

LITTER ACCUMULATION PROMOTES DOMINANCE OF INVASIVE SPECIES OF CATTAILS (*TYPHA* SPP.) IN LAKE ONTARIO WETLANDS

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Abstract: Wetlands of the Great Lakes region are increasingly dominated by invasive cattails (*Typha angustifolia* and *Typha X glauca*) which form dense stands of live and dead biomass that may reduce plant diversity. We hypothesized that differences in plant litter accumulation explain cattail dominance under certain hydrologic regimes related to wetland hydrogeologic setting. We investigated cattail abundance, litter accumulation, and species density in three bayside wetlands hydrologically connected and three protected wetlands hydrologically isolated from Lake Ontario. Mean litter biomass was higher in bayside wetlands (1.7–2.6 vs. 0.4–1.2 kg/m²) and negatively related to species density ($p = 0.004$) in both settings. A litter addition experiment demonstrated that fallen litter negatively influenced seedling survival ($p = 0.061$) and species density ($p = 0.024$). Decomposition rates accounted only partially for higher overall litter accumulation in bayside wetlands. Growing season water levels in bayside wetlands tracked Lake Ontario levels and showed less variation than protected wetlands. More stable water levels and higher density of standing dead stems in bayside wetlands may limit litter fragmentation, resulting in greater litter accumulation. Thus, anthropogenic and natural factors affecting cattail litter production, fragmentation, and decomposition could influence species diversity in coastal wetlands.

Key Words: barrier beach wetlands, decomposition, embayment wetlands, Great Lakes, hydrologic fluctuations, litter removal experiment, species richness

INTRODUCTION

Accumulation of plant litter in herbaceous ecosystems may mediate the relationship between soil nutrients, productivity, and plant species diversity (Berendse 1999). Numerous studies have established the positive relationship between nutrient availability and production of live plant biomass (e.g., Olde Venterink et al. 2001). In nutrient limited systems, 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 recruitment of new species and ultimately affect species diversity (Xiong and Nilsson 1999).

Results of fertilization and biomass removal studies that partitioned effects of litter and living biomass on plant community composition have been inconsistent. In some studies, living biomass or stem

density was most tightly correlated with species richness (Stevens et al. 2004), while in other studies litter biomass was a more important determinant of species richness (Tilman 1993, Foster and Gross 1998, Xiong et al. 2003). Still others found that availability of seeds and propagules influenced species richness more than amount of either living or dead biomass (Foster et al. 2004). Interestingly, fertilization and litter additions can have an identical effect on species recruitment, presumably because both treatments attenuate light levels (Berendse et al. 1994, Foster and Gross 1998). Both fertilization and litter additions also can influence competitive interactions between established plants, for example by changing rates of succession within communities. Thus, increasing plant productivity through fertilization may influence plant community composition because of the way that it affects litter accumulation.

Cattails (*Typha* spp.) have become dominant species in coastal marshes of the Great Lakes, often forming dense stands of live and dead biomass that

appear to reduce the diversity of other wetland species (Vaccaro 2005, Frieswyk and Zedler 2007, Tulbure *et al.* 2007). Unlike the native cattail, *Typha latifolia* L., percent cover of the invasive cattails, *Typha angustifolia* L. and *Typha X glauca* Godr. (pro sp.), is negatively correlated with plant species density and positively correlated with human population density and agricultural activity in Great Lakes coastal wetlands (Vaccaro 2005, Brazner *et al.* 2007). Given the potential for cattails to attain high levels of productivity (Brinson *et al.* 1981) and the resistance of their litter to fragmentation and decay (Davis and van der Valk 1978), accumulation of cattail litter might facilitate their own increasing dominance in Great Lakes wetlands by suppressing other species.

Typha angustifolia and *T. X glauca* occur more frequently around Lake Ontario than the other Great Lakes (Johnston *et al.* 2007); over the last 60 years, cover of these invasive cattails has been increasing, apparently at the expense of wet meadow communities in some Lake Ontario wetlands (Wilcox *et al.* 2008). Since 1960, the Moses-Saunders power dam on the St. Lawrence has regulated outflow of water from Lake Ontario in order to “reduce the range of Lake Ontario’s water levels, and to provide dependable flow for hydropower, adequate navigation depths, and protection for shorelines” (International Joint Commission 2004). The range of Lake Ontario’s water levels is roughly half that prior to regulation (0.7 m vs. 1.5 m), which has changed the natural disturbance regime in coastal wetlands and may have contributed to success of invasive cattails (Wilcox *et al.* 2005, Wilcox and Yichun 2007). Hydrologic modifications have been shown to decrease plant diversity of dammed lakes (Hill *et al.* 1998) and promote the expansion of cattail species in the Everglades (Newman *et al.* 1998) and a sedge meadow (Wilcox *et al.* 1984). Under controlled conditions, constant inundation in comparison with fluctuating water levels promoted the growth and phosphorus uptake of *T. X glauca* (Boers and Zedler 2008). Hydrologic differences also might help explain patterns of cattail dominance in Lake Ontario wetlands.

Wetlands around Lake Ontario differ in hydrogeologic setting and cattail dominance: bayside wetlands within large, open embayments are dominated by *Typha* species, while protected wetlands that lack a direct surface water connection to the lake, such as those behind barrier beaches, maintain a more diverse plant community. Hydrogeologic setting controls water flow patterns, fluctuations, and chemistry in a wetland (Bedford 1996), which likely will influence plant competition, production,

disturbance, and litter accumulation. Hydrologic regime can affect litter dynamics in several ways: by favoring growth of highly productive perennials like cattails (e.g., low disturbance, high fertility) (Wisheu and Keddy 1992), by influencing the amount of moisture, oxygen, and macroinvertebrates available for decomposition (e.g., Battle and Golladay 2001), by weakening and fragmenting standing litter, and by washing away live plants or litter fragments.

