IS PURPLE LOOSESTRIFE (*LYTHRUM SALICARIA*) AN INVASIVE THREAT TO FRESHWATER WETLANDS? CONFLICTING EVIDENCE FROM SEVERAL ECOLOGICAL METRICS

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Abstract: Conflicting interpretations of the negative impacts of invasive species can result if inconsistent measures are used among studies or sites in defining the dominance of these species relative to the communities they invade. Such conflicts surround the case of Lythrum salicaria (purple loosestrife), a widespread exotic wetland perennial. We describe here a 1999 study in which we quantified stand characteristics of L. salicaria and associated vegetation in arrays of 30 1-m² plots in each of five wet meadows in Connecticut, USA. We explored linear and non-linear relationships of above-ground plant biomass, stem density, and indices of species richness, diversity, and composition to gradients of L. salicaria dominance, including stem density, percent cover, and biomass. Species richness, other diversity metrics, and stem density of other species were not significantly correlated with the density or percent cover of L. salicaria stems. The relative importance values (number of quadrats in which they were found) of co-occurring species in low-density L. salicaria quadrats were significantly correlated with their relative importance in high-density L. salicaria quadrats, indicating that only modest shifts in abundance occurred as L. salicaria increased in density. No individual species were consistently associated with or repelled by the presence of L. salicaria across sites. In contrast to density and diversity features, however, the total biomass of species other than L. salicaria was significantly, negatively correlated with the total biomass of L. salicaria at each site surveyed. Lythrum salicaria in pure, dense stands maintained a greater above-ground standing biomass on invaded sites than uninvaded vegetation of similar physiognomy. This study demonstrates that hypotheses about L. salicaria effects can vary depending upon the ecological metric that is examined. Where one-time, correlative studies are the most feasible option, data taken on a range of metrics-especially biomass-should be taken to inform us about mechanisms by which L. salicaria invades and predominates in wetlands.

Key Words: Lythrum salicaria, purple loosestrife, invasive species, Connecticut, diversity, richness, wetland, plant ecology

INTRODUCTION

Invasive species, especially those that are rapidly expanding their habitat range, are increasingly recognized to be significant drivers of biotic interactions and resource fluxes in biological communities (Mack et al. 2000). In developing coherent strategies to address the control of these species, it is imperative to characterize thoroughly their actual ecological impacts on the communities they invade, particularly their capacity to displace existing species and alter species richness of plants and their associated consumers (Mack 1996, Blossey et al. in press). Only by systematically identifying the threats posed by these species can we determine which invasive taxa demand immediate attention from managers (Parker et al. 1999). It can be challenging to quantify the effects of invasive species, especially in sensitive ecosystems of conservation significance where direct, manipulative experiments or planned introductions are unfeasible. Thus, many studies have inferred negative impacts of invasive species from correlative data linking increasing prevalence of a given invasive species with a decrease in abundance of other associated species. Likewise, these data frequently are collected at a single sampling date and thus cannot capture temporal changes in community structure. Conflicting interpretations of "impact" can result if inconsistent ecological metrics measuring diversity, density, and other features are used from site to site in defining the relative dominance of these species.

Purple loosestrife, Lythrum salicaria L. (Lythraceae), has been the subject of such conflicting interpretations. Reportedly introduced in the early 1800s via ships' ballast and livestock, and widely cultivated for its ornamental and pharmacological values, L. salicaria has more than tripled its areal extent in North America since 1940 and now occupies more than 120,000 hectares of North American wetlands (Stuckey 1980, Thompson et al. 1987, Galatowitsch et al. 1999). Due to its explosive range expansion and its increasingly common occurrence in wetlands, L. salicaria has been identified as a serious threat to the species richness of wetland flora and fauna (Thompson et al. 1987) and has been targeted for intensive biological control efforts (Malecki et al. 1993, Blossey et al. 1994, Muth and Hamburg 1998). The hypothesis that L. salicaria is competitively dominant to other wetland species has been substantiated both by common-garden phytometer studies (Keddy et al. 1994, Gaudet and Keddy 1995, Weihe and Neely 1997) and by long-term data on L. salicaria performance-specifically, establishment and percent cover-in constructed wetlands (Weiher et al. 1996). Another study of 12 Minnesota wetlands (data re-examined from Emery and Perry 1995) shows that increased L. salicaria biomass was associated with decreased biomass of two Typha species. A common-garden experiment established in the Detroit River floodplain demonstrated that L. salicaria competitively displaces Typha angustifolia in terms of stem density, but only after several years of co-existence (Mal et al. 1997). A gradual recovery of the density of graminoids (specifically grasses, sedges, and/or Typha) has also been noted following removal of L. salicaria using herbicides (Gabor et al. 1996) and cutting (Wilcox et al. 1988). Although we are concerned with the relationship between L. salicaria and other plant species in this paper, we note that the species composition of insect and bird species is also observed to change with an increase in the prevalence of purple loosestrife (reviews in Thompson et al. 1987, Blossey 1999, Brown 1999).

