred in mid-June, and seed maturation occurred in early July.

Discussion

Absolute growth

P. arundinacea has been noted for its rapid growth potential (140), and the amount of biomass produced by *P. arundinacea* on an individual basis in this study is generally greater than that for other species grown in similar conditions. *Urtica dioica*, a perennial wetland forb, produced 4.8 g plant⁻¹ of aboveground biomass, and 2.6 g plant⁻¹ of belowground biomass after 4 months of growth under mesic conditions in a uniform planting study (135). In the same growth period during our study, *P. arundinacea* produced 10 times the aboveground biomass (58.2 g plant⁻¹) and 30 times the belowground biomass (66.0 g plant⁻¹). *P. arundinacea* growth in this study is roughly double that of *Spartina pectinata*, a native wetland grass; when grown in a uniform planting study for 5 months, *S. pectinata* produced 18 g plant⁻¹ above ground biomass and 17 g plant⁻¹ of belowground biomass (48).

Miller and Zedler (48) found that belowground growth from a *P. arundinacea* rhizome fragment with a single vegetative bud expanded beyond the 25-cm diameter pot after 5 months of growth. In this study, we found that belowground growth exceeded a container with 4 times the diameter (1.2 m) after only 5 months of growth. At this point in our study, *P. arundinacea* had reached 58.16 g plant⁻¹ of aboveground biomass and 113.37 g plant⁻¹ of belowground biomass. In the smaller pots, *P. arundinacea* reached only 16-20 g plant⁻¹ of aboveground biomass and 23-32 g plant⁻¹ of belowground biomass, suggesting that *P. arundinacea* growth is proportional to the space provided.

Because belowground biomass growth was limited by the container by the beginning of the second growing season, we were only able to calculate unconstrained belowground spread for the first growing season, which was 1.2 m, the diameter of the container in this study. *Typha latifolia* L., a species common to wetlands throughout North America, outperformed *P. arundinacea* in a similar uniform planting study in which a single *Typha latifolia* plant achieved a belowground spread of 3 m in the first growing season (138). Yet *P. arundinacea* has been found to be an inherently better competitor than *Typha* sp. during the establishment phase (10, 46), indicating that some mechanism other than belowground spread may be responsible for *P. arundinacea*'s superior suppression of other species.

Growth patterns

What does the observed pattern of unconstrained *P. arundinacea* biomass production say about its invasion mechanism? During establishment (the first 2 months of growth), root:shoot ratios indicate that biomass allocation was primarily aboveground. Initially, *P. arundinacea* produced twice as much biomass above ground as below. These data support the idea that above ground suppression of neighbors by *P. arundinacea* is particularly intense in the early stages of establishment, giving *P. arundinacea* the ability to preempt establishment of other species. Perry (141) noted that *P. arundinacea* can cause a light limitation for its competitors by growing much faster after seedling emergence. Several studies have observed that *P. arundinacea* can preempt slower growing sedge meadow perennials, such as *Carex* spp. (11, 107). Early rapid above ground growth may facilitate this advantage of *P. arundinacea* over *Carex* spp.

After the first of two months of establishment, *P. arundinacea* produced proportionally more belowground biomass (root:shoot ratios changed from 2 to less than 1). Root:shoot ratios are known to change during the growing season for many perennial species and the ability to differentially allocate growth is characteristic of competitive plants (130). In this case, the multi-stage process of growth may mean that *P. arundinacea* competitive strategy shifts, such that the first stage is focused on aboveground competition, and the second stage consists of above and below ground competition. Given the two different growth strategies, *P. arundinacea* growth may be constrained by different factors at each growth stage. A similar mechanism has been suggested for *Phragmites australis*, in which emergence from rhizomes was constrained by soil drainage, and not by differences in salinity or sulfides, but survival, growth, and belowground biomass production was constrained by salinity (139).

Comparison when grown with neighbors

Our results suggest that, when unconstrained, *P. arundinacea* produces biomass at high rates. But can this growth be sustained in the presence of neighbors? In Miller and Zedler's (2003) pot experiment, *P. arundinacea*'s productivity when grown alone was greater than total productivity of *Spartina pectinata* and *P. arundinacea* grown together, indicating that *P. arundinacea* was suppressed by *Spartina pectinata*. Conversely, in a greenhouse experiment, *P. arundinacea* produced similar or more biomass per plant when grown with *Typha latifolia* or *Carex stricta* as compared to growth of *P. arundinacea* alone (46). In a greenhouse experiment, differential suppression of *P. arundinacea* by other species was linked to environmental conditions, when *P. arundinacea* was suppressed by *Carex hystericina* under depleted nitrogen conditions only (84).

In contrast, when *P. arundinacea* is forced to grow in an already established canopy, *P. arundinacea* growth appears to be suppressed relative to performance in this study. Mean aboveground biomass of *P. arundinacea* plants grown from uniform rhizome fragments in a wetland in the presence of already established native species after 4 months was 0.21 to 0.28 g plant⁻¹ (99). Similarly, when uniform rhizome fragments were planted into a pasture, after four months of growth mean aboveground biomass was 0.64 g plant⁻¹ (142). Although comparison with these studies cannot be direct (immature seedlings were used in our study instead of rhizome fragments), it is interesting to note that after 4 months of unconstrained growth in our study, *P. arundinacea* produced around 100 times more above ground biomass (58.16 g plant⁻¹) than in either of these studies.

Suppression of *P. arundinacea* by a native species canopy has been demonstrated in other studies, leading to the conclusion that establishment of a dense native canopy will limit *P.*

arundinacea invasion (14, 51, 99). In contrast to the suppression of *P. arundinacea* under a native canopy, the rapid growth potential of *P. arundinacea* when unconstrained indicates that when resources are available, *P. arundinacea* has the ability to rapidly expand. This suggests that even established native communities are at high risk of *P. arundinacea* invasion when 1) propagules are available and 2) environmental conditions provide open space, e.g. *during* the establishment of the native species canopy, following a hydrologic drawdown, or in early spring prior to growth of native species.

Table 4-1. Growth characteristics were measured for each of 7 plants for every harvest period. Values are discussed in the text.

date	aboveground biomass (g/plant)		belowground biomass (g/plant)		shoots/plant		average shoot weight (g)		root:shoot ratio	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
6/13/02	0.18	0.05	0.16	0.06	7.33	0.56	0.02	0.00	2.35	0.13
7/10/02	2.67	0.31	1.32	0.21	38.67	4.47	0.07	0.00	2.13	0.24
7/29/02	8.60	1.21	4.29	0.79	72.67	8.57	0.12	0.01	2.19	0.32
8/19/02	37.67	4.52	18.75	2.29	158.33	13.05	0.24	0.03	2.11	0.25
10/3/02	58.16	4.67	65.98	6.90	160.83	12.94	0.37	0.03	0.94	0.15
11/8/02	52.46	7.32	113.37	19.12	177.67	36.68	0.33	0.05	0.48	0.05
5/9/03	19.19	1.56	110.80	15.93	120.45	13.28	0.16	0.04	0.18	0.01
6/3/03	61.74	9.62	133.20	33.14	137.86	14.65	0.45	0.05	0.58	0.13
7/4/03	79.19	8.94	188.42	27.87	142.29	13.73	0.58	0.07	0.46	0.05
7/31/03	134.27	24.91	261.41	40.36	121.86	18.86	0.91	0.13	0.50	0.03
9/11/03	116.85	8.41	283.34	21.83	197.29	16.61	0.61	0.05	0.39	0.03
10/6/03	132.26	12.12	293.80	24.12	208.43	13.76	0.64	0.04	0.45	0.03
11/18/03	6.36	0.88	333.08	40.82	228.71	39.09	0.06	0.03	0.02	0.00