In this research we sought to determine if differences in cattail productivity and litter accumulation could explain why cattails dominate in certain hydrogeologic settings. High density of cattails observed in embayment wetlands led us to suspect that high litter production and accumulation were allowing cattails to out-compete other species in these bayside wetlands. Specifically, we hypothesized that: 1) litter biomass would be higher and species density would be lower in bayside wetlands compared to protected wetlands; 2) experimentally increasing the amount of cattail litter would reduce plant species density, inhibit seedling establishment by another species, and reduce the size of seedlings once established; and 3) litter dynamics, i.e., biomass production, fragmentation, and decomposition, would vary with wetland hydrogeologic setting and be correlated with degree of water table fluctuations or nutrient availability. To test the first and third hypotheses, we characterized live and dead biomass of cattail and other species, rates of litter decomposition for cattail, species density, nutrient availability, and hydrologic fluctuations in six Lake Ontario wetlands. We tested the second set of hypotheses with a litter manipulation experiment in one of the six wetlands to help explain observed patterns and determine if cattail litter directly affects other plant species.

METHODS

Litter Dynamics in Lake Ontario Wetlands

Study Area. We chose six study wetlands from two distinct hydrogeologic settings along the U.S. shore of Lake Ontario (Figure 1). Three sites (Sodus, Mudge, and Beaver) are located within embayments along the southern shore of Lake Ontario (hereafter, “bayside” wetlands). This area is characterized by north-south trending drumlin hills formed from calcium-rich glacial till; the bays and wetlands occupy valleys between the hills. Because these wetlands are located within bays they have no direct exposure to waves, but the lake controls wetland water levels. The other sites (Snake, Deer, and South) are located on the eastern shore of Lake Ontario behind sand bars, and are hydrologically

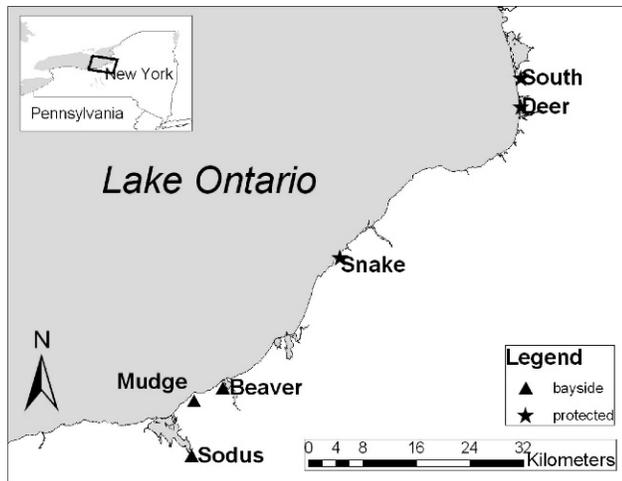


Figure 1. Location of study wetlands along Lake Ontario, New York, USA, showing the three bayside wetlands (Beaver, Mudge, Sodus) and three protected wetlands (Snake, Deer, South).

connected to Lake Ontario only by intermittent or indirect surface water openings or ground water (hereafter called “protected” wetlands). In each site, we quantified: 1) hydrologic fluctuations, 2) plant species composition, 3) live and dead biomass, 4) tissue nutrient concentrations, 5) land use in the watershed, and 6) decomposition rates.

Hydrology. In each wetland, hydrologic 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 every half hour at the fourth well from water’s edge from May to September 2004 by a capacitance rod connected to a data logger. Measurements made by hand indicated that water table elevations recorded by data loggers were within 1–3 cm of actual water levels.

Vegetation. Vegetation was sampled at the four intermediate water table well locations along the hydrology transect. Plant species were identified in four 1 × 1 m plots at each of the four wells and mean species density was calculated from the sixteen 1 × 1 m plots in each wetland. Plots were placed in a random direction and distance (1–3 m) from each of the four wells. We quantified aboveground biomass of the vegetation and litter by harvesting a randomly selected 0.5 m² area at each of the four sampling stations in late July 2003. We separated vegetation into five categories at 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. The measurement of live aboveground biomass will be called “live biomass” to distinguish it from “litter biomass” and is considered an estimate of annual aboveground biomass production because cattails reach their peak aboveground biomass in late July (van der Valk and Davis 1978a, Barlocher and Biddiscombe 1996). If the vegetation included woody species, we harvested and measured only leaves and small green stems. Shrubs were present only at one site, South Pond, and biomass measurements may underestimate new biomass production at this site.

Nutrient concentrations in leaves of mature cattails provided a comparative indication of nutrient availability within soil of each wetland (Bedford et al. 1999, Olde Venterink et al. 2002, Johnson and Rejmankova 2005). We harvested a large inner leaf from three cattail plants at each well location in each wetland (12 plants per wetland). A 50 cm leaf section located 50–100 cm from the tip was clipped out, dried, ground, and analyzed for nutrients. Concentration of phosphorus (P) in the leaf was determined through digestion with sulfuric acid and hydrogen peroxide followed by analysis with an ICP-MS. We determined percent nitrogen (N) by a standard dry combustion method using a CHN analyzer (FlashEA 1112 Elemental Analyzer). Percent P and N is reported by mass.

Decomposition Rates. To quantify rates of cattail litter decomposition in fallen litter, we 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 the decomposition process of recently toppled litter, we collected litter in July from *T. angustifolia* plants that had senesced the previous fall and remained upright during the winter (as in Kuehn et al. 2000). Litter was collected from a single wetland so that all variation in decomposition could be attributed to location of the litter bag. Litter bags measuring 10 × 20 cm were made out of fiberglass window screening with a 1 mm 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.