Other reviews, however, have found little conclusive, quantitative evidence for negative impacts of *L. salicaria* on plant species (Anderson 1995, Hager and McCoy 1998). Furthermore, a recent study of 41 plots along the Bar River, Ontario, Canada detected no relationship between the density of *L. salicaria* stems and the richness of other riparian plant species (Treberg and Husband 1999). Thus, despite two decades of accounts, the actual dynamics of *L. salicaria* and its capacity to displace other wetland species remain in doubt.

We suggest that part of this uncertainty is due to the fact that different studies employ different, and possibly incomparable, metrics to quantify the impacts of L. salicaria on co-occurring plant species. Numerous ecological methods exist for quantifying the spatial patterning of plant species and for detecting species affinities and competition (e.g., Mueller-Dumbois and Ellenberg 1974, Whittaker 1975, Pielou 1975, Dale 1999). Innumerable past studies of plant communities have made use of a variety of metrics, typically comparing two or more independent measures or devising composite metrics (i.e., the relative importance value) from measures of several attributes of the system. By contrast, few studies of L. salicaria have employed more than one metric to characterize spatial relationships between the invader and the invaded species (Table 1), nor have the metrics used to date reflected the broad range of analytical tools available. In part, this may be due to the fact that the perceived urgency of the invasive threat has demanded very rapid, often static, correlative field studies. Likewise, sophisticated equipment, including ordination software and geographic information systems technology, have not necessarily been widely accessible to the community of land managers who must address plant invasions head-on.

We describe here a study of five wet meadow sites in which we quantified multiple stand characteristics of L. salicaria and associated vegetation and investigated linear and non-linear relationships among these variables across gradients of L. salicaria dominance. We used many of the methods employed in previous studies, and added a few more simple measurements. We explored the null hypothesis that L. salicaria density and biomass are not significantly correlated with the density, diversity, and biomass of other plant species in these wetlands. We found, not surprisingly, that conclusions about L. salicaria effects vary widely depending upon the metric used to describe them. We propose that several metrics should be examined across a variety of wetland types-together with manipulative experiments where timing and conditions permit-in order to characterize these effects fully and consistently.

METHODS

We chose five wetlands (Figure 1) throughout Connecticut, each that contained a stand of *L. salicaria* having a range of stem densities from 0 to between 30 and 60 stems/m². These sites also possessed the following characteristics: 1) a riparian wet meadow vegetation assemblage (corresponding most closely to the

