PATTERNS, MECHANISMS, AND ECOLOGICAL IMPLICATIONS OF CATTAIL (*TYPHA* SPP.) DOMINANCE IN GREAT LAKES WETLANDS

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ABSTRACT

Many wetlands of the Great Lakes region are increasingly dominated by species of cattails, including the native *Typha latifolia*, the introduced *Typha angustifolia*, and their hybrid *Typha glauca*. Cattails are observed to form dense stands of live and dead biomass that may reduce plant diversity and compromise wetland habitat value. Cattail expansion has been used as an indicator of environmental change in the Everglades, but a broad analysis of the distribution and impacts of the northern species has not been conducted. In this study, I examined the patterns of cattail distribution across the Great Lakes, explored one mechanism by which cattails attain dominance in several Lake Ontario wetlands, and experimentally measured the effect of cattail biomass on plant species diversity in one wetland.

Patterns at the regional scale were addressed by analyzing vegetation surveys of 90 wetlands around the Great Lakes. Surveys were conducted in collaboration with scientists from the University of Minnesota – Duluth and the University of Wisconsin – Madison as part of an EPA-funded research program, the Great Lakes Environmental Indicators project. I compared patterns of dominance of invasive *Typha* (*T. angustifolia* and *T. glauca*) with those of five co-occurring, native graminoids, *Typha latifolia, Sparganium eurycarpum*, *Calamagrostis canadensis*, *Carex lacustris* and *Schoenoplectus tabernaemontani.* In contrast to the native species, the invasive *Typha* species represented a larger proportion of the plant cover in wetlands where they occurred (16% vs. 2 - 9% for natives), and their occurrence was associated with lower species density (7.1 vs. 8.6- 9.7 spp/m^2 for natives). Unlike the native species, the relative cover of invasive *Typha* was positively related to an index of agricultural intensity calculated for a wetland's watershed ($p<0.001$).

Agriculture uniquely explained 10% of the variation in the relative cover of invasive Typha, after accounting for variation due to lake identity (21%) and mean water depth (6%).

Among six Lake Ontario wetlands, I investigated the relationship between cattail abundance, litter accumulation, and species density in two hydrogeologic settings. I hypothesized that litter biomass would be higher in the *Typha*-dominated, open embayment wetlands than the protected wetlands that contained a mixed marsh meadow community. The mean biomass of all litter was higher in the open wetlands (1.7 - 2.6 vs. 0.4 -1.2 kg/m^2 for protected sites) and litter biomass was negatively related to species density (r^2=0.88, p=0.005). I further explored whether variation in litter biomass could be explained by differences in production, decomposition or hydrology. Peak live biomass was similar across the six sites. Decomposition rates in the fallen litter layer explained some of the variation in total litter (standing and fallen), but could not account for the overall higher accumulation in the open wetlands. Between May and September 2004, wetlands open to the lake experienced a narrower range of monthly water levels than the protected wetlands. The more stable water levels and the higher density of standing cattail litter in the open wetlands may be limiting the physical removal of litter, resulting in greater litter biomass.

Within one cattail-dominated wetland, I experimentally tested the hypothesis that an accumulation of cattail litter reduced species density. I added and removed both standing and fallen litter, and transplanted test seedlings into all plots. After 14 weeks, I found that fallen litter negatively influenced seedling survival (p=0.061) and species density (p=0.024), but the effect of standing litter was insignificant. In summary, both

observational and experimental data indicate a negative relationship between cattail litter biomass and species density. Therefore, factors affecting cattail litter production (e.g., agriculture) and decomposition (e.g., water levels) could have important implications for cattail dominance and species diversity in Great Lakes wetlands.

BIOGRAPHICAL SKETCH

Lynn Vaccaro was born on February 15, 1976 in Brattleboro, MA, and spent most of her childhood in Portsmouth, NH. She attended Phillips Exeter Academy as a day student and graduated cum laude in 1994. In college at Brown University, Lynn balanced three areas of interest: environmental science, education, and Latin American studies. She ultimately concentrated in Geology –Biology and graduated with a Bachelor of Science in 1998. Lynn fostered her broader interests by coordinating an ESL tutoring program, leading backpacking trips for students, and studying tropical ecology in Costa Rica for a semester.

After graduating from Brown, Lynn worked for 6 months as an environmental educator at an international school in Lenk, Switzerland. She then accepted a position as an education specialist for the Monterey Bay Aquarium in California, where she refined her teaching, diving, and sea kayaking skills. While helping teachers and students explore coastal ecosystems, Lynn decided she wanted to strengthen her own background in ecology and scientific research. She realized that graduate work would improve her effectiveness as both a science teacher and a liaison between the scientific and educational communities. In January of 2002, Lynn initiated work on her Masters degree in the department of Natural Resources at Cornell, and in September 2004 she began taking education classes to earn a teaching credential. She hopes that by engaging teachers, students and citizens in participatory research projects, such as wetland and watershed monitoring, she can help communities better manage their natural resources.

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Fellow graduate students in the Department of Natural Resources and the Biogeochemistry program have provided incredible support, guidance, and friendship during my Masters work. I am particularly grateful for the intellectual enthusiasm and editorial support provided by the F house residents and the Bruckner lab group.

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CHAPTER ONE

Establishing a framework: Species invasiveness or wetland invasibility?

INTRODUCTION

Loss of plant diversity and increasing dominance by invasive species are widespread phenomena in wetland environments, particularly around the Great Lakes (Mills et al. 1993). Plant species that invade and dominate new environments may influence ecosystem development (Vitousek et al. 1987), nutrient cycling (Ehrenfeld 2003), marsh formation (Rooth et al. 2003), water relations (Smith et al. 1998), and wildlife value (Chambers et al. 1999) and impose heavy societal costs (Pimentel et al. 2000). When an exotic species or foreign genotype appears that is very similar to a native relative, as in the case of *Phragmites australis* or the hybrid *Typha glauca*, evaluation of the invasion and its impacts may be delayed (Saltonstall 2002; Petit 2004).

In many marshes of the Great Lakes region, cattails (*Typha latifolia* L, *Typha angustifolia* L., and *Typha glauca* Godr. (pro sp.)) have become the dominant species, often forming dense, nearly monotypic stands of live and dead biomass. In Lake Ontario wetlands, an increasing abundance of cattail over the last 60 years has been associated with a simultaneous decrease in species of wet meadow communities (USGS 2004; Wilcox et al. 2004). Although there is some debate about the origin of *Typha angustifolia,* most wetland ecologists agree that it is a potentially invasive species that is detrimental to wildlife and plant diversity (Newman et al. 1998; Galatowitsch et al. 1999; Keddy 2000; Woo and Zedler 2002; Farnsworth and Meyerson 2003; King et al. 2004). Galatowitch (1999), Stuckey and Salamon (1987; 1993) have documented the range expansion of *Typha angustifolia* from isolated

Atlantic marshes in 1820 to its current cosmopolitan status throughout the Eastern and Midwestern US. Such increases in the abundance of a native or non-native plant species will only occur when both the species' characteristics and environmental conditions are favorable.

Because *Typha* species are well studied and morphologically plastic, they present an interesting case study for understanding how the environment, a species' biology, and plant-environment feedbacks could facilitate invasion and dominance. The abiotic conditions and competitive abilities enabling *Typha domingensis* Pers. (southern cattail) to invade and dominate saw grass marshes in the Florida Everglades have been investigated through several experimental and observational studies (e.g., Newman et al. 1998; Lorenzen et al. 2000; Miao et al. 2000; Weisner and Miao 2004). Although wetland managers around the Great lakes have a keen interest in controlling the expansion of northern *Typha* species (Motivans and Apfelbaum 1987), a careful examination of *Typha* species distributions, competitive interactions, and ecological impacts in the region has not been conducted (Ruiz et al. 1999).

The overall objective of this thesis is to identify distributional patterns and evaluate the mechanisms of cattail dominance across the Great Lakes region. This first chapter reviews the relevant plant community and invasion ecology literature in order to establish a theoretical framework for the subsequent species-specific and regional-focused investigation. Previous work on cattails is examined to develop hypotheses about factors facilitating their success in the Great Lakes. This introduction reviews theoretical and empirical work that address three factors likely to influence *Typha* spp. in the Great Lakes region: (1) characteristics of invasive species, (2) environmental parameters associated with invasion and dominance, and (3) feedbacks between a species' ecology and its environment (sensu Lonsdale 1999).

THE ECOLOGY OF INVASION AND DOMINANCE

Species Characteristics: Predicting Invasiveness

Many studies have sought to generalize about the characteristics of invasive species by comparing them with co-occurring, native species. Such studies have addressed differences in growth and physiology (Baruch and Goldstein 1999; Nagel and Griffin 2001), nutrient use (Kuhn et al. 2002; Miao 2004), reproduction (Cadotte and Lovett-Doust 2001; Smith and Newman 2001; Woitke and Dietz 2002) , competitive effect (Farnsworth and Meyerson 2003; Hager 2004), morphology (Williamson and Fitter 1996a), natural enemy assembly (Agrawal and Kotanen 2003), and genetics (Ainouche et al. 2004; Petit 2004). Few consistent patterns have emerged. For example, in a study of the invasive and native flora of Ontario, Cadotte and others (2001) found that ruderal life history traits were more common in exotic than the native species (short life span, flowering season of four or more months, hermaphrodite sex habit, and small fruit size). In contrast, Williamson and Fitter (1996a) conducted a similar analysis of the British native and exotic flora and found that distribution (near populated areas), abundance (in a plant's native range), and morphology (tall, broad) were more important than life history and reproductive traits in distinguishing native and exotic species. Although plant trait comparisons have provided important insights into how specific invasive species are able to compete in their new environments, [e.g., *Myrica faya* in Hawaii (Vitousek et al. 1987), or *Typha domingensis* in the Everglades (Weisner and Miao 2004)], cross-habitat, cross-taxa generalities and the ability to predict future invaders have remained elusive (Mack 1996; Daehler 2003).

Successful exotic plant invasions are subject to the same principles governing competition and dominance within established plant communities, despite historical dissociation (Davis et al. 2001; Thompson et al. 2001). Brown (1984) demonstrated that locally abundant native species also occur across a broad geographic range. The characteristics (e.g., environmental tolerance) that allow a species to occupy many sites within an area should also permit that species to occur across a wide geographic range. Thus invasive species that achieve high population densities locally would be expected to have a broad ecological range. In some cases the data supports this expectation, as in the analysis of exotics of the British Isles (Williamson and Fitter 1996a) but there are numerous exceptions. *Typha angustifolia* and *T. latifolia*, are both described as cosmopolitan species with broad ecological amplitude. The genus *Typha* is one of 50 genera that are found on all the continents, except Antarctica. (Good 1974). In the US, *T. latifolia* occurs in all 50 states, and *T. angustifolia* is found in 40 (USDA and NRCS 2004). The wide distribution of *Typha* species suggests that they should also be abundant locally.

It is difficult to determine the rate at which a particular exotic species has been imported to a new region, and thus evaluate the role of propagule pressure in determining invasive success. Almost all generalizations about species or ecosystem properties governing exotic introductions will be hindered by the challenges of quantifying propagule pressure (Lonsdale 1999). Williamson and Fitter (1996b) have argued that differences in propagule pressure may underlie many of the observed relationships. For example, characteristics, such as frequent cultivation, high abundance, and establishment in populated or disturbed areas, are correlated with successful invasions because these characteristics contribute to high levels of seed transport (Williamson and Fitter 1996a; Mack et al. 2000).

The investigations described here are primarily focused on the causes and impacts of the wide variation in cattail dominance among Great Lakes wetland sites. The three northern *Typha* species occur in all the states bordering the Great Lakes (USDA and NRCS 2004). In the vegetation surveys made in conjunction with my work, at least one of the three *Typha* species was found in 81% of the Great Lakes wetlands visited (Chapter Two). We can assume that *Typha* seeds reached and will continue to reach most Great Lakes wetlands; thus differences in propagule pressure are probably less important to its success than its competitive abilities and the characteristics of the wetland site.

Ecosystem Properties: Predicting a Site's Vulnerability

Ecologists have attempted to explain the success of an invader in terms of the "invasibility" of an area, either as a function of the existing plant or animal community, or as a function of the abiotic environment. Several aspects of community composition are thought to influence its invasibility, including the competitive abilities of native species; the phylogenetic and functional groups present (Mack 2003); the abundance of natural enemies (Agrawal and Kotanen 2003); and species or trophic diversity (Tilman 1997; Prieur-Richard and Lavorel 2000; Kennedy et al. 2002). Lonsdale (1999) found that globally, exotic and native species richness were positively correlated after controlling for island or reserve status. This result has two important implications: 1) on a community or regional scale, local diversity does not seem to be a barrier to invasion; and 2) the factors controlling native species richness also influence exotic species establishment, e.g., habitat diversity, latitudinal gradients or abiotic conditions. Thus, an understanding of dominance and diversity in natural plant communities may help to explain patterns of invasion.

The abiotic environment also will influence the success of an invading plant. Daehler (2003) reviewed studies that compared the growth of native and non-native co-occurring species under different environmental conditions. He found that invading species consistently out-competed native species under all growth conditions in only 6% of 55 studies. Interestingly, the native species most often out-performed the invasive species under low resource conditions (nutrients, light, or water) or under a simulated natural disturbance regime (Daehler 2001; Daehler 2003). Such work suggests that habitat parameters and anthropogenic activities partially explain plant community invasion and dominance.

Grime's view of dominance

The causes of diversity and dominance have been the subject of extensive theoretical and conservation-oriented research (e.g. Ehrlich and Ehrlich 1981; Huston 1994), with important implications for understanding the patterns of *Typha* spp. dominance of wetland communities. J. P. Grime's (1974; 1977; 2001) investigations of plant strategies and vegetation processes provide a useful framework. Grime theorized that biological communities are controlled primarily by the degree of stress (e.g., resource limitation, salinity, or anoxia) and the degree of disturbance (herbivory, fires, erosion, or storms) in a given area. The level of stress and the frequency and intensity of disturbance will determine which species are able to survive and compete over time, and in turn, influence the balance between species co-existence and dominance

Species diversity may be reduced at both the high and low ends of the stress or disturbance gradients, but for different reasons. Few species are adapted to highly stressful or highly disturbed habitats; thus, low species richness will be observed under physically challenging conditions (e.g., salt marshes). In contrast, low stress and low disturbance (e.g., ungrazed, fertile grasslands) will promote the growth of highly competitive plants capable of excluding other species (Grime 1973a; Grime 1973b). In productive environments, light and/or space become limiting, granting larger plants an advantage disproportionate to their size because they can better access resources *and* prevent light from reaching smaller neighbors. This size asymmetric competition is thought to reduce species co-existence (Zobel 1992; Newman et al. 1996; Rajaniemi 2003). These processes predict a hump-backed curve of species richness in response to stress or disturbance gradients. Grime's work suggests that changes in resource availability or physical disturbance will influence community dominance.

Resource availability

Consistent with Grime's predictions, plant productivity and soil fertility have been widely associated with species richness, observationally and experimentally; however, the patterns depend on the scale of the study and the range of soil fertility studied. Evaluations of natural productivity gradients across biomes or across communities most frequently find a unimodal relationship, with diversity peaking at intermediate productivity levels; however, within communities the relationship varies widely among studies or shows no clear pattern (Waide et al. 1999; Gross et al. 2000; Mittelbach et al. 2001). Fertilization experiments most frequently reveal that species richness declines with experimental additions of nutrients (Ditommaso and Aarssen 1989; Gough et al. 2000).

Although less well studied, similar patterns have emerged in wetland systems, both along gradients and in response to fertilization treatments (Wisheu and Keddy 1989; Moore and Keddy 1989a; Wheeler and Shar 1991; Bedford et al. 1999). In contrast to terrestrial systems, species richness appears to peak at the low end of a fertility gradient in wetlands. Such a difference might develop because factors other than soil nutrients strongly influence productivity in wetlands, complicating the relationship between productivity and diversity (Cornwell and Grubb 2003).

Disturbance and stress

In wetlands, environmental stress (anoxia, salinity) and disturbance (water fluctuations, wave action) exert important controls over plant community composition. In salt marshes, salinity is a stronger predictor of species richness than standing biomass, although both are significant (Garcia et al. 1993; Gough et al. 1994). In highly variable systems such as riverine wetlands, time since flooding and fertility together influence species richness (Shipley et al. 1991). Keddy and colleagues have established a predictive relationship between water level fluctuations and river or reservoir shoreline vegetation, demonstrating that increasing fluctuations increase plant diversity until a threshold is reached (Keddy and Reznicek 1986; Hill and Keddy 1992; Hill et al. 1998). Indeed, both hightly amplified and damped annual water level fluctuations in regulated lakes reduced community and species diversity of lake shore communities in Minnesota (Wilcox and Meeker 1991), in a range of natural New Zealand lakes (Riis and Hawes 2002), and in regulated rivers in Sweden (Nilsson et al. 1991; Jansson et al. 2000). These patterns are consistent with Grime's hump-backed relationship between species richness and disturbance.

Disturbance also can promote greater environmental variation and community diversity. In naturally fluctuating lakes, high water levels limit the downward encroachment of upland shrubby species, and low water level periods limit the upward spread of aggressive emergents, such as cattails, creating a zone of wet meadow (Keddy 1991; Keddy 2000). The diversity of both plants and animals is often positively correlated with environmental heterogeneity, presumably because spatial variation limits direct competitive interactions and competitive exclusion (Huston 1994; Vivian-Smith 1997; Lundholm and Larson 2003; Pausas et al. 2003; Tews et al. 2004). In wetlands, topographic variation occurs as a result of sedge tussocks, tipped trees, muskrat mounds, groundwater flow, channelization, wave exposure or animal trampling (Hewitt and Miyanishi 1997; Zedler et al. 1999), and can be vulnerable to human activities (Werner and Zedler 2002; King et al. 2004). Thus, factors that affect temporal or spatial variability in a wetland may influence competition and dominance of the plant community.

Feedbacks Promoting Dominance

There is increasing recognition that feedbacks between a plant and its environment may help predict invasion trajectories and plant succession. Grime (2001) and others have described a species' ability to dominate as the result of two factors: (1) its ability to achieve a larger size (vertically or horizontally) than its neighbors, and (2) its ability to reduce the fitness of its neighbors, either through resource depletion or physical inhibition. In many cases a feedback between these two components develops, in which increased growth allows the dominant species to further inhibit other species. The production and accumulation of plant litter is one mechanism by which a plant's success may reduce the fitness of its neighbors or impede the colonization of new species. *Typha* species are highly productive (Mitsch and Gosselink 2000) and their dead stems remain upright for longer than other wetland graminoids (Davis and Van Der Valk 1978). As a result, a litter layer is common in cattail-dominated marshes and may influence plant species co-existence. The role of litter is discussed in detail and addressed experimentally in Chapter Three.

The role of plant litter

In a quantitative review of 35 studies that experimentally measured the effects of persistent litter on vegetation, Xiong and Nilson (1999) found that: (1) litter had an overall negative effect on germination, establishment, above ground biomass and species richness when all studies were combined; (2) germination and species richness were most strongly affected by litter; and (3) the effect of litter depended on the type of litter and the ecosystem. In some systems, such as grasslands, litter can aid regeneration of certain species by retaining moisture, insulating the soil, protecting seeds from predators (Jarvis 1964), altering competitive interactions (Facelli 1994), adding nutrients, or changing pH (Dzwonko and Gawronski 2002). Negative responses result from chemical inhibition of germination (McNaughton 1968), a reduced probability of seeds reaching the soil (Foster and Gross 1997), diminished light penetration (Facelli and Pickett 1991), increased seed and seedling herbivory (Facelli 1994), elevated risk of fungal attack (Facelli 1994), alteration of germination cues such as temperature fluctuations (Sydes and Grime 1981b), or physical interference with root or shoot growth (Sydes and Grime 1981b). Although not reviewed by Xiong and Nilson (1999), the few litter removal or addition experiments conducted in wetlands revealed similar results; litter reduced seedling density and species richness in lacustrine marshes (Van der Valk 1986), salt marshes (Jordan et al. 1990), and temperate riparian areas (Nilsson et al. 1999).

The mechanism by which litter affects plant communities is not always clear; but it is often considered to be a physical inhibition of seedling regeneration (e.g., Van der Valk 1986). Experiments comparing plastic pseudo-litter and plant litter have shown that surface area was more important than the composition of litter (i.e., plastic pseudo-litter and organic litter caused similar results), further indicating that litter induces a primarily physical effect on seeds or seedlings (Sydes and Grime 1981b; Jordan et al. 1990). Some litter also may contain allelopathic chemicals that inhibit the growth of other species. Ecologists have identified allelopathic effects among aquatic angiosperms, which may use the compounds to compete for light and space (Gross 2003). Potentially allelopathic compounds in marsh plants have been isolated and bio-assayed in the lab (McNaughton 1968; Bonasera et al. 1979; Gallardo-Williams et al. 2002); however, field investigations of allelopathy have yielded mixed conclusions. High leaching and decomposition rates are thought to dampen the effects of allelopathic chemicals in wetlands. However, a full understanding of the role of phenolic compounds in decomposing litter may require improved methodologies.

Litter and community composition

Several lines of evidence suggest that litter may mediate the relationship between fertility and plant species diversity (Berendse 1999). Many models predicting species diversity have included litter, typically as an additional component of aboveground biomass (Grime 1973a; Moore and Keddy 1989a; Foster et al. 2004). In a nutrient limited system, fertilization increases living and dead biomass over time, but in herbaceous communities litter can accumulate faster than living biomass (e.g. Tilman 1993). Litter in turn may influence seed germination and establishment, thus factors causing an increase in litter biomass may inhibit the recruitment of new species (Xiong and Nilsson 1999). Results of fertilization and biomass removal studies that partitioned the effects of litter and living biomass on plant community composition have not been consistent. In some studies litter biomass was closely correlated with species richness (Tilman 1993; Foster and Gross 1998; Xiong et al. 2003), while in other studies the living biomass or stem density was a more important determinant of species richness (Stevens et al. 2004). Therefore, the role of litter varies among systems and may depend on the importance of seedling recruitment to plant community composition.

Plant responses to litter vary among species; thus, the way litter accumulates has the potential to structure communities (Sydes and Grime 1981a; Facelli and Pickett 1991; Facelli 1994; Xiong et al. 2001). In some cases, litter perpetuates a given dominance structure, as in the case of tree litter suppression of forest herbs that compete with tree seedlings (Sydes and Grime 1981b). Xiong (2001) determined that seed mass and seed persistence were positively correlated with a species' ability to survive under riverine litter deposits, and that relative growth rate and plant height were not related or were negatively correlated with success under litter. In riparian areas, the presence of litter may favor species that otherwise would be less competitive, thus promoting species co-existence.

If a feedback is to promote the continued dominance of a species, the dominant must be immune to its mechanism of suppression; otherwise, vegetative succession or boom-bust population cycles will result (Grime 2001). The litter of a number of macrophytes inhibits the germination of conspecific seeds, as in the case of *Typha latifolia* (McNaughton 1968), *Phragmites australis* (Van der Putten et al. 1997), or *Scirpus maritimus* (Clevering and Vanderputten 1995). Many monocots, particularly hydrophilic species, maintain and expand their populations primarily via vegetative growth. Translocation of energy reserves along rhizomes may help new shoots push through dense layers of litter. Clonal species do not need to propagate from seeds in their immediate vicinity; therefore, an accumulation of recalcitrant litter or a release of allelochemicals would not reduce their own reproductive fitness.

Litter accumulation patterns also have the potential to shape plant communities indirectly through impacts on soil properties. For example, the litter of *Phragmites australis* traps sediment better than native species; therefore its invasion enhances marsh accretion (Rooth et al. 2003). Deciduous tree litter can raise the fertility and pH of forest soils (Dzwonko and Gawronski 2002) and the litter of heathland grasses can elevate rates of N mineralization (Berendse et al. 1994). In marshes, dead cattails contribute to the buoyancy of vegetation stands (Hogg and Wein 1988). Thus litter and the factors that influence the production or accumulation of litter can create multiple feedback effects with implications for ecosystem and community structure.

CATTAIL EXPANSION IN THE GREAT LAKES

Species Characteristics: The Genus *Typha*

In North America, the genus *Typha* includes four morphologically similar species that can colonize a wide range of wetland habitats. *Typha latifolia* (wide-leaved cattail) is found from Alaska south into the tropics, and from sea level up to 2125 m (Grace and Harrison 1986). *T. latifolia* is common in late-successional, stable, peat-forming wetlands, in addition to more disturbed habitats (Smith 1967; Grace and Harrison 1986). *T. angustifolia* (narrow-leaved cattail) has spread across most of Eastern and Midwestern North America in the last 150 years, but its distribution remains restricted to areas south of 50°N (Smith 1967; Galatowitsch et al. 1999). *T. angustifolia* is more prevalent in early-succesional wetlands, on mineral soils, and in saline or alkaline environments (Mcmillan 1959; Grace and Wetzel 1982; Grace and Harrison 1986). When the two species co-occur, *T. latifolia* generally occupies the shallower water zone and *T. angustifolia* colonizes water depths up to 100 cm (Grace and Wetzel 1981). *Typha domingensis* usually occurs well south of 40°N and therefore is not considered in this evaluation of *Typha* in the Great Lakes region. A viable hybrid between *T. latifolia* and *T. angustifolia* (*Typha glauca*) has been recognized in Europe for over 100 years, but only recently has this hybrid been synthesized experimentally (Smith 1967) and validated with molecular techniques in the United States (Kuehn 1999b). The limited ecological information known about this highly variable hybrid is discussed below.

Invasion and hybridization

Although there is some doubt about the nativity of *Typha angustifolia*, its distributional history suggests an exotic origin (Stuckey and Salamon 1987) and its aggressive expansion in the last 100 years qualifies it as invasive (Galatowitsch et al. 1999; Woo and Zedler 2002; Farnsworth and Meyerson 2003). It is thought that *T. angustifolia* originally came from Europe, where both *T. latifolia* and *T. angustifolia* are native, although this has not been substantiated with molecular evidence. Stuckey and Salamon (1987) report that the narrow-leaved cattail was absent from early botanical surveys in Boston, Philadelphia, and New York until 1820, when subsequent floras began noting the sparse presence of *T. angustifolia* in Atlantic high marshes. In 1880 a narrow- and a wide-leaved cattail were documented in Central New York (Dudley 1886), and in 1890 *T. angustifolia* was first reported in southern Lake Michigan (Stuckey and Salamon 1987). The use of cattail species for food, pillow stuffing, and matting, and the development of canals, railroads, and highways probably facilitated its spread (Grace and Harrison 1986; Mills et al. 1993).