We placed 39 bags at each study site 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 remained at each of the four intermediate water table well locations in each wetland. We collected litter bags four times during the following year: November 2003, and April, June, and August 2004. During the first three collection dates, eight bags were retrieved from each site (two from each well location); we collected the remaining 12 bags per site on the final pick-up date. The remaining litter was gently rinsed with de-ionized water to remove silt and macroinvertebrates, oven dried to constant weight at 65°C, and weighed. An annual decomposition rate (k) was calculated for each wetland by using the final mass remaining in the litter bags after one year of decomposition and the model, $e^{-k*(years)} = \text{fraction of mass remaining}$. The exponential decay model provided a reasonable fit to the mass loss data; the R^2 ranged from 60 to 86%.

Land use. Watersheds draining to each of the six wetlands were previously delineated for the Great Lakes Environmental Indicator project (Hollenhorst *et al.* 2007). We used a geographic information system to summarize each watershed's land use from a modified version of the National Land Cover Dataset (Wolter *et al.* 2006, Johnston *et al.* 2009). Percent "developed" land was calculated as proportion of high-intensity residential, commercial, and agricultural lands (e.g., row crops, pasture, orchard) relative to total watershed area.

Analysis. We averaged measurements within each wetland before assessing variation among sites. We assessed differences between the two wetland settings and relationships between biomass production, decomposition rates, species density, and litter biomass using general linear model analyses in SAS (PROC GLM, SAS 2002). Pearson correlation analyses were completed using Minitab 13.1 to test whether the biomass of litter was correlated with species density or non-*Typha* biomass, whether tissue nutrient concentrations (N and P) were correlated with watershed development, decomposition, *Typha* biomass or live biomass, and whether watershed development was correlated with live biomass or *Typha* biomass. In addition, we evaluated the degree of correlation between decay rates and a wetland's mean and average monthly standard deviation of water depth. Assumptions of normality and equal variance were met in all cases. We considered differences and relationships significant if the statistical model had a p value < 0.05 .

Litter Manipulation Experiment

Study Design. To assess the role of cattail litter in structuring wetland plant communities, we manipu-

lated litter cover in Mudge Creek, one of the cattail-dominated, bayside wetlands used in our vegetation study. The wetland plant community was dominated by *T. angustifolia* with an understory of *Thelypteris palustris* Schott (marsh fern).

In May 2003, we manipulated the cover of standing and fallen litter in plots and monitored changes in the plant community through the growing season. We replicated litter manipulations in three areas of the wetland where the biomass of live *T. angustifolia* varied from 595–1070-g/m² and species richness varied from 1.75–6.25 species/m² under natural conditions. A completely randomized block design was used in which each of the three areas was considered a block. Each of the three blocks contained six 1 × 4 m plots, which received one of the litter treatments: addition, removal, and control for both fallen and standing litter. Thus, each of the six treatments had three replicates. To minimize edge effects, a half-meter wide buffer of similar treatment conditions surrounded the 4-m² treatment plots.

We developed three standing litter treatments: removal, addition, and a control. For the removal treatment, we cut and removed all dead stems and attached leaves that remained upright at an angle of $> 45^\circ$ relative to the ground surface. For the addition treatment, we used all the standing litter from the removal plots and inserted it upright into the addition plots where a network of persistent litter held the new stems in place for the experiment's duration. The standing litter control plots had an untouched layer of fallen and standing litter.

We established three fallen litter treatments after first removing all the standing litter from this series of plots. For the fallen litter removal treatment, we cut and removed the surface litter layer to the depth where root colonization was evident. For the addition treatment, we evenly distributed the removed fallen litter into the addition plots, doubling the biomass of fallen litter. The control plots had an untouched fallen litter layer and no standing litter. Aboveground biomass measurements were made adjacent to each of the blocks, allowing estimation of litter biomass within manipulation plots.

In addition to measuring changes in the existing plant community, we transplanted eight test seedlings into each of the treatment and control plots to provide a standardized assessment of growth conditions. We gathered 144 *Peltandra virginica* (L.) Schott. seedlings from a neighboring wetland in May 2003. At 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 had not yet rooted in the substrate. Within 24 hours, the seedlings were placed in the study plots. The base of each plant was placed into the litter layer such that at least 5 cm of the stem and all of the leaves emerged. In plots with a thick fallen litter layer, the roots rested partially or fully within the dense litter layer rather than within the organic soil substrate. After one month, over 80% of the seedlings were alive and after four months, 55% were alive. In mid-September seedlings were measured, dried, and weighed. We calculated seedling survival as proportion of live seedlings relative to the original eight seedlings in each plot in mid-September.

Analysis. Differences in final species density, test seedling survival, and test seedling biomass were assessed using analysis of variance performed with the general linear model procedure (SAS 2002). When litter treatments were considered categorically (addition, control, removal), standing and fallen litter treatments were analyzed separately and Tukey's error correction was used for all pairwise comparisons. When testing effect of litter biomass as a continuous variable, block was included as a second predictor variable to account for natural variation across the wetland. The partial p value indicates the effect of litter biomass after accounting for variation due to block. Block locations were selected to represent a natural gradient in cattail biomass and therefore are considered fixed effects. Because litter manipulations were not replicated within blocks, interaction between treatment and block could not be evaluated. The degree of correlation between two response variables, seedling survival and species density, was tested using Pearson correlation analysis in Minitab 13.1. Assumptions of equal variance and normality were met in all cases.