Study	Metrics Used	Impact Detected? Apparent negative correlation between <i>L. salicaria</i> density and <i>Typha</i> density, increasing through time; but no statistical analyses		
Rawinski and Malecki 1984	Three-year study comparing stem density of <i>L. salicaria</i> and <i>Typha</i> spp.			
Gaudet and Keddy 1988	44 wetland plant species, including <i>L. salicar-ia</i> , examined for correlation between 12 plant traits and competitive performance.	Plant biomass was the most significant pre- dictor of competitive ability, explaining 63% of variance among species.		
Keddy et al. 1994	Derived competitive effect rankings from bio- mass at final harvest for <i>L. salicaria</i> and 19 other wetland plant species grown in 3 treatments: flooded, control, and infertile.	In all 3 environments, <i>L. salicaria</i> caused an average reduction of 60% in yield of neighboring species.		
Emery and Perry 1995	Aboveground biomass and phosphorus con- centrations of <i>L. salicaria</i> and <i>Typha</i> (2 spp.) in 12 Minnesota wetlands.	<i>Typha</i> had significantly higher standing bio- mass than <i>L. salicaria</i> but increasing <i>L. salicaria</i> biomass was correlated with low- er <i>Typha</i> biomass; <i>L. salicaria</i> had signifi- cantly higher tissue P.		
Gaudet and Keddy 1995	Compared relative abilities of 40 plant species to suppress growth (biomass) of the target phytometer, <i>L. salicaria</i> .	Correlation between the competitive ability of a species and its position along resource gradients in its habitat of origin.		
Twolan-Strutt and Keddy 1996	<i>L. salicaria</i> and <i>Carex crinita</i> were grown in three competition treatments (no neighbors, roots only, and roots and shoots of neighbors present) at low and high wetland fertility levels. Biomass at final harvest measured and relative growth rate calculated.	<i>Lythrum salicaria</i> less sensitive to competi- tion than <i>C. crinita;</i> sensitivity of <i>L. sali- caria</i> above-ground competition higher in fertile wetland; sensitivity to below-ground competition lower in fertile wetlands.		
Weiher et al. 1996	Five-year study of 120 wetland mesocosms inoculated with 20 wetland species under 24 experimental treatments involving water level, phenology, fertility, and soil texture. Percent cover and presence/absence of each species measured annually	After 5 years <i>L. salicaria</i> dominated most mesocosms and other dicots were eliminat- ed. Initial planting conditions were not pre- dictive of longer-term trends in species composition.		
Mal et al. 1997	Four-year replacement series experiment with differing initial densities <i>of L. salicaria</i> and <i>Typha angustifolia</i> in field; overall rate of ramet production and proportion of total stems contributed by each species measured.	<i>Lythrum salicaria</i> exceeded <i>T. angustifolia</i> in ORP after first year; <i>L. salicaria</i> exceeds <i>T. angustifolia</i> in proportion of stems by Year 4.		
Weihe and Neely 1997	Replacement series with different initial ratios of <i>L. salicaria</i> and <i>Typha latifolia</i> planted in sun and shade (40% PAR); above-and below-ground biomass measured after one season of growth.	<i>L. salicaria</i> exceeded <i>Typha</i> in both above- and below-ground biomass in both sun and shade.		
Templer et al. 1998	Porewater ammonium/N and phosphate; tis- sue N and P; sediment organic matter, moisture, and redox potentials; above- and below-ground biomass of <i>L. salicaria</i> , <i>Phragmites australis</i> , and <i>Typha angustifolia</i>	L. salicaria showed significantly lower pore- water ammonium/N and phosphate; species did not differ in sediment organics, mois- ture or redox; L. salicaria had highest tis- sue P concentration and intermediate tissue N; L. salicaria had lowest below-ground biomass and intermediate above-ground biomass.		
Brown 1999	Impact of <i>L. salicaria</i> presence on pollina- tion and subsequent seed set by its conge- ner, <i>Lythrum alatum</i> .	Pollinator visitation and seed set lower in <i>L.</i> <i>alatum</i> when <i>L. salicaria</i> (<i>a</i> competitor for pollinators) is present.		
Treberg and Husband 1999	One-time survey of correlations between <i>L.</i> <i>salicaria</i> percent cover and plant species richness at 41 wetlands in Ontario.	No significant correlation; richness of floating aquatic species higher in plots with <i>L. salicaria</i> .		

Table 1. A summary of previous published studies that have directly collected data on the impacts of *Lythrum salicaria* on plant populations and on community structure. Metrics directly relevant to inferring an ecological impact of *L. salicaria* are shown in boldface type.



Figure 1. Map Connecticut, USA, labeling the five sites surveyed during this study. Sites correspond to town names: "Wethersfield" (41°41′30″N, 72°38′58″W); "Hamden" (41°21′21″N, 72°55′11″W); "Rocky Hill" (41°40′51″N, 72°38′24″W); "Bloomfield" (41°49′40″N, 72°42′35″W); and "Southbury" (41°28′23″N, 73°15′31″W).

Eupatorium-Ludwigia palustris community of the May 2000 draft Vegetation Classification for Connecticut [Metzler and Barrett, unpublished data] or the palustrine emergent, seasonally flooded, wet meadow sensu Cowardin et al. 1979); 2) at least 1 hectare in size; 3) flat topography and altitude between 10 and 35 meters a.s.l; 4) underlain by a non-calcareous bedrock of gneiss or schist; and 5) accessible for transect sampling and destructive harvest.

