

Impacts of *Lythrum salicaria* invasion on plant community and soil properties in two wetlands in central New York, USA

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Abstract: While the spread of the exotic *Lythrum salicaria* L. across wetlands in North America is thought to negatively affect the performance and diversity of native species, the actual impacts of *L. salicaria* invasion on community dynamics and ecosystem properties are not well understood. To determine whether *L. salicaria* affects community aboveground biomass, native species biomass, or soil properties, we studied two common situations in central New York State where *L. salicaria* invaded (i) an abandoned agricultural field and (ii) a relatively pristine wetland with low species diversity. In the agricultural site, nearly monospecific stands of *L. salicaria* and *Phalaris arundinacea* L. had nearly identical shoot mass (approx. 850 g·m⁻²) but divergent soil characteristics. Inorganic nitrogen was significantly higher under *L. salicaria* than under *P. arundinacea*. The low-diversity site is dominated by *Carex lacustris* Willd., with distinct areas codominated by either *L. salicaria* or *Typha latifolia* L. In this site, we found that areas with a codominant species had significantly more total aboveground biomass than those dominated by *C. lacustris*, suggesting that *L. salicaria* invasion does not significantly lower native species biomass. However, most soil nutrient levels did not differ among vegetation zones, indicating that species composition changes did not alter soil properties in the short term. This study supports a growing literature suggesting that *L. salicaria* invasion may not negatively impact relatively pristine wetlands as previously believed.

Key words: functional group, invasion, *Lythrum salicaria*, *Phalaris arundinacea*, wetland.

Résumé : Bien qu'on pense que l'invasion de l'adventice *Lythrum salicaria* L. à travers l'ensemble des terres humides de l'Amérique du Nord affecte négativement la performance et la diversité des espèces indigènes, le véritable impact du *L. salicaria* sur la dynamique des communautés et sur les propriétés des écosystèmes demeure mal compris. Afin de déterminer si le *L. salicaria* affecte la biomasse épigée des communautés, la biomasse des espèces indigènes, ou les propriétés du sol, les auteurs ont étudié deux situations courantes au centre de l'État de New York où le *L. salicaria* est envahissant : (i) un champ agricole abandonné; (ii) une terre humide relativement vierge avec une faible diversité d'espèces. Sur le site agricole, des peuplements presque mono-spécifiques de *L. salicaria* et de *Phalaris arundinacea* L. ont des biomasses presque identiques (approx 850 g·m⁻²) mais des caractéristiques édaphiques sont divergentes. L'azote inorganique est significativement plus élevé en présence du *L. salicaria* que du *P. arundinacea*. Le site à faible diversité est dominé par le *Carex lacustris* Willd., avec des surfaces distinctes dominées soit par le *L. salicaria* ou le *Typha latifolia* L. Sur ce site, on constate que les surfaces avec une espèce co-dominante présentent significativement plus de biomasse épigée totale, que les celles dominées par le *C. lacustris*, ce qui suggère que l'invasion par le *L. salicaria* ne réduit pas significativement la biomasse des espèces indigènes. Cependant, les teneurs de la plupart des nutriments du sol ne diffèrent pas selon les zones de végétation, ce qui indique que la composition en espèces ne modifie pas les propriétés du sol, du moins à court terme. Cette étude supporte une littérature de plus en plus importante qui suggère que l'invasion par le *L. salicaria* n'aurait pas d'impact négatif sur les terres humides relativement vierges, comme on le croyait auparavant.

Mots clés : groupe fonctionnel, invasion, *Lythrum salicaria*, *Phalaris arundinacea*, terre humide.

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Introduction

There has been considerable debate in the literature regarding patterns and processes of plant species invasions. Evidence suggests that invasions tend to be most successful

in low-diversity environments (Elton 1958; Tilman 1997; van Ruijven et al. 2003) or in disturbed environments (Hobbs and Huenneke 1992; Burke and Grime 1996; Galatowitsch et al. 1999; Alpert et al. 2000). One strikingly successful example is the spread of *Lythrum salicaria* L., a