Figure 4-1. Above and below ground biomass differed significantly with harvest date for both growing seasons (first growing season: aboveground biomass $F = 32.67$, $p < 0.01$, belowground biomass $F = 27.66$, $p < 0.01$, second growing season: aboveground biomass $F = 18.96$, $p < 0.01$, belowground biomass $F = 8.39$, $p < 0.01$). Although no plants were harvested for data collection following ground freeze, live aboveground biomass would have measured 0 g plant^{-1} at some time after November of each growing season after complete senescence. Values are means \pm SE. Letters indicate significant differences for Tukey's HSD test for difference between means ($\alpha = 0.05$).

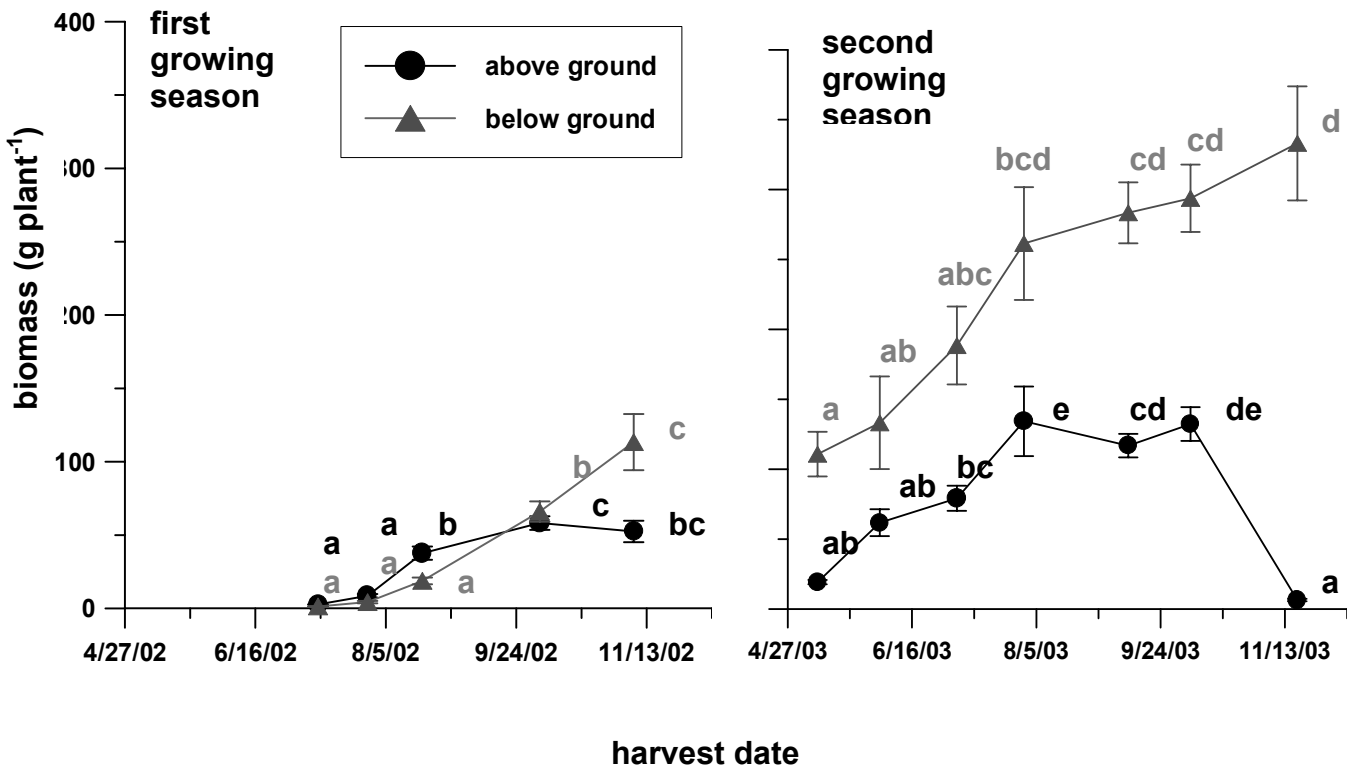


Figure 4-2. Belowground biomass was observed to reach the edges of the 1.2 m diameter container by May of the second growing season. In this photo, aboveground biomass has been clipped, and soil has been rinsed from a portion of the belowground biomass.

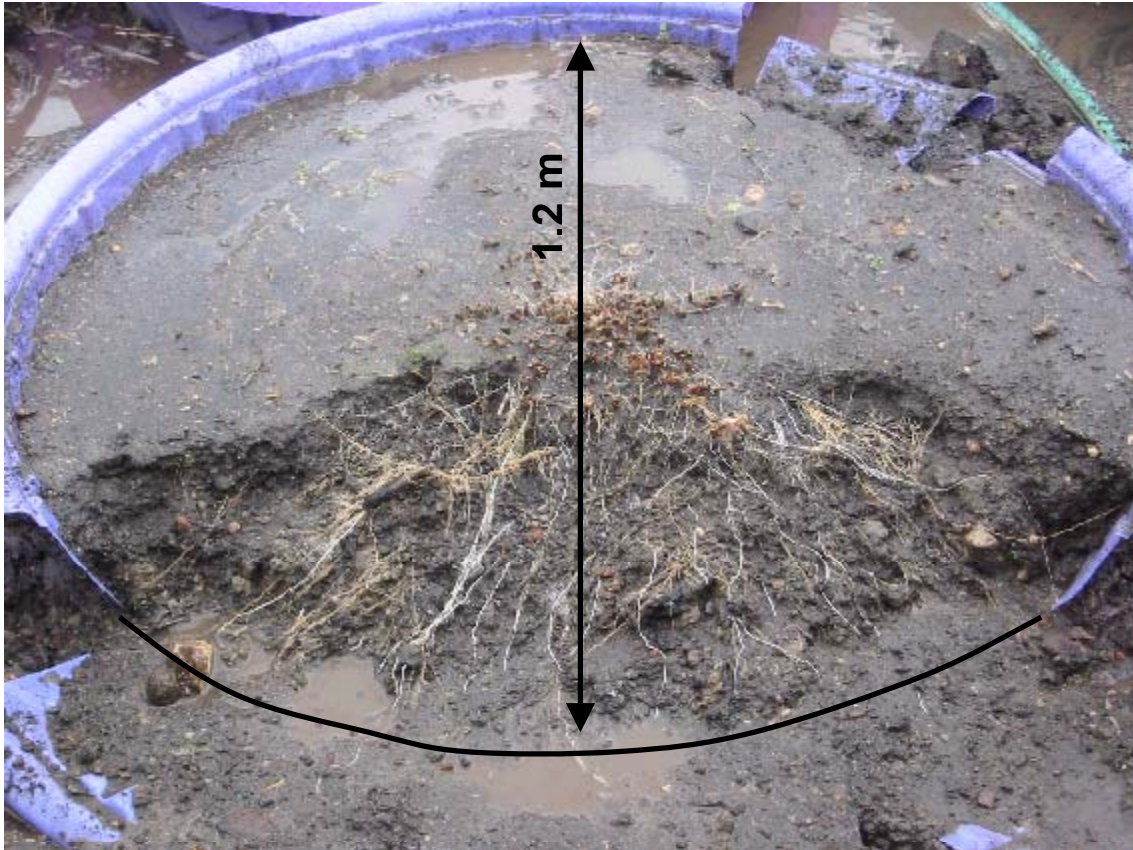
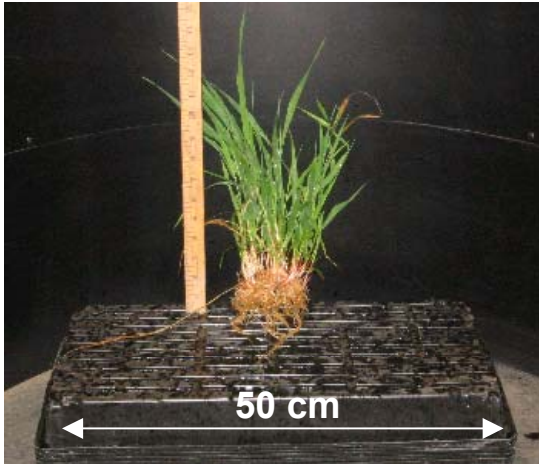