RESULTS

Litter Dynamics in Lake Ontario Wetlands

Hydrology. Patterns of water table fluctuations varied according to wetland hydrogeologic setting. Bayside wetlands tracked the fluctuations and seasonal trends of Lake Ontario, but not the daily cycle of seiches and wind-driven currents (Figure 2a,b). Water levels decreased between June and September in Lake Ontario and the bayside wetlands with the exception of Sodus Bay. The water level recorder at Sodus Bay measured virtually no change because it was located close to a water channel in a stand of cattails that was floating and thus rising and falling with lake water level. In

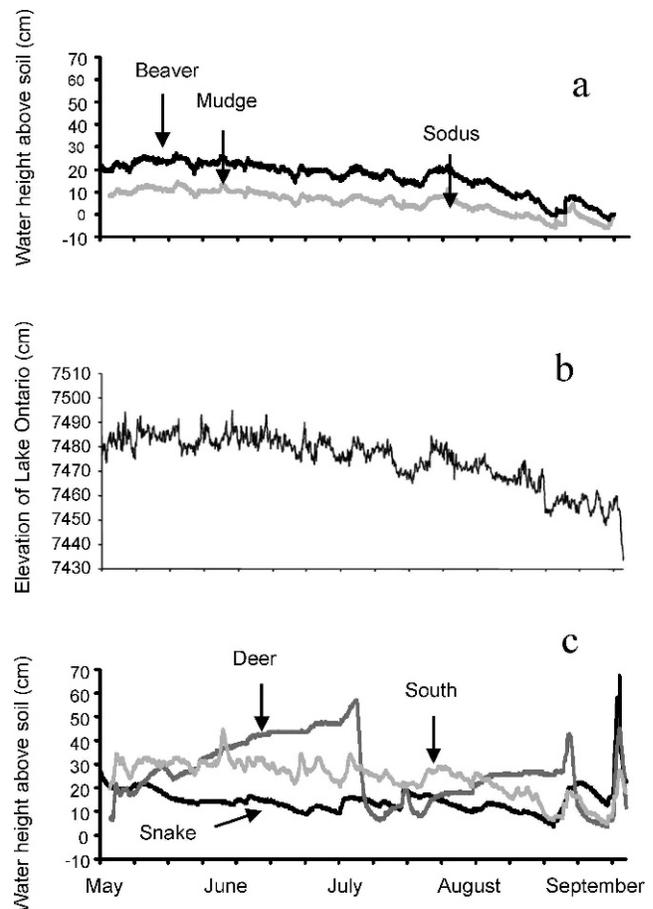


Figure 2. Hydrologic fluctuations in A) the bayside wetlands, B) Lake Ontario, and C) the protected wetlands. Water level measurements are relative to the soil surface in each wetland and relative to sea level for Lake Ontario. Data were collected every half hour from May to September, 2004.

contrast with the bayside wetlands, protected wetlands with only indirect or temporary connections to Lake Ontario experienced a more variable pattern of water table fluctuations and an overall greater range of water levels (Figure 2c, Table 1).

Vegetation. Relative abundance of live cattails and biomass of plant litter differed between bayside wetlands and protected wetlands (Table 1, Figure 3). Biomass of cattails was, on average, 89–92% of live biomass in bayside wetlands, and only 25–47% of live biomass in protected wetlands. Live biomass did not differ significantly between wetland settings; mean above-ground biomass was between 816 and 1172 g/m² at all sites, with the exception of one protected wetland, South Pond, which produced 414 g/m² above-ground herbaceous biomass (Table 1). In contrast, mean biomass of standing and fallen litter was significantly higher in bayside

Table 1. Characteristics of the water levels, vegetation, and watershed for each study wetland (mean \pm standard error, $n = 4$). Differences between bayside and protected wetlands are tested with ANOVA ($df = 1,4$), and significant differences are indicated in bold.

	Bayside Wetlands						Protected Wetlands						Test of wetland setting difference		
	SODUS	MUDGE	BEAVER	SNAKE	DEER	SOUTH	DEER	SNAKE	BEAVER	SNAKE	DEER	SOUTH	F	P	
WATER LEVELS															
Mean height above soil (cm)	4.3	5.5	16.4	15.0	27.0	24.2	27.0	15.0	16.4	15.0	27.0	24.2	6.39	0.065	
Maximum (cm)	7.7	14.7	27.5	67.9	57.2	44.7	57.2	67.9	27.5	67.9	57.2	44.7	20.31	0.011	
Minimum (cm)	2.7	-6.2	-2.5	3.5	3.7	4.8	3.7	3.5	-2.5	3.5	3.7	4.8	2.45	0.193	
Range (cm)	5.0	20.9	30.0	64.4	53.6	39.9	53.6	64.4	30.0	64.4	53.6	39.9	11.16	0.029	
Avg. monthly std dev.	0.4	1.9	2.8	4.5	9.4	4.5	9.4	4.5	2.8	4.5	9.4	4.5	13.58	0.021	
VEGETATION															
Biomass of live cattails (g/m^2)	1095 \pm 233	808 \pm 98	763 \pm 120	487 \pm 152	356 \pm 54	119 \pm 62	356 \pm 54	487 \pm 152	763 \pm 120	356 \pm 54	119 \pm 62	14.42	0.019		
Total living biomass (g/m^2)	1172 \pm 167	910 \pm 96	816 \pm 106	995 \pm 73	1031 \pm 242	415 \pm 64	1031 \pm 242	995 \pm 73	816 \pm 106	1031 \pm 242	415 \pm 64	0.45	0.537		
% P in live cattail leaves	0.40 \pm 0.08	0.10 \pm 0.01	0.15 \pm 0.002	0.29 \pm 0.01	0.17 \pm 0.02	0.11 \pm 0.02	0.17 \pm 0.02	0.29 \pm 0.01	0.15 \pm 0.002	0.17 \pm 0.02	0.11 \pm 0.02	0.09	0.785		
% N in live cattail leaves	2.30 \pm 0.07	1.53 \pm 0.05	1.95 \pm 0.04	2.24 \pm 0.13	1.94 \pm 0.11	1.73 \pm 0.11	1.94 \pm 0.11	2.24 \pm 0.13	1.53 \pm 0.05	1.94 \pm 0.11	1.73 \pm 0.11	0.03	0.879		
Decay rate constant (k), (yr) ⁻¹	0.42 \pm 0.05	0.25 \pm 0.03	0.27 \pm 0.02	0.49 \pm 0.04	0.37 \pm 0.02	0.23 \pm 0.01	0.37 \pm 0.02	0.49 \pm 0.04	0.25 \pm 0.03	0.37 \pm 0.02	0.23 \pm 0.01	0.25	0.642		
Total litter biomass (g/m^2)	1865 \pm 343	2596 \pm 224	2531 \pm 209	438 \pm 149	981 \pm 263	1252 \pm 289	981 \pm 263	438 \pm 149	2596 \pm 224	2531 \pm 209	1252 \pm 289	18.53	0.012		
Species density (spp/ m^2)	8.00 \pm 1.2	7.75 \pm 2.6	6.75 \pm 0.9	9.75 \pm 0.6	9.00 \pm 1.1	8.75 \pm 1.3	9.00 \pm 1.1	9.75 \pm 0.6	6.75 \pm 0.9	9.00 \pm 1.1	8.75 \pm 1.3	11.76	0.026		
WATERSHED															
% of watershed developed	73.5	35.8	46.2	50.1	35.3	29.2	35.3	50.1	46.2	35.3	29.2	1.13	0.348		