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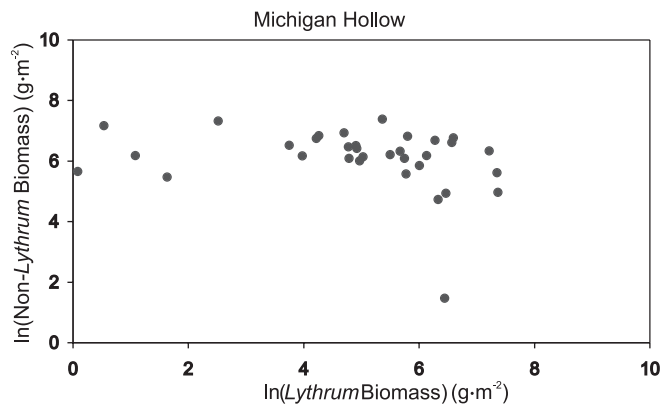
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Fig. 1. Correlation analysis showing how *Lythrum* and non-*Lythrum* biomass are related for each plot where *Lythrum* is present across all vegetation zones in Michigan Hollow ($r = -0.267$).



native Eurasian species, across wetlands in eastern North America in the early 1800s (Stuckey 1980; Thompson et al. 1987; Blossey and Schat 1997; Galatowitsch et al. 1999). Concern that *L. salicaria*, in turn, reduced species diversity in wetlands (Fernald 1940; Thompson et al. 1987) has spurred a large control effort (Malecki et al. 1993; Blossey et al. 2001; Landis et al. 2003), although some have questioned whether it has been truly responsible for altering biological diversity (Anderson 1995; Hager and McCoy 1998; Treberg and Husband 1999; Hager and Vinebrooke 2004).

A less obvious, but equally important, question is whether introduced plant species alter ecosystem properties and processes, such as pool sizes and turnover of nutrients and biomass (Vitousek 1990). It has been suggested that relatively similar species are interchangeable with respect to their effects on ecosystem properties (Johnson and Mayeux 1992; Grime 1997). Conversely, the addition of unique plant species can significantly alter ecosystem processes. For example, the invasion of an N-fixing plant species in Hawaii altered the competitive dynamics among plant and soil organisms by increasing biologically available soil N (Vitousek and Walker 1989). A less dramatic example is the invasion of C_4 species into C_3 -dominated environments, which altered nitrogen cycling and decomposition rates (Mack and D'Antonio 2003a, 2003b). One potential explanation for the large magnitude of these impacts is that those species each represent the introduction of a novel functional group into a plant community. Evidence from plant functional group studies have found that altering functional diversity can impact ecosystem processes (Tilman et al. 1997; Hooper and Vitousek 1998; Reich et al. 2004). Thus, an introduced species that represents a novel functional group in a community may be more likely to alter ecosystem processes.

Despite support for the idea that plant species can have unique functional roles in ecosystems, defining the functional traits of species is ambiguous and open to debate (Wilson 1999; Lavorel and Garnier 2002; Blondel 2003). Boutin and Keddy (1993) identified distinctive traits for wetland plant species, such as nutrient acquisition, competitive ability, stress tolerance, and dispersal ability. They identified three functional groups: interstitial, matrix, and ruderal species. Interstitial species, such as *Carex lacustris* Willd.,

have relatively low seed production, a low compact growth form, shallow rooting, and invest more energy into light capture than acquisition of belowground resources. Ruderal species, such as *L. salicaria*, are characterized by prolific seed production; a single mature *L. salicaria* plant has been estimated to produce as many as 2.7 million seeds annually (Thompson et al. 1987; Malecki et al. 1993). The seeds are long-lived, resulting in a large seed bank in sites where *L. salicaria* is present; however, its spread to other wetlands may be dispersal limited (Yakimowski et al. 2005). Other functional traits of *L. salicaria* are a tall clumping growth form, rapid regeneration following cutting, a shallow root system, and possibly rapid and efficient nutrient acquisition (Edwards et al. 1995). Matrix species, such as cattail (*Typha latifolia* L.) and canary grass (*Phalaris arundinacea* L.), are clonal dominants with very tall shoots and deep, well-developed roots and rhizomes that make matrix species competitive for belowground resources. Functional differences between these groups of species in resource use and allocation may impact wetland ecosystem processes and properties, such as carbon and nutrient pools and cycling rates.