Most of the sympatric *Typha* species can form hybrids, although the hybrids are not always fertile (Les and Philbrick 1993). Both early morphological analyses of *T. glauca* and the more recent molecular investigation indicate that *T. glauca* occurs wherever the two parent species overlap (Fassett and Calhoun 1952; Smith 1967;

Galatowitsch et al. 1999; Kuehn 1999b). As part of a broad survey of *Typha* genetics, Kuehn (1999b) found that 65% of specimens from the eastern Great Lakes region were *T. glauca*, demonstrating its importance in this area. Kuehn also (1999a) documented the extreme phenotypic variability within *T. latifolia*, *T. angustifolia,* and their hybrid, and the resulting challenges for field identification. Presently, stands of *T. glauca* are largely F1 hybrids. Although its abundance is thought to be increasing, clear evidence for introgression and advanced generation hybrids remains scarce (Kuehn 1999b). Vegetative reproduction often allows moderately sterile hybrids to persist, particularly in aquatic environments (Les and Philbrick 1993). Reportedly low fertility and developmental difficulties of hybrids may currently maintain their distinct genetic identity; however, given the extent of hybridization and the massive seed production of *Typha* species, fertile hybrids and introgression may become more widespread (Kuehn 1999b). To date, limited isozyme evidence indicates more prevalent backcrossing of *T. glauca* with *T. angustifolia* than with *T. latifolia* (Lee and Fairbrot 1973; Sharitz et al. 1980).

It is likely that the widespread hybridization of all *Typha* species has contributed to their genetic variability and wide environmental tolerances. In contrast with current understanding of *T. glauca*, Smith (1967) found higher fertility and more robust evidence for introgression in putative *T. latifolia* x *T. domingensis* hybrids. He argues that backcrossing between the hybrid and *T. latifolia* contributed to the development of ecotypes that are surprisingly well adapted to the distinct central California climate. The hybrid of *T. latifolia* and *T. angustifolia* also seems to be well suited to its environment. Initial experimental work suggests that *T. glauca* individuals have inherited the wide-leaf morphology of *T. latifolia*, the deep water tolerance of *T.*

angustifolia, and a greater plasticity in response to environmental gradients (Smith 1967; Waters and Shay 1990; Waters and Shay 1992).

Around the Great Lakes, the native *Typha latifolia*, the introduced *Typha angustifolia*, and their hybrid *Typha glauca* co-occur, hybridize, and form a structurally similar part of the plant community (Kuehn 1999b). In this document, the term cattail is used to refer to all three species collectively. References to the "invasive *Typha* species" apply to *Typha angustifolia* and *Typha glauca.* Genetic work indicates that most hybrids are F1 generation with limited fertility. Thus, the presence of *T. glauca* is dependent on the relatively recent invasion and colonization of *T. angustifolia* at a site and the two species are tightly linked. *T. latifolia* is native to North America, although Chapter Two investigates whether its distribution and ability to dominate are quantitatively different from the invasive species around the Great Lakes.

Competitive ability

Typha species are among the most productive plant species (Wetzel 1983; Mitsch and Gosselink 2000); however, their performance is strongly influenced by the environment. Cattails are physiologically better able to tolerate permanently flooded conditions than are many other emergent species. Cattail seeds can germinate without oxygen (Lorenzen et al. 2000), the adult plants are able to maintain high rates of photosynthesis under low soil redox conditions (Pezeshki et al. 1996; Lorenzen et al. 2000), and the roots are able to oxygenate their rhizosphere without showing signs of oxygen deficiency (Chabbi et al. 2000). Interestingly, the growth of *Typha latifolia* was sensitive to drought conditions; the species reduces immediate photysynthetic rates and long-term biomass allocation in dry soils (Li et al. 2004).

Grace and Wetzel (1981; 1982) demonstrated that, without competition, *T. latifolia* and *T. angustifolia* both reached maximum stand biomass in waters 50 cm deep. However, *T. latifolia* could exclude *T. angustifolia* from the shallower depths, and *T. angustifolia* could better colonize depths up to 100 cm, thus, producing consistent zonation patterns along lakeshores. Waters and Shay (1992) revealed that mono-typic, naturally occurring stands of *Typha glauca* reached maximal biomass at 25 and 100 cm depths, with relatively constant biomass (about 750g/m^2) between the two peaks. Shoot height, weight, and density varied widely along this water depth gradient, presumably allowing a stand to maximize light capture and tolerate different water depths (Waters and Shay 1990). These studies indicate that *T. glauca* demonstrates even greater morphologic and physiologic plasticity than its parental species, allowing it to survive more extreme water depths. This may explain the prevalence of *T. glauca* in highly variable Great Lakes wetlands.

Typha species also show higher plasticity in response to nutrient availability than do other emergent species, such as *Cladium jamaicense*, *Eleocharis interstincta* (Newman et al. 1996), and *Carex* species (Woo and Zedler 2002). Miao and others (2000) found that genetically identical genets of *Typha domingensis* growing in a nutrient-enriched area accumulated 11 times more biomass after 7 months and 16 times more biomass after 2.5 years than did individuals in the un-enriched area. In low-nutrient soils, the *T. domingensis* plants did not produce a single ramet, and instead allocated their limited resources towards larger, longer-lived shoots. Miao (2004) further observed that *T. domingensis* responded differently to soil nutrients from the native *C. jamaicence* in its ability to concentrate more phosphorus in its leaves, allocate more biomass to vegetative reproduction, and expand into a larger area when limiting nutrients became available. This work demonstrates that nutrient availability can accelerate the expansion of *Typha* species, and that *Typha* species can effectively modify their growth strategy in response to nutrient availability.

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Reproduction and clonal expansion

Typha species can produce large numbers of seeds and spread via lateral shoots, allowing them to expand within and among wetland areas. A single *Typha* inflorescence will produce 20,000 to 700,000 seeds, each with numerous gynophore hairs that facilitate wind dispersal when dry. When the fruit reaches water, the pericarp releases the seed, allowing it to sink into the sediment (as described by Grace and Harrison 1986). Seed germination requires saturated soils, high light, and alternating temperatures (Lombardi et al. 1997). Although germination can occur under low oxygen and nutrient conditions, cattail seeds will not germinate if buried (Stewart et al. 1997; Lorenzen et al. 2000). New seedlings seem to establish infrequently in mature stands of cattails and maintenance of the population primarily occurs through asexual production of new ramets (McNaughton 1968).

The degree to which cattails are able to spread vegetatively probably determines whether they co-exist with or dominate other species. Once established, an individual's growth rate, biomass allocation, morphology, and clonal expansion are highly dependent on a site's water depth and fertility (Waters and Shay 1990; Miao et al. 2000; Miao 2004; Weisner and Miao 2004). A single seedling can produce 6-7 new ramets and grow to cover a square meter over the course of a growing season under favorable conditions (Miao et al. 2000). Grace and Wetzel (1981) studied the intra- and inter- population differences in local ecotypes of *T. latifolia* through field surveys, a common garden experiment and reciprocal transplants. They found that biomass allocation to flowering, vegetative reproduction, and nutrient acquisition depended on both plant origin (genotypic) and the present growth conditions (phenotypic). Their work demonstrates the ability of cattails to modify its reproductive strategy in response to the degree of disturbance, nutrient stress and light limitation of a given environment. This flexibility could allow for powerful feedbacks between cattails and the environment.

Ecosystem Properties: The Great Lakes Basin

Experimental, observational, and modeling studies have identified conditions associated with the expansion of *Typha* species into different environments. The natural occurrence of *T. latifolia* on lakeshores has been associated with areas of high fertility and low disturbance (Day et al. 1988). Cases in which cattails are expanding into a new region generally support the theory that fluctuating resources promote invasion (Davis et al. 2000). For example, Woo and Zedler (2002) demonstrated that nutrient-rich run-off alone promoted the expansion of *Typha glauca* into a sedge meadow. In two cases, the invasion of *Typha angustifolia* was correlated with areas impacted by road salt (Wilcox 1986; Panno 1999). Salt contamination decreased native vegetation, which may have made resources available for *T. angustifolia*. Wilcox (1984) found that hydrologic alterations facilitated the invasion of *Typha* into a sedge meadow. Investigations of the expansion of *Typha domingensis* into sawgrass marshes of the Everglades re-affirm that *Typha* is able to spread aggressively when a combination of elevated nutrient levels, altered hydrology, and modified disturbance (e.g., muck fires or canal structures) co-occur (Newman et al. 1998; King et al. 2004). Lessons learned in other ecosystems have parallels in the Great Lakes region.

Wetlands have been impacted both directly by human activities and indirectly by invasive species introduced by humans. Mills and others (1993) documented the introduction of 139 non-indigenous organisms into the Great Lakes basin since the 1800s, including 59 plant and 24 algal species. The development of canals, railroads, and commercial transportation likely facilitated the spread of these organisms. Thirty percent of these invasions occurred after the opening of the St. Lawrence Seaway, demonstrating the importance of human activities in the spread of non-natives (Mills 1993). The Great Lakes have lost 70% of their original (pre-European settlement) wetland area due to filling, draining, and development of coastal areas (Dodge and Kavetsky 1995). There is evidence that the remaining wetlands have experienced both reduced natural disturbance and increased nutrient inputs, both of which may facilitate invasion and promote dominance.

Disturbance and productivity

The water levels of the Great Lakes fluctuate seasonally and inter-annually, altering the extent, flooding regime and community composition of the wetlands. Annual mean water levels of the unregulated Great Lakes can vary over a meter from year to year (Hunter and Croley 1993). High water years disrupt shrub and wet meadow species and low water years expose mud flats and allow the seed bank to germinate. Currently, dams on the outflows of Lake Superior and Lake Ontario regulate water levels dampening the natural cycle of disturbance and renewal. Lake Erie is shallow and holds the smallest volume of water of the major Great Lakes, making it very responsive to changes in inflow. Hydrograph's for lakes Huron and Michigan show high inter-annual variability and no effect of regulation. The headwater position and the large lake-to-watershed ratio of Lake Superior naturally stabilize the intra- and inter-annual water level variation, in comparison to the downstream lakes (Brinkmann 2000). As a result, most studies have been unable to detect changes in Lake

Superior's water regime that can be attributed to regulation alone (Quinn 2002; Changnon 2004).

Lake Ontario is the only Great Lake that shows a very clear response to flow modifications. In 1960, the Moses-Saunders power dam was constructed on the St. Lawrence River, on the outlet from Lake Ontario. The flow across the dam is regulated in order to "reduce the range of Lake Ontario water levels, and to provide dependable flow for hydropower, adequate navigation depths and protection for shoreline and other interests downstream in the Province of Quebec" (IJC 2004). Currently, there is no explicit mention of wetland or aquatic health in this mandate. Lake Ontario's levels are regulated within a target range of 74.15 and 75.37 m above sea level (IJC 2004). Given that annual discharge over the Moses-Saunders dam is about 13% of Lake Ontario's volume and monthly discharge reaches 22 km^3, regulation can influence lake levels on an annual and monthly basis. Since 1960, Lake Ontario has experienced a dampened inter-annual variation and an increased intra-annual fluctuation of water levels (Lenters 2001; Quinn 2002).

Given the importance of water level fluctuations for the maintenance of diverse wetland communities, (Keddy and Reznicek 1986; Wilcox and Meeker 1991; Wilcox 1995; Hill et al. 1998), increasing dominance on regulated lakes might be expected. Using historical imagery and field surveys at elevations with known water level histories, Wilcox argues that stabilized water levels on Lake Ontario are causing a decrease in sedge meadow plants and an increase in cattail-dominated communities (USGS 2004; Wilcox et al. 2004). He also suggests that post-regulation water levels have increased on average, which reduces the competitive ability of sedge meadow plants and improves the growth of cattails, as seen in the Everglades. Without the natural disruption of water-level extremes, cattails may be able to expand landward into marsh meadows.

Human activities also are adding growth-limiting nutrients to the water and wetlands of the Great Lakes. Total phosphorus inputs to the lakes have decreased due to the removal of phosphates from detergents and improved municipal sewage treatment; however, run-off from agricultural fields and urban areas continues to carry nutrients into the lakes (Elster 2000). Embayments are still vulnerable to eutrophication due to the high residential use of the shoreline, their large tributary input, and relatively slow flushing time (Makarewicz 2000). In many Great Lakes wetlands, nutrients may no longer be limiting due to phosphorus-rich run-off and atmospheric nitrogen deposition. Thus, space and light may be the primary limiting factors, promoting size asymmetric competition and diminished species co-existence (Rajaniemi 2003).

Interpreting vegetation patterns

Great Lakes wetlands are experiencing many types of environmental change that could be promoting the spread and dominance of invasive species like *Typha angustifolia* and *Typha glauca.* An analysis of cattail abundance in relation to the five lakes and different land uses could provide insight into which factors are most influential. Studies that have attempted to correlate plant composition and human activities have had mixed results. Wilcox et al. (2002) found that inter-annual water level changes, typical of the unregulated Great Lakes, created variation in vegetation such that the relationship between human activities and biotic communities was hard to quantify. However, other studies of wetlands along the Canadian Great Lakes coast have found that the percentage of agriculture in a watershed was correlated with turbid, nutrient rich sediments (Crosbie and Chow-Fraser 1999) and lower diversity of submerged aquatic plants (Lougheed et al. 2001). Lougheed et al. (2001) also discovered that land use was more tightly correlated with the water and sediment characteristics of inland wetlands than with coastal wetlands (Lougheed et al. 2001). Logically, lake currents and seiches will act to dilute pollutants delivered by streams; however, there may be other important abiotic gradients driving variation in Great Lake wetlands, such that the effect of land use is obscured.

Vegetation also is strongly driven by geologic and climatic variation around the Great Lakes (Smith et al. 1991; Lougheed et al. 2001). Smith (1991) suggests that the easily eroded sedimentary rocks of the southern Great Lakes produce shallow water zones with fine textured substrates favorable for marsh formation. In contrast, the older igneous and metamorphic bedrock of the northern Greats Lakes results in exposed shorelines and infertile wetlands (Smith et al. 1991) Indeed, Lougheed and others (2001) have observed that in comparison with the southern lakes, wetlands on lakes Huron and Superior contain species adapted to the short growing season and low substrate fertility, such as *Scirpus*, *Eleocharis*, *Equisetum,* and *Isoetes*. Productive marsh species, such as *Typha*, and a more diverse submerged aquatic community are typical of the southern eco-province. Agriculture and urban growth are also widespread in the southern province, due to the fertile soils and longer growing season. Thus, both wetland development and human settlement patterns are driven in part by these same physiographic factors, creating co-linearity between disturbance gradients when considering the Great Lakes as a whole.

Feedbacks Promoting Dominance: Lessons from the Everglades

In the Everglades, the importance of interactions between the biology of an invasive species and the environment has been widely recognized. Many experimental studies have investigated the competitive advantages of *Typha domingensis* over *Cladium jamaicense* (sawgrass). *T. domingensis* is able to vary its ramet and genet morphology and flourish in high water and high nutrient conditions, as described above (Newman et al. 1996; Miao 2004; Weisner and Miao 2004). In contrast, *Cladium jamaicense* has typical adaptations for low nutrient environments: slower growth rate, higher leaf longevity, chemically defended leaves, high tissue nutrient resorption, and effective vegetative spread (Richardson et al. 1999; Miao 2004). Comparisons have highlighted how each species' growth strategy could promote its own persistence by producing litter that either speeds (as in the case of *Typha*) or slows (*Cladium*) overall nutrient recycling. All *Typha* species are highly productive and their leaves senesce every fall in temperate climates; thus, substantial inputs of cattail litter could create important feedbacks for plant community and ecosystem dynamics.

The Everglades have become more vulnerable to invasion and dominance due to human settlement patterns. In the first half of the twentieth century, an extensive system of canals and levees was built to allow urban and agricultural expansion into the northern part of the Everglades. As a result, some sections of the remaining marshes now experience deeper waters, extended hydroperiods, and nutrient-rich agricultural run-off. As might be predicted from the physiological advantages of *T. domingensis*, elevated nutrient levels, higher water levels, longer flooding periods, muck fires, and canal structures are closely correlated with zones of cattail invasion (Newman et al. 1998; King et al. 2004). Neither hydroperiod nor nutrients alone predicts the distribution of *T. domingensis,* indicating that restoration of many aspects of the system is required (David 1996). The rapid invasion of *T. domingensis* into impacted sawgrass marshes demonstrates the importance of considering both the characteristics of the invading species and factors associated with habitat invasibility.

Unfortunately, the expansion of *Typha angustifolia* and *T. glauca* into more northern wetlands is not as well understood.

PRECIS OF THESIS

As described above, three primary factors influence the balance between dominance and diversity in plant communities:

1) Characteristics of the invading species' biology and ecology
2) Properties of the wetland environment
3) Feedbacks between a plant's ecology and its environment

The following two chapters present the results of research addressing the following two questions: *What factors and processes promote the dominance of cattails across the Great Lakes?* and *What are the implications of cattail dominance for plant community composition?* Because the ecology and biology of *Typha* species are fairly well documented, this research focuses on the second and third factors noted above. Chapter Two examines the relationship between the abundance of *Typha* species, species density and environmental conditions. Chapter Three addresses how litter accumulation may be acting as a feedback mechanism, promoting the dominance of cattails. A strong understanding of the physiology, ecology and variability of cattails, as outlined in this first chapter, provide a foundation for the interpretation of the forthcoming research results. The following objectives and specific research questions guide the next two chapters.

Chapter Two: Patterns of Typha dominance and species density in wetlands across the Great Lakes

The objectives of this study were to (a) identify how environmental conditions influence the distribution, percent cover, and dominance of *Typha* species across the Great Lakes, (b) assess the species richness associated with *Typha* species and (c) determine whether other dominant wetland graminoids show similar patterns. This work was guided by several predictions:

- The invasive *Typha* species, *T. angustifolia* and *T. glauca,* will occur across a range of hydrologic and physiographic conditions.
- Invasive *Typha* will occur more frequently and have a higher percent cover in wetlands around lakes with controlled water levels.
- The percent cover and the relative abundance of invasive *Typha* will be positively correlated with the amount of agriculture in a wetland's watershed.
- Species density will be negatively correlated with the percent cover of invasive *Typha* species.

By comparing the invasive *Typha* species (*T. angustifolia* and *T. glauca*) to other native members of the plant community, I hoped to determine if invasive *Typha* species exhibited similar ecological interactions compared to other plants, or whether the environment primarily determined diversity and dominance, regardless of plant species composition.

Chapter Three: The role of litter dynamics in mediating the dominance of cattails (Typha spp.) in Great Lakes wetlands

Around Lake Ontario the biomass of live and dead cattails varies: southern lakeshore wetlands within open embayments are visibly dominated by cattail, while wetlands behind barrier beaches along the eastern shore of the lake maintain a more diverse plant community. Given the potential for cattails to attain high levels of productivity (Brinson et al. 1981) and the resistance of its litter to fragmentation and decay (Davis and Van Der Valk 1978), an accumulation of cattail litter might be suppressing other species. I further hypothesized that litter dynamics would differ between the two hydrogeologic settings, potentially explaining their vulnerability to dominance by cattail. The objective of this research was to evaluate whether (1) the accumulation of cattail litter promoted the dominance of cattails by inhibiting other species, and (2) whether cattail litter production or decay differed among two hydrogeologic settings.

CHAPTER TWO

Patterns of *Typha* dominance and species density in wetlands across the Great Lakes

INTRODUCTION

The natural and anthropogenic factors influencing plant community diversity and dominance are of widespread interest from both a theoretical and a conservation standpoint (e.g., Ehrlich and Ehrlich 1981; Huston 1994; Grace 1999). An understanding of the relative importance of external factors (e.g., land use or disturbance) and intrinsic factors (e.g., the presence or identity of an exotic species) influencing species dominance will determine how we manage invasive species and potentially use plant community metrics as indicators of anthropogenic stress (e.g., Niemi et al. 2004a; Brazner et al. in review). In the last 50 years, North American wetlands have been particularly vulnerable to invasions by non-native species such as *Lythrum salicaria* (purple loosestrife), *Phragmites australis* (common reed), *Phalaris arundinacea* (reed canary grass), and *Typha angustifolia* (narrow-leaved cattail) (Galatowitsch et al. 1999; Zedler and Kercher 2004). Efforts to identify the characteristics of invasible ecosystems and invasive exotics have generally concluded that similar factors govern the dispersal, establishment and competition of native and non-native species (Levine 2000; Davis et al. 2001; Thompson et al. 2001). Because few introduced exotics ever become abundant or problematic, it is important to investigate the later stages of invasion, specifically, where, how and why exotic species dominate communities and impact invaded ecosystem (Levine et al. 2003). In some cases, the particular disturbances that create opportunities for invasive species can be identified; however, generalizations have been slow to emerge (Zedler and Kercher 2004). Few studies have been able to examine the pattern and impact of invasions across a large heterogeneous landscape like the Great Lakes basin. This study compares an invasive species to five native, co-occurring species with respect to their patterns of dominance, associated plant species diversity and the relative importance of natural and anthropogenic factors in promoting their abundance.

Anthropogenic activities and invasive species may be shifting the balance between dominance and diversity in Great Lake wetlands. The Great Lakes region has lost 70% of the original (pre-European settlement) wetland area (Snell 1987; Dodge and Kavetsky 1995) and many of the remaining wetlands experience dampened water level fluctuation and elevated nutrient loading (Williams and Lyon 1997; Crosbie and Chow-Fraser 1999; Quinn 2002). Agriculture, urban development, and atmospheric nitrogen deposition in the basin have increased nutrient and sediment loads into Great Lakes coastal waters (Detenbeck et al. 1999). Currently dams on the outflows of Lake Superior and Lake Ontario regulate water levels and minimize inter-annual variation, which provides a natural source of disturbance in the other lakes. Both highly amplified or dampened annual water-level fluctuations reduced wetland species diversity of managed lakes in Minnesota (Wilcox and Meeker 1991), in a range of natural New Zealand lakes (Riis and Hawes 2002) and in regulated rivers in Sweden (Nilsson et al. 1991; Jansson et al. 2000). A similar decline in plant diversity may be occurring in Great Lake wetlands.

Cattails (*Typha* spp.) dominate many Great Lake marshes, often forming dense stands of live and dead biomass (Frieswyk et al. 2005). On Lake Ontario, limited work has documented the expansion of cattail-dominated communities and the simultaneous decrease in wet meadow communities during the last 60 years (U.S.G.S. 2004; Wilcox et al. 2004). The three northern cattail species, the native *Typha latifolia* L, the introduced *Typha angustifolia* L., and their hybrid, *Typha glauca* Godr. (pro sp.), co-occur, hybridize and form a structurally similar part of the plant community (Kuehn 1999b). *Typha angustifolia* was first observed in Atlantic coastal marshes in 1820 and has since spread throughout much of the Southeastern and Midwestern US (Stuckey and Salamon 1987; Stuckey 1993; Galatowitsch et al. 1999). Both *Typha angustifolia* and *Typha glauca* are considered invasive species that can be detrimental to wildlife and plant diversity (Newman et al. 1998; Galatowitsch et al. 1999; Keddy 2000; Woo and Zedler 2002; Farnsworth and Meyerson 2003; King et al. 2004). However, it is unclear whether *T. latifolia* or other native graminoids are quantitatively different in their patterns of distribution and dominance. *Typha glauca* is described as more morphologically and ecologically variable than either parent species; thus, its distribution may be less responsive to hydrologic or climatic gradients than the distribution of other co-occurring native species (Waters and Shay 1990; Waters and Shay 1992).

Models of plant community dominance may help explain the success of the invasive *Typha* species, *Typha angustifolia* and *Typha glauca,* during the last 100 years. Factors that increase plant community biomass, such as elevated fertility and reduced disturbance, can promote the dominance of a few competitive species and facilitate the exclusion of subordinate species (Grime 1973a; 1973b). Consistent with Grime's model (as described in Chapter 1), an increasing abundance of *Typha* species has been associated with changes in nutrient-rich run-off (Woo and Zedler 2002) and hydrologic alterations (Wilcox et al. 2003). In the Everglades, *Typha domingensis* is expanding into areas of sawgrass marsh that are simultaneously affected by elevated nutrient levels, altered hydrology, and a modified disturbance regime (e.g., muck fires or canal structures) (Newman et al. 1998; King et al. 2004). Thus, theoretical and experimental work indicate hydrology and land use may affect the dominance of *Typha* around the Great Lakes.

The objectives of this study were to (a) identify how environmental conditions influence the abundance and dominance of *Typha* species across the Great Lakes, (b) assess the species richness associated with *Typha* species, and (c) determine whether other dominant wetland graminoids show similar patterns. A comparison of the invasive *Typha* species (*T. angustifolia* and *T. glauca*) and other native members of the plant community, will help determine if invasive *Typha* species exhibit unique ecological characteristics compared to other plants, or whether the environment is the primary determinant of diversity and dominance, regardless of plant community composition.

METHODS

Site Selection and Sampling Design

To evaluate abiotic factors associated with the distribution and abundance of *Typha spp.*, I analyzed data from an extensive wetland vegetation survey. The surveys were conducted on 90 wetlands across the five major Great Lakes as part of a large, multi-investigator project designed to identify biotic indicators of human disturbance to coastal systems, [Great Lakes Environmental Indicators project (GLEI), Gerald Niemi and Carol Johnston, principal investigators]. Michael Bourdaghs was responsible for the field sampling on lakes Superior and Huron, Christin Frieswyk sampled around Lake Michigan, and I conducted the surveys on lakes Erie and Ontario. Fieldwork focused exclusively on plant communities within non-forested wetlands with at least some emergent wetland vegetation.

Sites were selected using a stratified random sampling design, outlined by Danz et al. (2005). Sites were chosen to include roughly equal numbers of wetlands from the Laurentian Mixed Forest (northern) and the Eastern Broadleaf forest (southern) Eco-provinces (Bailey 1995) from three geomorphic settings (protected, river influenced, and coastal), and across several types of disturbance gradients, including intensity of agriculture, human population density, atmospheric deposition, and point source contamination (Figure 2.1).

Vegetation was sampled along linear transects whose end points were randomly pre-selected using a Geographic Information System and a program called Sample (http://www.quantdec.com/sample). Transects were initiated at the transition from woody to herbaceous wetland vegetation and continued until water depths exceeded 1 meter or the zone of submerged vegetation ended, roughly paralleling the hydrologic gradient. One-meter squared vegetation plots were placed at randomly generated intervals along each transect; plot spacing was approximately 20 m. The target number of survey plots in each wetland was proportional to the size of the wetland (20 quadrats/ 60ha). A minimum of 12 plots was surveyed in each wetland. Surveys were conducted during the summers of 2001-2003.

For each sampling plot, water depth and the coverage of water, soil, litter, moss, rocks, and all vascular plant species were recorded. Species were identified to the lowest taxonomic division possible according to the Interagency Taxonomic Information System (ITIS, http://www.itis.usda.gov). Coverage was estimated using a modified Braun-Blanquet cover class scale of 0 to 6, (1= <1%, 2= 1-5%, 3= 5-24%, 4 = 25-49%, 5= 50- 74%, 6= 75-100%) (ASTM 1997). The midpoint for each cover class was used (0.5, 3, 15, 37.5, 62.5 and 87.5 respectively) for analyses of percent cover.