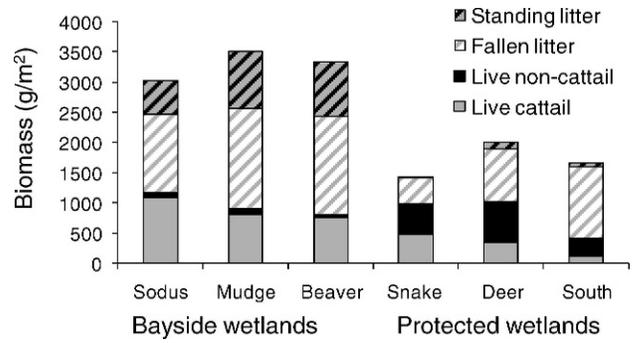


Figure 3. Mean biomass of vegetation and litter in late July 2003 in three bayside wetlands (left) and three protected wetlands (right).

wetlands than protected wetlands (mean = 2330 vs. 890 g/m^2 ; Table 1). On average, bayside wetlands had twice as much litter as live biomass, and protected wetlands had 50% more litter than live biomass.

Protected wetlands had significantly higher mean plant species density (8.8–9.8 species/ m^2) than bayside wetlands (6.8–8 species/ m^2) (Table 1). Mean litter biomass was negatively correlated with species density (Figure 4) and the biomass of non-cattail species ($r = -0.83$, $p = 0.030$). Thus, although aboveground biomass production was similar across sites, cattails constituted a larger proportion of live biomass, litter biomass was higher, and species density was lower in bayside wetlands.

Litter Dynamics. After a full year, percent of litter remaining varied from 59 to 79% among the six wetlands; however, the range of mean decay rates within the two hydrogeologic settings was similar (Table 1). The decomposition rate constant (k) was not correlated with mean ($r = -0.189$, $p = 0.720$) or

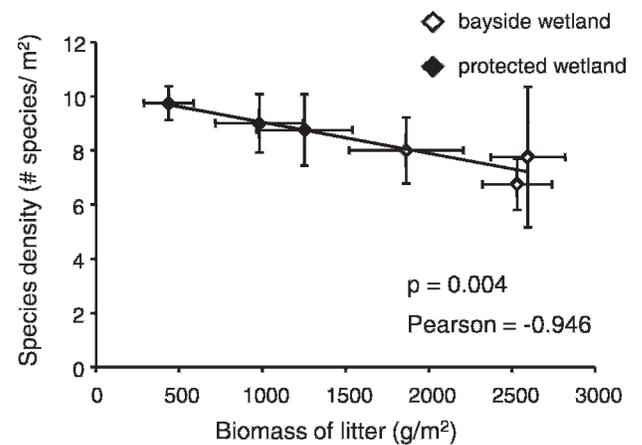


Figure 4. Relationship between mean biomass of all litter and mean species density in bayside and protected wetland sites. Bars indicate ± 1 SE ($n = 4$).

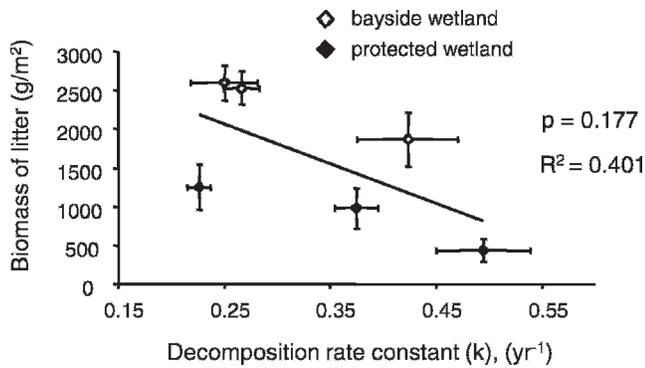


Figure 5. Relationship between mean litter biomass and mean rate of decomposition in bayside and protected wetland sites. Bars indicate ± 1 SE ($n = 4$).

average monthly standard deviation ($r = 0.005$, $p = 0.993$) in water table elevation. Hydrologic measurements taken at a single location within a wetland over the course of four months may not have captured the parameters most relevant to decomposition rates.