Figure 4-3. Belowground biomass is shown for a single plant one month after planting (July 2002) and 4 months after planting (October 2002). The same white tray is provided for scale in the lower pictures of belowground biomass only.

July 2002



October 2002

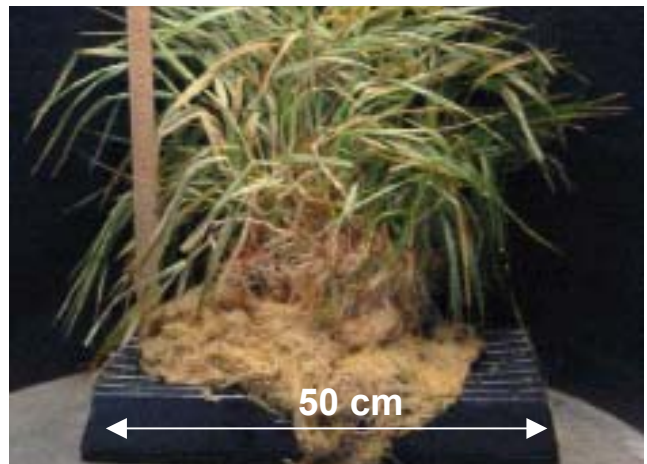


Figure 4-4. Number of shoots per plant differed with harvest date during year 1 ($F=10.77$, $p<0.01$) and year 2 ($F=4.25$, $p<0.01$). Values are means \pm SE. Letters indicate significant differences for Tukey's HSD test for difference between means ($\alpha = 0.05$).

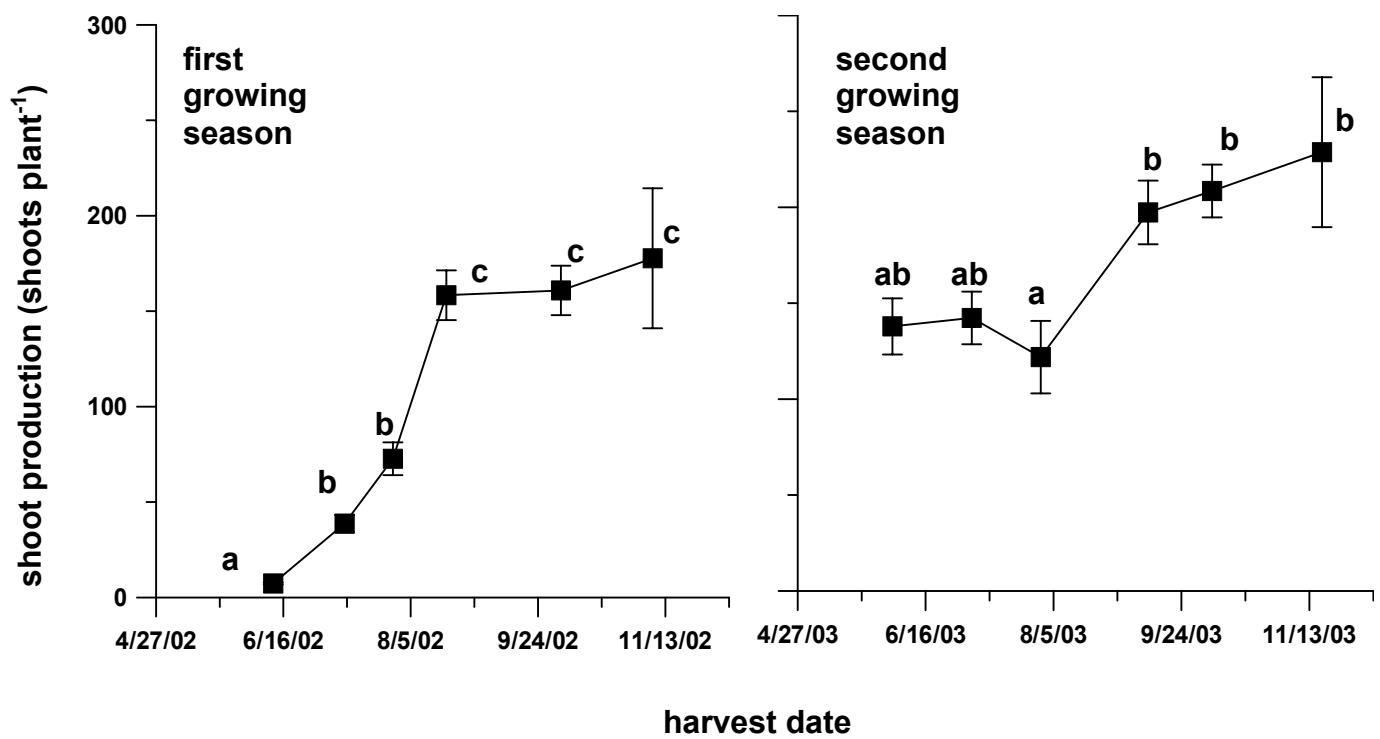


Figure 4-5. The average weight per shoot differed significantly over year 1 ($F=17.06$, $p<0.01$) and year 2 ($F=15.85$, $p<0.01$). At the end of the second growing season, many small shoots accounted for the weight of the aboveground biomass. Values are means \pm SE. Letters indicate significant differences for Tukey's HSD test for difference between means ($\alpha = 0.05$).