The purpose of this study was to compare ecosystem properties among sites in two wetlands with different amounts of *L. salicaria* present. Our objective was to determine whether *L. salicaria* affects community shoot biomass, native species biomass, or soil and plant tissue chemistry in two wetlands that included species from all three of Boutin and Keddy's (1993) functional groups. We hypothesized that the low-diversity wetland (Michigan Hollow) would experience an increase in total community shoot biomass but no change in native species biomass with *L. salicaria* invasion because *L. salicaria* increases functional diversity and thus may occupy a different niche than the dominant species. In contrast, we expected that shoot biomass levels of the two near-monoculture stands in the postagricultural wetland (Marten's Tract) would be similar because both dominant species (*P. arundinacea* and *L. salicaria*) are aggressive invaders known to achieve high biomass (Barnes 1999; Galatowitsch et al. 1999; Mahaney et al. 2004). We further hypothesized that *L. salicaria* gained a competitive advantage in both wetlands by superior nutrient acquisition and rapid growth. Therefore, we expected that vegetation zones with greater amounts of *L. salicaria* would correspond to lower levels of soil resources compared with the other vegetation zones. We also measured each species plant tissue nutrient concentrations to examine whether significant differences in a plant species' nutrient use and allocation might correspond to differences in soil resources.

Methods

Study areas

The two wetlands were located in central New York State. Michigan Hollow is a 15 ha nutrient-poor, low-diversity, riverine sedge meadow that sits in the lowest part of a small, forested watershed (42°21'N, 76°28'W) dominated by northern hardwood tree species. In the 1970s, the wetland was a monospecific stand of *C. lacustris* (Bernard and Macdonald 1974). In 1990, small isolated areas in the wetland became codominated by *T. latifolia*, and *L. salicaria* in-

Table 1. Mean (SE) biomass in five vegetation plots in two wetlands, with *P* values for each site to indicate significant differences across vegetation zones.

Zone	Total biomass (g·m ⁻²)	<i>Lythrum</i> biomass (g·m ⁻²)	Non- <i>Lythrum</i> biomass (g·m ⁻²)	% <i>Lythrum</i>
Michigan Hollow				
<i>Carex</i>	535.99 (54.33)a	0.46 (0.29)a	535.53 (54.42)a	0.2 (0.1)
<i>Typha</i>	1086.28 (109.02)b	124.28 (34.88)a	962.00 (116.75)b	13.5 (3.8)
<i>Lythrum</i> I	948.33 (118.48)b	477.35 (113.28)b	470.98 (76.47)a	42.2 (7.5)
<i>P</i> value	0.001	0.000	0.000	
Marten's Tract				
<i>Lythrum</i> II	879.65 (107.08)	824.55 (100.70)e	55.15 (21.02)e	95.3 (1.7)
<i>Phalaris</i>	839.90 (69.47)	24.45 (14.81)f	815.43 (66.86)f	2.4 (1.4)
<i>P</i> value	0.756	0.000	0.000	

Note: Letters denote significant differences between vegetation zones derived from post-hoc Tukey comparisons with *P* < 0.05.

vaded the wetland in 1993 and appears to be spreading in a northerly direction. There were no obvious disturbances to the wetland prior to the appearance of either *T. latifolia* or *L. salicaria* (J.B. Yavitt, personal observation). We established a transect along the invasion gradient and randomly selected one sampling area in each of three vegetation zones: the southernmost area was dominated by *C. lacustris* and *L. salicaria* (*Lythrum* I zone); the middle segment was dominated by *C. lacustris*, *T. latifolia*, and *L. salicaria* (*Typha* zone); and the northernmost region was dominated by *C. lacustris* (*Carex* zone). The soils were 50 cm deep Histic Peat.

The second site, Martens Tract, is a 99 ha postagricultural wetland in the Montezuma National Wildlife Refuge (42°58'N, 76°42'W). The preagricultural wetland was probably a swamp forest dominated by *Acer rubrum* L. (Vogelman 1972; Marks et al. 1992), and open *Carex* meadows and *Typha* marshes with scattered trees were known to occur in the region (Hunt-Joshi et al. 2004). The original wetland vegetation was removed more than 55 years ago, and potatoes and corn were grown annually until agriculture was abandoned in 1989 (Hunt-Joshi et al. 2004). *Lythrum salicaria* freely invaded the area after abandonment, while *P. arundinacea* was planted into monocultures (Hunt-Joshi et al. 2004). We examined two vegetation zones in one section of the wetland: a near-monoculture of *L. salicaria* (*Lythrum* II zone) and a near-monoculture of *P. arundinacea* (*Phalaris* zone). The soils were highly organic, calcium-rich and overlaid marl.