The sites have undergone a range of management activities, and the precise duration of L. salicaria's presence at each site is largely unknown. Although species composition varied, the sites shared many plant species in common. The Bloomfield site, a flat wet meadow, is mowed every fall, and the lower reaches of the meadow may be flooded seasonally. It is dominated by L. salicaria and by graminoid species including Agrostis alba, A. perennans, Carex scoparia, and Carex vulpinoidea, as well as Aster lateriflorus (see Table 2). Data on *L. salicaria* presence have been collected by one of us (D. R. E.) since 1997 as part of a study examining the feasibility of biological control. The Wethersfield site, an expansive wet meadow sloping gently to the banks of the Connecticut River, has been cultivated until the early 1990s as a hay lot. Following the cessation of active agriculture, the area subsequently recovered its characteristic wetland vegetation but is mowed yearly and floods periodically. The landowner noticed L. salicaria becoming abundant in 1994. The predominant species in addition to L. salicaria are Apios americana, Geum virginianum, Lycopus americanus, Agrostis perennans, and Aster novi-belgii (Table 2). The Rocky Hill site is situated Table 2. Taxa observed in the transects at five wet meadows in Connecticut. The "Quadrats" column indicates the total number of quadrats in which each taxon occurred. The "Sites" column indicates the number of sites at which each taxon occurred. No-menclature and authorities follow Gleason and Cronquist (1991) and Magee and Ahles (1999).

	Quad-	
Taxa	rats	Sites
Acalypha rhomboidea Raf.	9	4
Acer rubrum L.	13	5
Achillea millefolium L.	5	1
Agrostis gigantea Roth	46	4
Agrostis perennans (Walter) Tuckerman	56	4
Alisma triviale Pursh.	14	2
Allium vineale L.	11	2
Alnus incana (L.) Moench.	3	1
Ambrosia artemisiifolia L.	11	2
Andropogon gerardii Vitman.	7	2
Apios americana Medikus	33	2
Apocynum cannabinum L.	5	2
Asclepias incarnata L.	22	2
Asclepias svriaca L.	1	1
Aster novi-belgii L.	33	3
Aster puniceus L.	7	1
Aster lateriflorus (L.) Britt.	25	3
Avena sativa L.	3	1
Betula alleghaniensis Britton	1	1
Bidens frondosa L.	11	2
Bidens laevis (L.) BSP	3	1
Boehmeria cylindrica (L.) Swartz	18	4
Calamagrostis canadensis (Michx.) P. Beauv.	7	1
Calystegia sepium (L.) R. Br.	19	3
Carex lanuginosa Michx.	2	1
Carex bromoides Willd.	6	1
Carex scoparia Schk.	57	4
Carex stricta Lam.	4	2
Carex tribuloides Wahlenb.	19	2
Carex vulpinoidea Michx.	64	5
Celastrus orbiculatus Thunb.	2	1
Chenopodium album L.	1	1
Cinna arundinacea L.	19	3
Cornus ammomum Miller	16	4
Cornus sericea L.	1	1
Cuscuta gronovii Willd.	3	2
Cyperus strigosus L.	4	2
Decodon verticillatus (L.) Elliott.	2	1
Desmodium cuspidatum (Muhl.) Loudon	5	1
Dulichium arundinaceum (L.) Britton.	17	1
Echinochloa crusgalli (L.) P. Beauv.	1	1
Eleocharis sp. 1	6	2
Eleocharis sp. 2	2	1
Eleocharis sp. 3	21	1
Elymus virginicus L.	1	1
Epilobium coloratum Biehler.	29	3
Epilobium glandulosum Lehm.	1	1
Equisetum fluviatile L.	26	3
Eupatorium dubium Willd.	13	2
Eupatorium maculatum L.	4	2

Table 2. Continued.

