PLANT AND INSECT-MEDIATED INVASIVENESS OF *PHRAGMITES AUSTRALIS* AND THE LITTER DYNAMICS AND BIODIVERSITY OF SIX FRESHWATER MACROPHYTES

A Thesis

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Master of Science

by

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ABSTRACT

My thesis involves two distinct projects related to wetland plants. The first evaluates plant traits for their contribution to the success of invasive *Phragmites australis* in North America and their interaction with herbivores. The second investigates the relative effects of six plant species, with different growth forms, status (native v. nonnative) and tissue quality, on litter dynamics and invertebrate diversity in a New York freshwater wetland.

Prevention is the most cost-effective and successful means of managing invasive plants. Predicting future invasions depends on identifying plant traits that facilitate invasive success. We investigated the influence of above-ground growth phenology and increased stem height on the success of invasive *Phragmites australis* in North America, using a phylogenetically-controlled comparison with a native, non-weedy *P. australis* subspecies. We also measured the effects of specialist stem-galling *Lipara* flies and a generalist aphid (*Hyalopterus pruni*), both nonnatives to North America, on these above-ground traits. Comparisons were made in 1) a common garden at Cornell University, Ithaca, NY, in 2003 and 2004, and 2) a field site at Montezuma National Wildlife Refuge, Seneca Falls, NY in 2003. In the garden, but not the field, nonnative *P. australis* leaves remained green for about a month longer (native v. nonnative: 2003 = 59.93 v. 85.5 days, $P = 0.0002$; 2004 = 52.29 v. 87.39 days, $P = 0.02$). For nonnative *P. australis*, leaves of the upper canopy consistently lived longer while leaf lifespan in the lower canopy was shorter or the same. Greater investment in high canopy leaves may increase carbon gain efficiency of nonnative *P. australis*. Nonnative *P. australis* grew taller in the field but this was mediated by disproportionate *Lipara* attack rather than plant status (native or nonnative). *Lipara* attack reduced stem height of all stems but only increased the lifespan of nonnative *P. australis'* low canopy leaves. Aphids had no significant effect on measured plant

traits. Through increased carbon gain, leaf phenology may contribute to *P. australis'* competitive superiority over its native conspecific. Higher susceptibility of native *P. australis* to nonnative herbivores may also facilitate nonnative *P. australis'* competitive superiority.

Senesced plant litter from emergent macrophytes fuels freshwater wetland productivity and nutrient cycling. Litter nitrogen content generally has a direct, positive effect on quantity and rate of resource availability to wetland biota. Since plants vary in their nitrogen content, shifts in plant community composition may alter important wetland functions. To study the consequences of changing plant dominance, we compared litter mass loss and invertebrate richness and abundance of six common macrophytes in a central New York freshwater wetland. Plants studied include *Typha latifolia* L. (broad leafed cattail, Typhacea), *T. angustifolia* L. (narrow leafed cattail), *Phragmites australis* (cav.) Trin ex. Steudel (common reed, Poaceae), *P. australis* subspecies *americanus* Saltonstall, P.M. Peterson & Soreng, *Lythrum salicaria* L. (purple loosestrife, Lythraceae), and *Phalaris arundinacea* L. (reed canarygrass, Poaceae). After nine months, mass loss of most plant species diverged significantly. Plant effect on invertebrate colonization was season and species-specific, with *P. arundinacea* almost consistently supporting higher invertebrate densities. Although %N differed among some plant species, it was not a good predictor of mass loss or invertebrate abundance and richness. Including plastic drinking straws as a treatment revealed that several invertebrates used litter for substrate rather than food. We conclude that shifts in plant dominance among the six wetland macrophytes investigated could potentially alter wetland function, by changing decomposition rates and the invertebrate community. Net quality of litter resources, which depends on the combined influence of morphology, chemical quality of specific plant organs, and feeding ecology of specific taxa, may be a better predictor of species effects on decomposition and diversity.

BIOGRAPHICAL SKETCH

Mia Park was born to Noel and Mary in Vancouver, Canada, where she and her younger siblings, Angela and Derek, spent their early childhood years. Mia somehow got through her teens while living in Seoul, Korea and then San Jose, California, which she now calls home. Mia received her Bachelors of Science (Land, Air and Water Resources) and Arts (French) in 1999 from University of California, Davis. Attending UC Davis instilled in Mia a love for small towns and field biology. After graduation, she spent three years working as a field technician on various research projects, which ranged widely in study organism and location. Through these diverse experiences, Mia identified three core interests to pursue for graduate study: wetlands, invasive plants and invertebrates. She found a great match in the Ecology and Management of Invasive Plants Program (EMIPP) at Cornell University's Department of Natural Resources. During her time at Cornell University, Mia's passion for invertebrates deepened. While still interested in invasion biology, she now plans to study invasive ants and their impacts on native endemic ants and frogs in Madagascar. Ultimately, Mia hopes to increase general interest and support for invertebrate conservation.

In memory of Joe Stasulat
whose encouragement still urges me forward today.

ACKNOWLEDGMENTS

I would like to thank Bernd Blossey, my major advisor, for his constant support, confidence and ready laugh. I appreciate his drive for innovation and the thick skin I developed under his tutelage. I want to thank my committee member Mark Bain whose advice and reassurance contributed substantially to my thesis and to calming my nerves.

I extend great thanks to all members of the Ecology and Management of Invasives Plants Program (EMIPP)— past and present— for their support, feedback, enthusiasm, and friendship. Much of what I learned about invasion biology, ecology and good science comes from my interaction with this group. Needless to say, my field and lab work would not have been possible without them.

A special thanks to Jim Booth and Francoise Vermeylan whose statistical expertises were essential to completing this work. I am also grateful to Patrick Sullivan, Ted Treska and Beth Gardner for their statistical consulting at the early stages of my thesis.

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I am deeply grateful for the community of friends and colleagues I found in the Department of Natural Resources at Cornell University. No where have I met a group of people more genuine, intelligent, motivated and kind. Finally, I would like to thank my parents, Mary and Noel, and my siblings, Angela and Derek, who have supported me unconditionally in my pursuits to "save the planet".

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CHAPTER ONE

Influence of stem traits and herbivory on the success of invasive *Phragmites australis*

Abstract

According to theory, plant community structure results from the combined influence of inherent plant traits and external forces (e.g. herbivores); however, rarely are the two explicitly integrated in studies of plant invaders. Here we investigate whether above-ground growth phenology and increased stem height contribute to success of invasive *Phragmites australis* in North America, by using a phylogenetically controlled comparison with the native, non-invasive *Phragmites australis americanus* subspecies. We concurrently recorded the influence of herbivore attack by introduced specialist, stem-galling *Lipara* spp. flies and introduced generalist Peach aphid (*Hyalopterus pruni*) on plant growth and phenology. We used two different venues, a common garden and a field site in upstate New York, USA for our study. In the garden but not the field, nonnative *P. australis* leaves lived on average a month longer. Consistent across venue, the vertical age structure of nonnative *P. australis* demonstrated a potential for greater resource gain in dense canopy conditions. We found significant differences in plant height in the field, but height was mediated by *Lipara* spp. herbivory rather than native or nonnative status. *Lipara* spp. attack also influenced vertical age structure but not overall leaf senescence patterns. Aphids had no significant effect on traits measured. Differences in leaf phenology between native and non-native *P. australis* may contribute to the competitive superiority of nonnative *P. australis*. Consistent higher rates of herbivory on native *P. australis americanus* indicate that introduced herbivores may also facilitate replacement of this North American endemic subspecies by nonnative *P. australis.*

Introduction

Successful management of threats posed by plant invasions depends on prevention of new introductions (Rejmanek 2000). Increasing our ability to predict which plant species will be invasive in a new environment or have a negative impact on the invaded environment is, thus, fundamental to invasion ecology.

Leading hypotheses for invasive plant success stem from two general community ecology perspectives where external (e.g. plant-plant or plant-insect interactions) or endogenous (genetically-based) forces influence plant competitive ability. Enemy release (ERH)(Keane and Crawley 2002, Torchin *et al.* 2003, DeWalt *et al.* 2004), evolution of increased competitive ability (EICA)(Blossey and Notzold 1995), and biotic resistance (Case 1990, Kennedy *et al.* 2002) are largely exogenous in nature, relying on biotic forces influencing plant success and evolution. Endogenous-centered explanations of invasive success emphasize the importance of pre-adaptive traits that allow a plant to out-compete and dominate neighboring (native and introduced) flora in the introduced range (Sax and Brown 2000). High reproductive output, broad plasticity, superior levels of productivity and rapid growth are commonly observed traits of weedy plants (Baker 1965; Noble 1989; Roy 1990). Nonnative plant possession of novel weapons, the suppression of native flora and/or pathogens via root exudates, might also fall in this category (Callaway and Ridenour 2004, Prati and Bossdorf 2004).

Despite the importance of these hypotheses for experimental investigations, it is clear that they each have limitations, considering the fate of a novel plant may depend on the combined influence of 1) its evolutionary history and traits, 2) plant-plant interactions, 3) interactions with other trophic levels or the abiotic environment and climate, and 4) stochasticity (Lortie *et al.* 2004). While our understanding of the factors that influence successful invasions has certainly improved over the last few

decades (Sax and Brown 2000), lack of integration among different hypotheses may limit our ability to further improve understanding of invasion success and contribute to general predictive inability.

In this study, we hypothesized that leaf phenology and plant height contribute to the invasive success of P*hragmites australis* (cav.) Trin ex. Steudel in North America (NA). *Phragmites australis* (Type M haplotype) was introduced to NA ca. 200 years ago (Saltonstall 2002) and has spread throughout wetlands of the United States, particularly along the Atlantic Coast and in the Midwest (Marks *et al.* 1994). The presence of the native, non-invasive conspecific *P. australis* subsp. *americanus* Saltonstall, P.M. Peterson & Soreng in NA facilitates phylogenetically controlled comparisons to isolate plant characters that contribute to its invasive success (Trowbridge 1996, Agrawal and Kotanen 2003, Burns 2004).

In a common garden and a field site, we specifically predicted that 1) introduced *P. australis* will have a prolonged period of growth and 2) introduced *P. australis* stems will grow taller. Community dominance, linked to superior biomass production, requires relatively high levels of resource capture. By prolonging exploitation of resources, early and/or extended growth enables a plant to maximize productivity (Hulbert 1955, McKell *et al.* 1962, Fox 1984, Bazzaz 1986, Crawley 1987, Chikoye *et al.* 1996, Zotz *et al.* 2000, West *et al.* 2003). Plants may extend the duration of photosynthetic activity via early germination and establishment or through delayed leaf and stem senescence. Such advantages in resource use may determine plant fitness and, ultimately, the outcome of plant competition (Chikoye *et al.* 1996). Increased plant height, shown to be a good predictor of macrophyte invasive success (Gaudet and Keddy 1988), also facilitates greater access to light resources. Light limited plants may optimize carbon gain by quickly remobilizing nitrogen from shaded leaves in the under-story to new leaves of the upper canopy (Mooney *et al.* 1981). Since *P. australis* leaves emerge as the stem grows, increased height may be a product

of this tactic. Finally, the dense clonal stature of *P. australis* can limit light access to potential competitors (Haslam 1971).

To integrate an external force that may act on plant traits involved in the success of invasive *P. australis*, we recorded the influence of herbivory on plant growth and phenology. *Phragmites* plants are attacked by two conspicuous herbivores: specialist gall-forming flies of the genus *Lipara* and a generalist aphid, *Hyalopterus pruni* (Geoffroy), both of which are nonnative and attack the stem apex and leaves, respectively. *Lipara* spp. lay their eggs on the upper most leaves of *P. australis* stems (Chvala *et al.* 1974). Once hatched, larvae enter the tip of the stem and form a gall, which destroys the apical meristem, impeding stem growth (Tscharntke 1999). *Hyalopterus pruni* uses *P. australis* as a secondary host in late spring and early summer and feeds on phloem from leaf tissue (Mook and Wiegers 1999). Phloem-feeders have been shown to alter leaf phenology, which in turn, can negatively affect growth (Bazzaz and Hartnett 1984). At least 162 herbivores are associated with *P. australis* in Europe; whereas, only 26 species are known in NA, of which only five are native (Tewksbury *et al.* 2002). Given nonnative *P. australis* evolved under higher herbivore pressure than the native North American subspecies, we predicted that *Lipara* spp. and *H. pruni* would have a stronger influence on native *P. australis* stems.

Materials and methods

Study species

Extant populations of *Phragmites* throughout most of NA consist of the introduced Type M haplotype and an endemic North American subspecies *P. australis americanus* (Saltonstall *et al.* 2004). Due to the recent discovery of native endemic

North American haplotypes, little information on potential differences in ecology, plant-herbivore interactions and ecosystem function among the different haplotypes is available; however, in addition to genetic techniques, Type M can be separated from all endemic haplotypes using morphological traits (Blossey 2003). All *Phragmites* haplotypes are tall, clonal grasses growing in freshwater to oligohaline tidal wetlands, marshes, ditches and along roadsides. After initial establishment, plants produce annual cane-like 2 – 5 m tall shoots that produce flowers in late summer and disperse seeds over much of the fall and winter. Seeds are dispersed by wind, water, and adhesion to waterfowl; reproduction from seed is variable and usually low but important for colonization of new habitats (Haslam 1972a). Rhizome fragments are transported with construction equipment, water, or animals; clonal expansion after establishment occurs through an extensive rhizome system producing up to 200 stems/m^2 (Haslam 1958). Approximately two thirds of the biomass is allocated to the rhizome-system that can reach a depth of 2 m (Szczepansky 1969, Haslam 1972b).