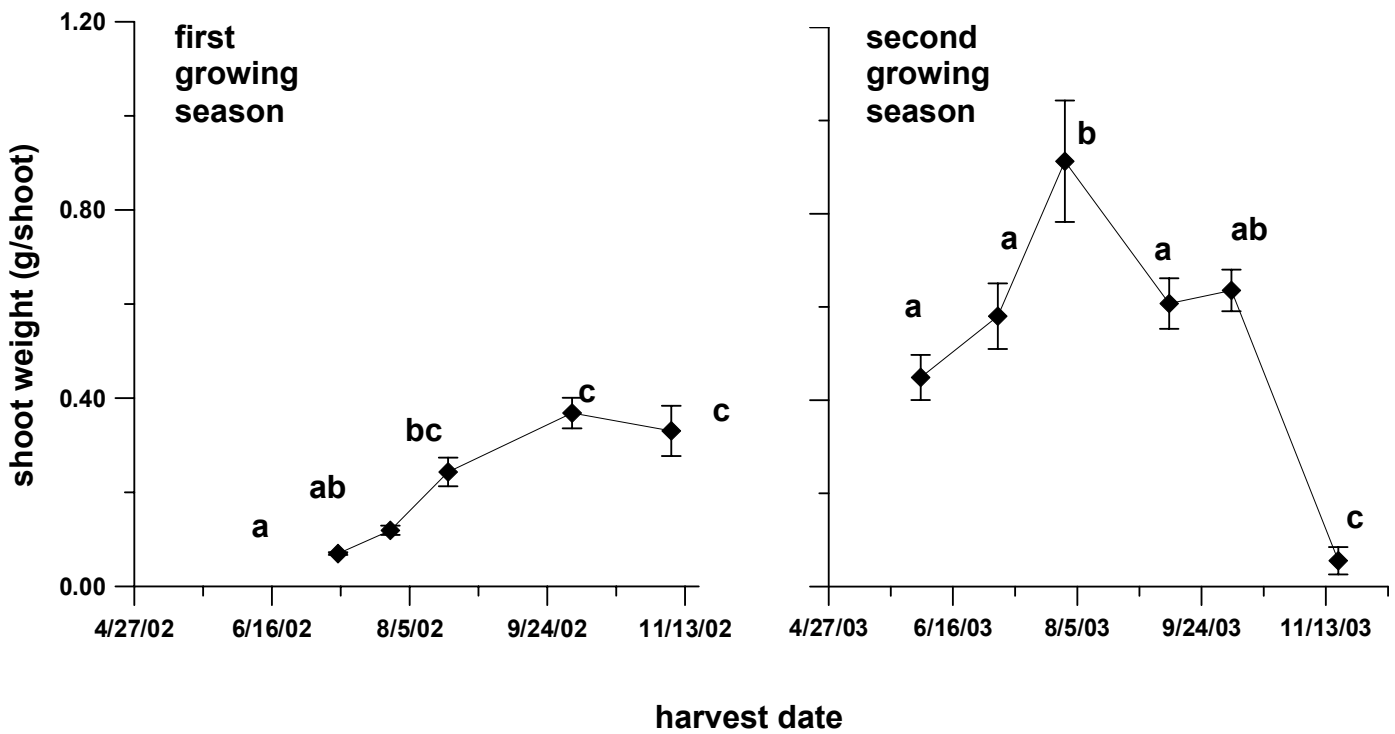
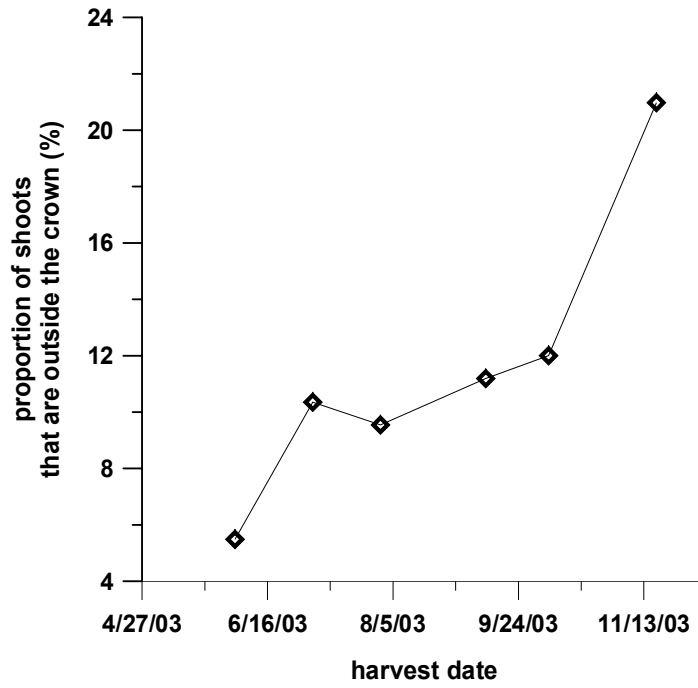


Figure 4-6. The proportion of shoots that surfaced outside of the crown increased throughout the second growing season.



CHAPTER 5

***Phalaris arundinacea* L. (reed canary grass) management plan and educational component**

Summary

A management plan is presented for the control of *Phalaris arundinacea* at the North St. Paul Sod Farm Site. The plan is supplemented by an outreach component that includes educational signage for the site and a fact sheet on *P. arundinacea* control for distribution. Control techniques involve late season glyphosate herbicide applications; broadcast applications are recommended where cover is almost exclusively *P. arundinacea*, and selective applications are recommended when *P. arundinacea* is present along with other desirable species. The site is divided into management units, and treatment of management units is staggered through time to prevent erosion from large-scale areas of bare soil. The fact sheet reflects these recommendations, and is also a document that can communicate research results to a wider audience, including land managers, state and local agency staff, and other interested parties.

Introduction

In 1997, the Ramsey Washington Metro Watershed District (RWMWD) designated a 20 acre abandoned sod farm in North St. Paul (hereafter referred to as the North St. Paul Sod Farm, or NSPSF) as a wetland restoration demonstration. The site, which is used to treat drainage from a residential area, is degraded by stormwater runoff and invasion by aggressive plant species, and provides an opportunity to learn from the restoration process. The area is of educational significance; the wetland is visible from the highly trafficked Gateway Trail, is easily accessible by large groups of students and community organizations, and is centrally located in an urbanized area.

The RWMWD has led a restoration effort on this site for several years. Staff have worked to improve the habitat of the site through adjacent upland prairie restorations, construction of a meandering drainage channel through the wetland, and native species revegetation of shores and channel edges. The site is accessible to the public through a visitor's parking lot, an observation mound, and a footbridge through the emergent marsh.

Creating a diverse native plant community in the wetland is central to the project goals for this site. A major barrier to that goal is the dominance of *Phalaris arundinacea* L., an invasive perennial grass, in the majority of the wetland area of the site. In order to investigate *P. arundinacea* control methods and subsequent native plant community establishment, research has been ongoing in a *P. arundinacea*-dominated area. Conclusions from this research have resulted in a series of *P. arundinacea* management recommendations specific to the NSPSF wetland site.

In this chapter, we recommend best management practices for control of *P. arundinacea* on the NSPSF site, and suggest public outreach that can be implemented in concert with the management activities. The objectives of this project are to: 1) improve wetland habitat of the wetland area by removing *P. arundinacea* and reestablishing native species, and 2) educate the surrounding community about the wetland restoration and the

value of biodiversity in an urban setting. Correspondingly, this document consists of two parts: 1) a management plan, and 2) a public education component.