	Quad-	
Taxa	rats	Sites
<i>Euthamnia graminifolia</i> (L.) Nutt	16	3
Fraxinus americana L.	2	2
Galium asprellum Michx.	23	4
Galium palustre L	30	3
Geum virginianum L.	21	1
Hieracium canadense Michx	1	1
Hierochloe odorata (L.) P. Beaux	2	1
Hypericum mutilum L.	9	3
Impatiens capensis Meerb	48	4
Iris versicolor L.	1	1
Juncus effusus L	34	4
Juncus tenuis Willd	21	4
Leersia oryzoides (L.) Swartz	19	2
Linaria vulgaris Miller	1	1
Ludwigia nalustris (L.) Elliott	21	1
Lycopus americanus Muhl	28	3
Lycopus unifloris Michx	20	2
Lysimachia ciliata L	5	1
Lystinaenia entata E. Lythrum salicaria I	113	5
Mentha arvensis L	3	2
Onoclea sensibilis L	24	4
Oralis stricta L	9	3
Panicum rigidulum Nees	6	2
Panicum clandestinum L	3	1
Parthenocissus quinquefolia (I) Planchon	2	1
Penthorum sedoides L	10	1
Phalaris arundinacea L	12	3
Phleum pratense I	12	1
Phraamites australis (Cay.) Trin ex Steud	3	2
Pilea numila (L.) A Gray	12	4
Polygonum hydroniner I	15	1
Polygonum hydropiper E. Polygonum hydropiperoides Michx	39	2
Polygonum lapathifolium L	15	2
Polygonum sagittatum L	47	5
Polygonum scandens I	2	1
Prunus seroting Fhrh	1	1
Rosa multiflora Thunh	6	4
Rubus hisnidus L	19	1
Rubus alleghaniensis T C Porter	9	1
Rudheckia hirta L	1	1
Rumex crispus L	11	1
Sagittaria latifolia Willd	6	1
Scirpus atrovirens Willd	2	2
Scirpus cynerinus (L.) Kunth	5	1
Scutellaria galeruculata L	4	1
Sedum purpureum (L.) L.A. Schultes	3	1
Senecio sp. (seedling)	1	1
Solidago canadensis var scabra Torrey & Grav	15	2
Solidago canadensis var. canadensis I	15	2
Solidago rugosa Miller	26	3
Sonchus oleraceus I	1	1
Sparganium americanum Nutt	7	1
Sphaonum sp	1	1
Spirea alba var Iatifolia (Aiton) Dinnel	1	1
Thelynteris palustris Schott	20	2
	20	-

Table 2. Continued.

	Quad-	
Taxa	rats	Sites
Triadenum virginicum (L.) Raf.	3	1
Toxicodendron radicans (L.) Kuntze	7	3
Trifolium pratense L.	2	1
Triticum aestivum L.	3	1
<i>Typha latifolia</i> L.	4	1
Verbena hastata L.	7	3
Viburnum acerifolium L.	2	1
Vicia cracca L.	6	1
Vitis riparia Michx.	3	1

in a floodplain of the Connecticut River, surrounded by patchy floodplain forest and agricultural fields planted to corn. The site itself was a wet meadow (not farmed) at the time of our visit, dominated by Impatiens capensis, Carex vulpinoidea, C. tribuloides, Polygonum hydropiperoides, and Epilobium coloratum in addition to L. salicaria (Table 2). The age of the L. salicaria invasion is unknown. The Hamden site occurs on a flat area traversed by a seep that delivers water into Lake Whitney. No maintenance occurs at this site, and flooding is rare. The meadow is dominated by L. salicaria (present since at least 1998), Polygonum sagittatum, Thelypteris palustris, Impatiens capensis, and Boehmeria cylindrica (Table 2). The Southbury site borders a wet field that has a history of agricultural use through 1990 and now is a town park. Lythrum salicaria was reported from the site in a 1995 report (Geotoxi Associates 1995). Management of the wetland appears minimal; the adjacent playing fields are mowed and possibly fertilized and/or sprayed for weed control. The site is dominated by L. salicaria, Ludwigia palustris, Alisma triviale, Carex scoparia, and *Polygonum hydropiperoides* (Table 2).

Sites were surveyed for species composition between 17 and 25 August 1999. At each site, we arrayed a transect line from a point randomly chosen within the *L. salicaria* stand, running roughly parallel to the orientation of the leading edge of the stand. Five parallel transect lines were then run perpendicularly at 5m intervals off this baseline. Six 1 m x 1 m quadrats were then laid at 5-m intervals along each transect line, for a total of 30 quadrats arrayed in a 25 m x 30 m grid per site.