Shoot mass

Because of the hypothesized northerly spread of *L. salicaria* across Michigan Hollow, we modified our sampling regime to avoid confounding time since invasion within the three vegetation zones. Therefore, the sampling design consisted of randomly establishing one 8 m × 10 m sampling area in each vegetation zone, with 20 plots (0.1 m²) set out on a regular grid with 2 m spacing between plots. This relatively clustered plot design was chosen to minimize the influence of time since *L. salicaria* establishment within a vegetation zone, thereby limiting the influence of its perceived northerly spread across the wetland. In Marten's Tract, we established 40 plots (0.1 m²) in a regular

grid across a 20 m × 20 m sampling area (plots separated by 2.5–4 m) in each vegetation zone. The size of the sampling area encompassed most of the area planted to *P. arundinacea*, and the *L. salicaria* zone was established immediately adjacent to this zone.

Shoot mass was determined for each plot in all five vegetation zones at the end of the growing season in late August 1998. Shoot biomass, including the current year's dead biomass, was clipped at ground level, and *L. salicaria* was separated from the other species. Since snow compresses *C. lacustris* biomass each winter, current year's biomass was easily distinguishable from older, partially decomposed biomass. Biomass of both *L. salicaria* and the other species was then dried for 24 h at 55 °C and weighed to the nearest 0.01 g.

Soil analysis

Soil cores (15 cm deep, 8 cm diameter) were taken from each plot, large roots were removed by hand, and portions were taken for individual soil analyses. Soil organic matter content (SOM) was estimated for one portion (approx. 0.5 g fresh weight) of each core, oven-dried at 55 °C, and combusted in quartz tubes at 450 °C. The ash was then dissolved in HNO₃ and concentrations of major cations and metals were analyzed by argon plasma emission spectroscopy on an inductively coupled plasma spectrophotometer (ICP) (Dahlquist and Knoll 1978). Soil pH was estimated on another soil portion (approx. 5 g) at field water content, using a 1:5 solution of soil to deionized water. Extractable NH₄⁺ and NO₃⁻ were estimated on a third portion (approx. 3 g) using 30 mL of 2 mol/L KCl and a continuous flow autoanalyzer. We also collected the pore water that filled the hole left by the soil core, passed it through a 0.45 μm filter, and analyzed it for concentrations of (i) major cations and metals on an ICP and of (ii) NH₄⁺ and NO₃⁻ colorimetrically on a continuous flow analyzer.

Tissue analysis

In August, foliar chemistry analyses were performed on the mature green leaves of each of the dominant species at both sites (*L. salicaria*, *T. latifolia*, *C. lacustris*, and *P. arundinacea*). The samples were dried for 24 h at 55 °C and ground to pass through a screen of mesh size 0.6 mm.

Table 2. Mean (SE) concentrations (mg·L⁻¹) of nutrients dissolved in soil pore water in five vegetation zones in two wetlands, with *P* values for each site to indicate significant differences across vegetation zones.

Zone	Ca ²⁺	Mg ²⁺	K ⁺	NH ₄ ⁺	NO ₃ ⁻	PO ₄ ³⁻
Michigan Hollow						
<i>Carex</i>	20.66 (0.44)a	3.16 (0.06)a	0.38 (0.04)	0.12 (0.02)	BDL	0.18 (0.06)
<i>Typha</i>	14.75 (0.50)b	2.58 (0.11)b	0.64 (0.27)	0.09 (0.01)	0.05 (0.00)	0.29 (0.07)
<i>Lythrum</i> I	24.44 (1.95)c	4.86 (0.52)c	1.03 (0.21)	BDL	BDL	0.14 (0.03)
<i>P</i> value	0.000	0.000	0.277	0.223		0.368
Marten's Tract						
<i>Lythrum</i> II	268.14 (13.15)e	30.95 (0.65)e	63.32 (1.95)e	0.31 (0.12)	0.29 (0.24)	BDL
<i>Phalaris</i>	363.00 (26.80)f	24.35 (0.80)f	37.73 (6.37)f	0.13 (0.08)	0.74 (0.36)	0.002 (0.002)
<i>P</i> value	0.013	0.000	0.005	0.915	0.557	

Note: Letters denote significant differences between vegetation zones derived from post-hoc Tukey comparisons with *P* < 0.05. BDL, values were below the detection limit.