Management Plan

Control of *P. arundinacea*

The management plan begins with a description of methods to control *P. arundinacea* prior to other wetland restoration activities (restoring hydrology, reestablishing native species). This plan is based on inference from the results of the research that has taken place on site, and is also a product of the best professional judgement of the authors of this document.

Current vegetation species composition of the site

Under this plan, the wetland areas of the property are divided into management units based on current vegetation species composition. Each area on the site is classified as one of several vegetation communities based on dominant species: 1) *P. arundinacea*-dominated emergent marsh (*P. arundinacea* cover is >75%, *Urtica dioica* and *Impatiens capensis* are present at 1-25%); 2) mixed native species/*P. arundinacea* emergent marsh (*P. arundinacea* cover is 50%, several native species are present at cover >25%); 3) native species-dominated riparian zone (several native species are present at high cover, *P. arundinacea* cover is <25%); 4) *Typha*-dominated emergent marsh (*Typha* cover is >75%, *P. arundinacea* cover is <25%); 5) oak/aspen woodland (shaded area where *P. arundinacea* cover is substantial in patches); and 6) upland prairie. These vegetation community areas have been mapped and described in Figure 5-1 and Table 5-1. Management recommendations are based on these units because *P. arundinacea* control strategy and subsequent native revegetation will vary according to the species composition of the area.

Hydrology

Flood pulsing and site hydrology will be important determinants of the resulting vegetation community. The site receives storm water runoff from a watershed of 480 acres, which is almost exclusively residential (143). A high percentage of impervious surface in the watershed contributes to hydrologic bounce, which inhibits the survival of key native wetland species but does not have significant negative impacts on *P. arundinacea*. Stormwater from urban areas is generally nutrient-rich, which increases the growth and competitive ability of *P. arundinacea*. Also, *P. arundinacea* propagules (i.e. seed, rhizome fragments) from upstream populations will likely be transported via stormwater inputs. Because hydrology of this site will likely create conditions that favor *P. arundinacea* persistence, long-term management of *P. arundinacea* on this site will be necessary, even after effective site management has minimized *P. arundinacea* populations. Although preventing dispersal of *P. arundinacea* propagules to the site is unrealistic, reducing hydrologic bounce and nutrient content of the stormwater will limit *P. arundinacea*'s competitive advantage and may reduce the level of aftercare needed to control *P. arundinacea*.

General recommendations for P. arundinacea control

The dense populations of *P. arundinacea* that currently exist on-site will need to be removed for native species to establish. In addition to the existing vegetation, in areas where *P. arundinacea* has been established for multiple years the *P. arundinacea* seed bank may be as high as 1200 seeds m⁻² (Chapter 2 of this document). Because this density of the *P. arundinacea* seed bank presents competition for any planting of native species, it must be considered in the management plan. Seeds near the surface will germinate when the *P. arundinacea* canopy is removed. Subsequent herbicide applications will remove these seedlings, and burning/herbicide treatments will deplete the seed bank in this way. For the *P. arundinacea* seed bank to deplete to levels that will not prevent native species establishment, *P. arundinacea* control will likely need to take place over several growing seasons. Minimize disturbance of the soil to prevent turning up additional *P. arundinacea* seed in these areas. While areas are undergoing herbicide treatment, large areas of exposed soil will need to be stabilized, e.g. through the use of stabilization blankets.

Herbicide applications are a major part of the plan to control *P. arundinacea*. A glyphosate-based herbicide is recommended because 1) it is relatively non-toxic, 2) its effect on *P. arundinacea* has been demonstrated, and 3) it is widely available and easy to apply. To maximize glyphosate herbicide effectiveness, apply herbicide in the later season, after late August, to ensure translocation of the herbicide to rhizomes (and therefore rhizome mortality). Apply glyphosate herbicide at the rate and concentration specified by the label for weedy perennial grasses; this will differ with respect to the glyphosate-based product chosen.

P. arundinacea-dominated areas will require herbicide control over several growing seasons. Removal of *P. arundinacea* will result in areas of temporarily exposed soil that are subject to erosion. Implementing control on selected management units separately through time will minimize erosion-related problems on site. Further discoveries about best management practices may result from observing the implementation of this plan over time, and the plan may be modified according to lessons learned during the management process.

Recommendations based on current species composition

For P. arundinacea-dominated emergent marsh

For *P. arundinacea*-dominated emergent marsh (management units 1 and 2), a broad-scale herbicide application is recommended, as damage to non-target species within these management units does not need to be considered. As described above, because of risks associated with soil erosion, management units will further be divided in sections (Figure 5-2). Control of *P. arundinacea* in sections will be staggered over time. Sections 1a, 1d, 2a and 2d will begin treatment in year 1, receiving herbicide applications in years 1-3, and be seeded in year 4. Sections 1b, 1c, 2b and 2c will be treated to prevent seed production (mowing, removing seed heads, etc.) before beginning treatment in year 3, receiving herbicide applications in years 3-5, and be seeded in year 6. Apply herbicide in late August and later as this application timing maximizes translocation of the herbicide to the rhizomes, ensuring maximum rhizome mortality, which is crucial to

control of *P. arundinacea*. Two herbicide applications can be implemented during this window if necessary.

After the standing *P. arundinacea* vegetation is killed in the first year of treatment, a heavy layer of thatch will remain. A controlled burn will be applied to remove thatch and encourage germination of *P. arundinacea* from the seed bank in the interests of reducing *P. arundinacea* seed bank density. Subsequent herbicide applications will control this flush from the seed bank. We recommend a late fall burn to remove thatch (spring burns may encourage growth from rhizome-based shoots).

Even after two years of effective herbicide application, *P. arundinacea* will recolonize, largely from the seed bank and from incoming propagules, and outcompete native vegetation that has begun to establish from a restoration seeding (Chapter 2, this document). Therefore, three years of herbicide application are recommended.

For areas with native species cover

Native species are present with substantial cover in management units 9 and 10, and native prairie species dominate management unit 10. For these areas, selective removal of *P. arundinacea* will be critical to the maintenance of these native populations. We recommend hand weeding of *P. arundinacea* seedlings in the early spring as soon as they reach an identifiable stage (removal will be easiest before the seedlings establish a network of rhizomes) and herbicide wicking of established *P. arundinacea* individuals in the fall (damage to non-target species will be lowest at this time when many native species have already senesced). Herbicide wicking is also an option in the early spring, but hand weeding is preferable, as herbicide applications during the early spring may not achieve complete mortality. We also recommend this treatment schedule for management units 4, 3, and 8, which are dominated by *Typha* sp. Selective control of *P. arundinacea* in these areas can begin immediately and continue for as long as needed.