Typically, established *P. australis americanus* populations are small (<1 ha), and the species grows in mixed communities of many other wetland plants. In contrast, Type M *P. australis*, introduced about 200 years ago from Europe (Saltonstall 2002), has spread across much of North America effectively replacing mixed, native wetland plant communities with extensive, dense monocultures (Saltonstall 2002). By 1960, historic *P. australis americanus* sites located in Connecticut, Massachusetts and Rhode Island had been replaced by Type M *P. australis* (Saltonstall 2002). The Type M haplotype has also expanded its range into the Southeast, where *Phragmites* did not occur previously.

Study sites and experimental conditions

In order to compare leaf phenology and growth, we monitored stem and leaf characteristics of native *P. australis americanus* and Type M *P. australis* haplotypes growing in a common garden at Cornell University's Resource Ecology and Management facility (REM) in 2003 and 2004. In 2003, a parallel field study was conducted at the Montezuma National Wildlife Refuge (MNWR), Seneca Falls, NY, where Type M and native Type E *P. australis* populations grew adjacently.

The common garden is a collection of *Phragmites* haplotypes (multiple plants/location) from across NA with a focus on temperate populations. All haplotypes were started from rhizome collections either excavated by us or provided to us by collaborators from across the continent. Plants were grown in 28 X 27 cm plastic nursery pots filled with potting soil (Farfard Canadian growing mix No. 1-P, Agawam, MA) and placed into shallow 4 x 4 m artificial pools (10 cm water depth) to provide them with sufficient moisture. Each pond contained a mix of native and Type M *P. australis* plants grouped according to collection location. Plants were weeded regularly and fertilized with 20 g Osmocote® slow release fertilizer (N-P-K: 18:6:12; The Scotts Company, Marysville, Ohio) each spring.

On 26 June 2003, 23 native and 25 Type M *P. australis* we randomly selected plants, representing 13 native and 5 introduced populations (Table 1.1) grown for at least one full growing season in the common garden. One stem per plant was tagged with flagging tape. Starting at the base of the plant (excluding basal leaves <10cm), fully expanded leaves were labeled with a unique ID number on the underside of the leaf using a permanent nursery marker. Leaves that had already emerged by the first date were not used in phenology comparisons as it was impossible to know their exact emergence date. We repeated this experiment in 2004 using identical labeling procedures but with a different set of plants, which were all placed at random in a

single pond (50 cm distance between pots). One plant was randomly chosen from each of 13 native and 11 Type M *P. australis* populations represented (Table 1.1). In order to test whether Type M and native haplotypes initiate growth at the same time, we began monitoring stems earlier, 5 May, in 2004.

At our field site (located 100 km north of the common garden), a Type M clone (10 x 8 m) grew immediately adjacent to a native Type E clone (7 x 5 m) in a spring-flooded, shallow depression in a meadow next to the visitor center of the MNWR. Both stands have existed at this location for at least ten years (Blossey, pers. obs.). As is typical, Type M grew in a virtual monoculture and continued to expand, while Type E stems grew interspersed with many other wetland and meadow species. On 6 June 2004, six stems (three on either side) were selected at 1 m intervals along a transect that ran through the adjacent native and nonnative clones, perpendicular to the inter-clone boundary. A total of 53 native and 55 nonnative stems were tagged, and fully expanded leaves were subsequently labeled as described for stems in the common garden.

Plant measurements

At the field site and in the common garden (both years), we measured stem height at least every two weeks from study initiation through December and recorded premature stem death and breakage. To establish whether Type M has a longer period of photosynthetic activity, stems in the common garden and field were visited weekly, at which point newly emerged leaves (fully expanded) were labeled and senescence (determined when leaf was completely devoid of green) of labeled leaves recorded. Monitoring in both the garden and the field continued through mid December. For

Table 1.1. Collection location, state or province, status (N= native, I= introduced), and Haplotype of *Phragmites australis* grown in the common garden.

Location	State/Province	Status	Haplotype[1]	Study Year[2]
Memramcook	New Brunswick	N	S	1,2
Hillsborough	New Brunswick	N	S	1
Sheppody	New Brunswick	N	E	1
Montezuma NWR	New York	N	E	1,2
Robert Moses State Park	New York	N	E	1,2
Deer Creek Marsh	New York	N	unknown	2
Brandy Brook	New York	N	G	1,2
TNC Choptanc	Maryland	N	AD	2
Drawer's Creek	Delaware	N	F	1,2
Occupacia Creek	Virginia	N	F	2
Marsh Lake	Indiana	N	E	1,2
Pipewort Pond	Indiana	N	AB	1
Marenisco	Michigan	N	E	1
Seminary Fen	Minnesota	N	S	1
Savage Fen	Minnesota	N	E	1
Medicine Lake NWR, site 1	Montana	N	E	1,2
Medicine Lake NWR, site 2	Montana	N	E	1
Sun Lakes Park	Washington	N	D	1,2
Ellensburg	Washington	N	A	1,2
Astoria	Oregon	N	E	1,2
Moncton	New Brunswick	I	M	1,2
New Haven	Connecticut	I	M	1,2
Robert Moses State Park	New York	I	M	1,2
Athens	New York	I	M	2
Galeville	New York	I	M	1,2
Ithaca	New York	I	M	1,2
Deer Creek at Lake Ontario	New York	I	M	2
TNC Choptanc	Maryland	I	M	2
Peoria	Illinois	I	M	2
Novato	California	I	M	1
Fish Access	Washington	I	M	1,2
Moses Lake	Washington	I	M	2

[1] genotyped

[2] study year 1 and 2 correspond to 2003 and 2004, respectively.

every leaf labeled after the initiation of the study, we recorded date of emergence, date of death, and subsequently calculated life span.

To account for the effects of herbivory on measured plant traits, attack by specialist gall flies, *Lipara* spp. and a generalist aphid, *Hyalopterus pruni*, on each stem was recorded. Gall fly damage is recognizable by cessation of stem growth and a thickened and wrapped apex (*L. rufitarsis*) or wrapped dead apical leaves (*L. similis*) but we did not distinguish between the *Lipara* species. The total number of native and Type M *P. australis* stems galled at the end of the growing season was noted. To quantify the intensity of aphid attack at the leaf level, we recorded aphid densities as percent cover of leaves, according to six categories: 0 = 0%, 1 < 1%, 2 =1-10%, 3 = 11- 25%, 4 = 26-50%, 5 = 51-75%, and 6 = 76%-100%.

Analyses

Since the experimental design differed between venues and years, all statistical analyses were performed separately for REM 2003, REM 2004 and MNWR. To determine if Type M *P. australis* benefits from early emergence, we compared mean number of leaves initiated per stem by the first date of monitoring in the garden and field site in 2003. Because we started earlier in 2004, we were able to compare timing of first leaf production between native and nonnative stems that year. We also compared leaf life span to see how long stems remained photosynthetically active. To test the influence of plant and insect-mediated effects on leaf life span, we employed a mixed linear model, with stem as our random variable. Specifically, we tested the main effects of continent of status (native or introduced), leaf position (vertical), stem galling and aphid attack on leaf life span. Vertical position of the leaf was determined by numbering leaves starting at the base consecutively up the stem. We included position of the leaf in the model because vertical age structure in plants whose leaves

grow successionally (from base to tip) has been shown to influence carbon gain (Hirose and Werger 1987). Aphid attack was consolidated into two categories: low (0 - 10%) and higher (10-100%).

The following interaction terms were also included: Aphid X Status, Gall X Status, Aphid X Gall, Status X Position, Position X Gall, and Status X Position X Gall. The Aphid X Status and Gall X Status terms allowed us to determine whether herbivores affected life span of native and introduced leaves equally. We also included Aphid X Gall to investigate a potential cumulative impact of the herbivores. Visual inspection of the data revealed a strong interaction between status and position on leaf life span. The interaction terms Position X Gall and Status X Position X Gall were included to investigate whether native and/or introduced stems compensate for the reduced number of leaves that resulted from galling.

A full factorial, repeated measures ANOVA was conducted to test the influence of status and galling on stem height through the growing season. To qualitatively compare temporal patterns in leaf phenology, the average cumulative proportion of leaves emerged and senesced per plant for each monitoring date was calculated. The frequency and intensity of herbivory by gall flies and aphids on native and introduced haplotype stems were compared.

Results

Leaf phenology and stem growth

Consistent between years and study sites, temporal patterns of leaf emergence were similar between native and Type M *P. australis* stems (Fig. 1.1). Average timing of leaf initiation, solely measured in the garden in 2004, was significantly earlier (t_{20} = 2.928, p = 0.0083) for Type M *P. australis* but only by about three days (mean julian

date for nonnative and native, respectively: 127.91 and 131.73). The small discrepancy in emergence time unlikely imparts a resource advantage; especially since there was no difference in average number of leaves emerged (Garden: native = 4.86, Type M = 5.00, $t_{45} = -0.1525$, $P = 0.88$; Field: native = 2.04, Type M = 2.16, $t_{89} = 0.5791$, $P = 0.56$). Thereafter, overall leaf production was synchronous through the growing season, except in the field where Type M haplotype stems continued to produce leaves after native stems had ceased to do so (Fig. 1.1).

A prolonged period of photosynthetic activity was observed in the garden but not in the field. In the garden, leaves of Type M *P. australis* stems lived significantly longer – over a month – than those growing on native stems (native v. Type M: 2003 = 59.93 v. 85.5 days; 2004 = 52.29 v. 87.39 days, Fig. 1.1; Table 1.2). In contrast, rates of leaf death in the field for native and Type M *P. australis* stems were similar (Fig. 1.1). Since leaf emergence did not differ among experiments, leaf life span paralleled senescence patterns. The opposite was observed in the field where native leaves lived on average 9.6 days longer than Type M haplotype leaves and where no significant effect of status was found on leaf life span (Table 1.2). Irregardless of status, leaf life span depended on vertical leaf position (Table 1.2). *Phragmites* leaves positioned midway on the stem lived longer than those found at the top or base (Fig. 1.2). Across venue, leaves in the upper canopy of Type M haplotype stems lived significantly longer than similarly placed leaves on native *P. australis* stems (significant Position X Status effect, Table 1.2). Leaves positioned on the lower half of native *P. australis* stems lived longer (field site) or as long (common garden) as similarly positioned leaves on stems of Type M haplotypes (Fig.1.2).

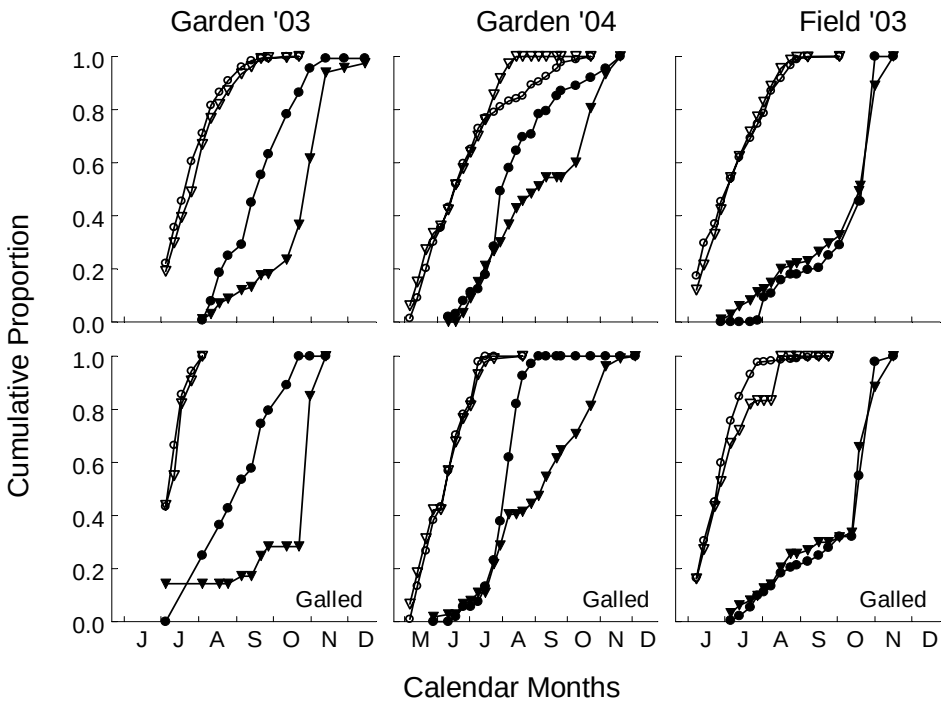

Figure 1.1. Leaf production (open symbols) and senescence (filled symbols) on native (circles) and introduced (triangles) Phragmites australis stems (cumulative proportion, separated by galled and ungalled stems) in the common garden (2003, 2004) and in the field (2003). Data represent means. Standard error bars were excluded for clear display of trends.