Samples were dry-ashed in quartz tubes at 450 °C, and the ash was dissolved in HNO₃ for elemental concentration analysis on an ICP. Tissue C/N was measured on an elemental analyzer (EA) by the Cornell Nutrient Analysis Laboratory (Department of Crop and Soil Sciences, Cornell University).

Data analysis

For Michigan Hollow, we used a Pearson's correlation on ln-transformed biomass values of all plots with *L. salicaria* present to examine the relationship between *Lythrum* and non-*Lythrum* biomass, combining all vegetation zones. We also performed a one-way analysis of variance (ANOVA) to determine whether there were significant differences in total and non-*Lythrum* biomass between plots with *L. salicaria* present or absent. In each wetland, we used one-way ANOVA to test for significant differences in shoot biomass (total, *Lythrum*, and non-*Lythrum* biomass) as well as soil, pore water, and tissue nutrient levels between the vegetation zones. Significant results were followed by Tukey post-hoc comparisons. Pore water sample values for nitrogen (N) and phosphorus (P) below machine detection limit were omitted from the analyses. All statistical analyses were performed using Systat version 11.

Results

Shoot biomass

In Michigan Hollow, the Pearson's correlation analysis showed only a very weak negative relationship between *Lythrum* and non-*Lythrum* biomass in all plots with *L. salicaria* present (*r* = -0.267; Fig. 1). ANOVA found no significant differences in total or non-*Lythrum* biomass between quadrats with and without *L. salicaria* (*F*_[1,58] = 3.83, 1.13; *P* = 0.055, 0.291, respectively). Total, *Lythrum*, and non-*Lythrum* biomass all differed among vegetation zones (Table 1). Total shoot biomass in Michigan Hollow in the *Typha* and *Lythrum* I zones was significantly greater than in the *Carex* zone (Table 1). While *Lythrum* biomass was significantly greater in the *Lythrum* I zone than in the *Carex* and *Typha* zones (Table 1), it did not correspond to a decrease in non-*Lythrum* biomass. In fact, non-*Lythrum* biomass was highest in the *Typha* zone and not significantly different between the other two zones (Table 1). In Marten's Tract, total shoot mass was not significantly different in the

Lythrum II zone compared with the *Phalaris* zone (Table 1). The dominant plant species contributed at least 90% of the community shoot mass in each of their respective zones (Table 1)

Soil resources

In Marten's Tract, there were no significant differences in concentrations of NH₄⁺ and NO₃⁻ in soil pore water between vegetation zones. The *Lythrum* II zone had significantly greater concentrations of pore water Mg²⁺ and K⁺ and significantly less pore water Ca²⁺ than the *Phalaris* zone (Table 2). In Michigan Hollow, there were no significant differences in soil pore water concentrations of NH₄⁺, PO₄³⁻, and K⁺ across vegetation zones. Nitrate levels were extremely low; mostly below the instrument detection limit. Pore water concentrations of Ca²⁺ and Mg²⁺ differed significantly between the vegetation zones (Table 2).

Element concentrations in soil samples from Marten's Tract were significantly higher in the *Lythrum* II zone than in the *Phalaris* zone for all variables measured (Table 3). Element concentrations in peat samples showed no significant differences in Mg²⁺, K⁺, and P across vegetation zones (Table 3). Soil organic matter, pH, and Ca²⁺ concentrations in peat soils were significantly higher in the *Carex* zone than in the *Typha* zone, while inorganic N (extractable NH₄⁺ and NO₃⁻) was significantly higher in the *Typha* zone than in the *Carex* zone (Table 3).

Plant tissue nutrients

At Michigan Hollow, there were no significant differences in species tissue N or C/N. *Carex lacustris* had the lowest tissue P and Ca²⁺, while *T. latifolia* had significantly higher K⁺ than the other two species (Table 4). *Lythrum salicaria* had significantly greater Mg²⁺ and Ca²⁺ than *T. latifolia* and *C. lacustris*. At Marten's Tract, *L. salicaria* had significantly greater Mg²⁺ and Ca²⁺ than *P. arundinacea*, while the opposite was found for tissue N (Table 4). There were no significant differences in tissue C/N, P, or K⁺ between species at Marten's Tract (Table 4).