For areas with woody species cover

Management units 5, 6, and 7 are areas with woody species cover. These areas are invaded by *P. arundinacea*, although other species exist in the understory. Similar to the areas with native species cover, selective removal of *P. arundinacea*, rather than homogeneous treatment over a large scale area, will be necessary. We recommend hand weeding of *P. arundinacea* seedlings in the early spring and herbicide wicking of established *P. arundinacea* individuals in the fall. Herbicide wicking is also an option in the early spring, but hand weeding is preferable, as herbicide applications during the early spring may not achieve complete mortality. Selective control of *P. arundinacea* in these areas can begin immediately and continue for as long as needed.

Reestablishment of native vegetation

Following control of *P. arundinacea*, seeding with a native species restoration mix will be needed to stimulate reestablishment of native vegetation. Given that there are no high quality wetlands nearby to serve as propagule sources, and that years of drainage have made the seed bank depauperate, it is highly unlikely that vegetation will establish through natural means of propagule dispersal to this site.

Areas that have been treated with broad-scale herbicide applications (management units 1 and 2) must be seeded uniformly. To prepare the soil for the native seeding in

mid- to late May, first burn the area (either in the previous fall or the early spring of that year) if necessary to remove dead vegetation. A wet meadow grass mixture will be seeded at 13 lbs/ac PLS or greater, and a wet meadow forb mixture will be seeded at 4 lbs/ac PLS or greater. The combined seeding rate of 17 lbs/ac pure live seed (PLS) was determined to be an average seeding rate, and increasing seeding rate will likely increase native species establishment.

For areas that have received selective removal of *P. arundinacea* (not broadcast herbicide application), interseeding is recommended for areas left open after *P. arundinacea* removal. Species-appropriate seedings will be necessary, e. g. woodland forb species in the understory of areas with woody species cover, and aquatic species in the *Typha*-dominated emergent marsh.

After seeding with native species, monitoring of *P. arundinacea* recruits will likely be necessary for as long as the site is exposed to an influx of new *P. arundinacea* propagules (i. e. indefinitely). As native species begin to establish, we recommend selective removal of new recruits of *P. arundinacea* as they emerge within the establishing native community, via hand-weeding or selective treatment with herbicide.

Educational component

To achieve the goal of educating the public about the project and the benefits of the project to the community and the ecology of the area, we have outlined an educational component to the management plan. The educational component involves: 1) educational signage for the site, and 2) a *P. arundinacea* control fact sheet for distribution.

On-site educational opportunities

Because areas managed for *P. arundinacea* control are visually distinct enough to be observed from both the observation mound and the Gateway Trail (Figure 5-1), this presents an opportunity to educate the public about the restoration process as it occurs at the NSPSF site. Educational signage will call attention to areas currently undergoing the restoration process and provide information about the project to the community and educate them about the importance of biodiversity and the contribution of their neighborhood wetland to ecosystem health.

One sign can be displayed permanently to explain why and how *P. arundinacea* is being removed from the site (Figure 5-3). Several other signs, constructed so as to make temporary posting possible, can be displayed when those specific management activities are underway (Figure 5-4, Figure 5-5).

P. arundinacea control fact sheet

A fact sheet communicates the results of the research presented in Chapters 2, 3, and 4 of this document (Figure 5-6). It gives a physical description of *P. arundinacea*, details why reed canary grass is a problem for wetland restoration, and recommends best management practices for control of *P. arundinacea*. In areas of educational signage around the NSPSF site, fact sheets can be made available for interested visitor to take with them. Or, a contact number for the RWMWD can be posted, so that visitors can obtain fact sheets after first contacting the RWMWD.

This fact sheet is also intended for distribution to managers with an interest in controlling *P. arundinacea*. This may include land managers from local agencies, federal agencies, environmental consultants, and academics.

Table 5-1. Each management unit has a designated vegetation species composition. See Figure 5-1 for location of management units.

Vegetation species composition	Management Units
<i>P. arundinacea</i> -dominated emergent marsh (<i>P. arundinacea</i> cover is >75%, <i>Urtica dioica</i> and <i>Impatiens capensis</i> are present at 1-25%)	1, 2
Mixed native species/ <i>P. arundinacea</i> emergent marsh (<i>P. arundinacea</i> cover is 50%, several native species are present at high cover)	9
<i>Typha</i> -dominated emergent marsh (<i>Typha</i> cover is >75%, <i>P. arundinacea</i> cover is <25%)	4, 3, 8
Native species-dominated riparian zone (several native species are present at high cover, <i>P. arundinacea</i> cover is <25%)	10
Oak/Aspen woodland (shaded area where <i>P. arundinacea</i> cover is substantial in patches)	5, 6, 7
Upland prairie	11

Figure 5-1. The NSPSF site has been divided into management units based on current vegetation species composition. Management units are numbered below. Corresponding vegetation species composition is provided in Table 5-1.