Differences in decomposition rates could not explain differences in litter accumulation among the six wetlands. When comparing wetlands with similar decomposition rates, bayside wetlands had a higher biomass of total litter compared to protected wetlands (Figure 5). Live biomass production and decomposition rate together explained 81% of the variation in litter biomass. However, decomposition rate combined with either hydrogeologic setting or proportion of cattails explained 99% of the variation (Table 2).

Land Use and Nutrients. The proportion of each wetland’s watershed that was developed (residential, commercial, or agricultural) varied from 29 to 73%, but did not differ significantly between wetland settings (Table 1). Percentage watershed developed was positively correlated with site fertility, as indicated by tissue N and P concentrations (Figure 6a). Tissue N and P concentrations showed no difference between wetland settings (Table 1). Total biomass was not significantly correlated with watershed development ($r = 0.693$, $p = 0.127$), tissue N concentration ($r = 0.584$, $p = 0.223$), or tissue P concentration ($r = 0.690$, $p = 0.129$). However, biomass of just the *Typha* species showed a weak correlation with watershed development ($r = 0.777$, $p = 0.069$).

Site fertility and litter decomposition rate were positively correlated (Figure 6b). Decomposition rates in litter bags were faster at sites with greater N or P concentrations in surrounding live cattail leaf tissues, even though we used standardized litter in litter bags at all sites.

Litter Manipulation Experiment

After altering the litter layer for 14 weeks within a single wetland we found that species density varied from 1.0 to 9.25 species/m² and depended on amount of litter and location within the wetland. Fallen litter significantly reduced species density ($F_{4,4} = 11.02$, $p = 0.024$), but the effect of standing litter treatments was not consistent ($F_{4,4} = 2.65$, $p = 0.184$) (Figure 7a). The location within the wetland

Table 2. 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-squared
Single variable model		
Live biomass (all species) ($p = 0.976$)		0.001
Decomposition rate ($p = 0.177$)		0.401
Relative abundance of cattails (cattail/ total live biomass) ($p = 0.046$)		0.669
Wetland setting ($p = 0.013$)		0.822
Multi-variable model		
Decomposition rate ($p = 0.037$)	Live biomass ($p = 0.085$)	0.809
Decomposition rate ($p = 0.006$)	Wetland setting ($p = 0.001$)	0.989
Decomposition rate ($p = 0.002$)	Relative abundance of cattails ($p = 0.0007$)	0.991

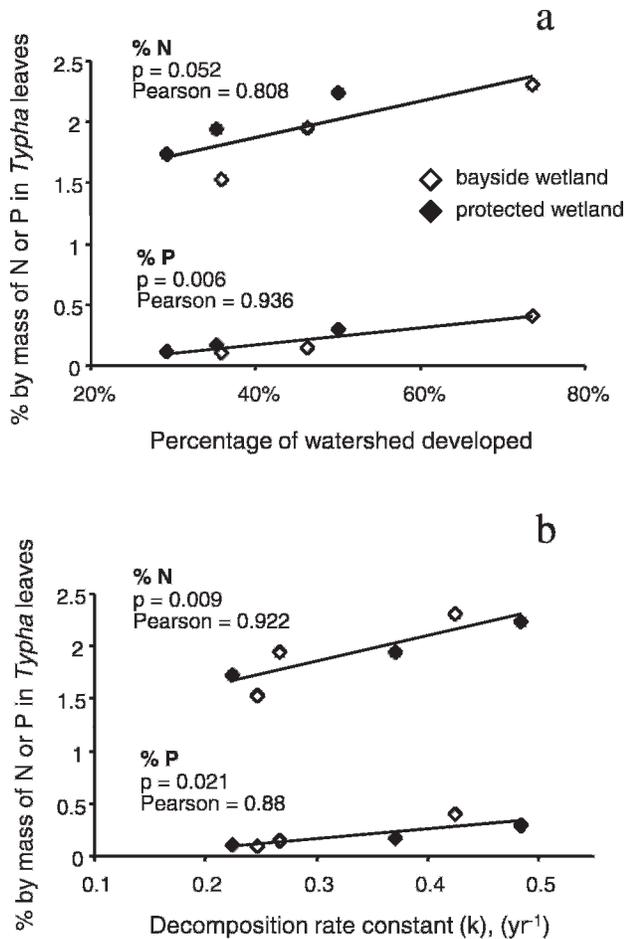


Figure 6. Correlation between percent N and P in live *Typha* leaves and A) percent of wetland watershed developed and B) decomposition rate.

(block) influenced the type and number of species observed within each treatment (Table 3). Block 3 with the lowest natural abundance of *T. angustifolia* maintained the highest number of species for a given treatment, but block 1 with the highest abundance of *T. angustifolia* had the most species when litter was removed.

Survival of the eight *P. virginica* seedlings planted in each 4-m² plot ranged from 0 to 100%, depending on litter treatment and location within the wetland block. Additions of fallen litter somewhat reduced survival of test seedlings ($F_{4,4} = 6.10$, $p = 0.061$); however, manipulating standing litter alone had no measurable effect ($F_{4,6} = 0.64$, $p = 0.561$) (Figure 7b). Neither standing nor fallen litter significantly affected seedling size (data not shown). Species density and seedling survival responded similarly to litter manipulations and were significantly correlated across all treatments ($r = 0.456$, $p = 0.044$).