Table 1.2. Effects of status (native or nonnative), aphid herbivory (low v. med to high), vertical position, and stem galling on *Phragmites australis* leaf life span as tested with mixed linear regression, treating stem as a random variable and position 2nd order.

	Garden 2003		Garden 2004		Field 2003	
Parameter	*F*	*P*	*F*	*P*	*F*	*P*
Status	16.84	0.0002	6.4912	0.0197	3.43	0.0677
Aphid	0.1994	0.6555	0.0044	0.9474	0.644	0.4223
Position[2]	29.1688	<0.0001	9.5161	0.0001	20.759	<0.0001
Gall	0.6674	0.4188	0.0001	0.9924	0.000476	0.6372
A x S	5.1768	0.0235	3.2981	0.0704	2.089	0.1486
A x G	0.2076	0.6489	3.8030	0.0521	0.00004	0.9948
S x G	0.0631	0.8030	0.0754	0.7866	0.2389	0.6251
S x P	11.8538	<0.0001	14.0151	<0.0001	4.659	0.0097
G x P	16.2584	<0.0001	22.7782	<0.0001	.1774	0.8375
S x P x G	-- [1]	-- [1]	7.1663	0.0009	1.502	0.2230
A x G x S	-- [1]	-- [1]	0.4929	0.4832	2.556	0.1102

[1] 3-way interactions were not run in the model due to inadequate sample size for specific combinations.

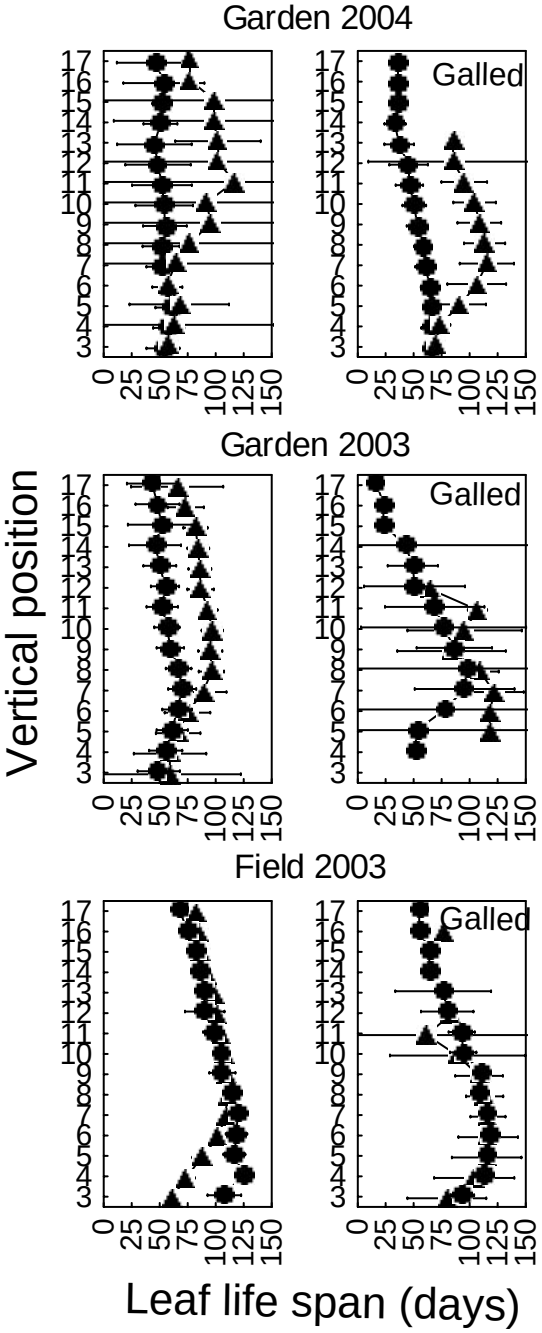

Figure 1.2. Leaf life span of galled and ungalled stems of native and introduced Phragmites australis at different vertical positions in the common garden (2003, 2004) and at Montezuma NWR (2003). Weighted means +/- 95% confidence interval are provided for leaves positioned from 3 to 17 since small sample size at the extreme positions resulted in extremely high variation at all study sites.

Stem heights between haplotypes were similar in the garden but not in the field, where Type M haplotype grew significantly taller (Fig.1.3). Plants grown in the common garden were on average shorter than those growing under natural conditions in the field.

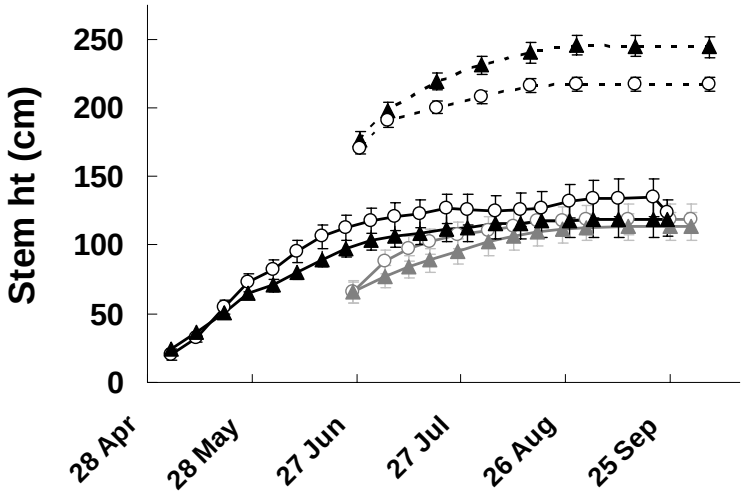

Figure 1.3. Stem growth (cm) of native (open circles) and introduced (filled triangles) *Phragmites australis* haplotypes in the common garden (2003 grey solid line, 2004 black solid line) and field site (hatched line). Data are means ± 1SE.

Natural enemies and plant measurements

Herbivory by specialist gall-forming *Lipara* spp. strongly influenced stem height and leaf production of both native and Type M haplotypes (significant Gall and non-significant Gall X Status effects, Tables 1.3, 1.4; Figs. 1.1, 1.4). These effects were consistent across venue and year except for 2003 stem growth in the garden, where galling had no main effect on height and reduced leaf production for the Type M haplotype only (Tables 1.3, 1.4; Fig. 1.4). Reasons for this annual effect in the garden

are unknown; however, possible causes include an improved ability to identify gall formation in the second year, population fluctuations of *Lipara* spp. within the garden, as well as within-population variation of response to *Lipara* spp. attack. While proportion of galled stems did not differ in the common garden (2003: Fisher's, p = 0.063; 2004: Fisher's, p = 1; Fig. 1.5), a significantly greater proportion of native *P. australis* stems suffered *Lipara* spp. damage in the field (Fisher's, p = 0; Fig. 1.4).

Table 1.3. Results of repeated measures ANOVA testing the effects of status (native or nonnative) and gall formation on *Phragmites australis* stem height in the common garden and in the field through the growing season.

	Garden 2003			Garden 2004			Field 2003		
Effect	SS	df	*F*	SS	df	*F*	SS	df	*F*
Status	760000	1	3.46	5207	1	0.5	289000	1	2.2
Gall	1836	1	0.08	177000	1	18***	250000	1	18.9***
S x G	368000	1	1.68	3898	1	0.4	2745	1	0.2
Time	89100	12	53.99***	325000	19	497.6***	185000	11	152.0***
T x S	2811	12	1.70	6033	19	9.2***	4673	11	3.8***
T x G	36900	12	22.36***	444000	19	68.0***	339000	11	27.9***
T x S x G	717	12	0.43	7607	19	11.6***	1852	11	1.5

*, **, ***, Effect significant at $P < 0.05$, 0.01, and 0.001, respectively.

Galling reduced stem height irrespective of haplotype, and the higher attack of native stems resulted in the observed height discrepancies between native and nonnative *P. australis* stems in the field (no significant Status effects on height, Table 1.3). Ungalled stems of both haplotyes grew taller than galled stems (significant Gall X Time effects, Table 1.2). *Lipara* spp. indirectly altered vertical leaf age structure. Across venues, *Lipara* spp. did not change seasonal patterns of leaf emergence nor senescence (Fig. 1.1). Additionally, this specialist herbivore did not affect overall leaf life span (significant Gall X Status term, Table 1.2). Although not statistically

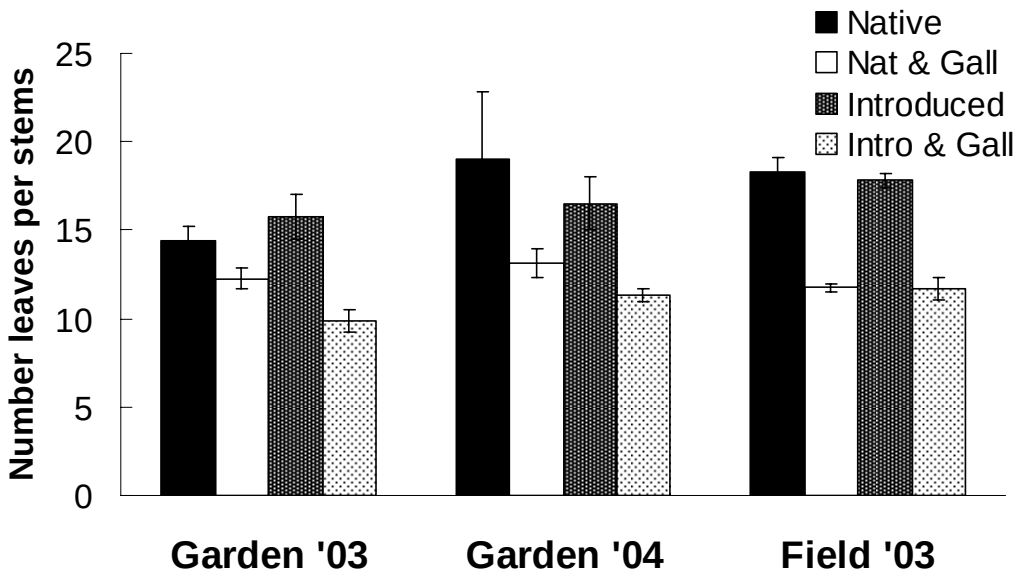

Figure 1.4. Number of leaves (means ± **2**SE) on galled and ungalled stems of native and introduced *Phragmites australis* in the common garden (2003, 2004) and at Montezuma NWR (2003).

Table 1.4. Results of two-way ANOVA testing the effects of status (native or nonnative) and gall formation on total leaf number per *Phragmites australis* stem in the common garden and in the field.

	Garden 2003		Garden 2004		Field 2003	
Effect	SS	*F*	SS	*F*	SS	*F*
Status	0.14	0.019	20.63	2.70	1.63	0.45
Gall	162.68	22.05***	131.03	17.17***	814.81	224.88***
S x G	35.27	4.78*	0.47	0.061	0.66	0.18

*, **, ***, Effect significant at $P < 0.05$, 0.01, and 0.001, respectively.

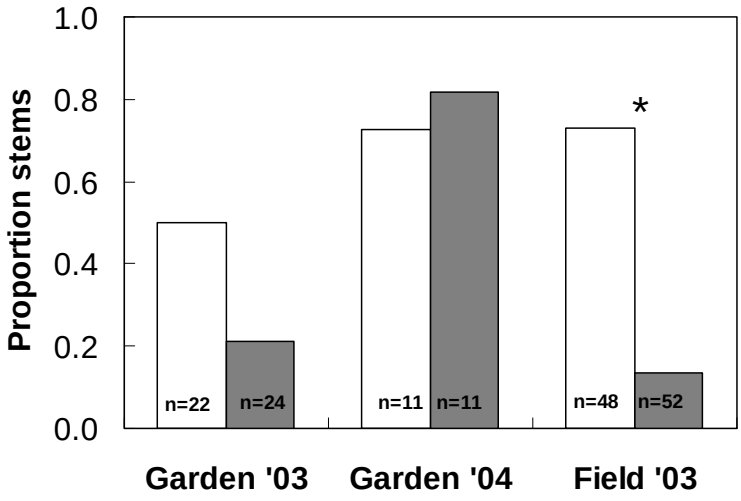

Figure 1.5. Apical attack (proportion of stems attacked) by *Lipara* spp. gall flies on stems of native (white) and introduced (grey) *Phragmites australis* haplotypes in the common garden (2003, 2004) and at Montezuma NWR (2003). The * indicates a significant difference in stem galling between haplotypes (Fisher's, p = 0).

significant in the field, there was a consistent trend for stems stunted by galling to retain already-emerged leaves longer, causing leaves positioned lower on the stem to live longer (Fig. 1.2; Table 1.2, significant Gall X Position in garden). This response was especially pronounced for Type M haplotype stems in 2004 (highly significant Status X Position X Gall effect, Table 1.2; Fig. 1.2).

Hyalopterus pruni reached higher densities more frequently on leaves of native haplotypes in both the common garden and field (Garden '03: $X^2 = 90.758$, df = 6, p = 0; Garden '04: $X^2 = 64.77$, df = 6, p = 0; Field: $X^2 = 159.469$, df = 6, p = 0; Fig. 1.6). However, there was no measurable effect of aphid herbivory on leaf life span (Table 1.2). Even though significant Aphid X Status and Aphid X Gall interactions were found on leaf life span in the garden, we attribute these results to a lack of higher aphid densities on Type M *P. australis* leaves and resulting inadequate sample sizes for higher aphid and Type M combinations.