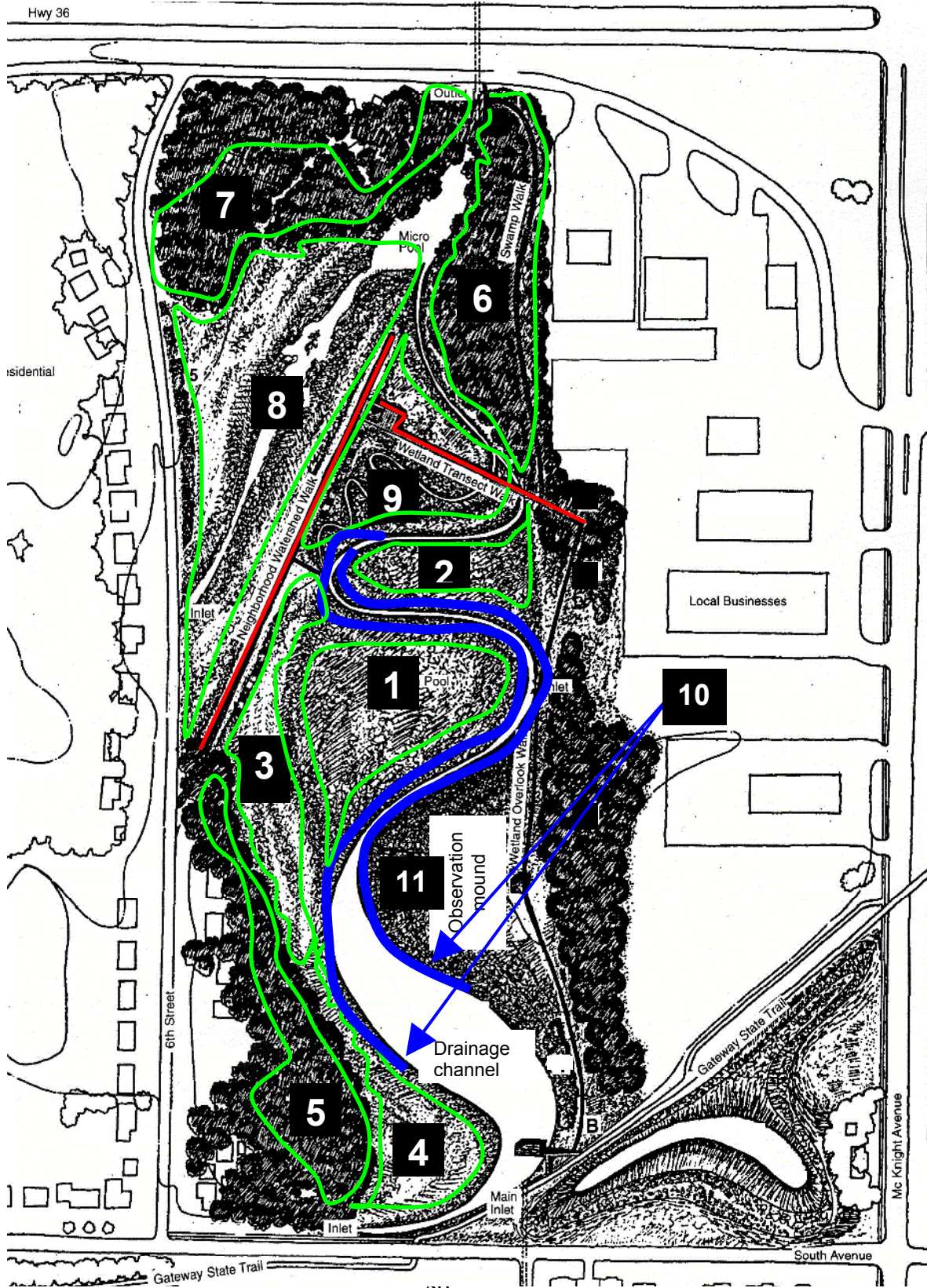


Figure 5-2. The *P. arundinacea* dominated management units 1 and 2 are further subdivided into 4 sections each for management recommendations. See Figure 5-1 for the location of management units.

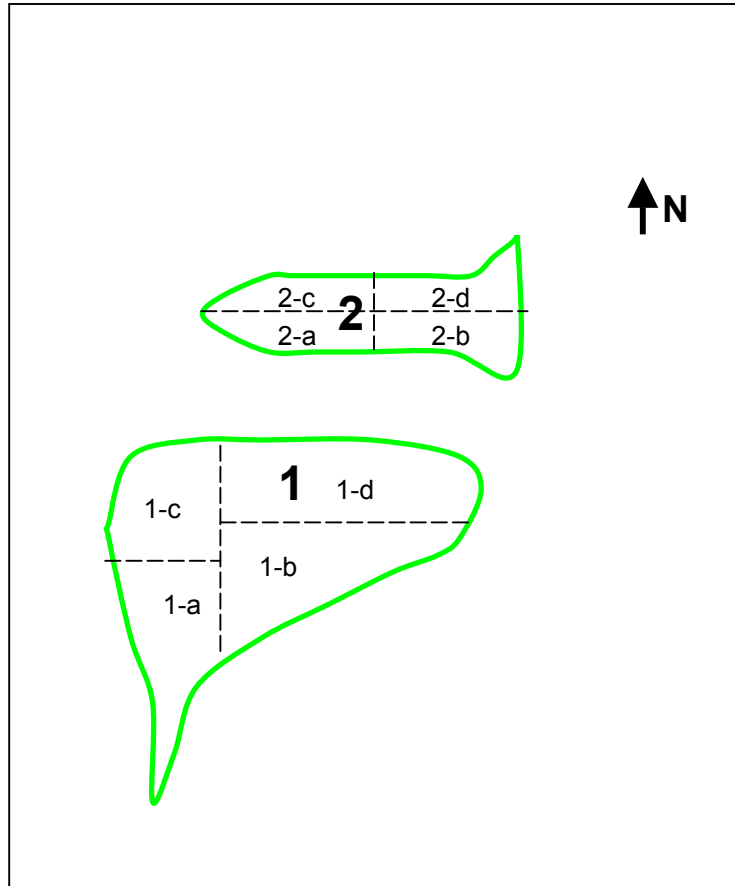


Figure 5-3. A general sign explains the purpose of *P. arundinacea* control activities that are currently being implemented on site.

Why does the wetland look like a war zone?

Restoration Underway!!

**The invasive species:
reed canary grass**



The native species:

Bottlebrush sedge



Swamp milkweed



That's right...the wetland doesn't look pretty now, but when we're done, this wetland will be much more valuable than it was before we got here. Reed canary grass invaded this wetland and is preventing native plants from growing here. Diverse native plant communities provide food and protection for other living things. If we can get rid of reed canary grass and get native plant species growing here, that will improve the biodiversity of this wetland.

Common yellowthroat



For more information, contact
Ramsey-Washington Metro
Watershed District:
www.rwmwd.org
651-704-2089

Figure 5-4. When burned areas of the site are visible from vantage points, this sign can be displayed to explain how burning facilitates the restoration process.

Why is the ground charred black?

We just did a *controlled burn* in the charred black section of the wetland. By carefully setting fire to a section of this wetland with the help of the North St. Paul fire department, we have made the wetland more suitable for native plants, and made it harder for the invasive reed canary grass to survive. A burn that is not carefully controlled could harm native vegetation or threaten the lives of people who live close to the wetland, so please leave the burning to us!



Figure 5-5. When herbicide use has created areas of dead vegetation, this sign can be displayed to explain how herbicide applications facilitate the restoration process.



Figure 5-6. A fact sheet describes the recommended best management practices that have resulted from this research (see next two pages).

Controlling Reed Canary Grass (*Phalaris arundinacea*) in Wetland Restorations

What is reed canary grass?

Reed canary grass is a sod-forming perennial grass that produces tall (2 to 8 ft) shoots, and reproduces by seed, underground spread, and from fragments (Figure 1). This plant forms thick, creeping underground stems called rhizomes (Figure 2). Reed canary grass is considered native to the temperate regions of all five continents. This species was bred to be an important cultivated forage grass for nearly two centuries, and has also been planted to stabilize slopes and drainage ways. Although reed canary grass had conservation value in the past, it is now considered an invasive species. The invasive character of some *Phalaris* populations may be the result of agronomic breeding for vigorous growth and drought tolerance. Most often, you will find reed canary grass growing in moist habitats, like wetlands, streamsides, lakeshores, and road ditches, but reed canary grass also grows well in upland habitats.



Figure 2. Thick creeping underground stems, called rhizomes, contribute to reed canary grass persistence.

Be careful not to confuse reed canary grass with native bluejoint grass (*Calamagrostis canadensis*). Bluejoint grass and reed canary grass seedlings are particularly difficult to distinguish. Look for the prominent transparent ligule (collar-like flap where the leaf attaches to the stem) on reed canary grass to positively identify this species (Figure 3).

Why is reed canary grass a problem?

Wetland restoration projects in Minnesota (and across temperate North America) are often invaded by reed canary grass before native plants can establish. Reed canary grass also invades natural wetlands, forming vast monotypic stands and displacing native vegetation. Development and urbanization alter the landscape, creating habitat for which reed canary grass is especially suited; it thrives in high nutrient, fluctuating hydrology conditions that are typical of sites that receive stormwater inputs. Reed canary grass also spreads through underground stems (rhizomes), allowing it to move into otherwise unsuitable conditions. This species is a problem for wetlands across the northern United States. Washington state lists reed canary grass as a noxious weed.



Figure 1. Reed canary grass in a wetland restoration in Minnesota.