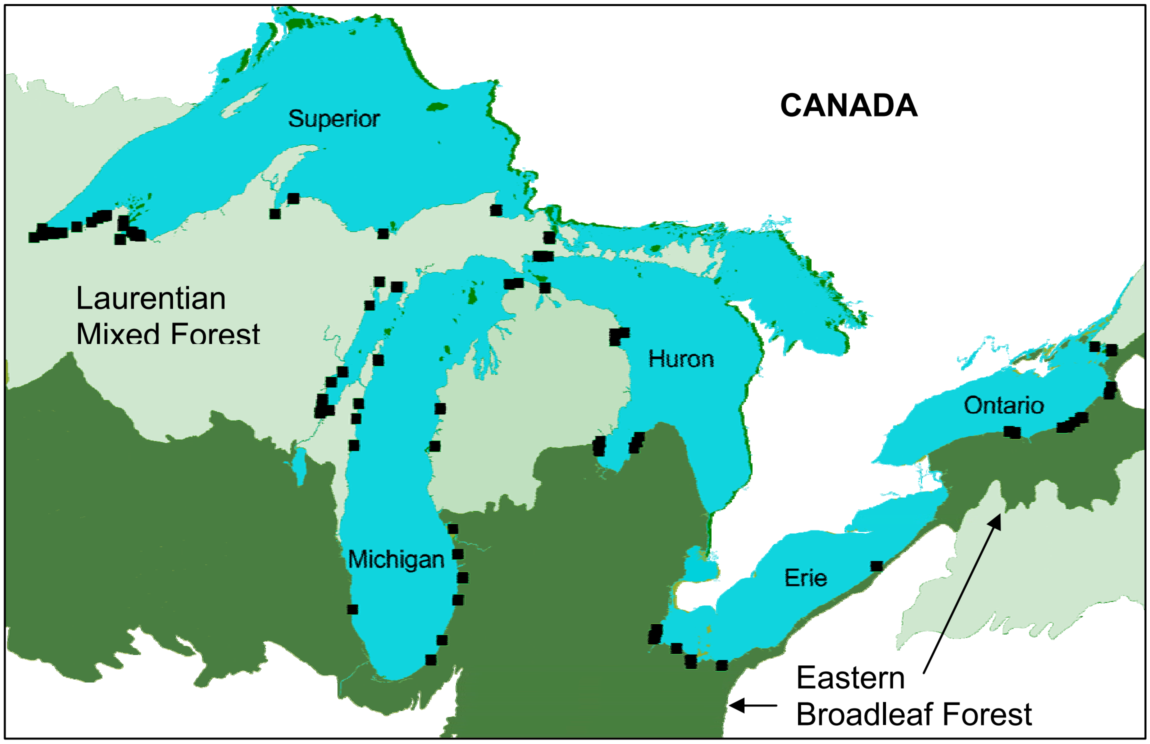


Figure 2.1. Map of the Great Lakes showing locations of wetlands sampled as part of the GLEI project and used in this study. Locations of the two eco-provinces in which study sites occurred are indicated.

Herbaceous plant communities are often layered; thus, the sum of all observations in a given plot could total more than 100%. The field teams met three times during the study period to improve consistency in species identification and cover estimates.

Study Species

Observations of *Typha angustifolia* and *Typha glauca* were combined into a single measurement, "invasive *Typha* species". Recent genetic work has revealed that *T. latifolia* and *T. angustifolia* readily hybridize wherever they co-occur; however, most hybrids appear to be F1 generations with limited ability to produce viable seeds and disperse (Kuehn 1999b). Vegetative reproduction generally allows F1 clones to spread throughout contiguous areas of suitable wetland habitat. Thus, based on current observations of hybridization, the presence of *T. glauca* is dependent on the relatively recent invasion and colonization of *T. angustifolia* in a site. Both *T. glauca* and *T. angustifolia* are considered invasive due to their recent spread across most of the United States and their aggressive growth within sites, and are often considered together ecologically (Motivans and Apfelbaum 1987; Stuckey and Salamon 1987; Galatowitsch et al. 1999; Woo and Zedler 2002). *Typha* species demonstrate wide phenotypic plasticity, limiting the utility of leaf width and flowering spike width in identification across a range of habitats, especially where hybridization is widespread, as in the Southern Great Lakes (Kuehn 1999a). I felt confident in our ability to consistently distinguish non-flowering *T. latifolia* from *T. angustifolia* and *T. glauca*, but because this data set combines observations from three different field teams that sampled over the course of three seasons, I was hesitant to separate our observations of the two invasive species. Field measurements reveal that in comparison with *T. latifolia*, *T. glauca* and *T. angustifolia* both had a higher mean percent cover, and in plots where they occurred there were fewer species and the vegetation canopy was taller (Appendix A). These observations indicate that *T. angustifolia* and *T. glauca* are structurally and ecologically similar in our Great Lake wetlands and can be considered together. Thus, I refer to *T. angustifolia* and *T. glauca* together as invasive *Typha*, but refer to *T. latifolia* explicitly by full name.

To determine whether *Typha* species exhibit unique patterns of distribution or abundance, I compared the invasive *Typha* species and *T. latifolia* to similar abundant, potentially co-occuring emergent species. I chose the four most frequently-observed graminoid species that typically occupy wetter areas of marshes: *Calamagrostis canadensis* (Michx.) Beauv. (blue joint grass), *Carex lacustris* Willd. (lake shore sedge), *Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla. (softstem bulrush), and *Sparganium eurycarpum* Engelm. ex Gray (giant burreed).

Indices of Anthropogenic Stress

To assess the relationship between the abundance of a species and urban or agricultural development, I used two comprehensive indicators of anthropogenic influence: an agricultural index and an urbanization index. Both indicators were developed and calculated by the Great Lakes Environmental Indicator (GLEI) project with leadership from Nick Danz, Tom Hollenhorst and Terry Brown (Danz et al. 2005). The region of land that drained into each wetland complex was delineated using digital elevation models and drainage maps. The potential impact from agriculture within a watershed was estimated using twenty-six publicly available GIS data layers from the United States Department of Agriculture (USDA) and Natural Resources Conservation Service (NRCS) that provide spatially referenced estimates of pesticide, nutrient and sediment run-off. The urbanization index was created using three variables: population density (calculated from the 2000 US Census Bureau data), road density (calculated from the US Census 2000 TIGER line files) and urban land cover (calculated using the United States Geological Service (USGS) National Land Cover Database 2001). A value for each variable was calculated for each of the watersheds that drained into a wetland study site. The 26 agriculture and the 3 urbanization variables were each combined in two principal components analyses designed to reduce the redundancy among the variables (Danz et al. 2005). The PC scores for the first axis explained 75% and 76% of the variance in the original variables for the agriculture PCA and urbanization PCA, respectively. The PC scores provide an integrated index of agricultural intensity and urbanization for each wetland's watershed.

Calculations and Statistical Analyses

I assessed patterns of abundance by determining the relative percent cover of each study species. For each wetland, all recorded cover values for a particular species were totaled and then divided by the summed cover of all plant species to yield a proportional cover for each species (0 – 100%), here termed as "relative percent cover" or "relative abundance". To equalize variances across the range of predicted values and normalize residuals, relative percent cover was square-root transformed. The pattern of dominance of the six study species was further assessed by looking at three characteristics: (1) frequency of occurrence across a wetland, calculated as the number of plots in which a species occurred divided by total number of plots per site; (2) the mean percent cover in plots of occurrence within a wetland, which was estimated visually in the field without considering how many other species or how many canopy layers might be present in a plot; (3) the mean species density in plots in which the species occurred within a wetland. Data from each wetland were averaged before assessing patterns across wetlands. Standard errors and regression statistics were calculated using SAS Version 9 (SAS 2002).

This work compares the effect of five main factors on the relative cover and the species density associated with each study species. Three natural factors are considered: (1) the mean water depth across a wetland, measured in the field at the time of sampling; (2) the lake on which a wetland is located (Superior, Huron, Michigan, Erie or Ontario); (2) the setting of a wetland, which combines the geomorphology (coastal, riverine or protected) and the eco-province (Eastern deciduous forest or Laurentian mixed forest, following Bailey 1995) resulting in 6 wetland settings. Two anthropogenic factors are also evaluated by using: (4) the urbanization index and (5) the agricultural index. Several of these variables may vary collinearly; for example, agriculture is more widespread in the southern eco-province, potentially obscuring the effect of a wetland's location on a particular lake. Thus, it is important to simultaneously analyze the five variables to determine the importance of each, independent of the other variables.

To compare the independent influence of external factors on the abundance of the study species, I used a hierarchical partitioning (HP) analysis (Chevan and Sutherland 1991). The technique evaluates the importance of each variable by comparing a nested series of models that utilize the factors of interest in all possible combinations. The average incremental improvement in model fit (R-square) with the addition of a variable is calculated across all models, including those with less than the original number of variables. HP does not select one best model, it assesses the independent and the joint explanatory power associated with each variable. As a result, the method is relatively robust against issues that plague multiple regression model building techniques, such as co-linearity among predictor variables and inflated R-square values (Mac Nally 2000; Graham 2003). I used the hier.part package in the statistical software R version 2.1.1 for this analysis (Walsh and Mac Nally 2004). The variance explained by a factor was compared to the results generated by 100 randomized datasets, providing an estimate of statistical significance (Z score).

RESULTS

In the 2010 plots from the 90 sites surveyed across the Great Lakes, we identified 488 taxa of vascular plants, nearly half of which occurred in only one or two wetlands (Johnston et al. in review). Twenty-four plants occurred in a third of the sites and were consistently abundant in wetlands where they occurred. The invasive *Typha* species were observed in more wetlands and in sites where they occurred exhibited a higher relative cover than all other vascular plant species (Figure 2.2).

An examination of patterns within each wetland indicates that the aboveground biomass of the native species typically covered a relatively small percentage of each plot (0.5- 25%) (Figure 2.3). In contrast, in 53% of the plots studied the cover of the invasive *Typha* species was greater than 25% (a mean cover of 37.5% or higher). The range in species richness values recorded in relation to the cover of each study species revealed that high cover of either the native graminoids or invasive *Typha* was associated with lower than average species density. However, the species density in plots with a low to moderate cover of the native species was higher than in plots with an equivalent cover of invasive *Typha*. For example, areas with 5-25% cover of *T. latifolia* had a mean species density of 9.0 (SE= 0.5) species/m^2, and areas with a similar cover of invasive *Typha* had a mean of 6.7 (SE= 0.3) species/m^2. Thus, the invasive *Typha* species when considered together were more dominant than the native

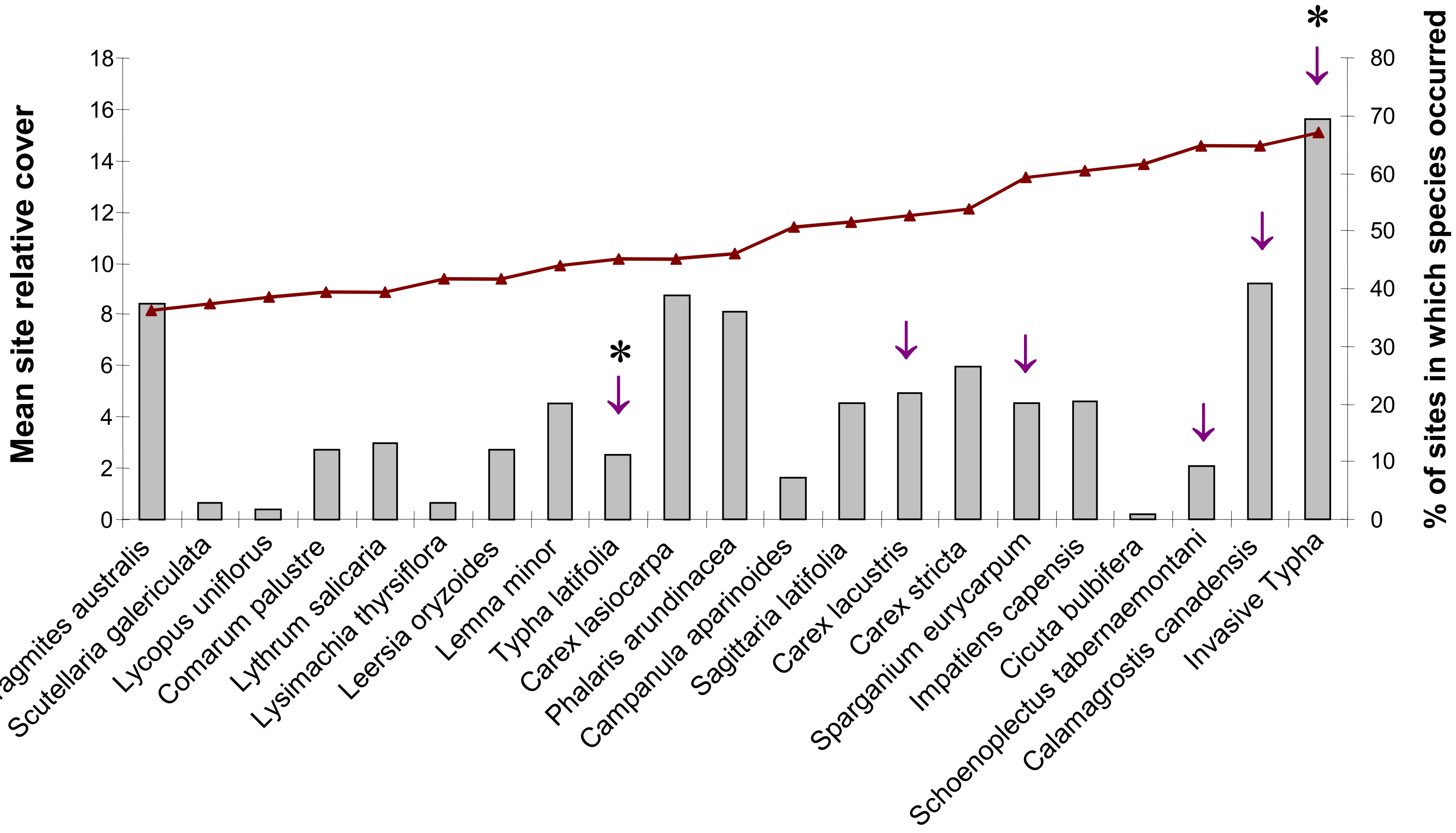


Figure 2.2. Mean site relative cover for the most common species in sites where each species occurred (bars). Triangles show percent of sites in which species occurred. Arrows indicate the plant species used in subsequent comparisons. Stars indicate the *Typha* species.

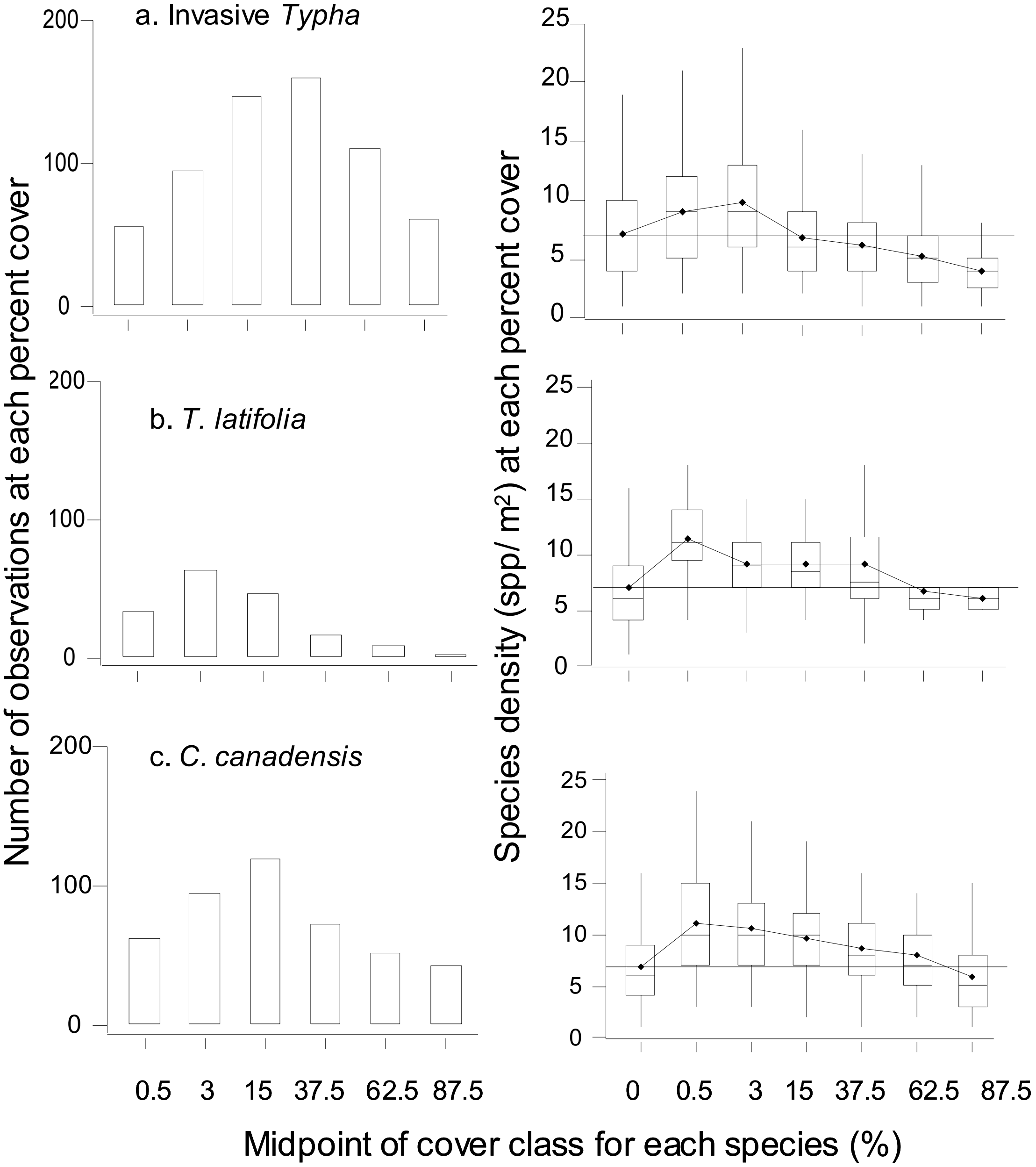
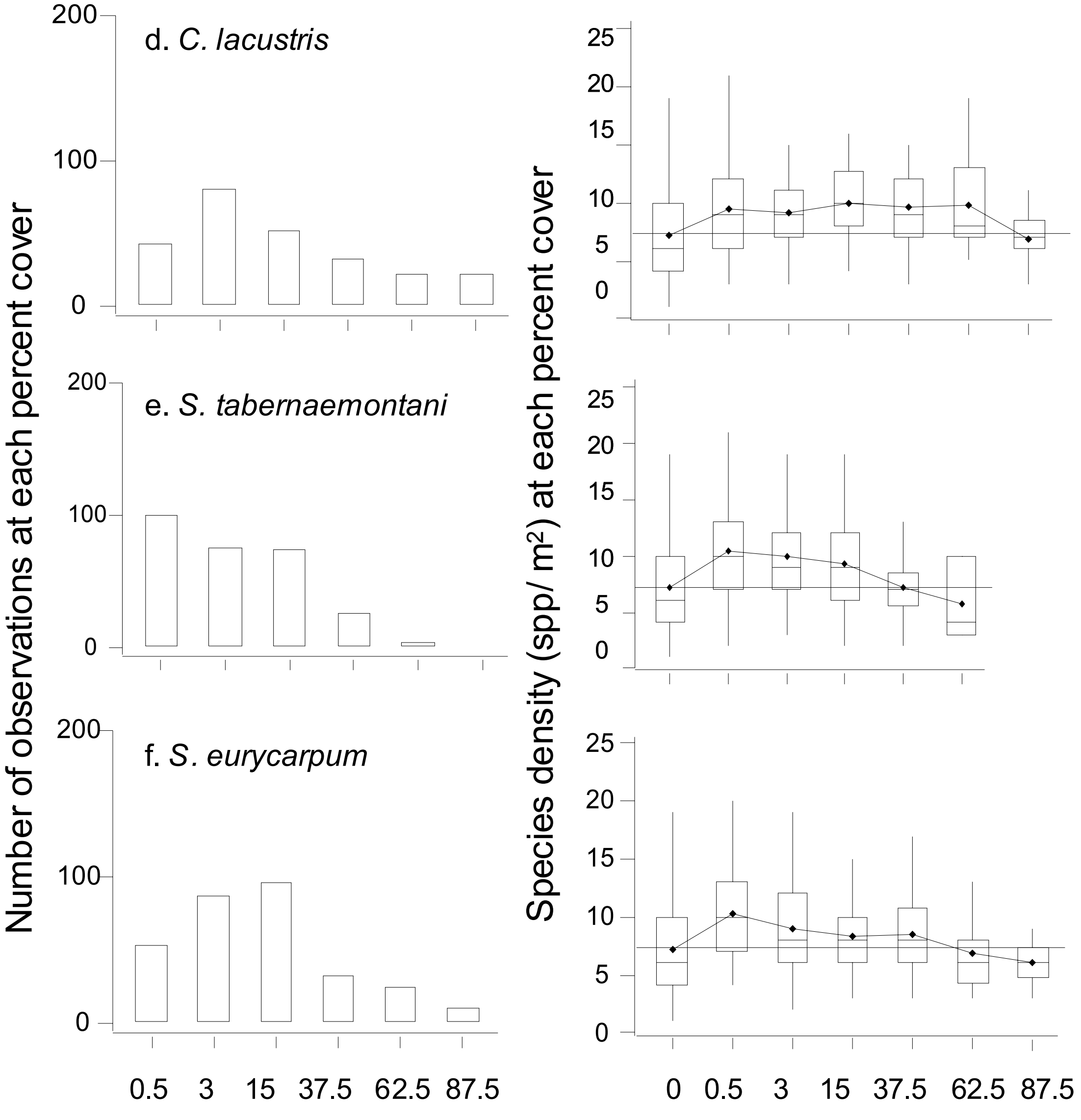


Figure 2.3 Number of times each species occurred at each percent cover class (left column) and the number of species in those plots (right column). Species density range box represents the middle 50% of observations at each percent cover value, line within box indicates the median value, and dot represents the mean value. Straight line marks the mean species density in plots without the species.

Figure 2.3 (Continued).



species in three respects: they occurred more frequently within a wetland (Figure 2.4b), they achieved a higher percent cover in plots where they occurred (Figure 2.4c), and they co-existed with fewer species even when occupying a similar percentage of a plot (Figure 2.4d).

The hierarchical partitioning analysis indicates that the mean water depth across a wetland, the lake on which a wetland is located, and the intensity of agriculture in the watershed draining into a wetland each had a significant independent influence on the relative cover of the invasive *Typha* species (Table 2.1). The urban index and the wetland setting (Northern riverine, protected or coastal, or Southern riverine, protected or coastal) were not significantly correlated with the relative cover of invasive *Typha* (Appendix B). The relative cover of the native graminoids, except *S. tabernaemontani*, was significantly related to at least two of the four factors: lake, water depth, agriculture index or the setting associated with a wetland. The cover of *S. tabernaemontani* did not exhibit a significant relationship with any of the factors.

The lake on which a wetland is located explained more variation in the cover of all six wetland species than the other natural and anthropogenic factors (Figure 2.5). The invasive *Typha* species were more abundant in wetlands around the southern lakes, Lake Ontario, Erie and Michigan (Figure 2.6a) *C. canadensis* occurred with a cover similar or greater than that of invasive *Typha* around Lakes Huron, Michigan and Erie. On Lake Superior, *C. lacustris* and *S. eurycarpum* exhibited high relative cover in wetlands where they occurred. The relative cover of invasive *Typha* and the mean depth of standing water in wetlands around Lake Ontario were significantly higher than in wetlands of the other lakes (Figure 2.6). The depth of standing water across a wetland explained 6% of the variation in the relative cover of invasive *Typha* and 11%

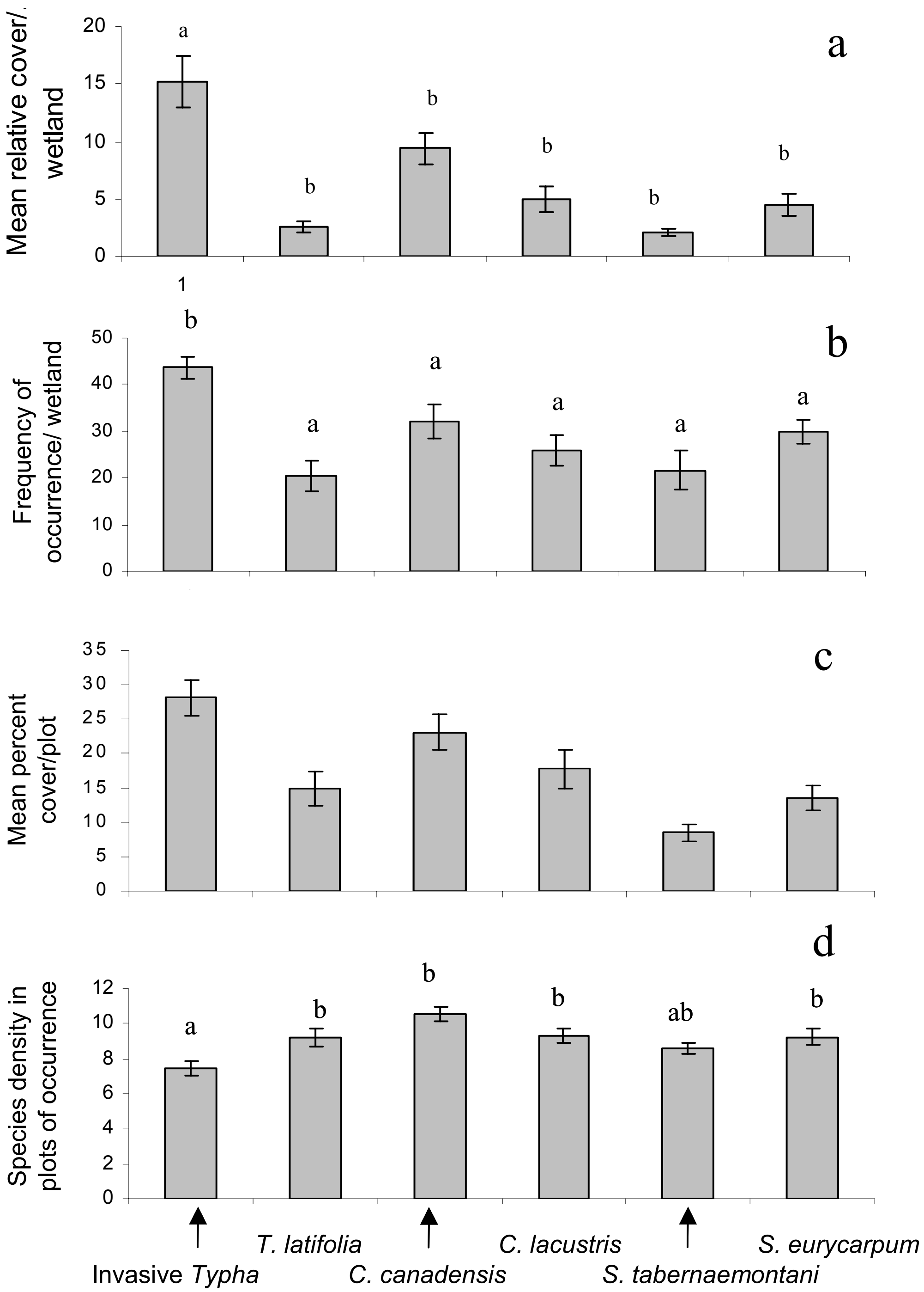


Figure 2.4. Comparison of dominance patterns of the invasive *Typha* species (*T. angustifolia* and *T. glauca*), *T. latifolia, C. canadensis*, *C. lacustris*, *S. tabernaemontani*, and *S. eurycarpum*, based on mean relative cover across wetland (a), mean frequency of occurrence within wetland (b), mean percent cover in plots of occurrence (c), and mean species density in plots of occurrence (d) in sites where each species was observed. Error bars represent 1 SE. Letters denote significantly different means at the alpha = 0.05 level using Hsu's multiple comparison with best.