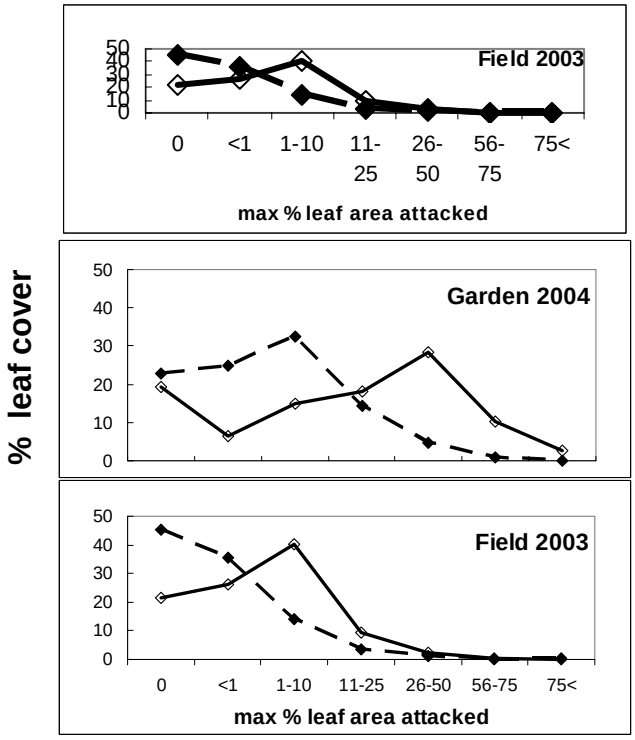

Figure 1.6. Frequency of aphid densities (% leaf cover, in categories) on leaves of native (solid line) and introduced (dashed line) *Phragmites australis* stems in the common garden (2003 and 2004) and in the field (2003).

Discussion

We found mixed support for prolonged growing period and increased stem height in nonnative *P. australis*, with results influenced by interactions with herbivores and venue. In the common garden, a one month delay in leaf senescence provides strong evidence that a prolonged period of photosynthetic activity contributes to the invasive success of Type M *P. australis* (Fig. 1.1). In their study of invasive *Bunias orientalis* L. in central Europe, Zotz *et al.* (2000) demonstrated empirically that delayed senescence relative to native plants can result in high carbon gains even late in the year. Longer leaf life spans can also translate into increased root production and, as a

result, increased stress tolerance (West *et al.* 2003). In light of the fact that two thirds of *P. australis* biomass resides in rhizomes (Szczepansky 1969, Haslam 1972b), a period of extended resource capture may be central to supporting extensive below ground structures, which in turn have been attributed to this invader's relatively high tolerance to suboptimal environments (Bart and Hartman 2000) and rapid vegetative spread (Tewksbury *et al.* 2002).

Despite the consistent pattern of senescence over two years in the garden, we did not observe an extended growing season for Type M *P. australis* in the field. Although herbivory rates differed between venues, neither *H. pruni* or *Lipara* spp. affected leaf phenology patterns. Latitude of source populations, applicable only to the common garden, has been shown to affect plant growth, but was also ruled out as a confounding factor since the phenology patterns were consistent when comparing populations within states (Park, unpublished). Given that senescence patterns similar to those in the common garden have been observed in other field populations, we hypothesize that the discrepancy in venue is a result of natural variation among populations for leaf longevity. However, these results highlight the need for future research to include multiple field sites even when combined with a common garden experiment.

Differences in age structure of leaves at the stem level provides initial evidence that Type M *P. australis* may be better equipped to compete in communities with a dense canopy than native haplotypes. Consistent with models of optimum carbon gain, leaves of nonnative *P. australis* were relatively short-lived in the shaded reaches of the lower canopy and longer-lived in the upper canopy where light resources were maximal (Mooney *et al.* 1981, Hirose and Werger 1987). However, whether this observed pattern increases the rate of photosynthetic activity and Type M's ability for greater carbon gain at both the stem and clone level needs experimental confirmation. By prohibiting stems from reallocating resources upwards, it seems that *Lipara* spp.

would inhibit efficient modes of carbon gain by Type M *P. australis*. Considering *Lipara* spp. caused stems to retain leaves in the lower canopy longer for both native and nonnative stems, follow up study of *P. australis* leaf dynamics should account for the indirect influence of stem-gallers. Similar to a longer period of resource capture, efficient resource capture would contribute to Type M haplotype's support of increased production.

As predicted, Type M *P. australis* stems grew taller than native stems in the field; however, the increased height was not a pre-adapted plant trait, but rather mediated by a specialist gall fly. The lack of height difference in the garden where galls occurred equally on native and nonnative stems confirms these results. These findings illustrate that naive conclusion about plant traits may be made if interactions with important herbivores are not considered. They also provide preliminary evidence that a top-down control may facilitate displacement of native *P. australis* haplotypes by the Type M haplotype.

That stems in general were shorter in the common garden than in the field illustrate the dependency of plant growth on environmental conditions and resource availability. As a result, height discrepancies commonly cited in the field may reflect variation in physiological responses of native and nonnative haplotypes to their environment (i.e. stressors or resources) or may reflect microhabitat variation within a site (Vasquez *et al.* 2005). Such variation would not be expressed in the common garden nor at our field site, since both were designed/selected to have similar abiotic conditions. It appears that stem height alone is not an appropriate surrogate of productivity for a clonal, rhizomatous plant like *P. australis*, known to suffer from apical herbivory.

The fact that introduced herbivores were responsible for the increased attack on native haplotypes is a twist on the enemy release hypothesis (ERH). ERH predicts that Type M *P. australis* will host fewer specialist herbivores in its introduced range

than in its native range (Keane and Crawley 2002, Mitchell and Power 2003, Torchin *et al.* 2003), and suffer less herbivory than the native flora of the invaded community because specialists of *native* species will not host-shift in sufficient frequency to make up for the lost specialists (Schierenbeck *et al.* 1994, Siemann and Rogers 2003). Type M P. *australis* in NA has certainly escaped many of its co-evolved European herbivores (Tewksbury *et al.* 2002), but the increased herbivore attack we observed on native *P. australis americanus* was caused by two introduced herbivores. Colautti *et al*. (2004) coined this inversion of ERH the 'enemy of my enemy' hypothesis (EEH). In this case, native haplotypes "naïve" to introduced herbivores appear to be more susceptible to the introduced specialists, whereas Type M's evolutionary history with introduced *Lipara* spp. has likely shaped this invader's ability to tolerate or develop increased resistance to the specialist gall-makers. Reasons for greater aphid herbivory on native *P. australis* leaves are unknown; however, *H. pruni* is known to respond to color (Moericke 1969) and plant tissue quality (Minks and Harrewijn 1986). Irregardless of cause, herbivores may influence competitive interactions between native and nonnative *P. australis* haplotypes; however, the advantages gained from enemy release alone probably do not explain Type M's general invasive success in NA (Colautti *et al.* 2004).

Our study focused on two herbivores and two stem traits, which is by no means exhaustive in understanding the mechanisms behind *P. australis*' competitive superiority. Considering rhizomes are important in Type M *P. australis* spread and establishment into "hostile" environments (Bart and Hartman 2000) and comprise a large part of this species' biomass (Szczepansky 1969, Haslam 1972b), future efforts to better understand what makes *P. australis* a successful invader should include a similar comparison of belowground traits, where phylogeny and environmental factors are also controlled.

Plants respond to and shape the biotic community in which they exist. Significant gall fly effects on both leaf life span and stem height0 reinforce that plant invaders do not thrive in a vacuum. Their growth and fitness are at once determined by genetically-based plant traits and exterior forces such as natural enemies. Further, the dynamic between endogenous and external factors is not unidirectional. For example, just as *Lipara* spp. herbivory stunted stem growth, unknown trait-mediated differences between native and introduced haplotypes resulted in higher rates of gall formation on native stems. Hypotheses such as enemy release, EICA, novel weapons, biotic resistance, as well as predictive models of invasion based solely on plant traits, have provided helpful mechanistic frameworks to address why some plants are invasive while others are not. However, each hypothesis alone fails to acknowledge the complex and dynamic interactions that direct the success or failure of plant introductions. Not until we integrate a holistic perspective on invasive success will our predictive abilities move beyond the individual case to the general.

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CHAPTER TWO

Decomposition dynamics and invertebrate diversity of six wetland macrophytes in a New York freshwater marsh

Abstract

As a major source of senesced plant material, emergent macrophytes influence wetland litter processing and decomposer food webs, both critical factors shaping nutrient cycling and total energy budgets. The influence of macrophytes on these wetland functions may be largely determined by the nitrogen content of the plant tissue, with high nitrogen tissues decomposing more readily due to their high palatability to decomposer microbes and invertebrates. Since plant species commonly vary in tissue quality, shifts in plant dominance within a wetland are likely to alter wetland function. To study the consequences of changing plant dominance, we compared litter mass loss and litter invertebrate richness and abundance in litter bags exposed to a central New York wetland. We used six common wetland plant species: *Typha latifolia* L. (broad leafed cattail, Typhacea), *T. angustifolia* L. (narrow leafed cattail), *Phragmites australis* (cav.) Trin ex. Steudel (common reed, Poaceae), *P. australis* subspecies *americanus* Saltonstall, P.M. Peterson & Soreng, *Lythrum salicaria* L. (purple loosestrife, Lythraceae), and *Phalaris arundinacea* L. (reed canarygrass, Poaceae). After nine months, significant species effects on mass loss, invertebrate richness and total density were observed. Most plant species supported significantly different rates of decay, while plant species effects on invertebrate communities were season and species-specific. Plant tissue nitrogen content differed significantly among plant species but did not predict mass loss patterns or invertebrate response. A combination of quality and quantity of litter resources, influenced by the morphology and quality of specific plant organs, may be a better predictor for species

effects on wetland biota and mass loss. Potential shifts in plant dominance among the six wetland macrophytes investigated can alter wetland function, by changing decomposition rates and the invertebrate community, an important prey-base for higher trophic levels in wetlands.

Introduction

Primary producers provide the basic "currency" for functioning of ecosystems. In freshwater wetlands, emergent macrophytes shape the physical environment and fuel most wetland food webs (Mitsch and Gosselink 1993, Kuehn *et al.* 2000). A small fraction of this macrophyte-derived energy enters wetlands through direct consumption of green leaf material by herbivores and omnivores. Most energy, rather, is released after plants have senesced through the microbial conditioning of dead plant tissues during the process of decomposition (Mitsch and Gosselink 1993, Moore *et al.* 2005). Microbial decomposers are consumed by invertebrates, which subsequently form the prey base for higher trophic levels. Decomposition of plant detritus is also critical for nutrient cycling as decomposers convert organic nutrients into inorganic forms useable by living plants (Naeem *et al.* 2000).

Decomposition rates and, thus, rates of nutrient and energy inputs, are largely controlled by the quality of the plant litter resource (reviews: Swift *et al.* 1979; Anderson *et al.* 1991). Generally, plant tissues with high concentrations of nitrogen (N) are preferentially colonized by microbes and invertebrate detritivores, resulting in relatively rapid decay (Melillo *et al.* 1982). Growth form and the allocation of nitrogen among plant organs also seems to affect decomposition patterns (Hobbie 1996). Tissue quality and physical structure have been shown to influence decomposition rates and biotic communities at multiple levels of plant taxonomy: plant type (Cornellissen 1996, 2004), species (Findlay and Arsuffi 1989, Hobbie 1992,

1996, Dudgeon and Wu 1999, Bailey *et al.* 2001), and even genotype (Driebe and Whitham 2000, Whitham *et al.* 2003, Schweitzer *et al.* 2005). Considering that tissue quality and physical form vary widely among plant species, shifts in plant community composition, especially shifts in plant dominance, may produce changes that reverberate through the entire ecosystem.

Both natural and human-induced environmental changes alter plant communities within freshwater wetlands; however, little is known about the consequences of such shifts on wetland function and biota. While litter N content provides a framework in which to predict directional changes in litter dynamics and decomposer communities, other factors, such as the physical structural traits of plants, also will play a role. Consequently, impacts of species-specific shifts in plant dominance remain unpredictable (Aertz 1997). Additionally, much of what is known about litter effects on ecosystem function comes from terrestrial and stream studies; much less is known about litter processing in wetlands.

To better understand the structuring forces of plant species in detrital systems of freshwater wetlands, we investigated the impacts of a suite of dominant wetland macrophytes on two ecosystem processes: decomposition and biodiversity. In a central New York wetland, we tested the following hypotheses: 1) plant species provide varying litter resources in terms of their tissue quality (i.e. N content), and 2) litter mass loss as well as invertebrate richness and abundance will increase with increasing N content. Macrophytes are important drivers of wetland processes, and shifts in the resident flora are expected to have extended effects on ecosystem processes.