Discussion

In a review of the literature, Anderson (1995) questioned the accuracy of many claims that *L. salicaria* reduces the biomass of other species. Rather, Anderson (1995) argued that

Table 3. Mean (SE) values for peat and soil characteristics (cation concentrations are in dry soil) from five vegetation zones in two wetlands, with *P* values for each site to indicate significant differences across vegetation zones.

Zone	Ca ²⁺ (mg·g ⁻¹)	Mg ²⁺ (mg·g ⁻¹)	K ⁺ (mg·g ⁻¹)	NO ₃ ⁻ + NH ₄ ⁺ (mg·g ⁻¹)	Total P (mg·g ⁻¹)	pH (in H ₂ O)	SOM (%)
Michigan Hollow							
<i>Carex</i>	16.69 (0.47)a	1.47 (0.03)	1.23 (0.04)a	8.96 (1.15)a	1.52 (0.05)	5.87 (0.04)a	74.76 (1.22)a
<i>Typha</i>	13.65 (0.61)b	1.59 (0.09)	1.39 (0.11)a	12.21 (0.86)b	1.55 (0.12)	5.59 (0.09)b	66.21 (2.84)b
<i>Lythrum</i> I	14.20 (0.55)ab	1.48 (0.06)	1.06 (0.07)a	NA	1.54 (0.06)	NA	68.88 (1.87)ab
<i>P</i> value	0.001	0.307	0.109	0.030	0.977	0.007	0.022
Marten's Tract							
<i>Lythrum</i> II	24.65 (0.40)e	2.47 (0.10)e	1.16 (0.04)e	20.40 (2.60)e	2.25 (0.19)e	7.94 (0.07)e	24.69 (2.14)e
<i>Phalaris</i>	12.86 (2.07)f	0.67 (0.11)f	0.73 (0.04)f	12.26 (0.86)f	1.54 (0.03)f	7.27 (0.06)f	19.29 (1.08)f
<i>P</i> value	0.000	0.000	0.000	0.004	0.002	0.000	0.037

Note: Letters denote significant differences between vegetation zones derived from post-hoc Tukey comparisons with *P* < 0.05. NA, no data were available from that vegetation zone; SOM, soil organic matter.

L. salicaria increases biomass production at a faster rate than most native species, and so only the proportion of native species biomass is decreasing. Our results from Michigan Hollow support this argument. The *Carex* zone, which had no *L. salicaria* present, had about 500 g·m⁻² of shoot mass. In contrast, total shoot mass was two times greater in the *Lythrum* I zone, but *C. lacustris* contributed roughly the same amount as in the *Carex* zone. Therefore, it appears that *L. salicaria* doubled the total shoot mass without diminishing the native species' biomass production. ANOVA further indicated no difference in non-*Lythrum* biomass between the *Carex* and *Lythrum* I zones.

However, when *L. salicaria* becomes dominant in a community (i.e., in Marten's Tract), it can maintain itself in near monocultures, even with other aggressive competitors (i.e., *P. arundinacea*) in the immediate vicinity. The total biomass in Marten's Tract was not significantly different between the two vegetation zones, suggesting that the site has a maximum attainable biomass level. This is not unexpected given that both dominant species in this site are aggressive species that are known to achieve high biomass levels (Barnes 1999; Galatowitsch et al. 1999; Mahaney et al. 2004). *Phalaris arundinacea* is an aggressive species with known exotic genotypes; however, it is unknown whether the *P. arundinacea* population in this site contains exotic genotypes or hybrids.

One reason for *L. salicaria*'s successful invasion into wetlands like Michigan Hollow simply may be that it represents a different functional group of plant species, rather than any advantage in competitive ability related to its exotic status. Ruderal plant species might be able to invade more readily into wetlands dominated by matrix and clonal species because they are prolific seed producers and can grow rapidly in areas "open" for establishment, and thus are not competing with plant species having similar traits. If ruderal species occupy microsites that are unsuitable for the other species, they would be less likely to have a negative impact on those species' biomass levels. Studies in prairie and grassland systems have shown that increased productivity can occur with increasing functional group diversity (Tilman et al. 1997; Reich et al. 2004). Additional support for this functional diversity hypothesis comes from the *Typha* zone, which had significantly higher total and non-*Lythrum* biomass than the other two zones. This was the zone with all three of Boutin and Keddy's (1993) functional groups present, which further suggests that increasing functional diversity may increase productivity. Because *L. salicaria* invaded Marten's Tract almost immediately after agricultural abandonment (i.e., not an intact community), this site could not be used to examine this functional group explanation.