In each quadrat, we counted the total number of separate *L. salicaria* stems originating at ground level. We also identified all other plant species in each quadrat (nomenclature follows Gleason and Cronquist 1991 and Magee and Ahles 1999) and counted the number of stems of all dicotyledon species. Dicotyledons included both herbaceous and woody species (seedlings and mature individuals). Because stems numbered in

the hundreds and the identity of separate ramets was problematic to quantify reliably for monocotyledons, we noted only their presence and species identity in each quadrat. From the field survey data, we calculated stem density per m² (dicots only), species richness, and the Shannon-Weaver and Simpson's indices for diversity. We also quantified the relative importance of each plant species at each site as the percentage of total quadrats surveyed (proportion of 30) in which the species occurred. A coefficient of variation was then calculated on the distribution of relative importance values across non-*L. salicaria* species at each site to determine whether increasing *L. salicaria* dominance was associated with less even (more hierarchical) distributions of other wetland species.

Twenty-five plots at each site were also photographed from 5 m elevation using a 35 mm camera mounted on an extendable surveyor's stadia rod equipped with a level. The target quadrat filled the frame at this height; therefore, each photograph showed the 1-m² plot at close resolution. The resulting photographs were inspected to estimate overlapping percent cover of L. salicaria and other species (pooled) in the plots for the purpose of designating high- and low-density categories of L. salicaria invasion. At each site, quadrats were divided into two categories: those with estimated percent cover > 30% of L. salicaria (representing stem densities of 20-54 stems/m² depending on the morphology of stems at each site) and those with estimated percent cover < 30% (as a test, we also contrasted 75% and 25% cover divisions and obtained the same results; data not shown). This categorization ensured that adequate numbers of quadrats in each category would be available for comparison. The ecological metrics described above were computed and compared among the two contrasting L. salicaria cover classes.

We returned to four of the five sites before 15 September 1999 to harvest all aboveground living biomass from a randomly placed subset of 8 quadrats per site. By the time we returned to the Rocky Hill wetland, flooding from Hurricane Floyd had inundated the site to a meter deep and precluded harvesting. Vegetative material was separated into *L. salicaria* and non-*L. salicaria* components and dried in large paper bags for 1 week at 70°C in drying ovens at the University of Connecticut Plant Science Research and Training Facility (Storrs, Connecticut). All dried material was subsequently weighed to ± 0.1 g. Data were transformed as necessary to normalize variances and were statistically analyzed using Systat version 8.0 and SigmaPlot 2000.

RESULTS

We identified a total of 115 species of vascular plants in the 150 quadrats we sampled at 5 sites. *Lyth*-



Figure 2. Relationship between density of *Lythrum* stems and the richness (number per m^2) of other vascular plant species in 150 quadrats at the five sites: "Wethersfield" (\blacklozenge), "Hamden" (\blacktriangledown), "Rocky Hill" (\blacksquare), "Bloomfield" (\blacklozenge), and "Southbury"(\blacktriangle).

rum salicaria occurred in 113 quadrats total, attaining the highest frequency and stem densities at Southbury (range 4-54 stems/m²) and the lowest at Hamden (range 1-17 stems/m²).

Species richness was not significantly correlated with the density of *L. salicaria* stems at any site, nor for all sites pooled (Figure 2). The slope of the linear regression describing the variables (b=-0.0052) did not differ significantly from zero.

We also investigated whether species numbers varied significantly among quadrats with high versus low stem densities of L. salicaria (Table 3). Species richness, the total number of species found in each quadrat, did not vary significantly among the two L. salicaria density levels at any site (by Mann-Whitney U tests, 0.409 > P > 0.167). Most quadrats with high *L*. salicaria densities showed greater mean species richness than those with low L. salicaria densities (whether or not L. salicaria itself was excluded from the analysis). Species richness was also examined separately for each of the following functional groups, as per the methods of Treberg and Husband (1999): annuals (20 spp.); woody perennials (15 spp.); herbaceous multistemmed perennials (66 spp.); and herbaceous singlestemmed perennials (13 spp.). No significant relationships between L. salicaria density and species richness were found for any subset (0.056 < P < 0.956), except for herbaceous multi-stemmed perennials, where a slight positive correlation existed ($r^2 = 0.10$; P =0.002).

Coefficients of variation were computed on the relative importance (number of quadrats in which they occurred) of all species at each site, affording an index

Table 3. Species composition of quadrats with low (<30%) and high (>30%) projected areal cover of *Lythrum salicaria*. *N* refers to the number of quadrats in each category sampled at the five sites. Parameters examined were "relative importance" (mean percentage of quadrats occupied by a given species; mean (S.D.)); species richness ("Richness" (S. D.), total number of species reported across all quadrats per site); Simpson's diversity index ("D"); Shannon-Wiener diversity index ("H"); Coefficient of variation of relative importance values ("C.V."); Wilcoxon signed-rank test results on species ranks (*Z*, *P*); and the correlation of species importance at low *Lythrum* density with that at high *Lythrum* density (r^2 , corresponding *P* value, and slopes are reported).