Methods

Study plants

Typha latifolia L. (Broad leafed cattail, Typhacea), *T. angustifolia* L. (narrow leafed cattail), *Phragmites australis* (cav.) Trin ex. Steudel (Common reed, Poaceae), *Lythrum salicaria* L. (Purple loosestrife, Lythraceae), and *Phalaris arundinacea* L. (Reed canarygrass, Poaceae) are common perennial macrophytes of northeastern freshwater wetlands. They represent multiple plant forms (herbaceous, graminoid) with differing leaf and stem morphologies and include both native and nonnative species (Table 2.1). *Typha angustifolia* has recently invaded the Midwest and West Coast; however, its status on the East Coast is less clear. Similarly, *P. arundinacea*'s current native status in the Northeast is under question due to its invasive nature, notably, in wetlands of the Midwest. *Phragmites australis* and *L. salicaria* are established exotic invasive plants that displace native flora, including *T. latifolia* and native *P. australis* subspecies *americanus* Saltonstall, P.M. Peterson & Soreng. Although less common than our other study plants, the native *Phragmites* subspecies was included as it was once more abundant in the Northeast but has been replaced by the introduced genotype and continues to be threatened by such replacement (Saltonstall 2002).

Site

The study site was located at Deer Creek Marsh in Oswego County, NY, a relatively undisturbed freshwater wetland located on the East Shore of Lake Ontario (N43º 35. 494, W76º 11.787). The hydroperiod of the marsh is regulated by the building and breaching of a sand barrier where Deer Creek empties into Lake Ontario (Bailey

Table 2.1. Growth form and status (native or introduced) in the Northeast of six wetland plant species studied.

Species	Habit	Height	Status
Lythrum salicaria	Erect herb; shrub form with woody, branched stems; small lanceolate leaves.	30 – 100 cm	Introduced invasive
Phragmites australis americanus	Erect graminoid but reed-like; 25-50 cm cauline leaves; tubular, hollow stem.	2 – 4 m	Native non-invasive
Phragmites australis	Erect graminoid but reed-like; 25-50 cm long cauline leaves; tubular, hollow stem.	2 – 4 m	Introduced invasive
Phalaris arundinacea	Erect graminoid, 7-30 cm long cauline leaves.	1 – 2 m	Native invasive
Typha angustifolia	Erect herb; long, relatively narrow, strap-like basal leaves, originating from shoot stalk.	2 – 2.5 m	Native
Typha latifolia	Erect herb; long, relatively broad, strap-like basal leaves, originating from shoot stalk.	50 – 150 cm	Native

1998). Consequently, water levels can fluctuate unpredictably. Water levels, dissolved oxygen, and pH differed between spring and fall collections (Table 2.2). Within the marsh complex, the study was situated in a medium rich fen, dominated by *Carex lasiocarpa.* Native and non-native *Phragmites* and *Typha latifolia* were present in the fen with *L.salicaria* growing along the perimeter of the fen.

Experimental design

Entire senesced stems of the six plant species were collected in October and November 2003. For each plant type, stems were collected from a single population,

Table 2.2. Site characteristics at Deer Creek Marsh during spring (June) and fall (September) collections.

Measure	Spring	Fall
Water depth (cm)	42.6	9.3
Temp (ºC)	28.3	17.6
pH	6.59	6.09
DO (mg/L)	3.45	1.53

with *L. salicaria, P. arundinacea*, both *Phragmites* and *T. angustifolia* collected within the Northern Montezuma Wetlands Complex (NMWC), Seneca Falls, NY. *Typha latifolia* was collected at a site near Ithaca, NY, about 83 km away from NMWC where identification could be confirmed by a regional expert (Robert Wesley). Stems were air dried at room temperature for a minimum of two weeks. Twenty-five 30 cm x 30 cm, individually-labeled plastic mesh bags (6 mm openings), were filled with 100 g of stem and leaf material in their natural ratios. Five additional 100 g samples of each plant type were weighed and oven dried at 65 ºC to calibrate oven dry mass placed in each bag. Standardized amounts of plant material within litter bags were used in this study because the focus was on the effect of the plant tissue character, *per se*, and not, for example, on a plant's effect due to increased relative biomass. Oven drying, however, revealed that both *Typha* litter bags contained about 60% plant biomass as other litter types. A control treatment, plastic drinking straws, was also included to measure invertebrate colonization of substrates as habitat and not as a food source (Angradi *et al.* 2001).

To allow for natural conditioning of litter, bags were placed in the field on 15 December 2003. To control for possible bias in invertebrate use of the plant treatments, the study was situated in a homogenous area of Deer Creek Marsh dominated by *Carex lasiocarpa*, where none of the plants included in the litter treatments were naturally found within the experimental grid. A total of 10 permanent

stations were created every 5 m along two parallel transects spaced 10 m apart. We placed two sets of seven litter bags at each station. Each set included one bag of each litter treatment fanned in a randomized order. To prevent loss of bags, litter bags were attached to a PVC stake with decoy cord and pinned flush to the marsh surface with 12-gauge galvanized wire. To account for materials that may have been lost in the initial transport to the field, five additional sets of litter bags were placed in exactly the same fashion adjacent to the grid but immediately collected the bags. This litter was oven-dried at 65 ºC for 48 hrs and weighed. On 8 June and 29 September 2004, six and nine months after placement in the field, we retrieved one of the paired sets of litter bags from each of the 10 stations, respectively. Litter bags were quickly placed in Ziploc bags and kept on ice for transport back to the lab.

Mass loss and invertebrate colonization

Within 24 hours of collection, invertebrates were rinsed from plant litter in a tub of water, which was sieved through a minimum 250 μm screen mesh. Although not an optimal extraction method, we refrained from using ethanol so that the litter could be analyzed for %N and %C. Invertebrates that were probably most underestimated include Nematoda, Acarina, and Collembola. Since we were interested in relative numbers among litter types this likely did not affect our conclusions. Invertebrates were stored in 70% ethanol, stained with Rose Bengal and subsequently hand-picked from detritus, identified and counted, under a dissecting stereoscope at 10X magnification. Most invertebrates were identified to family with the exception of a few groups: Ostracoda, Copepoda, Nematoda, Hymenoptera, Lepidoptera, and Odonata. Due to the time required to process samples, not all litter bags could be examined for invertebrate colonization. At least 5 out of 10 bags per treatment and collection time (spring or fall) were examined. These samples were paired by time,

meaning a treatment was processed for both spring and fall at a particular station. After rinsing, remaining plant litter was oven dried at 65 ºC for, at least, 48 hrs, weighed for mass loss, and subsequently analyzed for tissue quality.

Tissue quality

For all natural plant litter treatments, % N and %C (and C:N) were measured at three time periods: zero (initial), and after six (spring) and nine (fall) months incubation in the field. Five litter samples corresponding to bags processed for invertebrates as well as five samples used to standardize weight lost during transport (initial) were analyzed for %N and %C at the Cornell University Stable Isotope Lab, using a Carlo Erba NC2500 elemental analyzer machine.

Analyses

Differences in initial tissue chemical quality (N, C:N) among plant species was tested using one-way ANOVA. The effects of litter type, time and their interaction on percentage mass remaining (mass loss) were tested with a mixed general linear model (GLM) that included station as a random variable. This random term accounted for spatial variability commonly observed in our field data.

Similar GLM's were conducted on summary metrics of invertebrate abundance and diversity: total density (individuals per 100 g) and taxa richness. The use of density to describe abundance was most appropriate in our analyses due to low initial oven-dry mass for both *Typha* species (about 50-60 g oven-dried instead of the expected 100 g when measured as air-dried mass). To characterize the structure of the colonizing invertebrate community, principal component analysis, which identifies correlations among species, was employed. Additionally, individual GLM's were

conducted on composite taxonomic groups of invertebrates to test for differences in specific invertebrate response to the litter treatments over time; litter type X time interactions and the random station effect were also included in the model. Models were reduced to include only main effects if the interaction term was non-significant with $P > 0.1$. Total and composite group invertebrate densities were $\log_{10}$ (x+1) transformed to meet model assumptions of normality and homogeneity of residual variation. In the event transformation did not work (i.e. Bivalves and Hirudinae), logistic regression was first used to test for differences in the proportion of samples where composite taxa were present among litter types. A GLM was then conducted but only after samples that did not support the taxa in question were eliminated. Following all regressions described above, all pair-wise comparisons were conducted between plant species within a collection period and assessed for statistical significance using Bonferroni-adjusted *P* values.

To test litter N content's value as a predictor for mass loss and invertebrate colonization patterns observed, %N was included in GLM's used to analyze percent mass remaining and invertebrate densities (total and composite group). In the event that litter type was no longer significant with %N in the model, we concluded that differences in %N drove discrepancies observed among treatments. All analyses were performed using SAS software (SAS Institute Inc. 2004).

Results

Initial litter characteristics

Initial whole plant, leaf and stem %N and C:N were highly significantly different between species (ANOVA, $P < 0.0001$). Characteristic of rigid plant tissue, stems of all species had lower N concentrations than did leaves, resulting in intermediate values

of %N for whole plant litter (Table 2.3). Species ranked differently in their N concentration depending on the plant organs assessed. For whole plant litter, which likely best represents available litter resources, *P. arundinacea* boasted the highest N content which was more than two fold that of *T. angustifolia* (Table 2.3). In descending order, *P. australis americanus*, *P. australis*, *L. salicaria* and *T. latifolia* had intermediate levels of %N. Significant differences in N concentrations were also observed for leaf and whole plant litter in *Phragmites* (ANOVA leaf, $P = 0.031$; whole, $P = 0.014$) and *Typha* pairs (ANOVA leaf, $P < 0.0001$; whole, $P = 0.015$). Patterns observed in C:N mirrored those of N since C remained relatively constant among litter types (Table 2.3, Fig. 2.1B). Differences in leaf:stem mass ratio among species and congeners were found (Table 2.3). As described by Hobbie (1996), allocation patterns of nutrients and mass to stem and leaf tissues dictated whole plant tissue quality.

Table 2.3. Initial percent nitrogen (%N) in leaf, stem and whole plant (combined stem and leaf) litter; percent carbon (%C) in while plant litter; and leaf to stem mass ratios for *Phragmites australis americanus* (PAU-A), *P. australis* (PAU), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicaria* (LSA), and *Phalaris arundinacea* (PAR). +/- 1SE in parentheses following means.

	PAU-A	PAU	TLA	TAN	LSA	PAR
Leaf %N	1.18 (0.08)	0.90 (0.01)	0.93 (0.03)	0.50 (0.04)	1.13 (0.02)	1.13 (0.04)
Stem %N	0.32 (0.04)	0.28 (0.01)	0.24 (0.02)	0.19 (0.01)	0.34 (0.05)	0.54 (0.08)
Plant %N	0.69 (0.06)	0.52 (0.02)	0.48 (0.03)	0.31 (0.01)	0.51 (0.03)	0.81 (0.03)
Plant %C	47.0 (0.1)	44.9 (1.0)	43.7 (0.6)	45.5 (0.1)	46.22 (0.6)	43.3 (0.7)
Leaf:Stem (mass)	0.83 (0.1)	0.55 (0.05)	0.42 (0.05)	0.49 (0.07)	0.25 (0.04)	0.86 (0.08)

Mass loss and tissue quality

A highly significant difference in percentage mass loss of plant litter was observed among species ($P < 0.0001$). With the exception of *Typha* species litter, percentage mass loss diverged increasingly among species with time (Fig. 2.1A). After six months in the field (spring), mass loss was greatest for *L. salicaria* (23%), which was significantly higher than that of *T. latifolia* ($P = 0.01$) and both *Phragmites* species (both, $P < 0.004$). Litter with the lowest mass loss was *P. australis* (10%), significantly so relative to all but its conspecific (all comparisons, $P \leq 0.004$). Mass loss was intermediate for remaining plant species in the following rank order: *P. arundinacea* > *T. angustifolia* > *T. latifolia* > *P. australis americanus*. Of these, *P.* arundinacea had significantly higher mass loss both *Phragmites* species (both, $P <$ 0.004). Plastic straws had gained weight, likely due to the accumulation of periphyton, resulting in a percent mass remaining that was significantly higher than all other litter species (all comparisons, $P < 0.004$).

After nine months incubation in the field, *P. arundinacea* had the fastest decomposing litter, losing over 40% of its initial mass (Fig. 2.1) and resulting in a significantly lower mass remaining than all litter types (all comparisons, $P < 0.004$). In contrast, *P. australis* remained the slowest decomposing plant species, losing less than 20% of its initial litter mass, which was significantly lower than mass loss of *P. australis americanus*, *L. salicaria*, and *P. arundinacea* (all comparisons, $P < 0.004$). Second to *P. arundinacea*, *L. salicaria* had lost significantly more mass than remaining litter types (all comparisons, $P < 0.004$) except *P. australis americanus*. In turn, *P. australis americanus* had significantly less mass remaining than both *T. latifolia* ($P = 0.008$), *T. angustifolia* ($P = 0.02$), and *P. australis* ($P = 0.004$). All plant treatments had significantly less mass remaining than plastic drinking straws (all comparisons, $P < 0.004$).