While the presence of *L. salicaria* in Michigan Hollow indicates that it is able to invade an undisturbed wetland, *L. salicaria* had considerably less shoot mass in Michigan Hollow than in Marten's Tract. However, *L. salicaria* invaded Marten's Tract almost immediately after agriculture was abandoned and was potentially favored by the high disturbance levels and vegetation removal associated with agricultural activities. Five years after invasion began at Michigan Hollow, *L. salicaria* made up 42% of the total aboveground biomass in the most heavily *Lythrum*-dominated region of the wetland (*Lythrum* I zone), compared with 90% in Marten's Tract. While *L. salicaria* has the abil-

Table 4. Mean (SE) concentrations (in dry tissue) of nutrients in green leaf tissue of the different species from five vegetation zones in two wetlands, with *P* values for each site to indicate significant differences across vegetation zones.

Species	Ca ²⁺ (mg·g ⁻¹)	K ⁺ (mg·g ⁻¹)	Mg ²⁺ (mg·g ⁻¹)	P (mg·g ⁻¹)	N (%)	C/N
Michigan Hollow						
<i>C. lacustris</i>	3.77 (0.23)a	9.38 (0.40)a	1.08 (0.06)a	1.27 (0.03)a	1.68 (0.07)a	26.55 (1.10)a
<i>T. latifolia</i>	11.81 (0.98)b	13.68 (0.90)b	1.65 (0.10)a	2.32 (0.13)b	1.96 (0.14)a	23.97 (1.68)a
<i>L. salicaria</i>	19.33 (0.90)c	9.76 (0.41)a	5.34 (0.19)b	2.31 (0.18)b	1.64 (0.07)a	26.96 (1.25)a
<i>P</i> value	0.000	0.000	0.000	0.000	0.084	0.852
Marten's Tract						
<i>L. salicaria</i>	20.85 (0.84)e	17.71 (1.25)e	3.54 (0.11)e	3.91 (0.20)e	2.33 (0.27)e	19.72 (2.39)e
<i>P. arundinacea</i>	6.93 (0.17)f	18.13 (0.39)e	2.25 (0.06)f	3.99 (0.07)e	3.17 (0.17)f	13.89 (0.78)e
<i>P</i> value	0.000	0.754	0.000	0.739	0.048	0.089

Note: Letters denote significant differences between vegetation zones derived from post-hoc Tukey comparisons with *P* < 0.05.

ity to quickly colonize and pre-empt resources at a site, which is typical of ruderal species, perhaps it is less suited to competing for resources in a low-fertility environment with established vegetation. Other invasive wetland plant species are known to compete poorly when the vegetation at a site is intact (Burke and Grime 1996; Morrison and Moloisky 1998; Maurer and Zedler 2002), so perhaps *L. salicaria* invasion is repressed by the presence of intact vegetation as well. If correct, it could mean that it will simply take longer than the 5-year time span since invasion began at this site for *L. salicaria* to dominate an undisturbed wetland or that the species in this wetland will maintain a coexistence with *L. salicaria* until some disturbance in the wetland results in vegetation removal that may facilitate *L. salicaria* dominance.

One mechanism by which plant species attain dominance is by acquiring and storing nutrients in plant tissue. Nutrient acquisition can be a good index for comparing the competitive ability among plant species (Goldberg and Miller 1990). For example, because soil resources often are supplied in pulses, the individuals with the most rapid nutrient uptake are more likely to take advantage of the pulse and thus have greater tissue nutrient concentrations (Goldberg 1990). Based on Goldberg's hypothesis, we expected that *L. salicaria* would have higher tissue nutrient concentrations compared with the other plant species. This was not true consistently, except for the much higher tissue Ca²⁺ and Mg²⁺ concentrations in *L. salicaria* than in the other species. We do not know the mechanism for Ca²⁺ or Mg²⁺ accumulation in *L. salicaria* or the functional significance, although the accumulation was demonstrated in plants from Marten's Tract with extremely high soil Ca²⁺ concentrations and in Michigan Hollow where the soil Ca²⁺ concentrations were much lower.