Table 2.1. Variation in the relative cover of each study species, invasive *Typha* (*T. angustifolia and T. glauca*), *Typha latifolia, Calamagrostis canadensis, Carex lacustris, Schoenoplectus tabernaemontani,*and *Sparganium eurycarpum,* that can be independently explained by mean water depth, wetland setting, lake identity, agricultural index, and the urbanization index associated with a wetland.

		Species					
		Invasive *Typha*	*Typha latifolia*	*Calamagrosotis canadensis*	*Carex lacustris*	*Schoenoplectus tabernaemontani*	*Sparganium eurycarpum*
Mean water depth	Var	***0.06***	***0.11***	***0.1***	0	0.01	***0.08***
	Z	***3.14***	***5.32***	***2.62***	-0.47	0.25	***3.1***
Wetland setting	Var	0.08	0.08	***0.13***	***0.17***	0.09	0.08
	Z	0.53	0.63	***2.62***	***3.23***	1.09	0.58
Lake identity	Var	***0.21***	***0.15***	***0.16***	***0.17***	0.10	***0.18***
	Z	***6.33***	***3.75***	***3.14***	***3.97***	1.53	***4.12***
Agricultural Index	Var	***0.1***	0.03	0.02	***0.05***	0.01	***0.04***
	Z	***6.88***	0.9	0.12	***2.72***	0.3	***1.95***
Urbanization Index	Var	0.02	0.01	0.02	0	0	0
	Z	0.4	0.3	0.74	-0.31	-0.47	-0.38
MODEL STATISTICS							
Overall R-Square		0.47	0.38	0.43	0.39	0.21	0.38
Number of wetlands		61	41	59	48	59	54

Note: Relative percent cover was square root transformed to normalize variances. Var = proportion of variance independently explained by factor, Z = test statistic from a comparison with results generated by 100 randomized datasets. Overall R-Square indicates the variance explained by the full model. Factors significant at the alpha= 0.05 level are bolded and italicized.

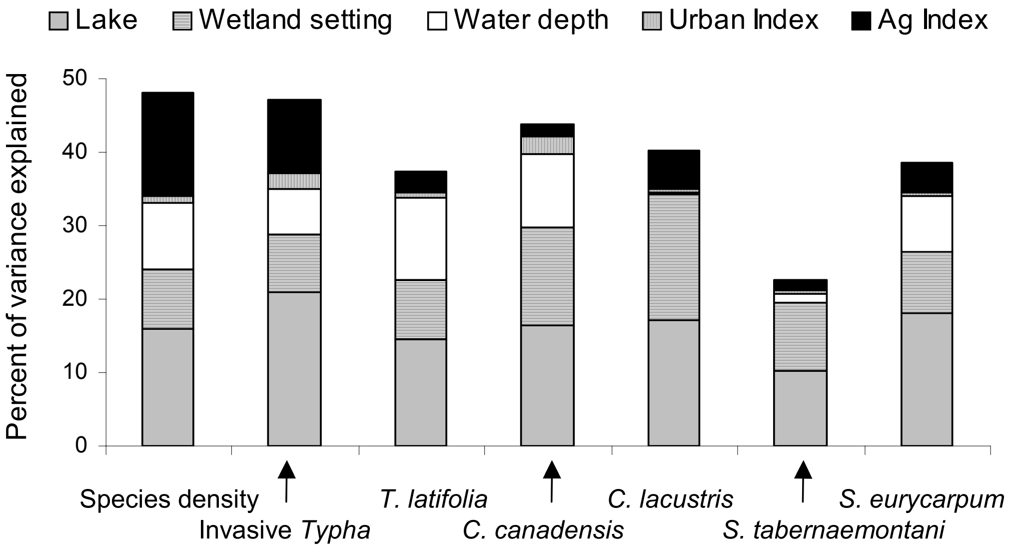


Figure 2.5 Percent of variance in mean species density and the relative cover of the invasive *Typha species (T. angustifolia and T. glauca)*, *Typha latifolia, Calamagrostis canadensis, Carex lacustris, Schoenoplectus tabernaemontani,*and *Sparganium eurycarpum* that could be independently explained by each natural and anthropogenic factor. Table 2.1 includes a test of significance for each factor.

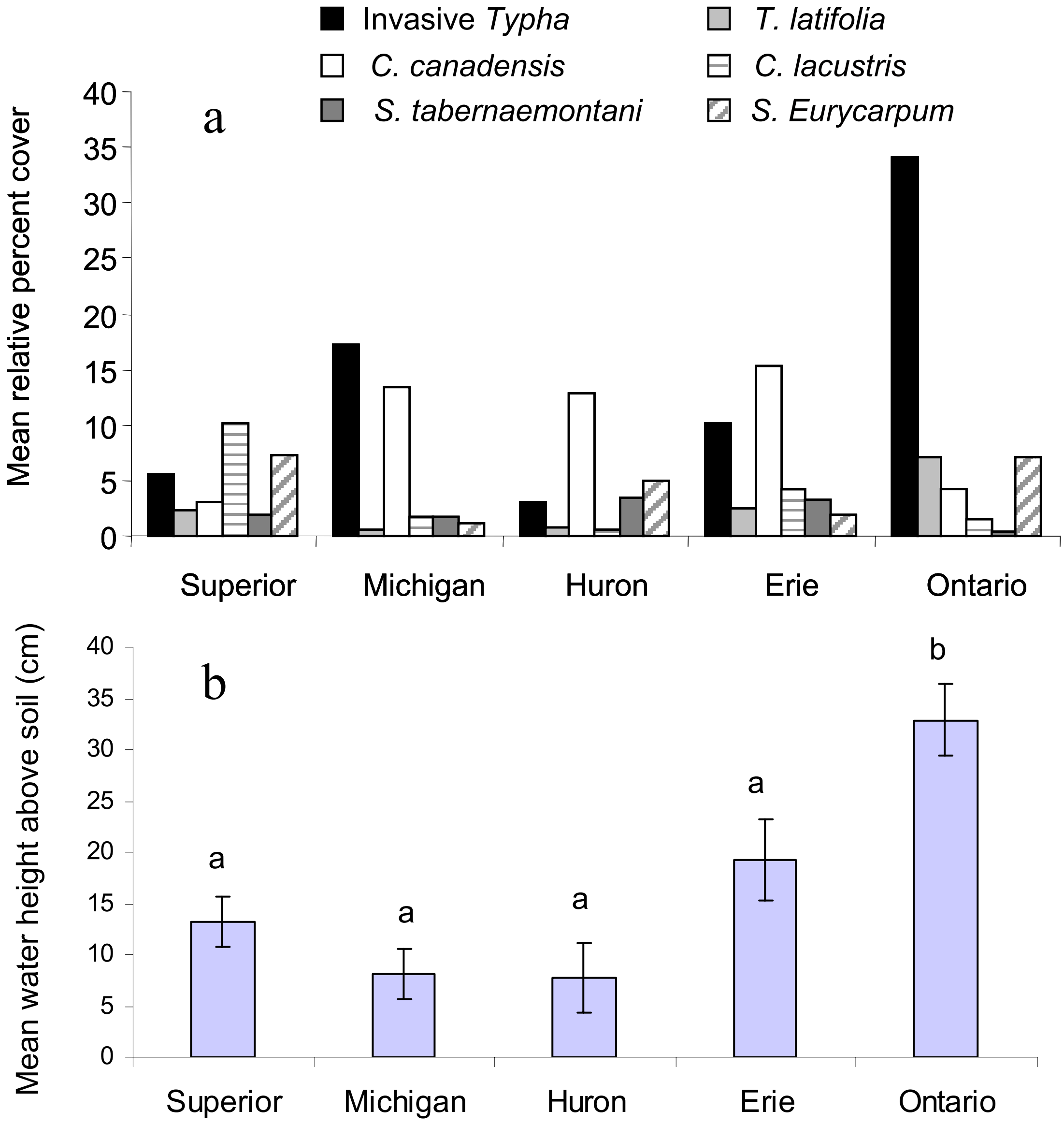


Figure 2.6. Mean relative cover of the study species: invasive *Typha* (*T. angustifolia* and *T. glauca*), *Typha latifolia*, *Calamagrostis canadensis, Carex lacustris, Schoenoplectus tabernaemontani* and *Sparganium eurycarpum* (a) and mean height of water above soil surface (+/- SE) (b) around each of the Great Lakes. Mean relative cover was calculated for wetlands where each species occurred.

of the variation in *T. latifolia* (Table 2.1). The mean water depth in plots occupied by the graminoid study species was slightly lower than the mean water depth across all sites, except in the case of *S. tabernaemontani* and *S. eurycarpum* which tended to occupy wetter areas (Figure 2.7). In addition, the frequency of different substrate types varied among lakes (Appendix C), and was correlated with the percent cover of many plants species, including the *Typha* species (Appendix D, Johnston et al. in review).

In wetlands more likely to be impacted by agricultural activities (i.e., wetlands with a high agricultural index value), the invasive *Typha* species were more abundant. The agricultural index uniquely explained 10% of the variation in the relative cover of invasive *Typha* after accounting for the lake, water depth and setting associated with a wetland. The invasive *Typha* species were the only taxa that showed a significant and positive relationship with the agricultural index; the native graminoid species tended to be less abundant in wetlands with a high agricultural index value (Figure 2.8). The urban index was not significantly correlated with the abundance of any of the six study species after accounting for the variation due to the other four factors.

To assess the relationship between a particular plant species and the mean number of species per meter-squared plot (species density), one must first evaluate factors that are simultaneously influencing species density and a plant species' abundance. Three external factors explained a significant component of the variation in mean species density: the identity of the lake (16%), the agriculture index (14%), and the mean water depth (9%) associated with a wetland (Table 2.2). These same three factors were similarly important in determining the relative cover of invasive *Typha* (Figure 2.5). An additional 5% of the variation in species density was correlated with the

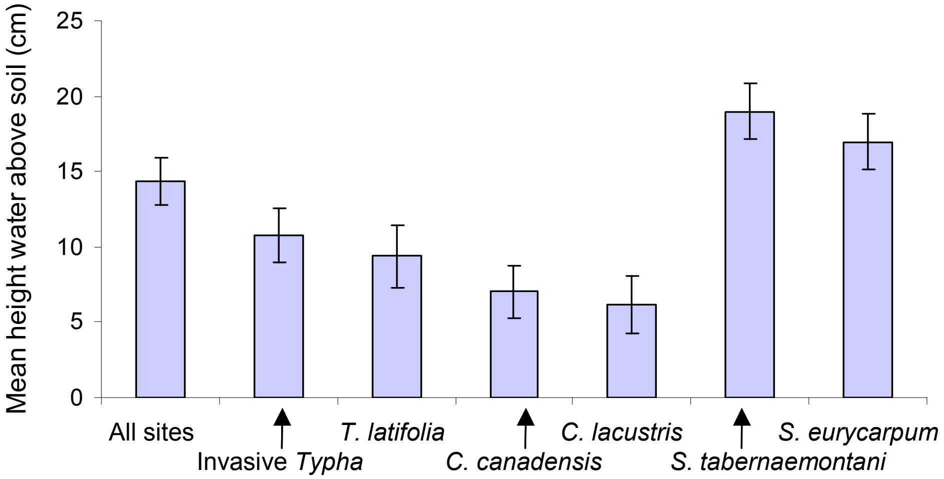


Figure 2.7. Mean height of water above soil surface (+/- SE) in areas of occurrence for each study species: invasive *Typha* (*T. angustifolia* and *T. glauca*), *Typha latifolia*, *Calamagrostis canadensis, Carex lacustris, Schoenoplectus tabernaemontani* and *Sparganium eurycarpum*.

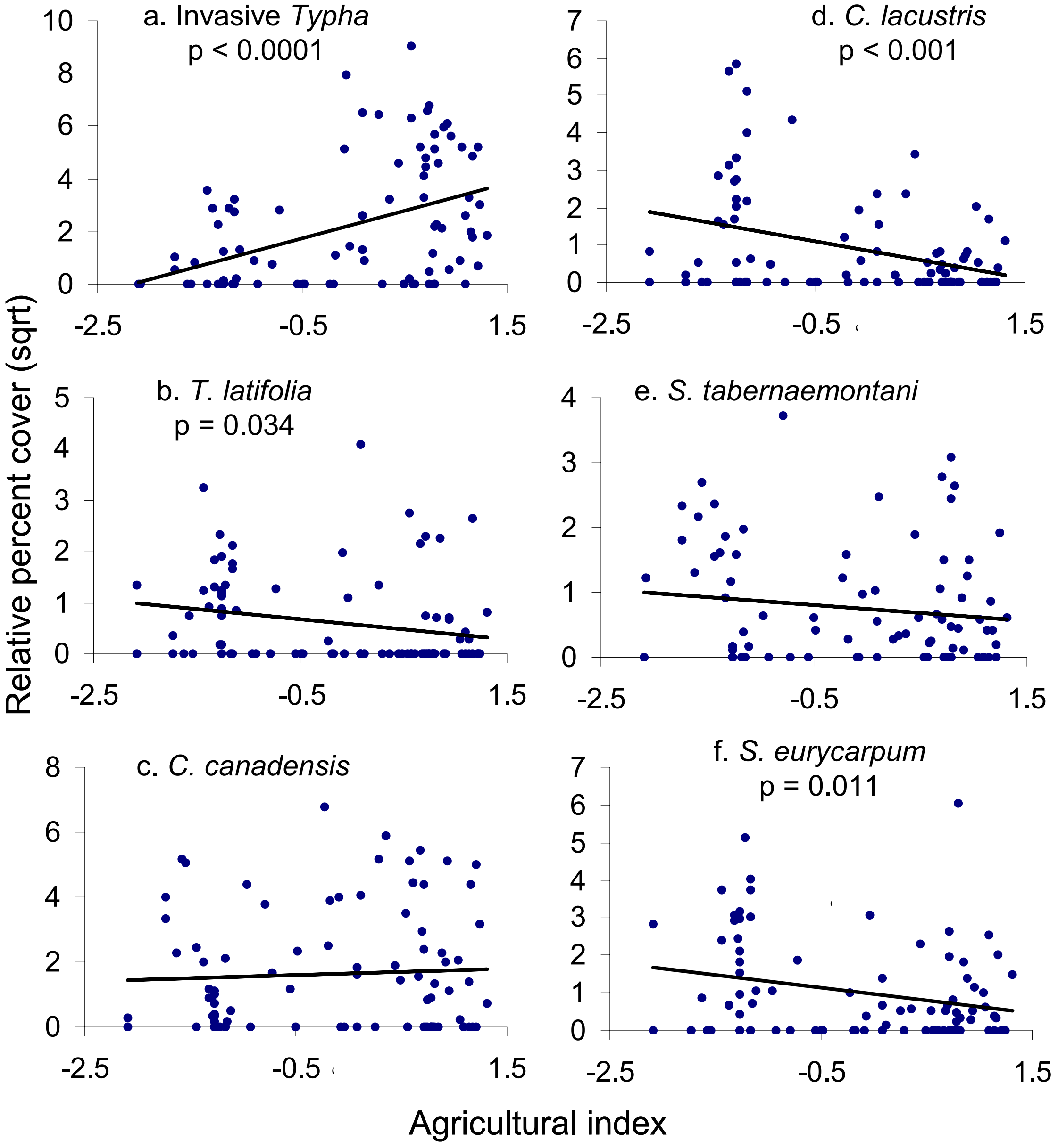


Figure 2.8. Relationship between the agricultural index and the relative cover of invasive *Typha* (*T. angustifolia* and *T. glauca*) (a), *Typha latifolia* (b), *Calamagrostis canadensis* (c), *Carex lacustris* (d), *Schoenoplectus tabernaemontani* (e) and *Sparganium eurycarpum* (f). Relative cover values are square-root transformed. The p-value is reported for relationships significant at the alpha = 0.05 level.

Table 2.2. Variation in mean species density that can be independently explained by mean water depth, wetland setting, lake identity, agricultural index, urbanization index, and relative cover of the six study species.

		Mean species density	Significant?
Mean water depth	Var	**0.09**	
	Z	**6.24**	*
Wetland setting	Var	0.08	
	Z	0.68	
Lake identity	Var	**0.16**	
	Z	**4.04**	*
Agriculture Index	Var	**0.14**	
	Z	**8.38**	*
Urban Index	Var	0.01	
	Z	-0.26	
Invasive	Var	**0.05**	
Typha	Z	**3.00**	*
Typha	Var	0	
latifolia	Z	-0.54	
Calamagrosotis	Var	0.02	
canadensis	Z	0.67	
Carex	Var	0.02	
lacustris	Z	0.37	
Schoenoplectus	Var	0.01	
tabernaemontani	Z	0.10	
Sparganium	Var	0	
eurycarpum	Z	-0.55	

Note: Var = variance independently explained by factor, Z = test statistic resulting from comparison with randomized data. Factors significant at the alpha= 0.05 level are bolded and marked with *. The importance of the relative cover of each species was tested sequentially, with only the upper variables included.

relative cover of invasive *Typha*; however, the cover of the other graminoid species was not significantly related to species density after accounting for external factors (Table 2.2).

Regionally, areas with invasive *Typha* tended to have a lower species density (Figure 2.5d) and the relative cover of invasive *Typha* across a wetland was negatively correlated with the mean species density of the wetland (Figure 2.9). Such a relationship could develop if the expansion of invasive *Typha* and plant species diversity were directly influencing each other or if both parameters were independently responding to external factors. For example, a higher agricultural index value for a wetland's watershed was associated with both lower species density (Figure 2.10) and a higher cover of invasive *Typha* (Figure 2.8a). The relationship between the agricultural index and species density was similar in areas with and without invasive *Typha*, suggesting that the presence of invasive *Typha* was not changing the way agricultural activities impacted plant species diversity (Figure 2.10). However, the lake on which a wetland was located did seem to influence the relationship between invasive *Typha* and species diversity. In plots where invasive *Typha* occurred, there was a significant negative correlation between the percent cover of invasive *Typha* and species density in wetlands around Lake Ontario and Lake Michigan, but not in the wetlands around the other lakes (Figure 2.11). A direct comparison of the mean species density in plots with and without invasive *Typha* within a wetland revealed that in 45% of the wetlands mean species density was higher in areas with invasive *Typha*. Thus, the degree to which the invasive *Typha* species dominate the plant community is variable and may be governed by external factors, such as agricultural run-off or the hydrology of particular lakes.

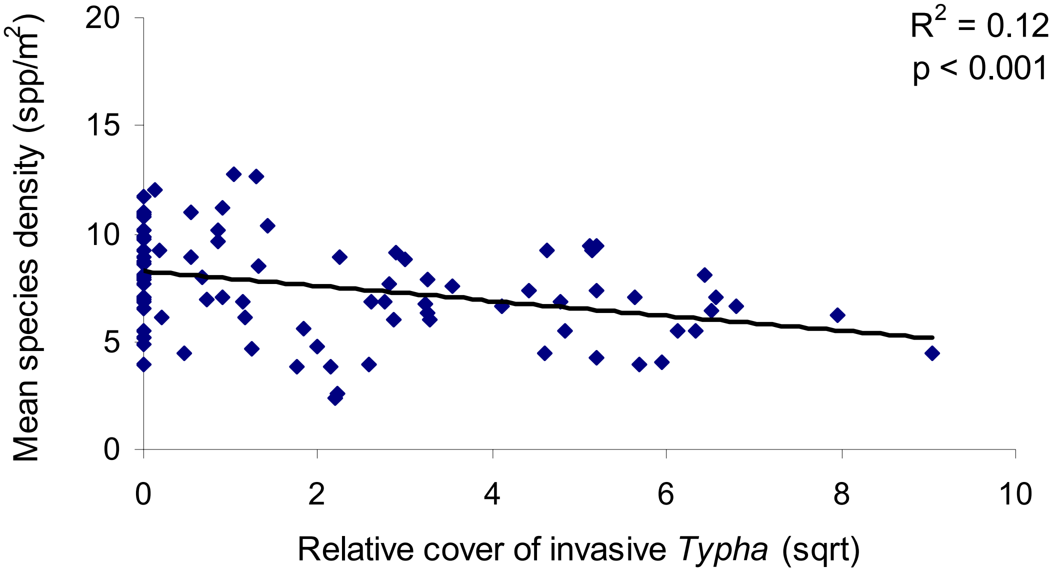


Figure 2.9. Relationship between the mean species density and the relative cover of invasive *Typha* (square root transformed). R^2 and p values for single variable regression are reported.

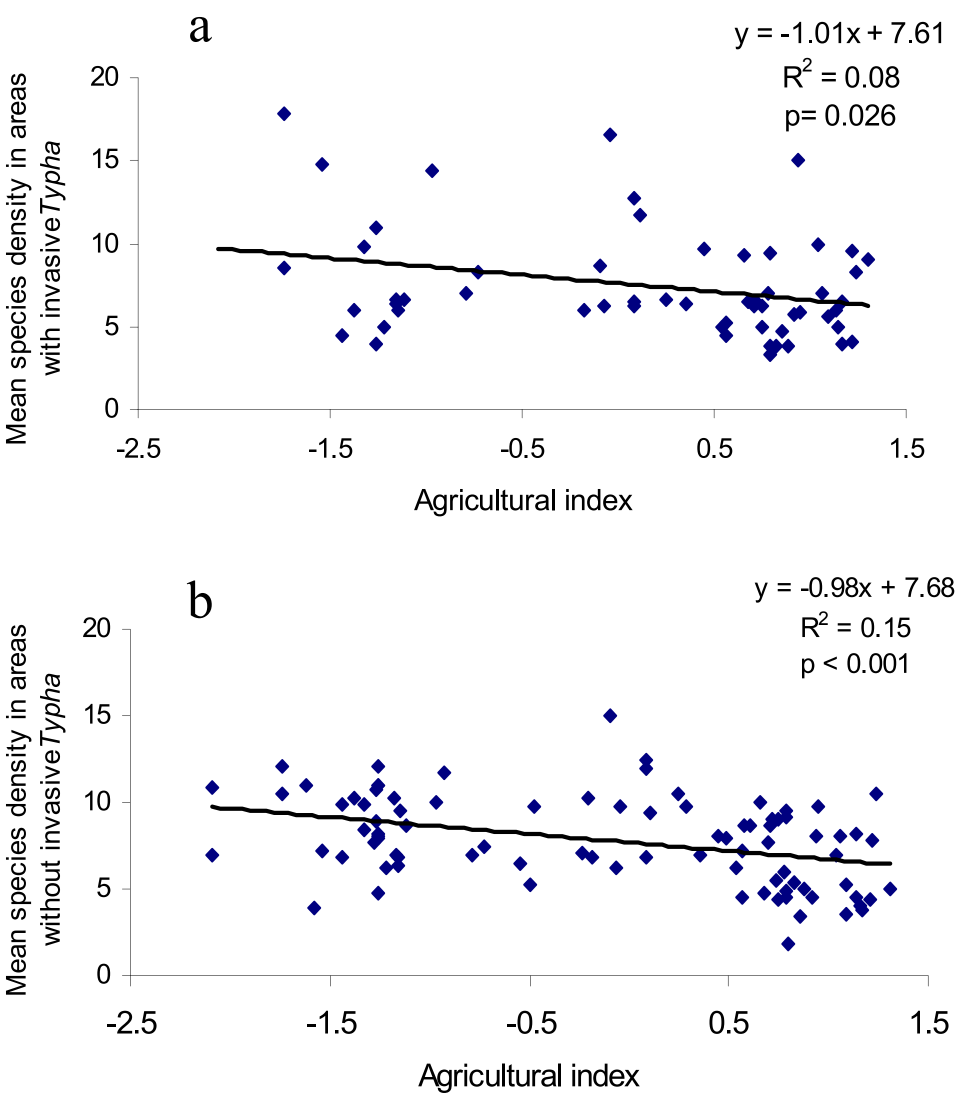


Figure 2.10. Relationship between the agricultural index and mean species density in areas with (n=60) (a), and without (n=90) (b) invasive *Typha* present. The regression equation, R^2 and p values are reported.

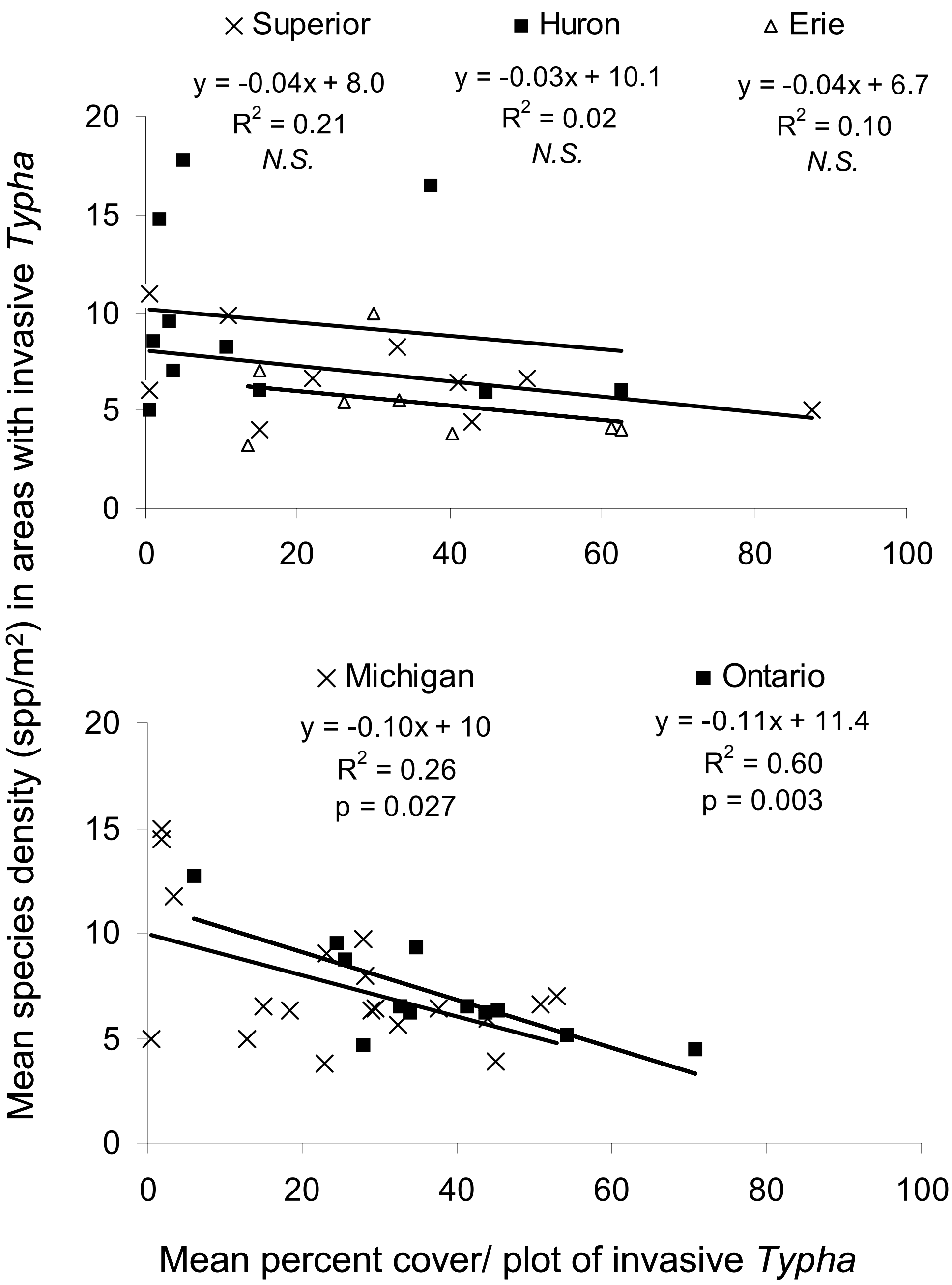


Figure 2.11. Relationship between mean cover per meter-squared of invasive *Typha* and the means species density in plots of occurrence within each lake. The regression equation, R^2 and p value are reported for the relationship within each lake.