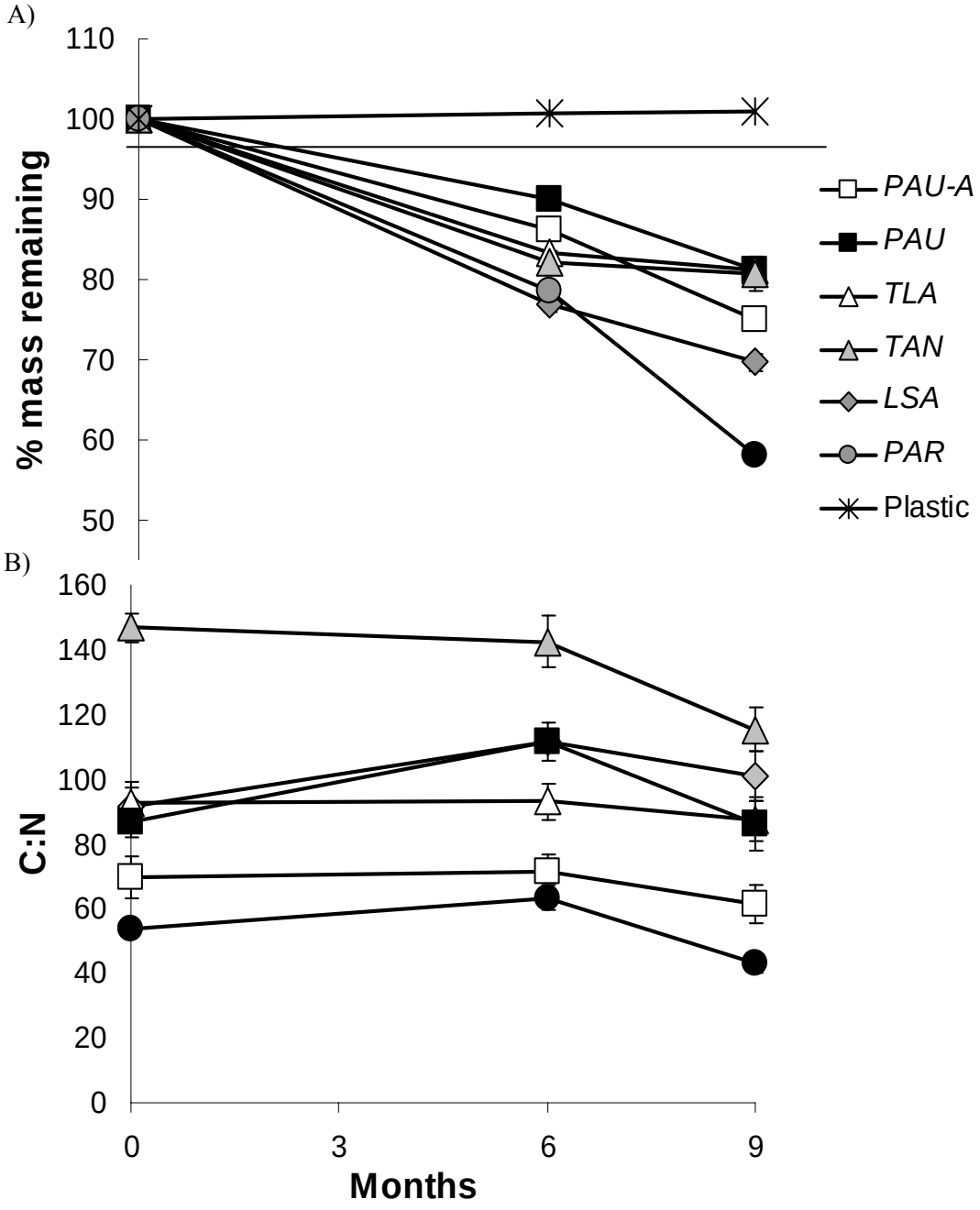

Figure 2.1. Decomposition (A, litter mass remaining [%] after six and nine months) and C:N over time (B) for *Phragmites australis americanus* (PAU-A), *P. australis* (PAU), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicara* (LSA), *Phalaris arundinacea* (PAR) and plastic drinking straws (Plastic, excluded for C:N). Data are means ±1SE for 5 replicates per species per sample time.

Constant C:N between initial litter and litter exposed for six months reveal that mass lost between these time points was mostly attributed to fragmentation, rather than decomposition, characterized by decreasing C:N. Due to their structure, L. *salicaria* and *P. arundinacea* comprised the smallest fragments of litter within the mesh bags, which may explain their greater loss by spring relative to other litter types. In contrast, decreasing C:N in the fall sample indicate divergence in decomposition rates, reflected by a highly significant litter type X time interaction ($P < 0.0001$).

Including C:N ($P = 0.1251$) or %N ($P = 0.1211$) in the regression model did not change the highly significant effect of species ($P < 0.0001$) on percent mass remaining, indicating that differences in mass loss among species was not explained by species-level variation in these quality metrics.

Invertebrate colonization

Overall, we observed a strong difference in total invertebrate density ($\log_{10}$ transformed abundance $100g^{-1}$) among litter types ($P < 0.0001$), which persisted through time (litter species X time: $P = 0.58$). This effect was driven almost entirely by statistically higher invertebrate abundance in *P. arundinacea* litter compared to all but one litter type (*P. arundinacea* v. *P. australis americanus*, $P = 0.004$; v. *P. australis*, $P < 0.002$; v. *L. salicaria*, $P = 0.008$; v. *T. angustifolia*, $P < 0.002$; v. plastic, $P < 0.002$; and v. *T. latifolia*, $P = 0.8$; Fig. 2.2B). Besides *P. arundinacea*, *T. latifolia* was the only other litter species that supported significantly more invertebrates than another litter type (i.e. plastic straws, $P = 0.3$). No significant change in invertebrate density was observed over time ($P = 0.38$).

Consistent through time, mean taxa richness varied significantly among litter species (P = 0.0028, Fig. 2.2A). This overall significant result was driven by the high taxa richness found within *P. arundinacea* packs (20 taxa $sample^{-1}$, time pooled),

relative to the low taxon rich invertebrate community supported by *T. angustifolia* (18 taxa sample^{-1}; time pooled, $t_{73} = 4.26$, $P < 0.001$). All other plant species shared equivalent species richness.

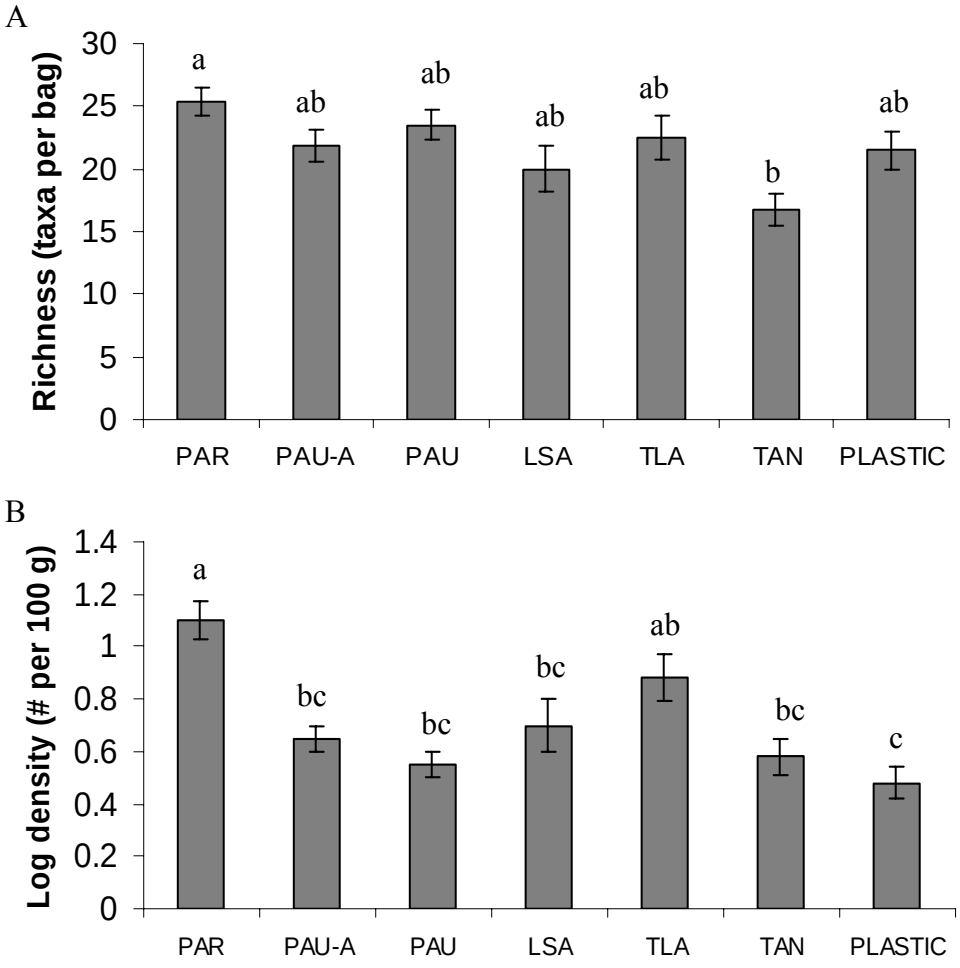

Figure 2.2. Taxa richness (A) and invertebrate density (B) in litter bags filled with *Phragmites australis americanus* (PAU-A), *P. australis* (PAU), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicara* (LSA), *Phalaris arundinacea* (PAR), and plastic drinking straws (PLASTIC). Spring and fall samples pooled. Plant species are ranked from highest (left) to lowest (right) %N. Data are means ±1SE for, at least, 10 replicates per plant species.

Forty-four abundant taxa, invertebrates that occurred in 5% or more of Spring and Fall samples combined, were identified from litter packs (see Table A.1 in Appendix for a complete list). Ten composite taxa were created to facilitate analysis: small crustaceans (copepods, ostracods, cladoceran), large crustaceans (isopods, amphipods), Diptera (Chironomidae, Ceratopogonidae), small Oligochaetes (Enchytraidae, Naididae), large Oligochaetes (Lumbricilidae, Naididae), nematodes, bivalves, Hirudinea (leeches), Acarina, and Collembola. For crustaceans and Oligochaetes, families and orders were categorized as "small" if their characteristic size was less than 2 mm; families and orders characteristically greater than 2 mm in size were categorized as "large".

Similar to patterns observed in total invertebrate density, most composite taxonomic groups with a significant litter species effect reflected relatively high densities of colonizers in *P. arundinacea* litter. Only for Nematoda, Acari, small Oligochaetes and bivalves did we observe significantly lower densities in plastic straws than in natural litter types (Fig. 2.3). Bivalves were unique in their preference for *P. australis americanus* over *P. australis*. After excluding two extreme outliers, Diptera was the only group where *L. salicaria* and not *P. arundinacea* had significantly more individuals 100 g^{-1} than other litter types – driven by abundance of individuals in the family Chironomidae. A significant litter species X time interaction for small Oligochaetes ($P = 0.0265$) demonstrate that aggregations changed with season. Large Oligochaetes, Hirudinea and Collembola responded more to season than they did to litter type. Thus, response to plant litter types was taxon specific and, in some cases, time dependent.

Principle components analysis of the invertebrate community demonstrated that individual taxa did not interact measurably in litter packs. The following are the first five Eigen values (%) ranked in descending order: 15.3, 10.4, 8.5, 6.1, and 5.6.

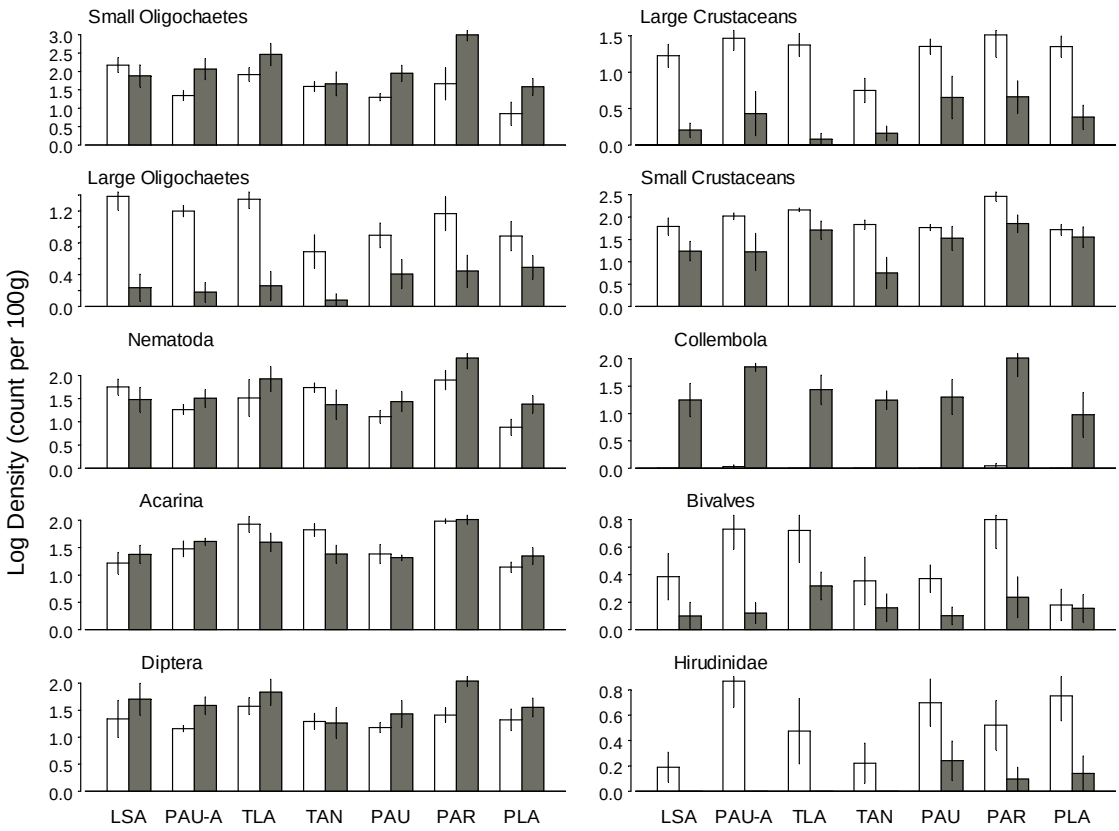

Figure 2.3. Invertebrate density and taxa richness in spring (open bars) and fall (gray bars) in litter bags filled with *Phragmites australis americanus* (PAU-A), *P. australis* (PAU), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicara* (LSA), *Phalaris arundinacea* (PAR), and plastic drinking straws (PLA) as litter source. Plant species are ranked from highest (left) to lowest (right) %N. Data are means ±1SE for at least 5 replicates per plant species per sample time.