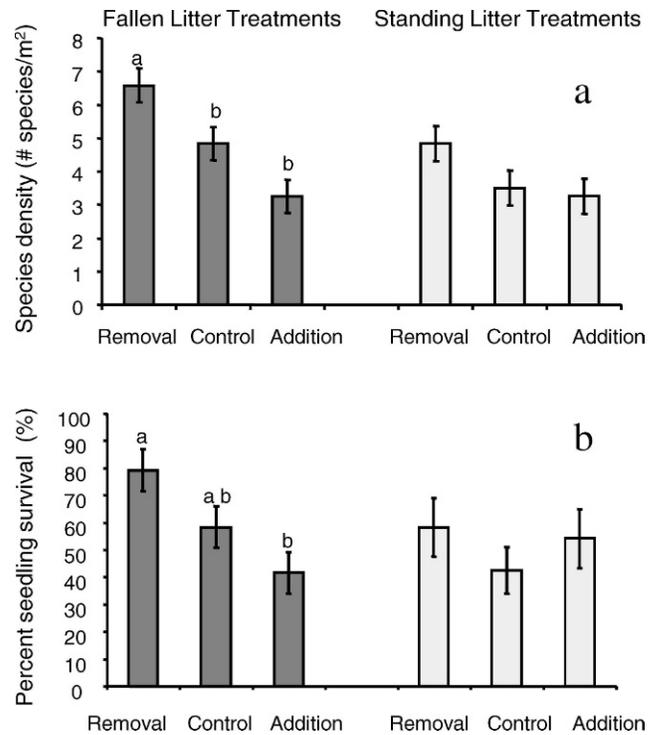


Figure 7. A) Species density (± 1 SE) ($n = 3$) and B) seedling survival (± 1 SE) ($n = 3$) after 14 weeks in litter manipulation treatments. Letters indicate significantly different means at the $p < 0.05$ level using Tukey's correction for all pairwise comparisons.

DISCUSSION

The Effect of Litter on Species Coexistence

This study aimed to determine if differences in plant litter accumulation could explain why invasive cattail species are able to dominate within certain hydrogeologic settings. Our data supported our hypothesis that a higher proportion of live biomass accumulates as litter within the wetland setting that is often dominated by cattails, i.e., bayside wetlands. Among the six study wetlands, species density was negatively correlated with litter biomass, but was not related to aboveground live biomass.

The field manipulation demonstrated that cattail litter, independent of other factors, influences species density in marshes. Increasing the cover of fallen cattail litter, without altering the density of live cattails, reduced species density and *P. virginica* seedling survival. In plots where all litter was removed, juvenile plants of many species were observed, more seedlings survived, and species density increased. Therefore, production and accumulation of plant litter is one mechanism by which cattails impede survival of other species.

Three lines of evidence suggest that cattail litter may reduce species density by affecting seed

Table 3. Species occurring in fallen litter treatment plots after 14 weeks.

	Block 1	Block 2	Block 3
	Higher abundance of live cattails	Intermediate abundance of live cattails	Lower abundance of live cattails
Species found in all fallen litter treatment plots	<i>Typha angustifolia</i> <i>Thelyptis palustris</i>	<i>Typha angustifolia</i> <i>Thelyptis palustris</i> unknown seedling	<i>Typha angustifolia</i> <i>Thelyptis palustris</i> <i>Lysimachia thyrsiflora</i> L. <i>Triadenum virginicum</i> (L.) Raf. <i>Impatiens capensis</i> Meerb. <i>Polygonum amphibium</i> L. <i>Boehmeria cylindrica</i> (L.) Sw. <i>Scutellaria galericulata</i> L. <i>Asclepias incarnata</i> L. <i>Cicuta bulbifera</i> L. <i>Cephalanthus occidentalis</i> L. <i>Galium tinctorium</i> L. <i>Acer rubrum</i> L. <i>Alnus incana</i> (L.) Ell.
Species found only in control and fallen litter removal plots	<i>Impatiens capensis</i>	<i>Cornus amomum</i> P. Mill. <i>Lythrum salicaria</i> L. <i>Galium tinctorium</i> L. <i>Lysimachia thyrsiflora</i> <i>Scutellaria galericulata</i> L. <i>Calamagrostis canadensis</i> (Michx.) Beauv.	<i>Solidago</i> seedlings <i>Carex</i> seedlings <i>Decodon verticillatus</i> <i>Osmunda regalis</i> <i>Poa</i> sp.
Species found only in fallen litter removal plots	<i>Lythrum salicaria</i> <i>Poa</i> sp. <i>Campanula aparainoides</i> Pursh. <i>Osmunda regalis</i> L. <i>Solidago</i> seedling <i>Galium tinctorium</i>	<i>Osmundo regalis</i> L. <i>Poa</i> sp. <i>Decodon verticillatus</i> (L.) Ell.	

germination and establishment processes: 1) fallen litter had a stronger impact than even a dense layer of standing litter, 2) survival of test seedlings and final plot species density were closely correlated, suggesting a similar mechanism may be responsible for both responses, and 3) growth of test seedlings that survived was not affected by litter cover, indicating that established plants were less sensitive to litter. In other studies, 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, type of litter, and the species involved (as reviewed by Xiong and Nilsson 1999, and Sayer 2006). Seeds in areas with a thick litter layer initially face a physical challenge. Recently dispersed seeds must germinate from the top of the litter layer and their roots must grow through the litter to reach the soil, as our test seedlings did. Alternatively, older seeds must germinate from the bottom of the litter layer and grow up through the litter to reach sunlight. Although our seedling experiment was relatively short (14 weeks), and seedlings likely experienced some stress from transplanting, survival rates paralleled the response to litter by the existing plant community and seed bank.

Our study could not 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 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). A recent experiment found that the litter of *Typha X glauca* modified soil chemistry (increased NH_4^+) and reduced light, which led to a loss of species diversity and further *T. X glauca* invasion in a marsh on Lake Huron (Farrer and Goldberg 2009). Cattail litter seems to be causing a similar change in the environment and plant community of Lake Ontario wetlands.