DISCUSSION

This work revealed several important ecological differences between populations of the invasive *Typha* species (*T. angustifolia* and *T. glauca*) and those of five native, co-occurring graminoids (*Typha latifolia*, *Calamagrostis canadensis*, *Carex lacustris*, *Schoenoplectus tabernaemontani*, and *Sparganium eurycarpum*). In comparison with the native species, the invasive *Typha* species occurred more frequently within a wetland, achieved a higher percent cover per meter-squared, and were associated with a lower density of plant species. The relative abundance of invasive *Typha* across a wetland was positively correlated with an index of agricultural intensity for the watershed draining into the wetland. This pattern contrasted with that of the native species, whose relative cover tended to decline, and from overall plant species density, which significantly decreased in relation to the agricultural index. These results demonstrate that *T. angustifolia* and *T. glauca* have the ability to grow at high densities around the Great lakes, their abundance is associated with reduced plant species diversity, and their growth is promoted by agricultural activities. Geographic patterns of plant species density and the dominance of invasive *Typha* across the Great Lakes suggest that the invasive *Typha* species are primarily a symptom rather than an independent cause of stress to native plant communities. Therefore an understanding of their distribution and abundance could lend insight into the threats facing the Great Lakes.

Geographic Patterns of Dominance

The higher abundance of the invasive *Typha* species in the southern lakes and the relatively constant abundance of *T. latifolia* among the five lakes may reflect differences in the species' climatic tolerance. *Typha latifolia* occurs from Alaska south into the tropics, and from sea level up to 2125m, and thus can tolerate the full climatic range across the Great Lakes. In contrast, in North America, *T. angustifolia*'s distribution remains restricted to areas south of 50° N; and therefore, it may be approaching a latitudinal limit in the Northern Great Lakes region (Grace and Harrison 1986). Climate warming may shift the distribution of *T. angustifolia* in the future.

Differences in each lake's history, geology or hydrology may be further influencing vegetation patterns. The lake on which a wetland is located was the most important determinant of abundance for the six plant taxa studied, after accounting for variation due to surrounding urban and agricultural development and the wetland's geomorphic setting. Each lake experiences a unique pattern of inter- and intra- annual lake level fluctuation, which affects wetland plant establishment and competition. Variable water levels provide natural disturbances in marshes; high water years inhibit the success of woody species and low water years allow marsh meadow species such as sedges to flourish. Keddy and colleagues have established a predictive relationship between water level fluctuations and river or reservoir shoreline vegetation, demonstrating that increasing fluctuations increase plant diversity until a threshold is reached (Keddy and Reznicek 1986; Hill and Keddy 1992; Hill et al. 1998).

Water level regulation could explain why the invasive *Typha* species are particularly abundant in wetlands around Lake Ontario (Figure 2.7). Currently, dams on the outflows of Lake Superior and Lake Ontario regulate water levels; however, most studies can only detect hydrologic changes attributable to regulation on Lake Ontario (Brinkmann 2000; Lenters 2001; Quinn 2002). Historical hydrographs of lakes Huron, Michigan and Erie show high inter-annual variability, low intra-annual fluctuations, and no effect of regulation. Since 1960, when the Moses-Saunders power dam was constructed on the outlet from Lake Ontario, water levels have been regulated within a target range of 75.15 and 75.37 m above sea level. Lake Ontario now experiences less inter-annual variation in water levels, but the intra-annual range from summer high water periods to winter low water periods has actually increased (Quinn 2002). Using historical imagery and field surveys at elevations with known water level histories, Wilcox (USGS 2004; Wilcox et al. 2004) argues that stabilized water levels on Lake Ontario are causing a decrease in sedge meadow plants and an increase in cattail-dominated communities. He believes that higher summer water levels since 1960, and the absence of extreme water levels, reduce the competitive ability of sedge meadow plants and allow *Typha* species to expand landward around Lake Ontario. Our field surveys, which were each conducted at discrete sampling dates during the summers of 2001-2003, indicate that mean water levels were higher in the wetlands of Lake Ontario than the other four lakes. These results support the hypothesis that the hydrologic regime of wetlands on Lake Ontario is distinct and facilitates the success of invasive *Typha*.

The high prevalence of invasive *Typha* species in the Eastern Great Lakes may also reflect the invasion history of *T. angustifolia*. In the last 150 years, *T. angustifolia* has spread across much of Eastern and Midwestern North America (Galatowitsch et al. 1999). Botanical records indicate that *Typha angustifolia* was first introduced into brackish marshes of the Atlantic coast in the early 1800s and has since spread westward through New York state (Stuckey and Salamon 1987; Galatowitsch et al. 1999). The time since *T. angustifolia* first established in a wetland could influence the degree to which it is able to dominate the plant community today, suggesting that western marshes may experience greater levels of dominance in the future.

The Role Anthropogenic Stress

The relative cover of the invasive *Typha* species was higher and mean species density was lower in wetlands with a higher agricultural index value, indicating that agriculture around the Great Lakes represents an important threat to coastal wetlands. Agricultural land uses have been shown to increase the sediment, pesticide and nutrient loads within downstream rivers and wetlands (Herlihy et al. 1998; Jones et al. 2001). Experimental work demonstrates that sedimentation can influence the establishment of seedlings, disrupt the plant canopy, lower species richness, reduce topographic heterogeneity, and ultimately promote the growth of a few competitive plants such as *Typha glauca* and *Phalaris arundinacea* (Werner and Zedler 2002; Kercher and Zedler 2004; Mahaney et al. 2004a). Nutrient enrichment also influences plant competition and has facilitated the invasion of *Typha* species in a sedge meadow (Woo and Zedler 2002) and in the Everglades (Childers et al. 2003). *Typha domingensis* has been a successful invader of sawgrass marshes in the Everglades in part because it is better able to respond to increased nutrient loading by concentrating more nutrients in its leaves, allocating more biomass to vegetative reproduction and growing faster (Newman et al. 1996; Lorenzen et al. 2001). Similar adaptations may explain why *T. glauca* and *T. angustifolia*, unlike the native graminoid species, are more abundant in wetlands more heavily impacted by agriculture. Many wetland ecologists have observed anecdotally that cattails seems to be more common in highly impacted wetlands (e.g., Grace and Harrison 1986; Keddy 2000). However, this is the first time a broad survey has revealed a relationship between agriculture and invasive *Typha* abundance outside of the Everglades.

Surprisingly, urbanization was not related to the abundance of any of the study species nor did it seem to influence overall plant species density, even though urban areas are known to influence aquatic ecosystems in several ways. Streams within urbanized catchments contain high levels of phosphorus and nitrogen; however, the area dedicated to agriculture in the Great Lakes region is much larger and probably constitutes a more important source of biologically available nutrients. Impervious surfaces and efficient storm water drainage systems associated with urban areas decrease infiltration and increase the frequency and magnitude of flooding events in connected streams (Allan 2004). Flashy flows can scour riparian areas, transport sediments and disrupt native wetland communities, potentially facilitating invasions (Kercher et al. 2004). Urban run-off and waste water treatment effluent elevate the conductivity, biological oxygen demand, suspended solids, hydrocarbons and metals in urban streams (as reviewed by Paul and Meyer 2001). Although fish and aquatic invertebrate populations are influenced by the amount of urban area in a watershed (Allan 2004), wetland plants may be less sensitive to chemical contaminants. Urbanization also causes an overall loss of wetland area, therefore wetlands heavily impacted by urbanization may be under-represented in this analysis. In summary, this work indicates that natural geographic variation and agricultural land uses are more important than urbanization in determining the abundance of invasive *Typha* species and overall species density in Great Lakes coastal wetlands.

Species Density

Across the Great Lakes, areas where the invasive *Typha* species occurred had lower species density than areas with the native graminoids (Figure 2.5), and the relative abundance of invasive *Typha* showed a significant negative correlation with a wetland's mean species density. Both species density and the cover of invasive *Typha* in a wetland were related to external factors, but 5% of their variation was uniquely and significantly correlated. Other observational studies have found a positive correlation between native species richness and invasibility (measured as number of exotic species), which indicates that factors governing diversity (e.g., immigration rates, disturbance and resource availability) affect both exotic and native species (Lonsdale 1999; Levine 2000; Brown and Peet 2003; Stohlgren et al. 2003). If an exotic is a “strong” invader it could exhibit a negative relationship with native species diversity if it competitively excludes other species (e.g., Ortega and Pearson 2005). Yet, even some strong invaders, such as *Lythrum salicaria*, are associated with high plant diversity in some cases (Farnsworth and Ellis 2001; Hager and Vinebrooke 2004). Thus many factors, including time since invasion, the environment, and species traits will influence the relationship between the cover of an established exotic and community diversity (Levine et al. 2003; Zedler and Kercher 2004).

The negative relationship between invasive *Typha* and species richness could result from several processes: (a) communities with lower species density may be less resistant to invasive *Typha*, (b) invasive *Typha* may be better able to tolerate stressful conditions or overcome dispersal obstacles that limit the survival of other species, or (c) invasive *Typha* may be directly inhibiting the co-existence of other species. Distinguishing between the above hypotheses requires that we separate the factors facilitating the abundance of invasive *Typha* from the processes limiting species density (MacDougall and Turkington 2005). Although it is impossible to establish a conclusive causative relationship with observational data, several lines of evidence suggest that external factors independently influence species density and the dominance of invasive *Typha*. Within a wetland, the species density of areas with and without invasive *Typha* is not significantly different, indicating that invasive *Typha* species are able to establish and co-exist within a diverse plant community in some cases. The relationship between mean species density and the agricultural index is similar in areas with and without invasive *Typha*. Although species density seems to decline as invasive *Typha* become more abundant, the cover of invasive *Typha* is positively correlated with the agricultural index. Thus, agricultural activities within the watershed seem to simultaneously lower wetland species density and promote the dominance of invasive *Typha*. Among the wetland graminoids studied, the invasive *Typha* species are unique is their ability to dominate a wetland, but their dominance is sensitive to external conditions, such as the lake or the degree of agriculture associated with a wetland. In summary, these analyses suggest that invasive *Typha* dominance is one mechanism through which natural and anthropogenic factors impact the plant community rather than an independent cause of plant diversity decline.

CONCLUSIONS

Although cattails are often lumped together as a single conservation issue, the distribution and associated species density of the native and invasive *Typha* species indicate that they exhibit important ecological differences. In the wetlands surveyed, *Typha latifolia* and the native graminoids, *S. eurycarpum*, *C. canadensis*, *C. lacustris* and *S. tabernaemontani* were on average a smaller proportion of a site's plant community, they were associated with higher species density and their relative cover was less responsive to agricultural impacts, in contrast with the invasive *Typha* species. Previous research on the ecology and physiology of cattails revealed that they tolerate a wide range of water depths and are able to rapidly utilize increases in available nutrients (Waters and Shay 1992; Newman et al. 1996; Miao 2004; Weisner and Miao 2004). As might be expected, in the Great Lakes region the invasive *Typha* species occur across a range of wetland settings and are more common and dominant in wetlands surrounded by greater agricultural activity.

Patterns observed across the Great Lakes have important implications for the management of invasive *Typha* species. Although apparently limited by climate in the northern regions, invasive *Typha* may be particularly hard to control around the southern lakes because they can flourish in wetlands impacted by agriculture. Invasive *Typha* species form a larger proportion of the plant community in wetlands around Lake Ontario, and these wetlands tend to have higher mean water depths and less inter-annual water level variation. The relationship between agricultural intensity and both species density and invasive *Typha* suggests that the abundance of invasive *Typha* is an indicator of the degree to which external factors are shifting the balance between dominance and diversity. In order to protect Great Lakes wetland plant communities, we may need to simultaneously alleviate agricultural impacts, alter Lake Ontario's water level regulation, and minimize the spread of invasive *Typha*.

CHAPTER THREE

The role of litter dynamics in mediating the dominance of cattail (*Typha* spp.) in Great Lakes wetlands

INTRODUCTION

Ecologists have long observed that plant species diversity varies in a uni-modal relationship with biomass (e.g., Grime 1973a; 1973b). Grime's original model considered biomass to include live and dead plant material but, according to a review by Grace (1999), only some of the many subsequent studies have explicitly incorporated litter biomass. Several lines of evidence suggest that litter may mediate the relationship between increased nutrient loading to terrestrial and aquatic ecosystems and plant species diversity (Berendse 1999). Numerous studies have established the positive relationship between nutrient availability and production of live plant biomass (e.g., Venterink et al. 2001). Increasing soil fertility also can cause litter biomass to accumulate at faster rates than living biomass, particularly in herbaceous communities (e.g., Tilman 1993). Litter in turn has been shown to influence seed germination and establishment (Xiong and Nilsson 1999).

Results of fertilization and biomass removal studies that partitioned the effects of litter and living biomass on plant community composition have been inconsistent. In some studies, living biomass or stem density was more tightly correlated with species richness (Stevens et al. 2004), while in other studies litter biomass was a more important determinant of species density (Tilman 1993; Foster and Gross 1998; Xiong et al. 2003). Still others found that propagule additions overwhelmed the effect of living and dead biomass (Foster et al. 2004). Foster and Gross (1998) showed experimentally that either additions of litter or fertilizer to an old field grassland caused an identical decline in species recruitment, presumably because each attenuated light to a low level. Berendse and others (1994) observed further that additions of fertilizer and litter to a Dutch heath not only had similar effects on plant biomass production but also affected rates of succession within the community, suggesting that litter influences competitive interactions between established plants.

Cattails (*Typha* spp.) have become the dominant species in many marshes of the Great Lakes region, often forming dense stands of live and dead biomass which appear to reduce the diversity of other wetland species (Frieswyk et al. 2005). On Lake Ontario, an increasing abundance of cattail over the past 60 years has been associated with a simultaneous decrease in wet meadow communities (USGS 2004; Wilcox et al. 2004). While these changes appear to be related to regulation of water levels on Lake Ontario, they have occurred simultaneously with increased nutrient loading to the lake and its wetlands (Detenbeck et al. 1999). Given the potential for cattails to attain high levels of productivity (Brinson et al. 1981) and the resistance of its litter to fragmentation and decay (Davis and Van Der Valk 1978), accumulation of cattail litter might facilitate its own increasing dominance in Great Lakes wetlands by suppressing other species.

The degree to which cattails dominate Great Lakes wetlands varies and offers an opportunity to examine both the factors associated with dominance by cattail and the relationship of cattail live and dead biomass to species diversity. Unlike the native cattail species, *Typha latifolia* L., the percent cover of the invasive cattails, *Typha angustifolia* L. and *Typha glauca* Godr.(pro sp.)*,* is negatively correlated with plant species richness and positively correlated with agricultural activity (Chapter 2). *T.*

angustifolia and *T. glauca* occur more frequently around Lake Ontario than the other Great Lakes, suggesting that this lake's unique water level regulation may be a contributing factor (Chapter 2). However, even around lake Ontario, cattail abundance varies; southern lakeshore wetlands within open embayments are visibly dominated by cattails while wetlands behind barrier beaches along the eastern shore of the lake maintain a more diverse plant community.

Approach and Predictions

In this study, I first characterized the litter dynamics of six Lake Ontario wetlands in terms of live and dead biomass of cattail and other species, rates of litter decomposition for cattail, and species density. Based on observed differences in cattail abundance between open embayment wetlands and those behind barrier beaches, I hypothesized that litter dynamics would differ between the two hydrogeologic settings, potentially explaining their vulnerability to dominance by cattail. Specifically, I expected that litter biomass and abundance of live cattail would be positively correlated and that litter biomass and species density would be negatively correlated, i.e., that litter biomass would be higher and species density lower in open embayment wetlands. I also expected that litter dynamics, i.e., plant production and decomposition, would be driven by water level fluctuations which would differ as a function of the wetland's hydrogeologic setting.

In the second part of this study, I conducted a litter manipulation experiment in one of the Lake Ontario wetlands to help explain the patterns observed in the first part of the study and identify the mechanisms by which cattail litter affects other plant species. To this end, I manipulated both standing and fallen litter, added seedlings of a common species to different litter treatments, measured seedling survival and growth, and determined the species density of treatment plots. I hypothesized that increasing the amount of cattail litter would reduce plant species diversity, that fallen litter would inhibit the establishment of seedlings, and that standing litter would reduce the size of seedlings once established.

METHODS

Litter Dynamics in Lake Ontario Wetlands

Study area

In order to characterize litter production and decomposition around Lake Ontario, I chose six study wetlands from two distinct hydrogeologic settings. Three of the sites are located along the southern shore of Lake Ontario in embayments that are open to the lake (hereafter termed "open" wetlands). Calcium-rich glacial till covers the bedrock in this area. The other three sites are located on the eastern shore of Lake Ontario where an extensive network of sand bars and barrier beaches has formed. The study wetlands are located behind sand bars and are hydrologically connected to Lake Ontario only by intermittent or indirect surface water openings or ground water (hereafter called "protected" wetlands). In each site, I quantified (1) hydrologic fluctuations, (2) plant species composition, (3) live and dead biomass, and (4) decomposition rates.

Hydrology

In each wetland, hydrologic and vegetation measurements were made along a transect that ran from upland to water's edge and bisected an area of herbaceous vegetation typical of that site. Water table wells were installed at six equally spaced locations along the transect, within the zone of emergent, non-woody vegetation. Water table elevation was measured monthly at each of the wells and recorded continuously at the fourth well from water's edge by a capacitance rod connected to a data logger, from May-September of 2004. Measurements made by hand indicated that water table elevations recorded by the data loggers were within 1-4 cm of actual water levels.

Vegetation

Vegetation was sampled at four intermediate locations along the transect where mean water depth was 5- 20 cm and *Typha* species (primarily *Typha angustifolia* and *T. glauca*) were most abundant. Sampling stations were 10-30 meters apart, depending on the length of the full transect. Plant species were identified in meter-squared plots placed at a random direction and distance (1-3m) from each water table well. Four plots were surveyed at each sampling station to calculate a mean species density. Aboveground biomass of the vegetation and litter were quantified by harvesting a 0.5 m^2 area adjacent to each of the four sampling stations in late July, 2003. The vegetation was separated into five categories at the time of harvest: Live cattail biomass, live non-cattail biomass, standing cattail litter, fallen cattail litter, and non-cattail litter. Plant material was dried at 65° C to constant weight and then weighed.

Decomposition rates

In order to quantify the rate of cattail litter decomposition in the fallen litter layer, I used standard litter-bag techniques (Robertson et al. 1999). Senesced cattail plants typically remain upright for 6-18 months before fragmenting, toppling over, and forming a litter layer (Davis and Van Der Valk 1978). To mimic this second stage of the decomposition process, I collected litter in July from *Typha angustifolia* plants that had senesced the previous fall and remained upright during the winter (as in Kuehn et al. 2000). Litter was collected only from the Mudge Creek wetland so that all variation in decomposition could be attributed to the location of the litter bag. Litter bags measuring 10 x 20 cm were made out of fiberglass window screening with a 1mm mesh size. Each bag was filled with 10 grams of intact, air-dried litter with roughly equal amounts of leaf and upper stem material. Fifty grams of litter were oven dried to provide a dry weight correction factor.

Thirty-nine bags were placed at each of the six study sites during the second week of August, 2003. Three bags were immediately collected from each wetland and processed in the lab to correct for any mass lost during transport. Nine bags were left at each of the four sampling stations in each wetland. Litter bags were collected at four points during the following year: November 2003, April 2004, June 2004, and August 2004. During the first three collection dates, eight bags were retrieved from each site (two from each sampling station), and the remaining 12 bags were collected on the final pick-up date. The remaining litter was gently rinsed with de-ionized water to remove silt and macro-invertebrates, oven dried to constant weight at 65° C, and weighed. An annual decomposition rate (k) was calculated for each wetland by fitting a fixed intercept, exponential curve to a graph of mean percent mass remaining for each plot over the course of the year. I assumed exponential decay: $e^{-k*(\text{years})}$ = fraction of mass remaining.

Analysis

Relationships between peak biomass production, decomposition rates, species density and litter biomass were assessed using general linear model regression analyses in SAS (PROC GLM, SAS 2002). Measurements within each wetland were averaged before assessing variation among sites. In addition, a ratio of litter biomass to the biomass of live aboveground tissue (the litter:live ratio) was calculated to provide an estimate of how much litter remains in a wetland relative to the amount produced.

In a temperate wetland, the aboveground production of cattails will die and become litter each fall; thus, peak aboveground biomass should be equivalent to annual litter fall. In an ecosystem with constant production and decomposition rates and negligible physical removal of biomass (e.g., due to fire, water transport, or herbivory), mass lost during decomposition should equal production of litter (inputs) and the system should maintain a predictable amount of organic litter (T). Annual cattail litter inputs and losses were calculated following the model of Olson (1963) for systems with discrete annual litter fall in which L = k' * T, where L is annual litter inputs (peak live biomass) within a meter-squared, k' is the annual fraction of mass lost from litter bags (1- e-kt), and T is the maximum litter layer biomass (peak live biomass + late summer litter layer). I compared peak live biomass of cattails (litter inputs) with estimated mass lost during decomposition to determine whether current rates of litter decay were equivalent to litter inputs. I also predicted the biomass of litter that should be maintained if cattail growth and decay were constant over time and T(predicted) = L / k' as described by Olson (1963). The predicted and measured litter layer were compared to determine how well current rates of production and decomposition explained litter biomass within each wetland setting. The difference between the predicted and measured litter layer is an indication of the importance of other litter input (e.g., changes in production over time) or loss factors (e.g., physical removal of litter).

Litter Manipulation Experiment

Study site

To assess the role of cattail litter in structuring wetland plant communities, I manipulated the litter cover in a cattail-dominated marsh. The study was conducted within Mudge Creek, a large wetland complex that was used in the previous comparison study as an open site. The wetland is located near Wolcott, NY, on East Bay, a shallow embayment that opens directly onto Lake Ontario. Water levels in the marsh fluctuate with Lake Ontario's water levels, with high water levels in the summer months and low water conditions in the winter. The embayment has a watershed of 66 km^2 of which 46 % is agricultural land (pasture or row crop), 43% is forested, 6% is residential and 5% is wetland or open water. During the growing season, the shallow groundwater of the site typically has a pH between 6 and 7, electrical conductivity between 250 and 350 Microsiemens/cm, and a temperature between 14 and 19° C.

The wetland plant community is dominated by *Typha angustifolia* (cattail) with an under story of *Thelypteris palustris* Schott (marsh fern). A number of herbaceous species are present in low densities, including *Impatiens capensis* Meerb., *Calamagrostis canadensis* (Michx.) Beauv. (blue joint grass), *Comarum palustre* L. (marsh cinquefoil), *Decodon verticillatus* (L.) Ell. (whorled loosestrife), *Polygonum amphibium* L. (water smartweed), and *Peltandra virginica* (L.) Schott (arrow arum). A few shrubs, such as *Alnus incana ssp. rugosa* (Du Roi) Clausen (alder), *Cephalanthus occidentalis* (button bush), and *Cornus sericea* L. (silky dogwood), are scattered throughout the marsh.

Study design

In May 2003, I manipulated the cover of standing and fallen litter and monitored changes in the plant community during the following growing season. Dead stems and their attached leaves that remained upright at an angle of 45° or greater were considered "standing" litter. "Fallen" litter was defined as the surface layer of dead leaves and the dead stems at an angle of less than 45°. Standing and fallen litter were removed and added to plots independently to produce six treatment combinations: removal, addition, and control for each litter type (standing and fallen). To avoid excessive disturbance to the plots and to simulate a more realistic scenario, standing litter was manipulated with a natural layer of fallen litter in place, while fallen litter was manipulated after removing all standing dead stems.

For manipulations of standing litter, the erect dead stems and attached leaves were cut from the standing litter removal plots and inserted upright into the standing litter addition plots. A network of persistent stems held these new stems in place for the duration of the experiment. For manipulations of fallen litter, I cut and removed the surface litter layer to the depth where root colonization was evident. These dead stems and leaves were then evenly distributed in the fallen litter addition plots. Thus, litter addition plots experienced approximately twice the amount of litter typical for that area of the marsh.

Litter manipulations were replicated in three areas of the wetland (blocks) that naturally varied in the abundance of *Typha angustifolia* (Table 3.1). A completely randomized block design was used, consisting of three blocks each with six 1 x 4 m subplots in which litter was removed, added, or left intact. Above ground biomass measurements were made adjacent to each of these blocks allowing estimation of litter biomass within the manipulation plots. To minimize edge effects, a half-meter wide buffer of similar treatment conditions surrounded treatment subplots. Measurements made within the four-m^2 subplot were averaged or totaled before performing statistical tests.

Table 3.1. Live and dead cattails, mean water depth, and species density in control plots within each block of litter manipulation treatments.