These weak associations among invertebrate taxa demonstrate that invertebrates responded independently to litter types and were not influenced by interactions with other invertebrates.

Total density was unaffected by season, but both positive and negative density shifts within specific taxonomic groups resulted in a no net change of total density. Aquatic taxa, notably large crustaceans, were generally more abundant in spring while taxa fit for a semi-aquatic existence (Collembola, small worms) or smaller volumes of water, like small crustaceans, had increased in density by fall (Table 2.4, Fig. 2.4).

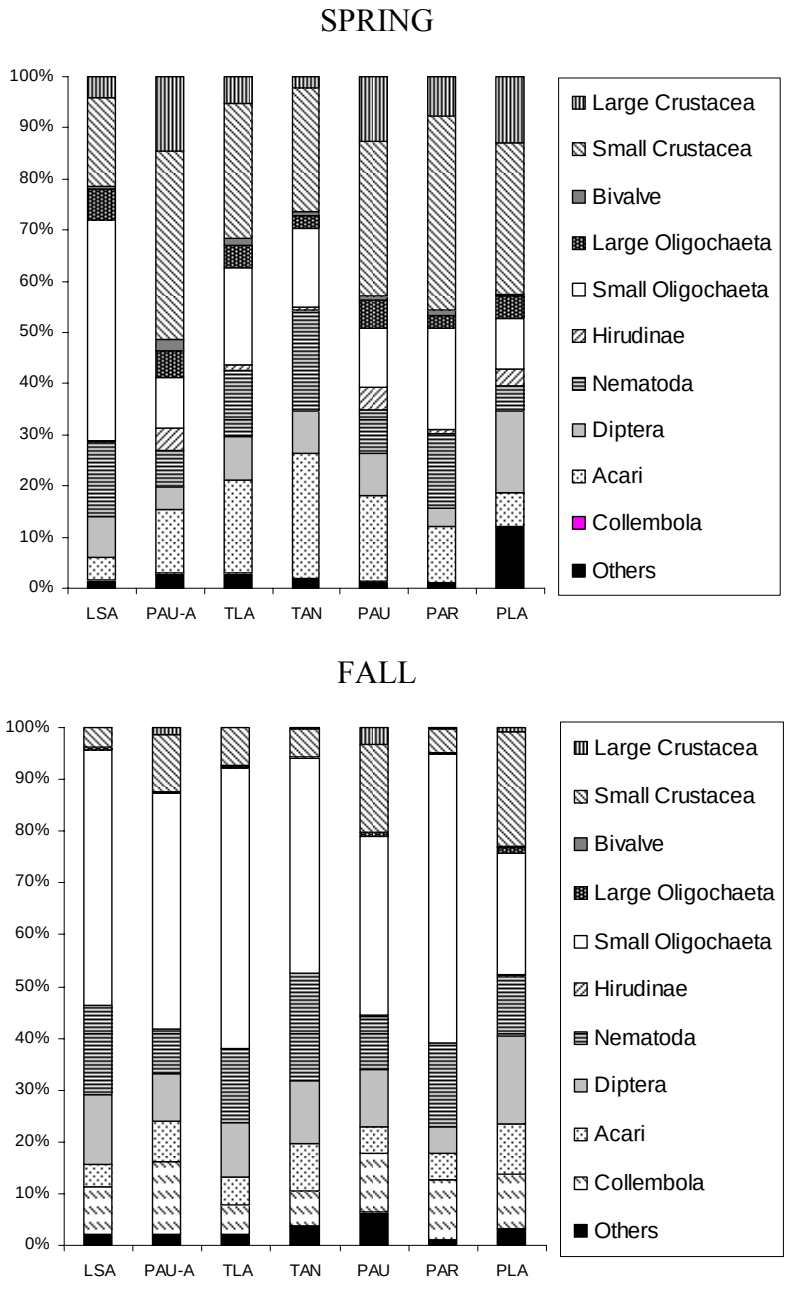

Figure 2.4. Invertebrate communities (proportion of composite taxa) in spring and fall colonizing litter bags filled with *Phragmites australis americanus* (PAU-A), *P. australis* (PAU), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicara* (LSA), *Phalaris arundinacea* (PAR) and plastic drinking straws (PLA).

Table 2.4. Densities (counts per 100 g) of invertebrate groups in large mesh bags filled with one of the following litter types: *Phragmites australis* (PAU), *P. australis americanus* (PAU-A), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicaria* (LSA), *Phalaris arundinacea* (PAR), and plastic drinking straws (PLA). Invertebrates were sampled spring (S) and fall (F) 2004. +/- 1SE in parentheses.

	PAU		PAU-A		TLA		TAN		LSA		PAR		PLA	
	S $_{n=10}$	F $_{n=6}$	S $_{n=10}$	F $_{n=5}$	S $_{n=5}$	F $_{n=6}$	S $_{n=7}$	F $_{n=6}$	S $_{n=5}$	F $_{n=7}$	S $_{n=7}$	F $_{n=5}$	S $_{n=6}$	F $_{n=5}$
Crustacea														
Large	27 (5.5)	12.8 (9.0)	46.7 (12.6)	7.4 (6.7)	29.0 (9.5)	0.3 (0.3)	7.3 (2.8)	0.7 (0.4)	20.8 (7.8)	0.9 (0.4)	69.4 (21.9)	6.4 (3.6)	27.0 (6.9)	2.4 (1.7)
Small	64.2 (10.6)	69.0 (33.8)	118.8 (21.7)	57.6 (33.5)	146.2 (12.7)	74.3 (22.4)	77.6 (15.1)	19.2 (10.8)	87.2 (35.6)	25.0 (5.7)	338.8 (73.0)	103.4 (44.6)	62.7 (19.6)	57.4 (26.3)
Oligochaeta														
Large	11.8 (3.9)	3.2 (2.1)	16.7 (2.7)	0.8 (0.6)	24.6 (6.5)	2.2 (1.8)	8.4 (4.4)	0.3 (0.3)	31 (10.8)	2.3 (2.0)	21.4 (6.4)	3.2 (1.9)	9.2 (2.3)	2.8 (1.2)
Small	24.5 (6.6)	139.5 (53.0)	31.5 (9.3)	239.4 (133.3)	105.2 (27.6)	551.0 (188.7)	49.7 (14.6)	149.7 (84.9)	216.4 (84.1)	336.9 (266.3)	179.1 (67.3)	1244.6 (369.5)	20.7 (13.4)	61.2 (26.9)
Nematoda	18.6 (6.5)	41.2 (12.5)	23.4 (5.8)	45 (18.8)	71.8 (26.8)	143.7 (48.0)	63.4 (14.5)	73.8 (41.2)	73.2 (23.8)	117.3 (93.7)	130.3 (41.9)	363.8 (135.1)	10 (3.9)	30.6 (9.9)
Hirudinea	9 (3.5)	1.5 (1.0)	14.1 (4.6)	0 (0)	5.8 (4.8)	0 (0)	1.9 (1.5)	0 (0)	0.8 (0.48)	0 (0)	5.1 (2.9)	0.4 (0.4)	7.2 (2.3)	0.8 (0.8)
Diptera	17.0 (3.2)	45.3 (17.1)	14.5 (2.1)	47.7 (13.8)	46.6 (14.8)	105.4 (31.6)	26.6 (8.7)	43.7 (25.2)	39.7 (13.3)	90.3 (20.8)	32.3 (8.8)	117.1 (23.0)	33.6 (15.9)	44.2 (12.6)
Bivalve	2.0 (0.8)	0.3 (0.2)	7 (2.0)	0.4 (0.2)	7.6 (4.1)	1.3 (0.4)	2.7 (1.6)	0.7 (0.4)	2.2 (1.11)	0.6 (0.6)	9 (2.5)	1.2 (0.8)	0.8 (0.5)	0.6 (0.4)
Acarina	35.7 (8.3)	20.2 (2.3)	39 (7.8)	41.2 (5.9)	100.8 (27.3)	54.3 (18.9)	79 (19.0)	32.8 (13.1)	22.8 (9.5)	30.4 (7.0)	98.0 (10.2)	109.2 (22.3)	14.2 (2.3)	25.4 (6.1)
Collembola	0 (0)	46.8 (20.8)	0.1 (0.1)	73.2 (10.2)	0 (0)	59.2 (28.4)	0 (0)	24.2 (9.5)	0 (0)	62.1 (42.0)	0.1 (0.1)	258.8 (135.6)	0 (0)	27.6 (13.5)
Total	213.7 (14.8)	405.5 (109.3)	321.8 (33.6)	524.6 (190.3)	554.2 (78.3)	1013.0 (255.7)	322.9 (40.6)	358.8 (161.1)	502 (118.4)	680.3 (360.0)	894.3 (107.7)	2235.2 (436.3)	210. 8 (56.5)	261.4 (77.8)
Taxa Richness	21.2 (1.5)	21.3 (2.6)	23.4 (1.1)	19.4 (2.5)	22.4 (2.2)	19.5 (2.1)	17.1 (1.5)	13.8 (1.9)	21.4 (2.2)	16.7 (2.4)	24.0 (1.4)	23.2 (1.0)	19.3 (1.6)	20.2 (2.4)

Additionally, crustaceans and Oligochaetes had swapped dominance status from spring to fall, which likely reflects increasing food availability for engulfers like small worms (Table 2.4, Fig 2.4).

Closer comparison of dominant taxa among litter treatments provides further support for an effect of litter type on community composition (Table 2.5). In spring, of the five most abundant (dominant) taxa, three were consistent across plant species: nematodes, Podocopa #1, Harpacticoida. *Phragmites* species and plastic straws were unique in that Harpacticoida was the top dominant. In contrast to all other natural litter types, *L. salicaria* supported disproportionately more Oligochaetes (~30%) and Chironomidae (~5%) and fewer Oribatida. By fall, strong distinctions between plant species had all but disappeared with all natural litter species having been colonized by proportionately high densities of Oligochaetes and Collembola. Chironomidae and nematodes continued to rank among the top five most abundant invertebrates. Even though crustacean numbers generally had declined by fall, plastic and *Phragmites* species continued to support relatively more crustaceans; however, Harpacticoida had seceded to Cyclopoida as the dominant taxon.

Discussion

Mass loss and quality

By the end of the experiment, significant differences among mass loss were observed as predicted, even between closely related conspecifics. Decomposition rates and N content of *T. angustifolia* and *P. australis* were similar to those found by Findlay *et al.* (2002). No comparisons were available for other litter types. Despite a positive correlation with mass loss, tissue %N (or C:N) alone did not significantly explain litter

Table 2.5. Composition (%) of top five dominant taxa in mesh bags filled with one of six macrophyte species: *Phragmites australis* (PAU), *P. australis americanus* (PAU-A), *Typha latifolia* (TLA), *T. angustifolia* (TAN), *Lythrum salicaria* (LSA), *Phalaris arundinacea* (PAR), or plastic drinking straws (PLA). Invertebrates were sampled spring (S) and fall (F) 2004. +/-1SE in parentheses. OL = Oligochaeta, NEM = Nematoda, PO = Podocopa, DIP = Diptera, HARP = Harpacticoida, ISO = Isopoda, CYCLO = Cyclopoida, AC = Acari, COLL = Collembola. Number represents morphospecies.