Factors Promoting Litter Accumulation

The observation that litter negatively impacts species density lends importance to the question of why litter biomass varies among wetlands. We hypothesized that litter dynamics would differ as a

function of the wetland's hydrogeologic setting and be correlated with hydrologic variability or soil fertility. In support of this hypothesis, we found that hydrogeologic setting was a better predictor of litter biomass than aboveground biomass production and decomposition rates considered alone or together. This suggests that environmental differences may explain why over twice as much litter occurred in bayside wetlands compared to protected wetlands.

For the six wetlands studied, the proportion of the watershed developed was closely correlated with percent N and P in live cattail leaves, strongly suggesting that surrounding land use influenced nutrient availability in the wetland. Nutrient enrichment has been linked to increased growth and expansion of cattails in the Everglades (King *et al.* 2004) and wet meadows of the Great Lakes region (Woo and Zedler 2002). Watershed development was weakly correlated with biomass of *Typha* species in our study. However, tissue nutrient concentrations were not correlated with total aboveground biomass production, live cattail biomass, or litter biomass, suggesting that other factors were influencing litter dynamics. Because aboveground biomass production was similar across the six wetlands, processes that occur after a plant senesces probably drive differences in litter accumulation.

Water levels fluctuated more in the protected wetlands than in the bayside wetlands, possibly altering the way litter fragments and decays. Water levels on Lake Ontario and the bayside 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, water levels were more variable in the protected wetlands and each hydrograph was distinct depending on its unique connection to Lake Ontario. In all three protected wetlands, barrier beaches restricted flow out of the wetlands, causing their water levels to rise more sharply in response to local precipitation events than did the water table of the bayside wetlands. Previous work at one of our protected sites revealed that steep drops in water levels correspond to flushing events (Bailey and Bedford 2003) which could transport litter fragments out of the wetlands, further affecting litter accumulation. Other studies have documented a net export of dissolved organic carbon (DOC) and particulate organic carbon (POC) from Great Lake coastal wetlands, but the movement of litter fragments has not been quantified (Bouchard 2007).

Decomposition is generally faster in an environment with fluctuating rather than stable water levels

because neither oxygen nor moisture limits decomposer activity (Anderson and Smith 2002). In this study the hydrologic regime was not well correlated with decomposition rates in the litter bags, perhaps because the bags were almost always inundated. However, water fluctuations would directly affect standing dead stems, which could promote their decay and shorten the time that dead plants remain upright. Typically decomposition accelerates after stems collapse and submerge because moisture limitation is relieved and micro- and macrofauna can access the litter (Dezozaya and Neiff 1991, van der Valk *et al.* 1991, Kuehn and Suberkropp 1998). The variable flooding regime of the protected wetlands may weaken and disrupt standing litter, accelerating the overall decay process and causing less litter to accumulate compared to the more hydrologically stable bayside wetlands.

The higher density of live cattails and upright dead stalks in bayside wetlands may further limit litter disturbance and decay. Sites with lower cattail abundance have less standing litter and have less litter accumulation relative to aboveground production. Davis and van der Valk (1978) found that 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 X 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). Standing dead plants likely support other upright stalks, slowing overall litter breakdown and likely inhibiting movement of litter during flooding. Thus as cattails expand in a wetland with stable water levels they may create a positive feedback that promotes persistent standing litter, greater litter accumulation, suppression of other species, and increased cattail dominance.

Implications for Great Lakes Plant Communities

Lake Ontario's water levels are currently regulated to minimize inter-annual variation. Before lake-level control began in 1960, water levels and plant communities varied episodically, more closely matching the vegetation cycles documented on other Great Lakes (Wilcox *et al.* 2005). Water level fluctuations are believed to increase wetland species diversity by killing woody and perennial vegetation during high water periods and allowing seeds to germinate along bare mudflats when water levels are low (van der Valk and Davis 1978b, Keddy and Reznicek 1986). Unfortunately, invasion by *Typha*

X glauca has been associated with reduced seed bank diversity in Lake Michigan wetlands, potentially limiting native species regeneration during low water years (Frieswyk and Zedler 2006). Stable water levels, the expansion of cattails, and litter accumulation may be causing a similar loss of seed bank and plant species diversity in Lake Ontario wetlands.

Plant community response to litter is often species specific and thus, factors promoting litter accumulation can influence community composition (Sydes and Grime 1981a, Facelli and Pickett 1991, Facelli 1994, Xiong et al. 2001). We found that seedling survival was sensitive to litter biomass, but the final size of live seedlings was not influenced by the amount of litter present. Other studies have also shown that seeds are more sensitive to litter than mature plants (Foster and Gross 1997). Therefore, annual or non-clonal herbaceous plants with less belowground storage are likely to be vulnerable to accumulation of litter. For example, *Campanula aparinoides*, *Cicuta bulbifera*, and *Galium tinctorium* were observed in several plots but never occurred in litter addition plots, indicating that they may have failed to germinate or emerge as a result of the thick litter layer. In contrast, clonal species, such as *Thelytris palustris* and *Lysimachia thyrsoiflora*, 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). The dense litter layer in the bayside wetlands may be preventing regeneration of sedge meadow species even during lower water-level periods. Species of the genera *Poa*, *Carex*, and *Solidago*, which occur widely in the protected but not the bayside wetlands, appeared as seedlings in our fallen litter removal plots of Mudge Creek. The relatively rapid response of Mudge Creek to litter removal indicates that restoration of a more diverse plant community might be possible if the litter of *T. angustifolia* were reduced. Thus, understanding how the expansion of cattail species and human activities (e.g., nutrient enrichment and lake level regulation) influence litter production, fragmentation and decomposition could help maintain diverse lakeshore wetlands.

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