	Block 1 Higher abundance of live cattails	**Block 2** Intermediate abundance of live cattails	**Block 3** Lower abundance of live cattails
LIVE CATTAILS			
Biomass of live cattails (g/m^2)	1070	777	595
Density of cattails in May (stems/ m^2)	21	17	15
Density of cattails in Sept. (stems/m^2)	27	25	26
Final height of cattails (cm)	251	245	252
LITTER			
Biomass of total litter (g/m^2)	3115	2812	2141
Ratio of standing:fallen	0.7	0.4	0.6
Fallen litter depth in May (cm)	28	20	16
HYDROLOGY			
Water depth in May (cm)	10	11	2
Water depth in September (cm)	0	0	0
SPECIES RICHNESS			
Control plot species density (spp/m^2)	1.75	2.5	6.25

In addition to measuring changes in the existing plant community, I transplanted eight test seedlings into each of the treatment and control plots to provide a standardized assessment of growth conditions for establishing plants. One hundred forty-four *Peltandra virginica* seedlings were gathered from a similar, neighboring wetland in May, 2003. At the time of collection, each seedling was 15-20 cm tall, with 1-2 leaf blades and no root branching. The seedlings could be collected with minimal disturbance because they were floating in standing water and were not yet rooted in the substrate. Within 24 hours, the seedlings were placed in the study plots where similar moisture conditions prevailed. I placed the base of each plant into the litter layer such that at least 5 cm of the stem and all of the leaves emerged. Initially, the roots did not necessarily contact the soil surface, depending on the depth of the fallen litter. After one month, over 80 % of the seedlings were alive and after four months, 55 % were alive. In mid September the seedlings were measured, dried and weighed.

Analysis

Differences in final species density, test seedling survival, and test seedling biomass were assessed. Analysis of variance was performed using the general linear model procedure (SAS 2002). Because litter was manipulated within a single treatment plot within each block, interactions between treatment and block could not be evaluated. Block locations were selected to represent a natural gradient in cattail biomass (Table 3.1), and are therefore considered fixed effects. The standing and fallen litter treatments were analyzed separately. Tukey's error correction for all pairwise comparisons was used when assessing differences among litter levels (SAS 2002). The assumptions of equal and normally distributed variance were met in all cases.

RESULTS

Comparison of Lake Ontario Wetlands

The relative abundance of live cattails and the biomass of plant litter differed between the open embayment wetlands and the barrier-beach protected wetlands (Figure 3.1). The biomass of cattails was, on average, 89-92% of the total live biomass in the open wetlands, and only 25 - 47% of the live biomass in the wetlands closed to Lake Ontario. Peak live biomass did not differ significantly between the wetland settings; the mean above-ground peak biomass was between 816 and 1077 g/m^2 at all sites, with the exception of one closed wetland that produced 414 g/m^2 in aboveground herbaceous biomass. In contrast, the mean biomass of standing and fallen litter was much higher in sites open to Lake Ontario. Thus the amount of total litter per unit of live biomass (ratio of litter:live biomass) was higher in the open wetlands (mean =

2.0) than closed wetlands (mean = 1.5), although the difference was not statistically significant. The ratio of cattail litter to live biomass was significantly higher in the open wetlands (mean = 2.0) than the closed wetlands (mean = 0.76), suggesting that a higher proportion of live cattail biomass accumulates as litter in the wetlands open to Lake Ontario.

The closed wetlands had a higher mean plant species density (8.75 - 9.75 species/ m^2) than open embayment wetlands (6.75 to 8 species/m^2). Simple regression analyses revealed that mean biomass of litter was negatively related to the species density of a wetland ($p=0.005$, $R^2 = .88$) and the biomass of non-cattail species ($p= 0.041$, $R^2=.69$) (Figure 3.2). Thus, although aboveground production was similar across sites, cattails constituted a larger proportion of the live biomass, litter biomass was higher, and species density was lower in the wetlands open to Lake Ontario.

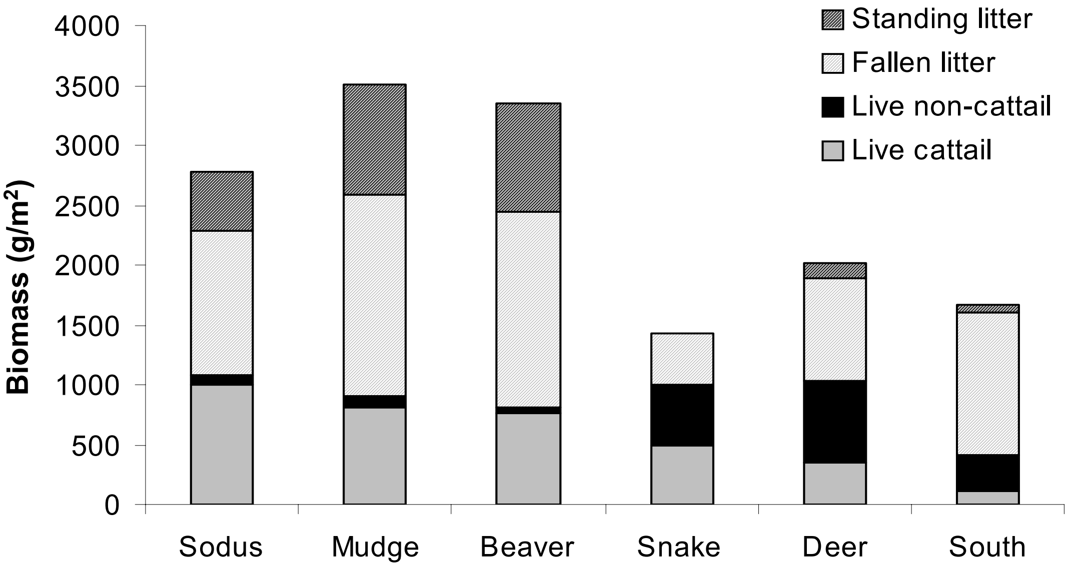


Figure 3.1. Mean biomass of vegetation and litter in late July 2003, in three open wetland sites (left) and three protected wetland sites (right).

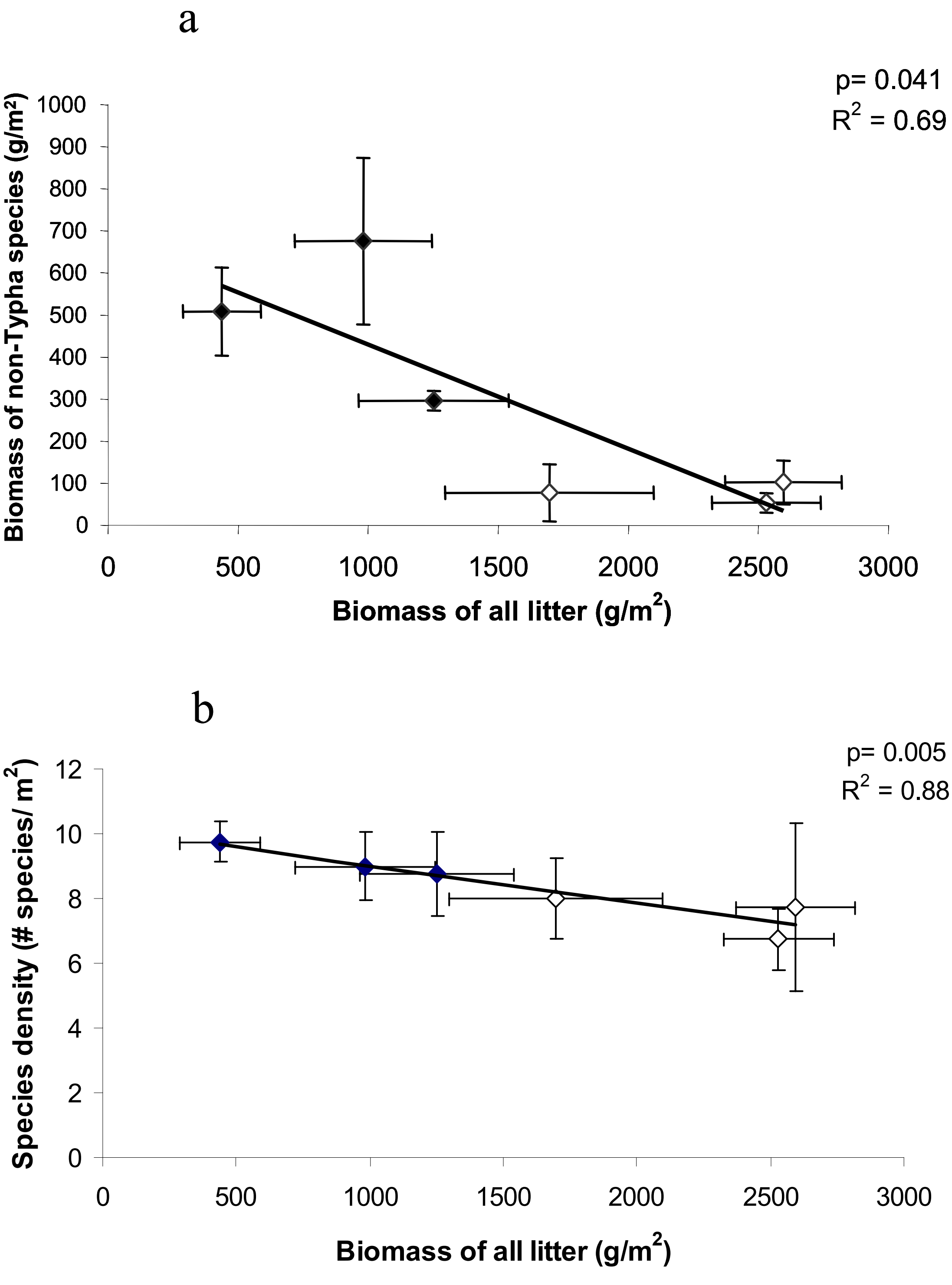


Figure 3.2. Relationship between the mean biomass of all litter and (a) the mean biomass of non-cattail species, and (b) mean species density in open and protected wetland sites. Bars indicate +/- 1 SE (n=4).

Hydrology

The pattern of water table fluctuations in the six wetlands varied according to their hydrogeologic setting (Figure 3.3). The wetlands open to the lake tracked the weekly fluctuations and seasonal trends of Lake Ontario. The daily lake level fluctuations were not as pronounced within the open wetlands, because the embayment moderates wind driven currents. Water levels decreased between June and September in Lake Ontario in the open wetlands with the exception of Sodus Bay, which exhibited virtually no change. The water level recorder at Sodus Bay was located close to a water channel in a stand of cattails that may have been floating and thus rising and falling with the lake water level. As *Typha* species are known to form floating mats (Hogg and Wein 1988), such an interpretation is reasonable. Water levels on Lake Ontario and the open wetlands are influenced by precipitation patterns across the entire Great Lakes basin, but remain relatively stable due to the large volume of water in the lake and the regulated outflow across the Moses-Saunders dam on the St. Lawrence River.

In contrast with the open wetlands, the wetlands with only indirect or temporary connections to Lake Ontario experienced a more variable pattern of water table fluctuations and an overall greater seasonal and monthly range of water levels (Table 3.2). The hydrograph for each of the closed wetlands differed, depending on its unique connection to Lake Ontario (Figure 3.3). For example, the outlet from Deer Creek into Lake Ontario is usually filled with sand, but it periodically blows open causing gradual increases and sharp drops in water levels. South Pond wetland is connected to Lake Ontario via a series of channels and ponds, such that the seasonal trends in water level correspond with those of Lake Ontario, but the water table rises more dramatically after rain events due to slower drainage. Seasonal water levels in

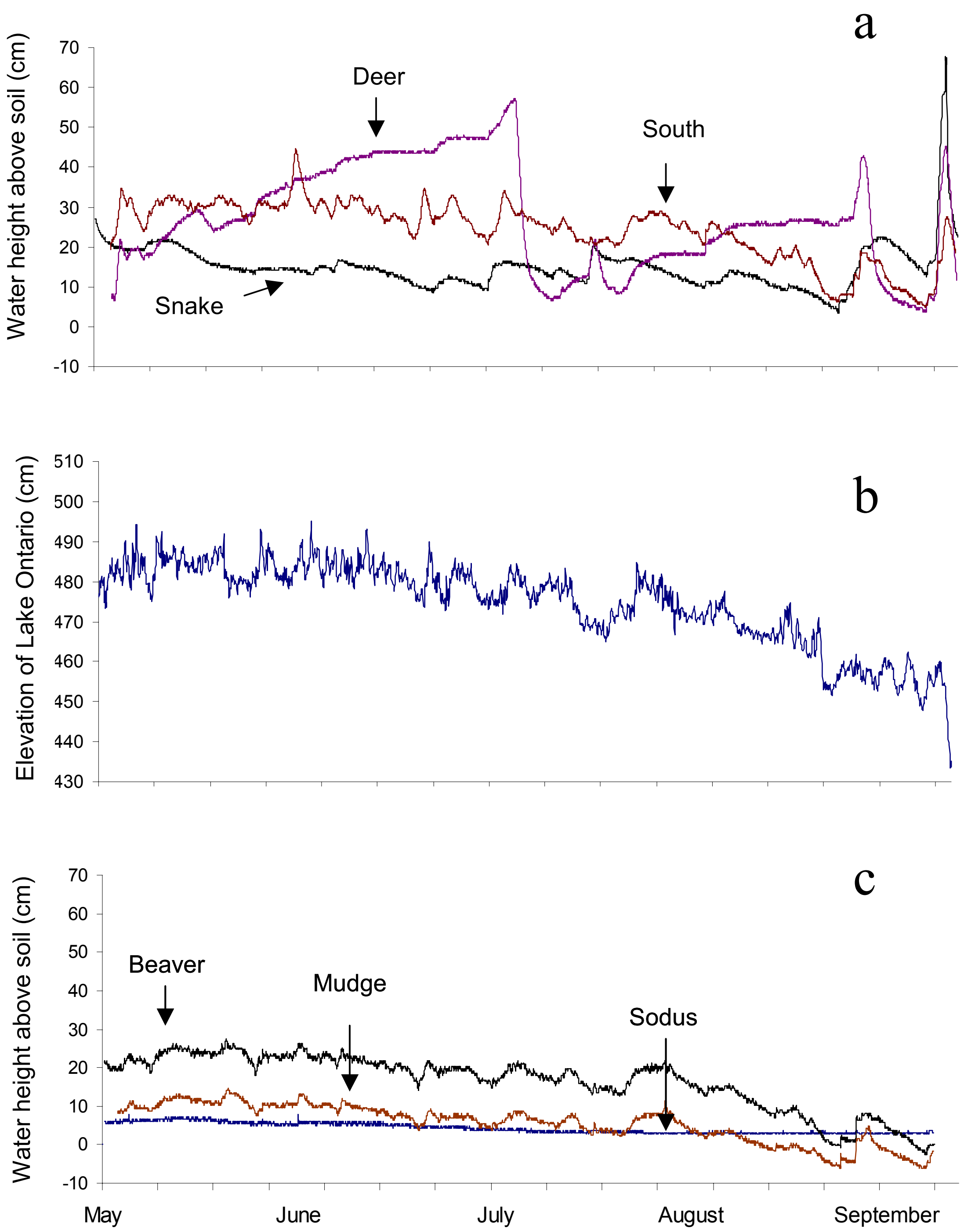


Figure 3.3. Hydrologic fluctuations in the protected wetland sites (a), in Lake Ontario (b), and in the wetlands open to the lake (c). Water level measurements are relative to the soil surface in each wetland. Data were collected every half hour from May to September 2004.

Table 3.2. Characteristics of seasonal and monthly water levels relative to soil surface (cm), between May and September 2004, in the six study sites. ANOVA was used to test whether a parameter differs significantly (bolded) between open and protected wetlands.

	Wetlands open to lake			Wetlands protected from lake			setting difference
	SODUS	MUDGE	BEAVER	SNAKE	DEER	SOUTH	
SEASONAL							
Average (cm)	4.3	5.5	16.4	15.0	27.0	24.2	*p = 0.065*
Standard deviation	1.3	5.0	7.2	5.9	13.1	7.4	*p = 0.196*
Maximum	7.7	14.7	27.5	67.9	57.2	44.7	***p = 0.011***
Minimum	2.7	-6.2	-2.5	3.5	3.7	4.8	*p = 0.083*
Range	5.0	20.9	30.0	64.4	53.6	39.9	***p = 0.029***
MONTHLY							
Standard deviation	0.4	1.9	2.8	4.5	9.4	4.5	*p = 0.066*
Range	2.0	8.4	11.3	20.4	33.4	19.1	***p = 0.033***

Snake Swamp were variable but did not track Lake Ontario because this wetland has no surface water connection to the lake. Precipitation was higher than average during the summer of 2004 and water levels remained high overall. Barrier beaches restricted flow out of the protected wetlands, causing them to respond more strongly to local precipitation events than did the open wetlands.

Litter dynamics

Given the similarity in peak production across wetland sites, rates of decomposition were expected to be lower in the open wetlands where litter biomass was higher. After a full year, the percent of litter remaining varied from 78.8 % (+/- 1.3) to 59% (+/- 1.2) among the six wetlands; however, the range of mean decay rates within the two hydrogeologic settings was comparable (Figure 3.4). Surprisingly, the estimated decomposition rate constant (k) did not directly correspond to the mean or variance in

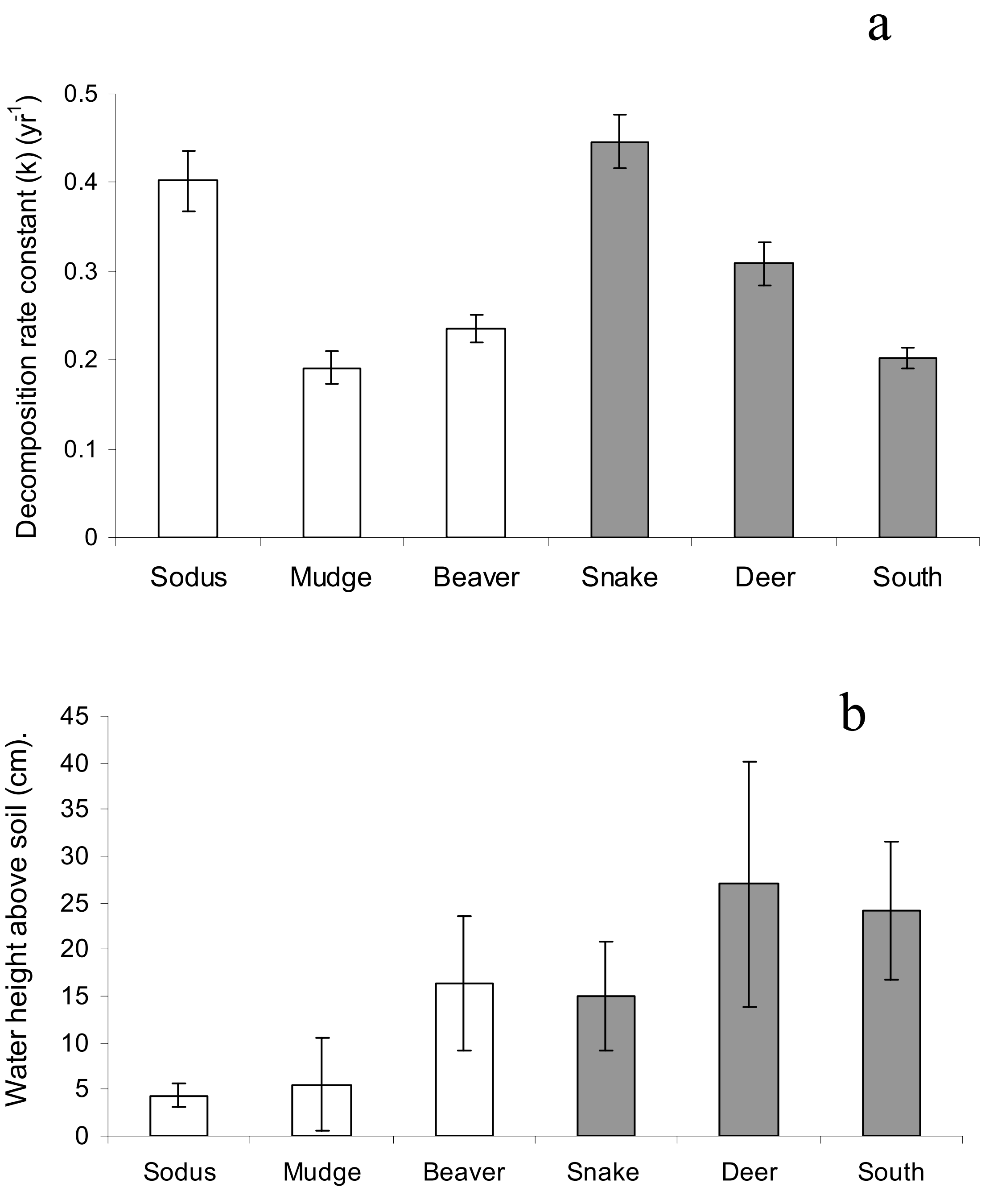


Figure 3.4. Annual decomposition rate constant (+/- SE) (a), and mean summer height of water above the soil (+/- STD) (b) in the six study sites.

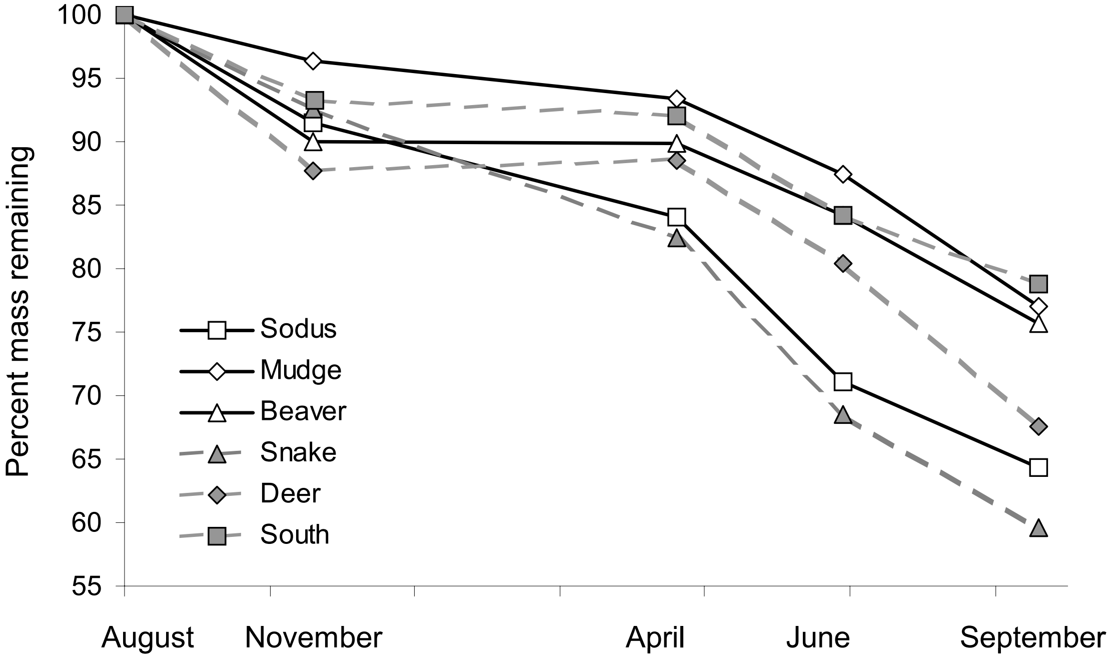


Figure 3.5. Percent of original mass of cattail litter remaining at each of the four collection dates during the 12-month study. Points represent mean values for each of the open wetlands (open symbol) and protected wetlands (filled) (n = 4).

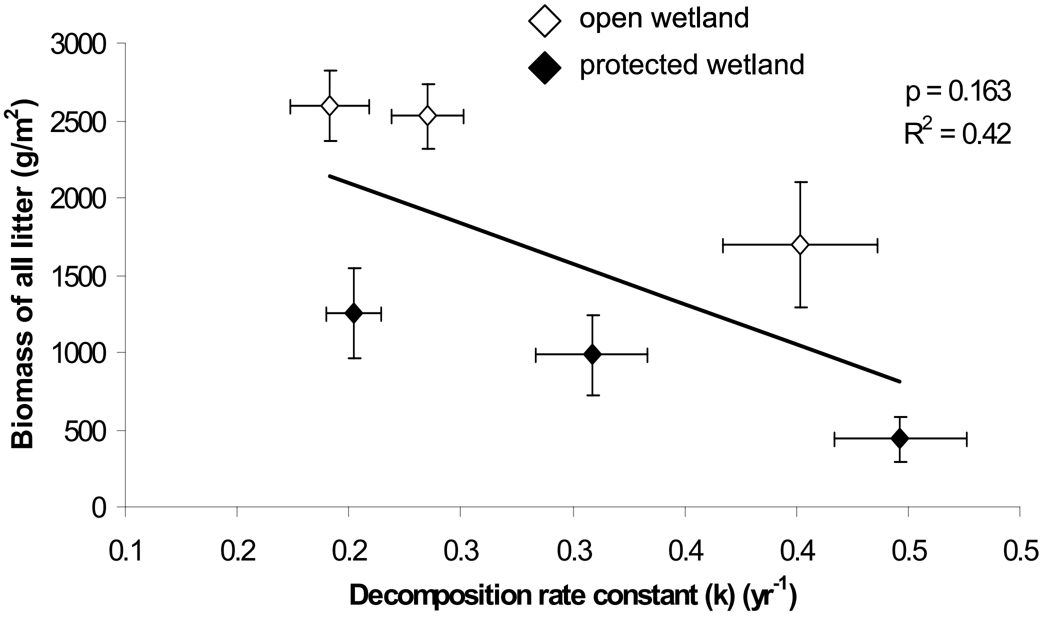


Figure 3.6. Relationship between mean litter biomass and mean rate of decomposition in open and protected wetland sites. Bars indicate +/- 1 SE (n = 4).

water table elevation (Figure 3.5). Hydrologic measurements taken at a single location within a wetland over the course of four months may not have captured the variation relevant to decomposition rates.

Differences in decay rates could not account for the overall higher amounts of all litter types in the open wetlands (Figure 3.6). Peak live biomass and decomposition rate together explained only 66% of the variation in litter biomass. However, decomposition rate combined with either wetland setting or the proportion of cattails could explain 99% of the variation in litter biomass (Table 3.3).

In all six wetlands, peak aboveground cattail biomass (litter inputs) was higher than the estimated cattail litter decay losses. However, the ratio of cattail decomposition to production differed significantly between wetland settings ($p = 0.006$); estimated decay losses were on average 79% of live cattail biomass in the open wetlands, and only 45% of peak live biomass in the protected wetlands (Figure 3.7). Current rates of cattail production and decomposition could maintain 42% more litter biomass than actually measured in the open wetlands, and 400% more cattail litter biomass than measured in the protected wetlands (Figure 3.8). Deviations from the 1:1 line for both results indicates that either: (1) cattail growth and decay are not constant, i.e., aboveground production was lower or decomposition was higher in past and the systems are accumulating litter; or (2) some litter is physically transported out of the wetland, explaining with the biomass of litter is lower than predicted. The larger discrepancy for the protected wetlands suggests that cattail abundance or litter accumulation are changing more rapidly, or more litter is transported out of these wetlands in comparison with wetlands open to Lake Ontario. In sites where cattails are less abundant there is a larger imbalance between decomposition and production (Figure 3.9).

Table 3.3. Relationship between mean litter biomass and potential predictor variables (live biomass, proportional abundance of cattails, wetland setting and decomposition rate). Results from several single and multi-variable regression models are compared.