SPRING	LSA		PAU-A		TLA		TAN		PAU		PAR		PLA	
rank	taxon	%	taxon	%	taxon	%	taxon	%	taxon	%	taxon	%	taxon	%
1	OL6	29	HARP	13	NEM	13	NEM	19	HARP	11	NEM	15	HARP	9
2	NEM	14	ISO	10	AC8	11	AC8	19	AC8	10	OL6	12	DIP2	9
3	OL4	8	PO1	9	OL6	11	OL4	9	PO1	9	HARP	10	AMPH	9
4	PO1	6	NEM	7	PO1	10	HARP	9	ISO	9	PO1	10	PO1	9
5	DIP2	5	CYCLO	7	HARP	9	PO1	9	NEM	8	OL4	7	OL6	7

FALL	LSA		PAU-A		TLA		TAN		PAU		PAR		PLA	
rank	taxon	%	taxon	%	taxon	%	taxon	%	taxon	%	taxon	%	taxon	%
1	OL4	48	OL4	31	OL4	37	OL4	34	OL4	22	OL4	51	OL4	13
2	NEM	17	COLL	14	OL6	17	NEM	20	COLL	11	NEM	16	NEM	11
3	DIP2	12	OL6	14	NEM	14	DIP2	8	NEM	10	COLL	12	DIP2	9
4	COLL	9	NEM	8	DIP2	7	COLL	7	DIP2	9	DIP2	5	COLL	10
5	AC8	3	DIP2	7	COLL	6	OL6	6	OL6	8	OL6	5	OL6	9

species effects on percent mass remaining, suggesting that plant species differed in additional ways that drove mass loss patterns (discussed below). The rate at which plant litter decomposes directly influences rates of nutrient and energy cycling and, consequently, plays a vital role in food web dynamics (Moore *et al.* 2005). Therefore, divergence in decay rates observed among our six plant species suggests that these plants are not functionally equivalent and that ecosystem-level consequences may be born due to shifts in plant dominance among these wetland plants. Distinct mass loss rates between *Phragmites* species support findings that even genotypes can support varying ecosystem processes (Driebe and Whitham 2000, Whitham *et al.* 2003, Schweitzer *et al.* 2004).

Invertebrate colonization and quality

We found mixed support for our prediction that invertebrate colonization would differ among plant litter species. Invertebrates did respond differentially among litter species; however, litter effects on biota were species specific, varying with the taxa observed and season. Litter type exerted a strong effect on invertebrate richness, overall density, and abundance of 7 out of 10 composite taxa. However, these trends were largely driven by significant density differences between the most preferred and least preferred litter types or by the overwhelming preference for one litter type. Where densities diverged among litter types, invertebrates almost exclusively preferred *P. arundinacea* litter (i.e. total, large crustaceans (spring), small crustaceans (spring), nematodes, small Oligochaetes (fall). With the exception of Diptera, small Oligochaetes (spring), and bivalves, invertebrate abundances on other natural litter types did not differ significantly despite a wide variety of plant form and tissue chemistry represented. Only two studies are known to have compared invertebrates using a subset of our study plants. With litter bags, Fell *et al*. (2003) did not detect

differences in macroinvertebrate richness and abundance between *T. angustifolia* and *P. australis* litter. Similarly, field-sampled macroinvertebrates in *T. latifolia* and *L. salicaria* stands had comparable densities and richness but were found to be smaller in *L. salicaria* (Gardner *et al.* 2001).

Stream studies have shown that tissue palatability is an important factor in colonization by microbes (Melillo *et al.* 1982, Findlay and Arsuffi 1989) and invertebrates (Dudgeon and Wu 1999). Except *P. arundinacea* (highest N) and plastic straws (lowest N), ranking of plant species according to invertebrate colonization (total density) was not as predicted based on N content, indicating that palatability of our tissues may have been influenced by other factors such as physical leaf toughness and/or anti-herbivory compounds, such as tannins and phenolics (Campbell and Fuchshuber 1995, Grime *et al.* 1996). Consistent with other studies that included synthetic substrates (Dudgeon and Wu 1999, Angradi *et al.* 2001), plastic straws supported, overall, fewer fauna than natural litter types. However, this pattern was not ubiquitous among composite taxa, suggesting that while some taxa exploit plant detritus directly for food and substrate, others may use litter for habitat only and/or consume the periphyton that grows on detrital surfaces (Melillo *et al.* 1982, Dudgeon and Wu 1999, Royer *et al.* 1999, Angradi *et al.* 2001).

Other factors controlling mass loss and invertebrate abundance

Our results indicate that in addition to N content, plant structure (Bailey *et al.* 2001, Varga 2001, Robertson and Weis 2005) and life history of colonizing fauna (Varga 2001) drove mass loss and invertebrate density patterns observed. Plant structure (morphology and quantity of leaves and stems) determines the quantity of palatable detrital material (leaf tissue), the accessibility of that material to biota through surface-to-volume ratios, and ultimately, dictates the phenology of decay (the development of

detritus) (Moore *et al.* 2005). All of these influence the food and habitat resources available to decomposer fauna. In turn, variable feeding ecologies (e.g. shredder v. filter feeder) and habitat needs (e.g. refugia) among invertebrates will also direct invertebrate responses to litter resources.

We argue that invertebrates responded favorably to *P. arundinacea* for the same reasons this grass is cultivated for cattle forage in North America (Cherney *et al.* 2003) and Europe (Sahramaa *et al.* 2004). Not only does *P. arundinacea* have relatively high N concentrations, but it has a very high leaf to stem mass ratio (Table 2.1). As leaves are thin and leaf toughness is low (Park, personal obs.), they break down relatively quickly. The leaves of *L. salicaria* are also very thin and even more fragile than those of *P. arundinacea*. Despite *L. salicaria*'s recalcitrant stem, the rapid decay of leaves by spring resulted in higher rates of mass loss and attracted an advanced invertebrate community comprised of proportionately more Oligochaetes, which require particulate matter for food and habitat (Brinkhurst and Gelder 2001). By fall, other litter types supported equal densities of Oligochaetes probably due to the fact that 1) leaf litter comprised a small portion of *L. salicaria* biomass and disappeared from bags over time, and 2) other litter types had adequately broken down after 9 months to support Oligochaetes. Persistent through time, hollow-stemmed *Phragmites* species and plastic straws supported a higher percentage of Hirudinae and crustaceans, revealing their potential preference for tubular structures. The combination of higher %N and leaf:stem mass of native *P. australis americanus* likely contributed to its rapid decay relative to introduced *P. australis*. A lack of discrepancy in invertebrate abundance between plants as different in form as *Typha* and *Phragmites* but similar in whole plant N content, indicates that a difference in plant architecture is influential only if quantity and quality of litter resources also differ.

In general, we anticipated stronger species effects between the litter types tested, especially between natural litter species and plastic drinking straws. Taxonomic resolution above the species level, a common issue for invertebrate studies, may have oversimplified invertebrate response to various litter types as different genus and species are known to exploit resources and habitats with differing efficiencies (Bjelke and Herrman 2005). Additionally, while litter bags have proven to be a useful tool for mechanistic understanding of litter dynamics, the small spatial scale of litter bags does not fully represent conditions produced by an entire shift in plant dominance. Because we controlled for biomass, our results speak exclusively to species effects founded in tissue quality and/or structure of that tissue plant. Even within that context, specific plant species effects may be drowned by the signal of surrounding field conditions. Indeed, the responses observed may be more akin to those predicted for plants just initiating community dominance. Given that a plant effect on ecosystem function is expected to be proportional to its landscape-level biomass, a plant's influence at this stage is likely small but predicted to increase as it becomes increasingly dominant (Grime 1998). Moreover, litter bags cannot imitate alterations in biomass produced by dominant plant species at the wetland-scale. Given that changes in litter quality, quantity and timing of litter, as well as environmental conditions, alter nutrient and energy cycling (Aerts and de Caluwe 1997), our investigation provides just one part of the story.

Status effects on mass loss and invertebrate colonization

In a review of decomposition rates for native and non-native plants, Ehrenfeld (2003) found that non-native plants tended to decompose more quickly than native plants. Ashton *et al*. (2005) recently confirmed this pattern holds true, using phylogenetically controlled pairs in an invaded and non-invaded site. We observed no general trend

between native and nonnative plant species, as both the highest and lowest values for mass loss and invertebrate abundance came from invasive plant litter. Opposite to findings by Agrawal *et al*. (2005) that invasive plants have lower C:N ratios (higher N content) than native plants after controlling for phylogeny, native plants in our study had higher N within congener pairs.

Implications

Species identity of litter entering wetlands influenced decomposition rates and wetland biota, indicating that shifts in dominance among the six wetland macrophytes tested could alter wetland function. In our study system, decomposability and palatability of plants depended on the net effect of plant form/architecture and N content of plant stems and leaves. In general, fast decomposing litter produces rapid pulses of nutrients and energy that can quickly support high invertebrate numbers, e.g. *P. arundinacea*. In the short-term, this may increase overall productivity of wetland biota and be seen as beneficial. In the long-term, however, litter with rapid decay rates provides a relatively ephemeral resource, whereas slower decomposing litter stabilizes and sustains detritus-based, aquatic ecosystems (Findlay and Arsuffi 1989, Wetzel 1995). Distinct temporal advantages of slow and fast decomposing litter may explain why diversity of decomposer communities can increase with detrital diversity and provide additional support for the value of diversity in ecosystem health and function (Wetzel 1995).

The effect of changing plant dominance will also depend on the original plant community composition. The more similar litter dynamics of the new plant dominant resemble those of the old, the lower the impact may be on wetland food webs. Despite intermediate N content and tough leaf tissues, *T. latifolia* attracted relatively high densities of several invertebrates (i.e. small crustaceans, Nematoda, Acari and small

Oligochaetes). This may be associated with the fact that the invertebrates at our study site have evolved with dominant Carex *lasiocarpa,* which has been found to have similar decay rates as *T. latifolia* (Thormann and Bayley 1997). Thus, the evolutionary context of a wetland system may be important, where the biota of historically stable wetlands respond more strongly to changes in plant dominance than biota adapted to historically dynamic wetlands. Improving our general understanding of the consequences plant shifts may impose on freshwater wetland systems requires future studies that investigate litter processing at larger spatial and temporal scales that include multiple historic contexts.

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APPENDIX

Table A.1. Complete list of invertebrate taxa collected from litter bags placed in Deer Creek Marsh, NY. Common (C), abundant (A) and rare (R) taxa occurred in greater than 10%, between 5% and 9%, and less than 5%, respectively, of pooled samples.

Class/order	Family	Genus	Abundance
Isopoda	Caecidotea		C
Cladocera			R
Amphipoda	Crangonyx		C
Copepoda	Cyclopoida		C
	Harpacticoida		C
	Calanoida		C
Ostracoda	Podocopoda 1		C
	Podocopoda 2		C
	Podocopoda 3		C
	Podocopoda 4		C
	Podocopoda 5		C
	Podocopoda 6		A
	Podocopoda 7		C
	Podocopoda 8		R
Diptera	Ceratopogonidae		C
	Chironimidae		C
	Psychodidae		R
	Stratiomyidae		R
	Tabanidae		R
	Tipulidae		R
	Diptera 1		R
	Diptera 2		R
Ephemeroptera	Caenidae	*Caenis*	C
	Ephemeroptera 2		R
Hymenoptera			C
Coleoptera larvae	Scirtidae	*Cyphon*	A
	Dytiscidae	*Hydroporus*	R
	Gyrinidae		R
	Coleoptera L1		R

Table A.1 (Continued).

Class/order	Family	Genus	Abundance
Coleoptera larvae (cont')	Coleoptera L2		R
	Coleoptera L3		R
	Coleoptera L4		R
	Coleoptera L5		R
Coleoptera adult	Dytiscidae 1	Hydroporus	R
	Dytiscidae 2	Hygrotus	R
	Dytiscidae 3		R
	Staphylinidae		R
	Carabidae		R
Odonata			R
Lepidoptera larva			R
Oligochaeta	Lumbriculidae	*Lumbriculus variegatus*	C
	Enchytraidae 1	*Pristinella*	C
	Enchytraidae 2		A
	Naididae 1		C
	Naididae 2		C
	Naididae 3		C
	Naididae 4	*Dero* A	C
	Naididae 4	*Dero* B	C
	Oligocheata 1		A
Hirudinea	Hirudinidae	*Helobdella stagnalis*	C
	Glossophonidae		A
	Hirudinidae		A
Nematoda			C
Collembola	Sminthuridae		C
	Hypogasturidae		C
	Isotomidae		C
Thripsera			R
Acari	Prostigmata	unknown	R
	Prostigmata	Trombidiidae	C
	Prostigmata	Bdellidae	C
	Prostigmata	Tydeidae	C
	Mesostigmata	unknown	C

Table A.1 (Continued).

Class/order	Family	Genus	Abundance
Acari (cont'd)	Mesostigmata	Ascidae	C
	Oribatida	Hydrozetidae	C
	Oribatida	Oribatulidae	A
	Oribatida	Camisiidae	A
	Oribatida	Hydrozetidae	C
	Oribatida	Malaconothridae	C
	Oribatida	unknown	C
	Oribatida	Phenopelopidae	C
	Oribatida	Mycobatidae	C
	Acari 1		C
	Acari 2		C
	Acari 3		A
Bivalvia			C
Gastropoda	Snail 1		C
	Snail 2		C
	Snail 3		C
	Snail 4		A
	Snail 5		C
	Snail 6		A
	Snail 7		A
	Snail 8		A
	Slug 1		C
Planaria			C