In contrast with the higher tissue nutrient concentrations expected for the superior competitors above, McJannet et al. (1995) analyzed tissue N and P concentrations for 41 wetland plants from diverse habitats and found significantly lower tissue N and P concentrations, especially N, in plants with ruderal functional traits (including *L. salicaria*). They argued that ruderal species had very high growth rates, and thus they did not store nutrients in leaf tissue. Our findings do not agree with this hypothesis; moreover, we found much higher tissue N concentrations of 16–23 mg·g⁻¹ compared with values of <10 mg·g⁻¹ (McJannet et al. 1995) for

L. salicaria. Our N values for *L. salicaria* were similar to those found by Nagel and Griffin (2001). We found similar concentrations of P in *L. salicaria* leaf tissue (0.23–3.9 mg·g⁻¹) compared with values of 1.4 to 4.0 mg·g⁻¹ reported by Emery and Perry (1995) for plants growing in 11 sites in Minnesota. Templer et al. (1998) reported even higher tissue P concentrations (5 mg·g⁻¹) for *L. salicaria* in an estuary in New York State. We found higher tissue N concentrations than did McJannet et al. (1995) and Mahaney et al. (2004) for *P. arundinacea*, but the P concentrations we found were similar to those found by Mahaney et al. (2004). In addition, although not statistically compared, the *L. salicaria* tissue values for several of the elements we measured differed more between the two sites than did those element concentrations between the different species within a site (see Table 4). This contrasts with the results of McJannet et al. (1995), who found no consistent differences in tissue N and P for plant species growing in fertile and infertile sites.

In Marten's Tract, we found major differences in all soil and water chemistry variables except pore water PO₄³⁻, NH₄⁺, and NO₃⁻ concentrations. Concentrations of dissolved PO₄³⁻ were extremely low in both zones in Marten's Tract, even though it was the more fertile wetland. It is possible that P is insoluble and bound to Ca²⁺ given the abundance of Ca²⁺ and the higher soil pH in Marten's Tract. Differences in soil variables could be caused by species-specific impacts of the dominant species on soil properties. Because we are unable to determine the initial soil conditions, we cannot establish whether *L. salicaria*, *P. arundinacea*, or both species caused the divergence of these soil resources. Nevertheless, we are confident in assuming that there were no major pre-existing soil differences between these two sites because of their close proximity, identical agricultural history, and lack of any obvious differences in hydrology or topography. In contrast with Marten's Tract, we found only subtle effects of *L. salicaria* on peat and water chemistry in Michigan Hollow. However, *L. salicaria* could have effects on ecosystem processes that we did not measure (e.g., N transformations and trace-gas fluxes). Otto et al. (1999) studied rates of microbial N transformations in a stand of *L. salicaria* versus ones dominated by *Typha angustifolia* L. or *Phragmites australis* (Cav.) Trin. ex Steud. and found no large differences in N cycling among the sites. Furthermore, we cannot assess changes in N cycling due to increased

L. salicaria biomass and associated changes in decomposition processes, some of which may become evident at a later date.

In conclusion, our findings suggest that *L. salicaria* invasion into a low-diversity wetland does not necessarily alter ecosystem functions and processes such as nutrient cycling, nor does it lead to a striking decrease in the shoot biomass of native species. As a ruderal species, *L. salicaria* may add to the total community biomass by colonizing microsites that are not suitable for other wetland plant species and could have future implications for short-term ecosystem carbon storage. While the emergent ecosystem properties investigated in this study were unaffected in the short term, it is unknown whether *L. salicaria* will increase in dominance through time, potentially leading to significant changes in ecosystem properties in the long term. For instance, other aspects of native species besides biomass, such as lifetime reproductive fitness, may be impacted in the longer term. In addition, our study only examined soil and pore water chemistry at one point in the growing season, and so any shifts in chemistry throughout the growing season would be missed. Therefore, broader studies, in both space and time, should be undertaken to examine whether these results are applicable across an array of wetlands and whether these results hold over longer time periods.

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