Variable predicting mean litter biomass *(partial p value)*		**Full model R-square**
Single variable model		
Live biomass (all species) *(p=0.8913)*		0.005
Decomposition rate *(p=0.163)*		0.422
Relative abundance of cattails (cattail/ total live biomass) *(p=0.0600)*		0.628
Wetland setting *(p= 0.0211)*		0.772
Multi-variable model		
Decomposition rate *(p=0.1094)*	Live biomass *(p=0.2830)*	0.631
Decomposition rate *(p= 0.0004)*	Wetland setting *(p= 0.0002)*	0.996
Decomposition rate *(p=0.0029)*	Relative abundance of cattails *(p=0.0007)*	0.992

Note: Full model R^2 indicates the proportion of the variation in biomass that can be explained by the variables in the model. The p value in parentheses indicates the significance of the predictor variable, within the regression model.

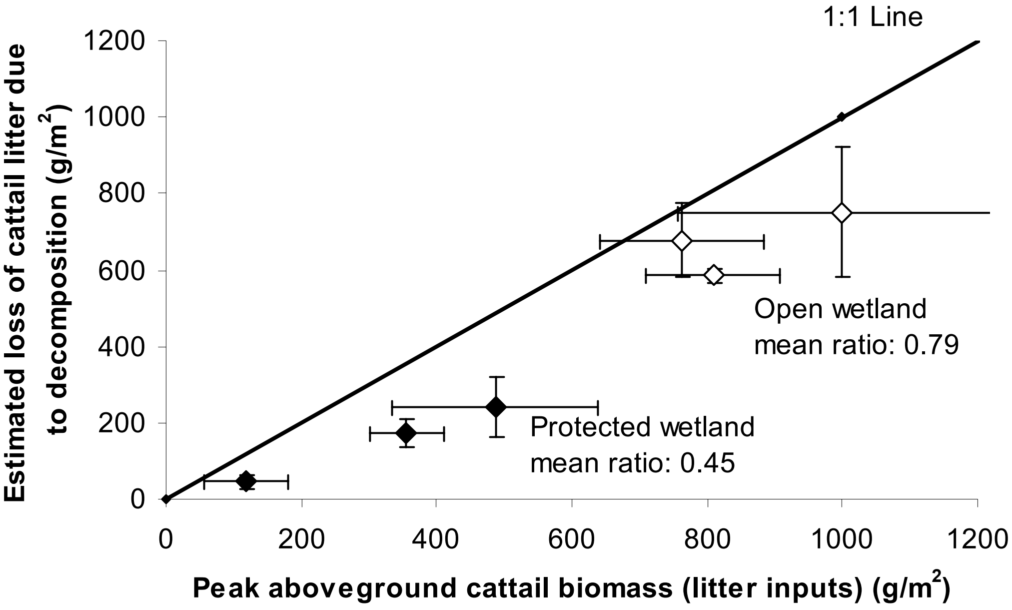


Figure 3.7. Relationship between the peak above ground production of cattails (litter inputs) and the estimated decomposition losses based on measured values for litter decay and litter layer biomass. Error bars represent 1 SE. The mean ratio of losses to inputs is reported for each wetland setting.

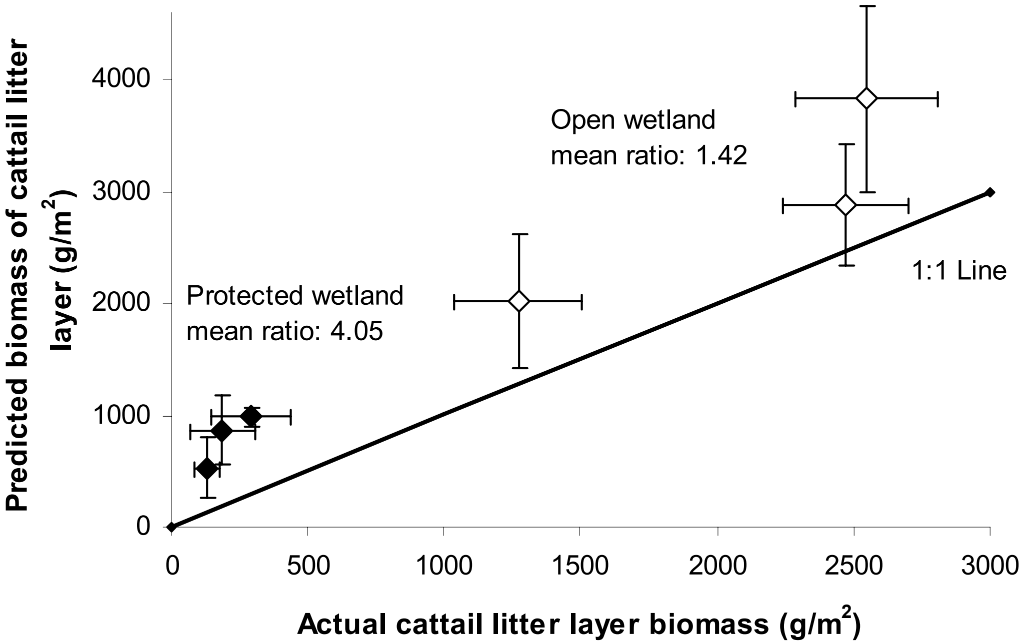


Figure 3.8. Relationship between the measured cattail litter biomass and the predicted litter layer based on measured values for litter production and decomposition. Error bars represent 1 SE. The mean ratio between predicted and actual litter biomass is reported for each wetland setting.

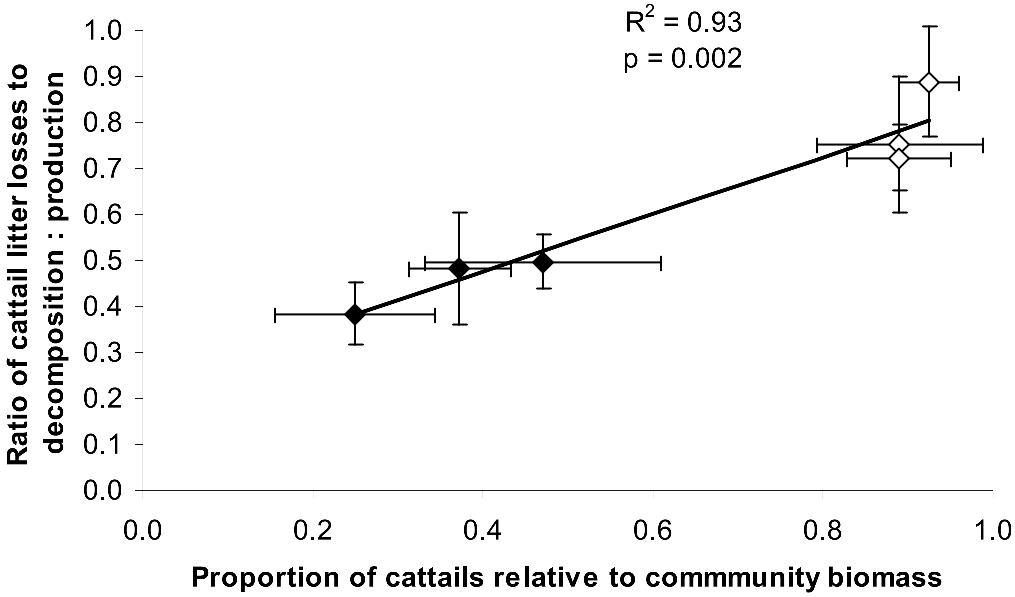


Figure 3.9 Relationship between the relative abundance of cattails and the ratio of estimated cattail litter decomposition to litter production. Error bars represent 1 SE.

Litter Manipulation Experiment

At the end of the 14-week experiment, in which we investigated the relationship between cattail litter accumulation and the co-existence of other plant species, species density varied among litter manipulation treatments and locations within the wetland, from a mean of 9.25 to one species/m^2. Fallen litter significantly reduced species density ($p= 0.024$), but the effect of standing litter treatments was not consistent (Figure 3.10).

Survival of the test seedling, *Peltandra virginica*, provides a standardized indicator of how litter additions and removal affected conditions for seedling establishment. On average, 55% of the transplanted seedlings were alive, green and apparently established in September 2003. The survival of the eight phytometer seedlings planted in each 4-m^2 plot ranged from 0 to 100 %, depending on the litter treatment and location within the wetland block. Additions of fallen litter reduced the survival of the test seedling ($p = 0.061$); however, manipulating the standing litter alone had no measurable effect ($p = 0.651$) (Figure 3.11a). Contrary to expectation, neither standing nor fallen litter treatments significantly affected the final size of the seedlings (Figure 3.11b).

The biomass of live and dead *Typha angustifolia* and community composition naturally varied among the three blocks within Mudge Creek (Table 3.1) and influenced experimental results (Table 3.4). Litter-addition treatments were applied by adding all of the litter from an equally sized, neighboring plot; therefore the biomass of litter in the control and addition plots differed among blocks. Final species density and seedling survival were negatively related to the combined biomass of fallen and standing litter in the treatment plots (Figure 3.12). Species density and seedling survival responded consistently to litter biomass, despite natural variation among blocks. In fact, both response variables, species density and seedling survival, were significantly correlated ($p= 0.0027$), particularly within blocks 1 and 2 (intermediate and high abundance of *Typha glauca*) (Figure 3.13). The three treatment blocks capture a range of both cattail abundance and species richness that may reflect an underlying abiotic gradient. At a given biomass of litter, both species density and seedling survival were lower in blocks with a higher abundance of *Typha angustifolia.* The significant influence of the location within the wetland (block effect) indicates that litter is only one factor controlling species density within a cattail marsh.

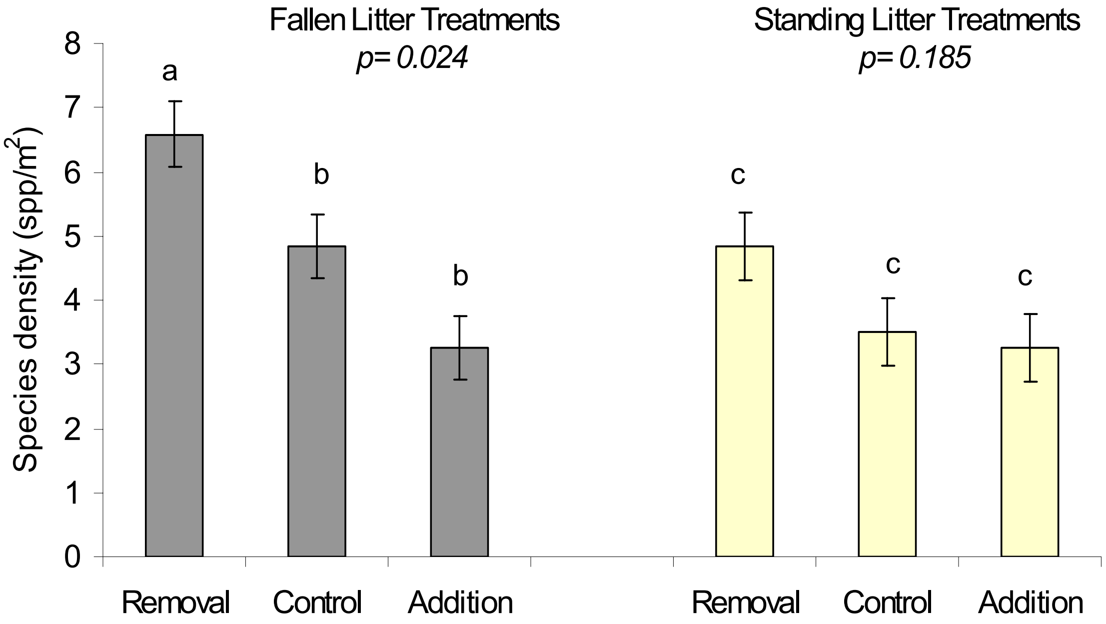


Figure 3.10. Species density (+/-1 SE) after 14 weeks (*n* = 3) in litter manipulation treatments. Letters indicate significantly different means at the $p < 0.05$ level. The significance of the overall effect of each type of litter is reported (p-value).

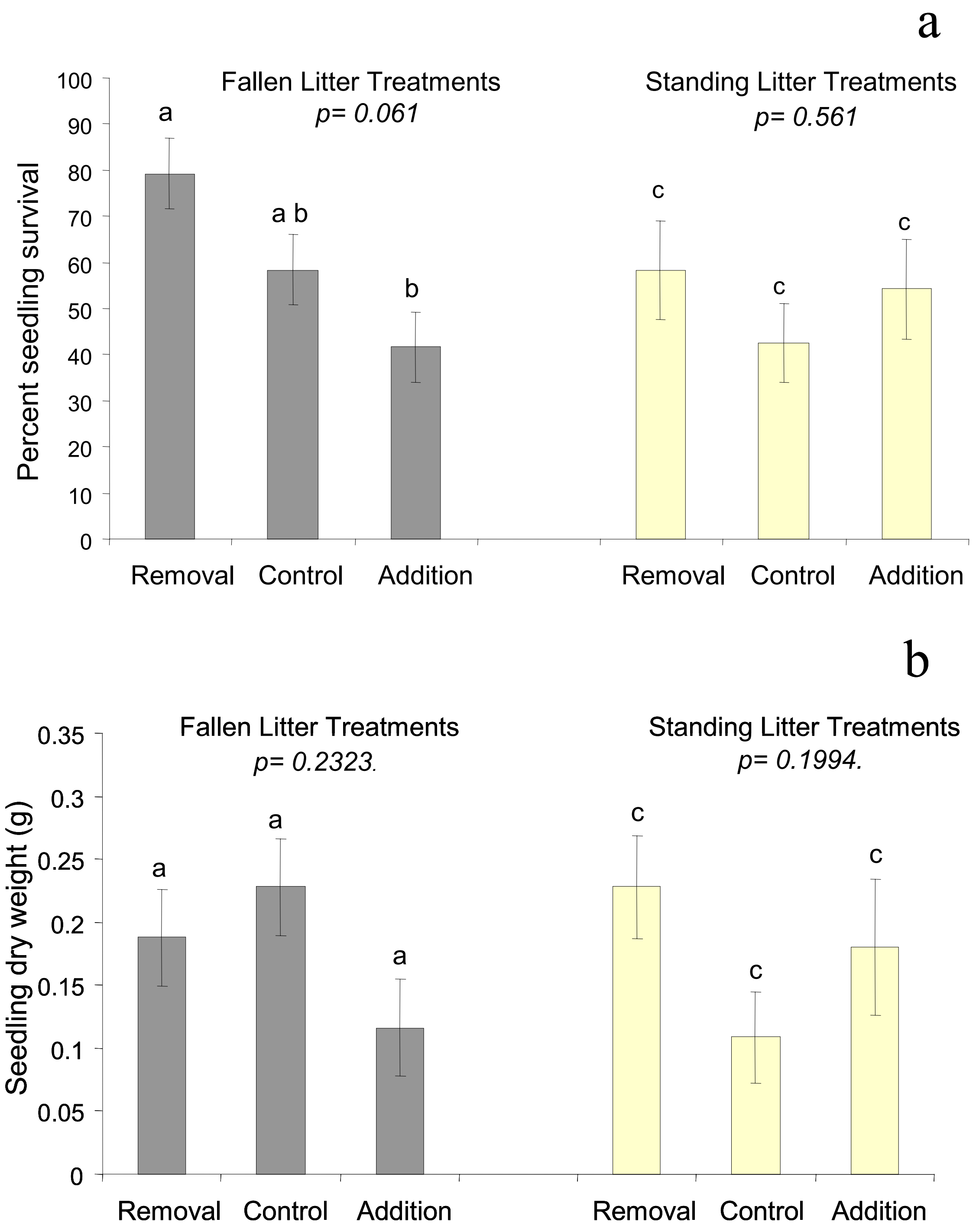


Figure 3.11 Seedling survival (+/- 1 SE) (*n* = 24) (a), and dry weight of surviving test seedlings (+/- 1 SE) (*n* = 10 - 24) (b) after 14 weeks in litter manipulation treatments. Letters indicate significantly different means at the $p < 0.05$ level. The significance of the overall effect of each type of litter is reported (p-value).

Table 3.4. Species occurring in fallen litter treatment plots after 14 weeks, listed by block.

	Block 1 Higher abundance of live cattails	**Block 2** Intermediate abundance of live cattails	**Block 3** Lower abundance of live cattails
Species found in all fallen litter treatment plots	*Typha angustifolia* *Thelyptris palustris*	*Typha angustifolia* *Thelyptris palustris* *unknown seedling*	*Typha angustifolia* *Thelyptris palustris* *Lysmachia thyrsiflora* *Triadenum virginicum* *Impatiens capensis* *Polygonum amphibium* *Boehmeria cylindrica* *Scutellaria galericulata* *Asclepias incarnata*
Species found *only* in control and fallen litter removal plots	*Impatiens capensis*	*Cornus amomum* *Lythrum salicaria* *Galium tinctorium* *Lysmachia thyrsiflora* *Scutelaria galericulata* *Calamagrostis canadensis*	*Cicuta bulbifera* *Cephalanthus occidentalis* *Galium tinctorium* *Acer rubrum* *Alnus incana*
Species found *only* in fallen litter removal plots	*Lythrum salicaria* *Poa* sp. *Galium tinctorium* *Campanula aparinoides* *Unknown seedling* *Osmunda regalis*	*Osmundo regalis* *Poa* sp. *Decodon verticillatus*	*Scutellaria galericulata* *Asclepias incarnata* *Solidago* seedling *Carex* seedling *Poa* sp. *Osmunda regalis* *Decodon verticillatus*

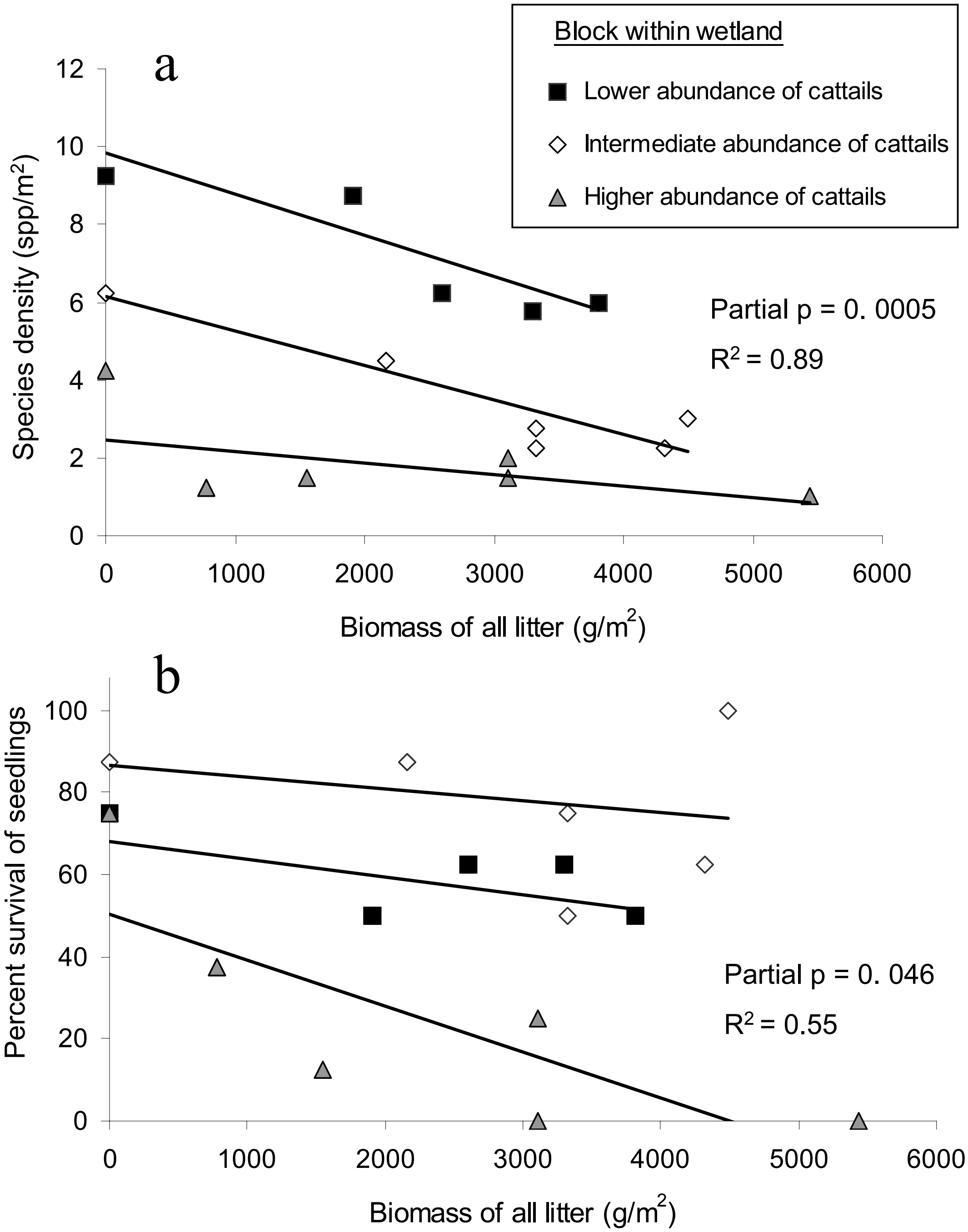


Figure 3.12. Relationship between the biomass of all litter and (a) species density, and (b) seedling survival, within the three blocks after 14 weeks of experimental litter manipulation. R^2 indicates how much variation is explained by both block and litter biomass. The partial p value indicates the significance of the relationship between litter biomass and species density (a) or seedling survival (b), after accounting for the natural variation due to block.

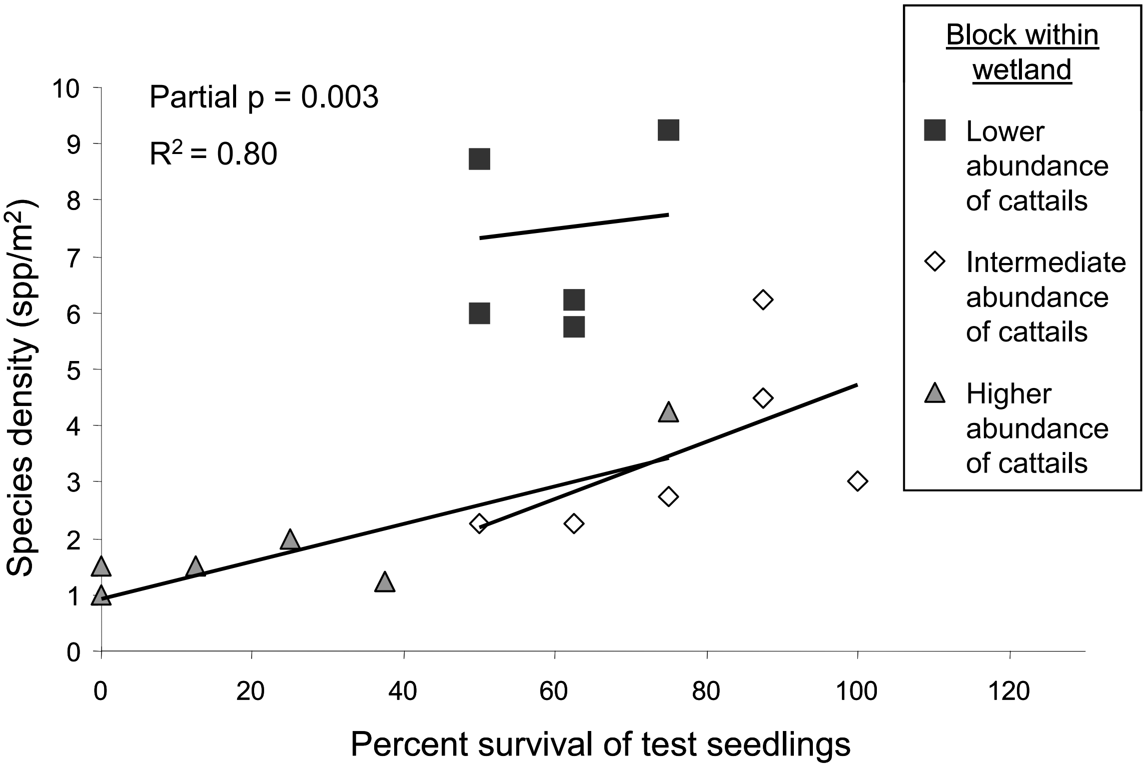


Figure 3.13. Relationship between seedling survival and species density within the three blocks after 14 weeks of experimental litter manipulation. R^2 indicates how much variation is explained by both block and litter biomass. The partial p value indicates the significance of the relationship after accounting for the natural variation due to block.

DISCUSSION

The Effect of Litter on Species Co-existence

A comparison of Lake Ontario wetlands indicates that total litter biomass or live cattails could be directly inhibiting other species; however, an underlying factor could be influencing both species density and litter accretion independently. Among the six study wetlands, species density was negatively correlated with the biomass of litter, but was not significantly related to aboveground live biomass. This pattern was underlain by differences in the vegetation of wetlands hydrologically open and closed to Lake Ontario. Although aboveground live biomass was similar across wetland settings, cattails constituted a larger proportion of the living biomass and there was more organic litter in the wetlands open to the lake, where species density was lower. All six wetlands had relatively deep peat soils (1-4m) and the water table was consistently above the soil surface during the growing season. However, the more diverse, closed wetlands tended to have deeper, more variable water levels and more microtopographic variation, both factors that influence plant diversity (Vivian-Smith 1997; Hill et al. 1998; Riis and Hawes 2002; Werner and Zedler 2002) and may influence litter decay.

My field manipulation demonstrated that cattail litter, independent of other factors, does influence species density in marshes. Experimentally increasing the cover of cattail litter, without changing the density of live cattails, reduced species density and seedling survival. In plots where all litter was removed, juvenile plants of many species were observed, the standard test seedling survived better, and species density increased. This field experiment isolated the role of cattail litter, but environmental variation and long term competitive interactions also drive differences in species density within or between wetlands.

Litter has been shown to have a positive or negative effect on seed germination, seedling establishment, plant growth, and species diversity, depending on the ecosystem, the type of litter, and the species involved (as reviewed by Xiong and Nilsson 1999). In the cattail marsh studied, three lines of evidence suggest that cattail litter may reduce species density by impacting seed germination and establishment processes: (1) fallen litter had a stronger impact than even a dense layer of standing litter, (2) the survival of the test seedling and the final species density of a plot were closely correlated suggesting a similar mechanism may be responsible for both responses, and (3) the growth of the test seedlings that survived was not affected by litter cover, indicating that established plants were less sensitive to litter.