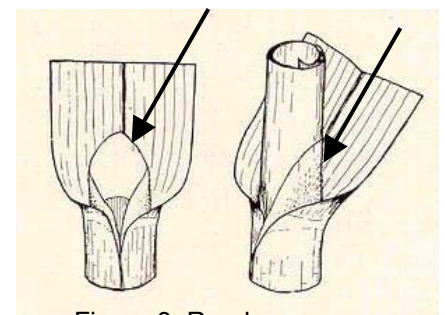


Figure 3. Reed canary grass has a prominent ligule.

Controlling reed canary grass: what works?

Herbicide treatments reduce reed canary grass when applied at the right time. Glyphosate-based herbicides are most commonly used to control reed canary grass because they are relatively non-toxic and they are known to be effective for this species. Because of glyphosate's mode of action, later season herbicide applications (late August or later in Minnesota) are more effective than spring herbicide applications (April and May in Minnesota) (Figure 4). Glyphosate moves with carbohydrates in the plant. A herbicide application in spring, when the plant uses carbohydrates to produce shoots, will kill the shoots of the plant but rhizomes will survive and resprout. But glyphosate herbicide applied in the later season, when the plant is storing carbohydrates in the rhizomes, will translocate directly to rhizomes, killing both the above and belowground parts of the plant.



Figure 4. This photo was taken one year after these plots had been treated with herbicide in Minnesota. The late August and late September application plots have no living reed canary grass. These applications were more effective than the late April herbicide application, as evidenced by the living reed canary grass in this plot.



Figure 5. A dense cover of native species can really slow down reed canary grass invasion.

Reed canary grass is less likely to invade a site that has a dense cover of native plant species (Figure 5). If managers can quickly establish native plants, by seeding and planting, they will spend less effort controlling reed canary grass. While the native species are establishing, however, managers will probably need to selectively remove new reed canary grass juveniles, especially if it is easy for reed canary grass seed to get to the site from other nearby populations.

Controlling reed canary grass: what doesn't work?

Mechanical control (mowing, grazing, tilling) alone does not reduce established reed canary grass populations. Mowing and grazing removes top growth and stimulates more shoot production. Tilling splices rhizomes into pieces and triggers dormant buds to produce new shoots, producing a more dense reed canary grass stand than if nothing had been done in the first place. Burning alone also doesn't work. In fact burning increases reed canary grass shoot density as new shoots sprout from rhizomes rapidly following a burn (Figure 6). And implementing a controlled burn prior to a glyphosate herbicide application does not increase the effectiveness

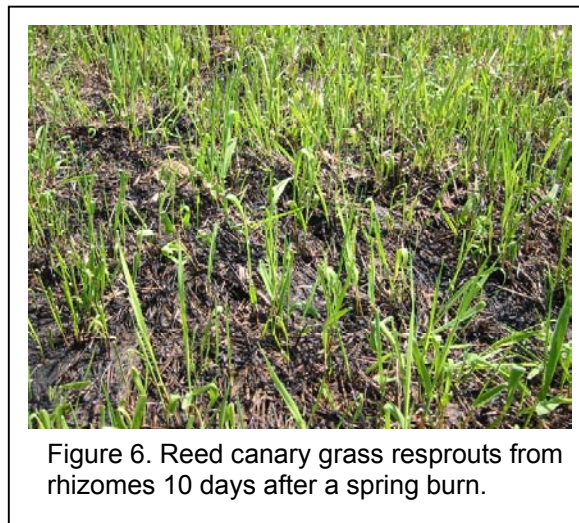


Figure 6. Reed canary grass resprouts from rhizomes 10 days after a spring burn.

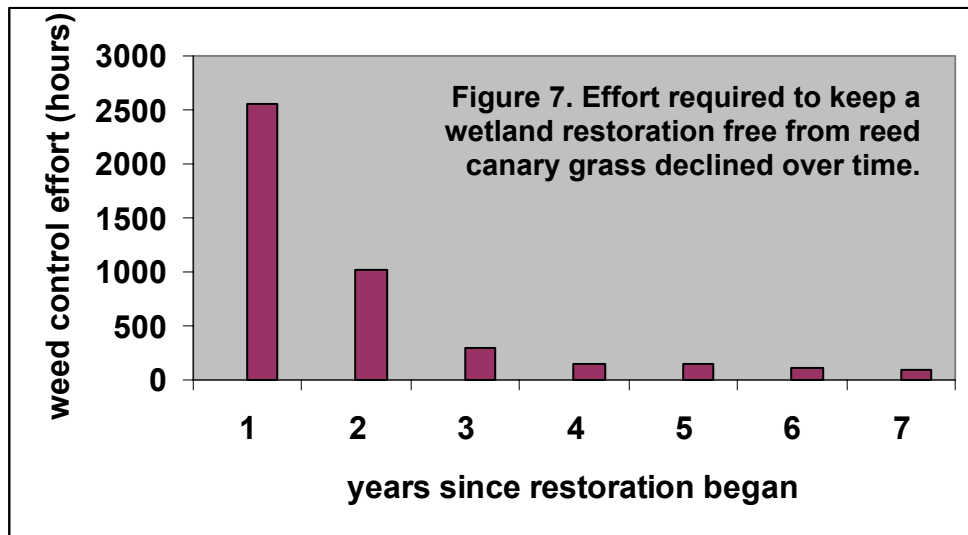
of the herbicide. Just partial contact with live tissue is enough for absorption of glyphosate herbicide, it isn't necessary to burn to get a flush of new green shoots.

Although mechanical removal methods are not successful for established stands of reed canary grass, if other aggressive native species are established on site, burns or mechanical removal may create gaps into which already established native species may expand. However, created gaps are also at risk for reed canary grass reinvasion if reed canary grass seed is available to the site.

Is one year of control enough?

Following control, reed canary grass can rapidly recolonize, possibly from rhizomes, from seeds on site, or from dispersal of seeds to the site. If reed canary grass has dominated a site for many years, managers will definitely need to control reed canary grass for more than one year, and

maybe more than 2 years. Although the effort required to keep reed canary grass out of the site diminishes over time, hand weeding might be necessary indefinitely. At the Spring Peeper Meadow wetland restoration demonstration at the University of Minnesota Landscape Arboretum, effort to keep the wetland reed canary grass-free was substantial at first, but declined over time (Figure 7).



The devil is in the seed bank

For sites that have had reed canary grass for more than 20 years, many reed canary grass seeds (Figure 8) are stored in the soil, forming a reed canary grass seed bank. After clearing away the existing reed canary grass, seeds in the seed bank have enough light exposure to germinate and grow, and the site is recolonized with reed canary grass. How do you diminish the reed canary grass seed bank? There are several options:

1. Spray the reed canary grass, till the seed bank to encourage germination of a new generation of reed canary grass plants. Kill that generation of plants, and repeat.
2. Excavate and remove the top 4-6 inches of soil.
3. Turn and fill under the layer of soil containing reed canary grass.



Figure 8. Reed canary grass produces many seeds.

For more information:

- The Nature Conservancy Wildland Invasives Team <http://tncweeds.ucdavis.edu/esadocs/phalarun.html>
- Wisconsin Department of Natural Resources <http://www.dnr.state.wi.us/org/land/er/invasive/factsheets/reed.htm>

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