The mechanism by which litter impacts plant community composition is often hard to determine. In some systems, such as grasslands, litter is thought to benefit the regeneration of certain species by retaining moisture, insulating the soil, protecting seeds from predators (Jarvis 1964), altering competitive interactions (Facelli 1994), and adding nutrients or changing the pH (Dzwonko and Gawronski 2002). In other situations, litter has been shown to hinder species recruitment due to chemical inhibition of germination (McNaughton 1968), reduced chances of seeds reaching the soil (Foster and Gross 1997), diminished light penetration (Facelli and Pickett 1991), increased seed and seedling herbivory (Facelli 1994), elevated risk of fungal attack (Facelli 1994), alteration of germination cues such as temperature fluctuations (Sydes and Grime 1981b), and physical interference with root or shoot growth (Sydes and Grime 1981b). In wetlands, two experiments comparing plastic pseudo-litter and plant litter, found that the amount of litter was more important than the actual type of litter (i.e., plastic pseudo- or organic litter) indicating that litter induced a primarily physical effect on seeds or seedlings (Sydes and Grime 1981b; Jordan et al. 1990). Potentially allelopathic compounds in marsh and aquatic plants have been isolated and bio-assayed in the lab; however, field investigations of allelopathy have yielded mixed results (McNaughton 1968; Bonasera et al. 1979; Gallardo-Williams et al. 2002; Ervin and Wetzel 2003; Gross 2003). This study cannot distinguish between potential physical or chemical causes of the reduced seedling survival, as both mechanisms would be more pronounced in a thicker layer of litter.

Litter Dynamics

The observed relationship between litter and species density in marsh systems lends importance to the question of why litter biomass varies among wetlands. It is surprising that peak herbaceous biomass and decomposition rates, when considered alone or together, were relatively poor predictors of a wetland's mean biomass of litter, but the hydrogeologic setting of a wetland was significantly related to litter biomass (Table 3.3). These patterns indicate that abiotic, or compositional differences between the open and protected wetlands are responsible for the unexplained variation in litter biomass.

The type of plant material, the way litter is fragmented, microbial activity, and flooding will influence the rate at which litter is transformed into soil organic matter, DOC or CO_2. Litter also may be physically removed from wetlands regularly impacted by waves, fires, or ice scouring. The litter-bag technique used in this study provides an integrated measure of conditions affecting decomposer activity (e.g., oxygen availability, pH, moisture, light) for a specific type of litter, in the spot where the bag is located. My litter bags incorporated both the stem and leaf material that constitute fallen litter. The calculated decay rates are somewhat lower than other studies using *Typha* litter, in part due to the inclusion of stems (Mason and Bryant

1975; Davis and Vandervalk 1978). Aquatic invertebrates are important decomposers in wetlands (Dezozaya and Neiff 1991) and many were found inside the litter bags. This study did not measure decay rates of dead leaves or stems that remained upright. Thus, measuring mass loss from litter bags quantifies only one component of litter loss; factors influencing plant senescence, aerial decay, standing litter fragmentation or litter removal may be equally important and variable among wetlands.

An analysis of just cattail biomass minimizes variation due to plant species and further illustrates the differences between wetland settings. In the hydrologically variable, protected wetlands the estimated losses due to decomposition were equivalent to only half of the annual production of cattail litter; and the layer of cattail litter measured was four times lower than would be predicted based on the current rates of production and decomposition (Figure 3.7 and 3.8). Estimated losses due to decomposition better matched current rates of litter production in the open wetlands. There are two likely explanations for the discrepancy, both of which could be more pronounced in the protected wetlands: (1) cattail abundance is increasing, resulting in more live biomass relative to litter; and (2) biomass is physically removed from the system, accounting for the difference in litter inputs and losses. Cattail communities may be expanding, particularly in the diverse wet meadows of the protected wetlands. Limited documentation indicates that cattails have become more abundant around Lake Ontario in the last 40 years (Wilcox et al. 2004). In addition, some litter fragments are probably transported out of the wetlands during flooding events, even from the areas sampled, which were at least 20m from open water. The protected wetlands are adjacent to small ponds or slow moving creeks and the open wetlands occupy shallow embayments that are not exposed to waves. The more variable flooding regime in the protected wetlands likely removes more plant material than the relatively stable water levels in the open wetlands, affecting the degree to which litter accumulates and inhibits the growth of other species.

The higher density of live cattails and upright dead stalks in the open wetlands may further limit the movement and breakdown of litter. Sites with a lower abundance of cattails have less standing litter (Figure 3.1) and have a larger imbalance between litter inputs and decay losses (Figure 3.9); if the imbalance indicates the degree to which litter is physically washed out of the wetlands, then cattails may be limiting the movement of litter in wetlands open to Lake Ontario. Davis and Van Der Valk (1978) found that fully 50% of the biomass of a senesced cattail stand remained standing through the winter until the following June, and some stems remained upright for two years. They further observed that this standing litter stage lasted longer for *Typha glauca* than for ecologically similar graminoids from the genera *Scirpus*, *Sparganium,* and *Carex*, even though decomposition rates of fallen litter were similar among the species (Davis and Van Der Valk 1978). Although the hydrologic regime was not well correlated with measured decay rates, flooding could weaken or fragment dead stems, influencing the transfer of standing litter to the fallen litter layer. Typically decomposition accelerates after stems topple and flood because the moisture limitation is relieved and micro and macro fauna can access the litter (Dezozaya and Neiff 1991; Van der Valk et al. 1991; Kuehn and Suberkropp 1998). Thus wetland communities with a higher proportion of cattails likely have a more persistent layer of standing litter, which in turn may slow overall litter breakdown and inhibit the movement of litter during flooding.

Implications for Great Lakes Plant Communities

A wetland's response to litter will depend on the degree to which it relies on regeneration by perennial species and vegetative growth as opposed to seed recruitment and colonization. Results of the litter manipulation experiment indicated that seedling survival was sensitive to litter biomass, but the final size of the established test seedlings did not depend on the amount of litter present. This is consistent with the finding of Foster and Gross (1997) that litter inhibited the success of seeds but did not affect mature transplanted individuals. Variable systems, such as prairie potholes and riparian wetlands, typically rely on the germination of buried seeds after cycles of flooding and drawdown (Van der Valk and Davis 1978; Wilson 1993), and litter has been shown to influence seed germination and community composition in these systems (Van der Valk 1986; Xiong and Nilsson 1997; Xiong et al. 2001).

Lake Ontario's water levels are currently regulated to minimize inter-annual variation, but before lake-level control began in 1960, wetlands open to the lake probably experienced more temporal variation and species turnover. The increase in species in the litter removal plots at Mudge Creek, a wetland open to the lake, indicates that species adapted to take advantage of ephemeral openings in the canopy or litter layer are still present Even though cattails make up 89% of aboveground biomass in Mudge Creek wetland, natural seed dispersal or seed banks appear to be a viable and diverse source of new species. Water levels fluctuations have been shown to increase wetland species diversity by killing vegetation during high water periods and later exposing bare mudflats (Van der Valk and Davis 1978; Keddy and Reznicek 1986). This study suggests that moderate fluctuations that remove litter but not necessarily live plants could also increase species diversity.

Plant community response to litter is often species specific and thus, the way litter accumulates has the potential to structure communities (Sydes and Grime 1981a; Facelli and Pickett 1991; Facelli 1994; Xiong et al. 2001). Annual or non-clonal, herbaceous plants with less below ground storage may be particularly vulnerable to the accumulation of litter. For example, *Scutelaria galericulata*, and *Galium tinctorium,* were observed in the control but not in the fallen litter addition plots, indicating that they may have failed to germinate or emerge as a result of the thick litter layer (Table 3.1). In contrast, clonal species, such as *Thelyptris palustris* and *Lysmachia thyrsiflora,* occurred even in plots with additional fallen litter. Cattails also store resources in their network of rhizomes, allowing them to regenerate quickly in the spring and push through dense layers of litter (Grace 1993). Species like cattails that reproduce vegetatively do not need to propagate from seeds in their immediate vicinity, making them insensitive to their own litter accumulation or allelochemicals that might suppress other species (Ervin and Wetzel 2003).

The dense layer of litter in the lake controlled, open wetlands may be preventing the regeneration of sedge meadow species, even during lower water-level periods. Given that water levels are similar or lower in the open wetlands, it is surprising that wet meadow species are nearly absent from the cattail-dominated, open wetlands. This study found that many of the wet meadow species common to the protected wetlands are present as subordinate plants and seeds in the open wetlands. For example, species of the genera *Poa, Carex* and *Solidago,* which occur widely in the protected wetlands, appeared as seedlings in the fallen litter removal plots of Mudge Creek. Many *Carex* species regenerate from rhizomes and should be relatively tolerant of litter. Sustained high water levels or a major disturbance, followed by years of competition with the taller cattail species probably eliminated them. The relatively rapid response of

Mudge Creek to litter removal indicates that restoration of a more diverse plant community may be possible if the litter of *Typha angustifolia* was reduced and a natural disturbance to the litter layer was recreated.

CONCLUSIONS

A species' ability to dominate is determined, in part, by its ability to achieve a larger size and reduce the fitness of its neighbors (Grime 2001). This study reveals that the production and accumulation of plant litter is one mechanism by which cattails can impede the survival of other species. Across Lake Ontario wetlands, litter biomass was negatively correlated with species density and litter biomass was higher in cattail-dominated marshes. Experimental results indicate that a persistent layer of fallen cattail litter can negatively influence seedling survival and, as the biomass of litter increases, species density and seedling survival decline.

In Lake Ontario wetlands, the proportion of cattail production that accumulates as litter appears to depend on both the decomposition rate and the hydrogeologic setting. More litter relative to the amount produced remains in cattail-dominated wetlands that are stabilized by Lake Ontario's water levels. In contrast, protected wetlands experience more hydrologic variability, both standing and fallen litter are less persistent, and more litter appears to move out of the wetland. Cattail stems and leaves are known to remain upright longer than those of other wetland graminoids and a network of standing stems may inhibit the removal of litter during flooding. Thus hydrologic stability and cattail abundance may be creating a positive feedback promoting a persistent layer of standing litter, greater fallen litter accumulation, and increased cattail dominance.

The relationship between plant biomass and species diversity has been the subject of much research; however, the importance of senescence and the fate of plant litter has been under-appreciated. This research demonstrates that litter dynamics in Lake Ontario wetlands are influenced by hydrology and community composition, and litter, in turn, can influence the structure and diversity of these wetlands. Understanding these dynamics is crucial because production and decomposition processes are sensitive to anthropogenic activities. In the Great Lakes, nutrient enrichment could increase plant production of litter, and regulated water levels could reduce the fragmentation of standing litter. Understanding how the live and dead phase of cattails is influenced by human activities, and how this ultimately affects plant communities will be vital to the preservation of lakeshore wetlands.

CHAPTER FOUR

Conclusions

The overarching objectives of this research were to describe the patterns and investigate the mechanisms of cattail dominance in the Great Lakes region. Cattails have become a ubiquitous component of natural and created freshwater wetlands throughout temperate North America. Because cattails represent such a familiar icon, the species does not evoke the widespread concern associated with other invasive species such as *Lythrum salicaria* or *Phragmites australis*. Botanists have called *Typha* species "weeds" (Grace and Harrison 1986) and assigned *Typha latifolia* the lowest ranking within a floristic quality assessment, an indication that the plant is common to many habitats (Herman et al. 2001). However, a thorough investigation into the causes and implications of its dominance has not been conducted outside of the Everglades. This work investigated the relationship between cattail dominance and internal (e.g., species density) and external (e.g., surrounding land use) characteristics of wetlands across the Great Lakes (Chapter Two). More intensive work around Lake Ontario explored the hypothesis that litter accumulation creates a positive feedback promoting cattail dominance (Chapter Three).

Results of this research demonstrated, as have previous studies, that cattails can survive under a variety of wetland conditions, but the extent to which cattails dominate wetland plant communities depends upon the environment. In an analysis of their distribution across the Great Lakes, I found that the relative cover of cattails varied among wetlands, depending on the associated ecoprovince, land use, lake, and water depth. Further investigation of Lake Ontario wetlands revealed that although cattails occurred in both protected and open wetlands, they had a greater aboveground biomass and were associated with lower species richness in wetlands hydrologically open to Lake Ontario.

A study of the five Great lakes revealed that cattails were most abundant around Lake Ontario, the one lake where regulation has noticeably damped inter-annual water level fluctuations. Around Lake Ontario, cattails were more dominant in wetlands that closely tracked the water levels of Lake Ontario in contrast with hydrologically more variable protected wetlands. This suggests that stabilized water levels positively influence the growth and competitive ability of cattails and/or negatively influence the survival and competitive ability of other species. This interpretation is consistent with findings from other regulated lakes in which diminished water level fluctuations promoted the growth of certain species and reduced species diversity (e.g., Keddy and Reznicek 1986; Wilcox and Meeker 1991).

In both observational and experimental studies, I found a negative relationship between invasive cattail abundance and species density, at the plot and site level. Native species did not exhibit this relationship. Experimental manipulation of cattail litter indicated a causal relationship between cattail biomass and the survival of other species. Although cattails probably affect neighboring plants in several ways, this work highlights the role of cattail litter as one mechanism by which cattails reduce species density. Thus, factors that promote the production of cattails and the accumulation of their litter will promote further exclusion of other species.

This work underscores the importance of litter as a component of community biomass in herbaceous wetlands. In a regional survey of Great Lakes wetlands, I found that litter cover was associated with lower species density. Among six intensively studied

Lake Ontario wetlands, where litter biomass sometimes exceeded peak live production by a factor of three, species density was negatively correlated with litter biomass, but was not related to live biomass. During an experimental manipulation of cattail litter, species density declined as litter biomass increased, even when live cattail biomass remained constant. These results are consistent with the hypothesis that litter accumulation mediates the relationship between cattail abundance and species diversity in herbaceous wetlands.

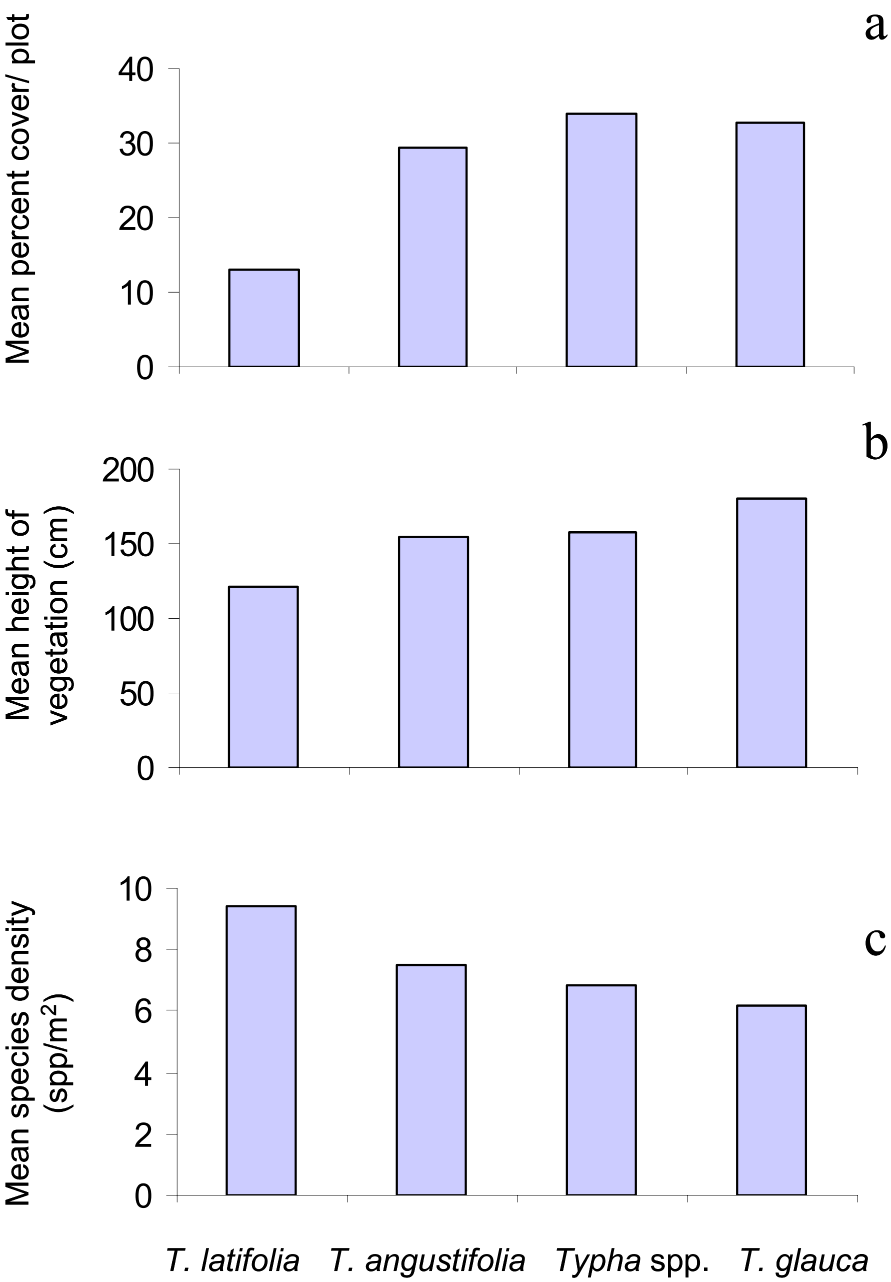
Results of the litter manipulation confirmed that cattail litter reduces species density and seedling survival. Species density was higher in plots without a litter layer, in part, because seed germination and establishment were higher, as evidenced by the high number of new seedlings and the improved survival of the test seedlings. This mechanism by which cattail litter affects species density has implications for how my results apply to other wetlands or other types of plant litter. The litter manipulation experiment was conducted in a cattail-dominated marsh, in which water levels were only slightly above the soil surface during the growing season. Within the marsh, the degree to which litter removal increased species density varied, suggesting that the response to litter might vary even more widely among systems. If seed germination requires exposed, dry soils, a marsh with higher water levels might not experience a similar increase in seedling recruitment. In deeper water, the physiological tolerance of seeds and seedlings will limit their survival, and therefore accumulated litter might provide a dry substrate for the establishment of some species. For example, tussocks produced by *Carex stricta* roots and litter are associated with higher species diversity because they provide a range of seed germination conditions (Werner and Zedler 2002). Thus, the effect of litter in wetlands will depend on the species involved and the wetland environment.

The study of litter dynamics in Lake Ontario wetlands indicates that litter accumulation depends on a wetland's hydrogeologic setting and the abundance of cattails. In the study, both hydrology and plant composition varied between the two hydrogeologic settings (open and protected); thus it was impossible to determine which was a more important determinant of litter biomass. Cattail stems and leaves are known to remain upright longer than those of other wetland graminoids and a network of standing stems can probably support itself. Water level fluctuations could weaken or disrupt standing litter. Thus hydrologic stability and cattail abundance may both promote a persistent layer of standing litter, and ultimately speed litter breakdown

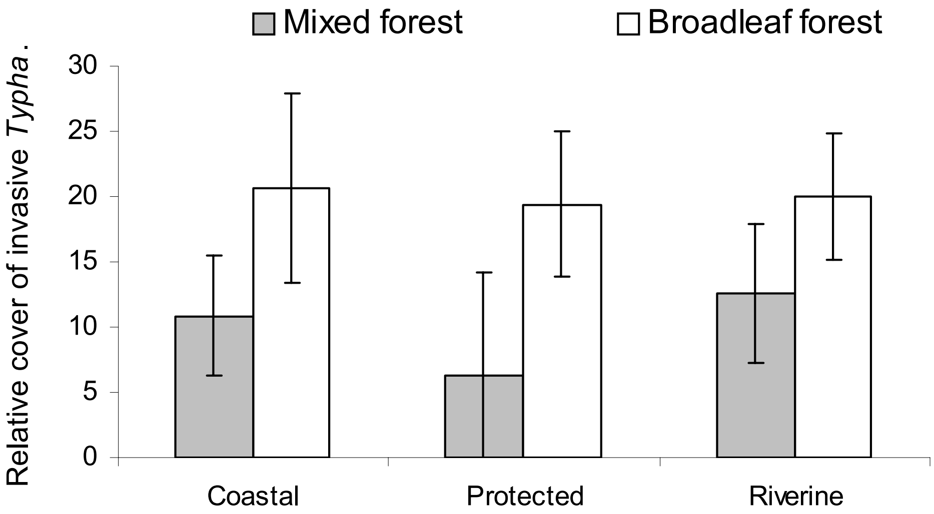
I proposed that, under the right conditions, cattail production promotes a positive feedback by increasing litter accumulation, thus excluding other species, and in turn promoting further dominance of cattails. This mechanism implies that cattail abundance is promoted by slower decay of its litter. This feedback process contrasts with other theories about how competitive plants modify their environment. For example, leaves typical of fast growing, competitive plants (e.g., leaves with a shorter lifespan, less chemical and physical defense, and higher nutrient content) decompose more quickly (e.g., Reich et al. 1992; Wright et al. 2001). The more rapid cycling of organic matter and nutrients promoted by their litter is thought to be advantageous to fast growing plants with high nutrient demands. Although cattail growth is known to respond positively to increased nutrient availability, my work implies that cattails gain an advantage from slower decomposition. This study did not test whether cattails grow better under a high accumulation of litter, or whether they benefit by excluding other species, which are important aspects of a positive feedback cycle. Although not formally tested here, cattails also may benefit indirectly by an accumulation of organic matter. Persistent cattail litter can form floating mats that allow cattails to colonize open water areas, thereby increasing their habitat. Thus in wetland systems the traits associated with competitive plant species may not speed organic matter decomposition, and faster decomposition necessarily be advantageous for a species like cattails.

This work contributes to our understanding of the conditions and processes that allow one group of species to become dominant. The relationship between plant community biomass and species diversity has received considerable attention; however, the importance of plant litter dynamics in determining competitive interactions has been under-appreciated. Factors affecting cattail litter production and decomposition could have important implications for plant communities, and thus should guide future restoration and preservation efforts. Although not experimentally tested within my studies, my results strongly suggest that agriculture within a wetland’s drainage basin influence cattail growth, especially that of the invasive species, and water level regulation influences the way senesced plants fragment and decompose. Thus both watershed and lake factors may need to be addressed simultaneously in order to protect Great Lakes wetlands.

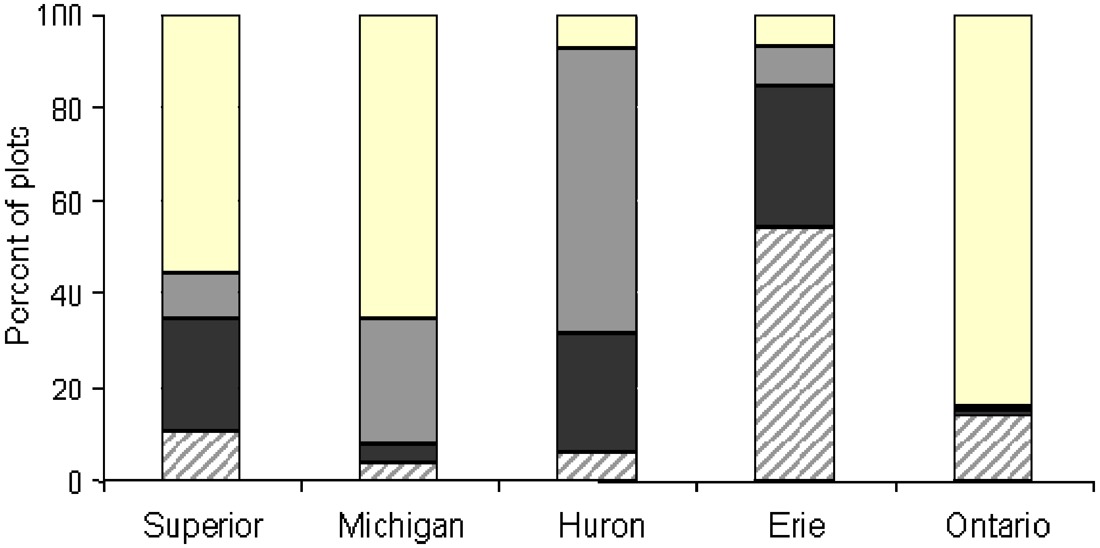
APPENDICES



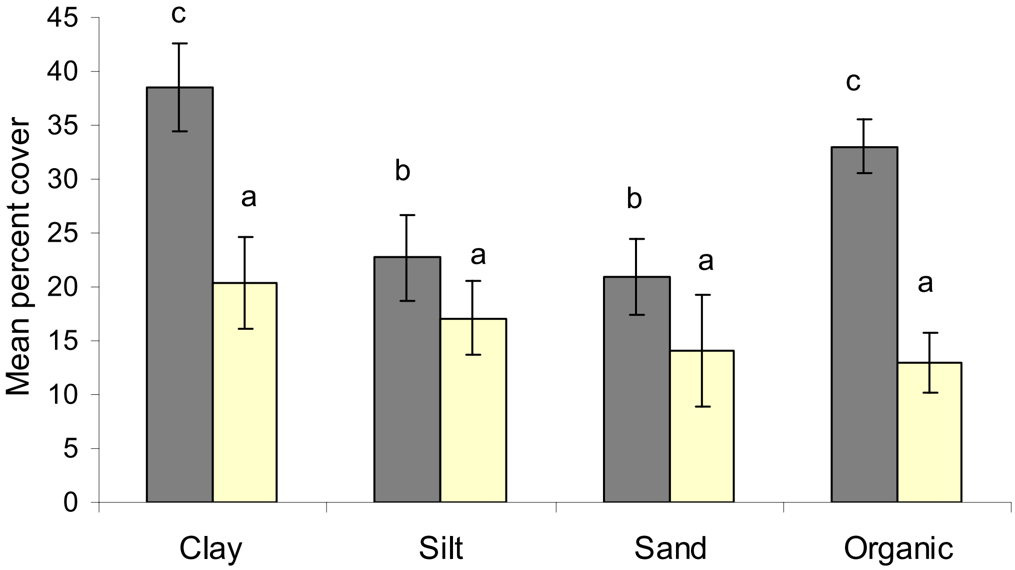
Appendix A. Comparison of *T. latifolia*, *T. angustifolia*, *Typha* spp. and *T. glauca* with respect to their mean percent cover per meter-squared (a), the mean height of vegetation in plots of occurrence (b), and the mean species density in plots of occurrence (c) across 90 Great Lakes wetlands. Observations recorded as *T. angustifolia*, *T. glauca* or *Typha* spp. were combined in calculations of invasive *Typha* species in Chapter Two.



Appendix B. Relative cover of invasive *Typha* (+/- SE) in six different wetland settings: coastal, protected and riverine wetlands within the Laurentian mixed forest and the Eastern broad leafed forest eco-provinces. The means are not significant at the alpha = 0.05 level. Results reported in Chapter Two.



Appendix C. Frequency of occurrence in different Great Lakes of four types of substrate: organic soil (□), sand (▒), silt (■), and clay (▨). Data recorded during vegetation surveys conducted for the Great Lakes Environmental Indicators (GLEI) project. Variation in wetland substrate may explain or reflect the differences in plant community composition described in Chapter Two.



Appendix D. Mean percent cover (+/- SE) in plots with different substrates, for the invasive *Typha* species (■), and *Typha latifolia* (□). Means and standard errors were calculated based on plots where each species occurred. Letters indicate significant differences at alpha= 0.05. Substrate type was recorded during vegetation surveys conducted for the Great Lakes Environmental Indicators (GLEI) project. Variation in wetland substrate may explain or reflect the differences in plant community composition described in Chapter Two.

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