Site/Density	Ν	Importance	Richness	D	Н	C.V.	<i>Z</i> , <i>P</i>	<i>r</i> ² , <i>P</i> , b
Bloomfield/High	11	27.5 (5.2)	10.5 (3.6), 28	16.12	2.98	1.16	3.06, 0.002	0.83, 0.0001, 0.83
Bloomfield/Low	19	24.8 (4.8)	9.6 (2.9), 32	15.93	3.01	1.34		
Rocky Hill/High	12	24.3 (4.3)	9.8 (2.3), 32	17.31	3.00	0.89	2.15, 0.003	0.72, 0.0001, 0.80
Rocy Hill/Low	18	24.2 (4.3)	9.6 (2.4), 26	17.95	3.07	0.86		
Southbury/High	12	24.0 (4.3)	8.5 (3.7), 29	16.52	3.03	1.19	2.79, 0.005	0.83, 0.0001, 0.81
Southbury/Low	18	21.2 (3.6)	7.6 (3.6), 29	16.64	3.03	0.96		
Wethersfield/High	11	21.1 (2.7)	14.9 (3.5), 54	31.87	3.69	1.46	3.89, <0.0001	0.64, 0.0001, 0.73
Wethersfield/Low	19	19.8 (2.6)	13.9 (2.2), 56	32.02	3.68	1.31		
Hamden/High	6	17.6 (2.6)	9.8 (3.1), 33	24.15	3.34	1.08	4.04, <0.0001	0.01 0.416 0.09
Hamden/Low	24	13.9 (2.5)	7.9 (3.2), 46	19.88	3.36	2.37		

of dominance by one or a few species that would create an uneven distribution around the mean. Coefficients of variation did not vary markedly or consistently with L. salicaria density, except at Hamden, where it was greater among quadrats with low L. salicaria densities (Table 3). The Shannon-Wiener diversity index (computed as $-\Sigma P_i \ln(P_i)$ where P_i is the proportion of total species observations comprised by species i) did not differ among high and low-density L. salicaria stands (Table 3). Likewise, the Simpson's diversity index (computed as $1/(\Sigma P_i^2)$ with P_i defined as above) did not vary among high and low-density L. salicaria stands (Table 3). The mean percentage of quadrats in which each species occurred also did not vary with L. salicaria stand density (paired t-tests on transformed data, Table 3).



Figure 3. Relationship between density of *Lythrum* stems and the density of other dicotyledon stems in quadrats at the five sites: "Wethersfield" (\blacklozenge), "Hamden" (\blacktriangledown), "Rocky Hill" (\blacksquare), "Bloomfield" (\blacklozenge), and "Southbury"(\blacktriangle).

To determine whether species composition varied among quadrats with contrasting L. salicaria densities, Wilcoxon signed-rank tests were performed on relative importance values for all species at each site (Z parameter and probability levels are reported in Table 3). Species rank distributions varied significantly with L. salicaria density at all sites, but shifts in the relative rankings of each species were not consistent among sites. Also, the relative importance of each species at low L. salicaria density was significantly correlated with its relative importance at high L. salicaria density $(0.641 < r^2 < 0.834)$, except at Hamden $(r^2 = 0.013)$. The slopes of these regressions were all < 1.0, indicating that species in general tended to appear more frequently in quadrats with high densities of L. salicaria (Table 3). No individual species were consistently associated with or repelled by the presence of L. salicaria across sites. Inspection of the low-elevation photographs we took of each plot indicated that percent cover of L. salicaria was not correlated with percent cover of other species (pooled), largely because L. salicaria overlapped in vertical space with many other species and was not dense enough at any site except Southbury to eliminate species from the "understory" ($r^2 = 0.029$, N = 125 photographs).

The density of dicotyledon stems was slightly negatively correlated with the density of *L. salicaria* stems (b = -1.1, P = 0.051) in quadrats across all sites. However, less than 3% of the variance in the data was explained by either linear or non-linear equations (linear regression is shown in Figure 3), and negative relationships were not consistently observed at each site. The few species that attained densities in excess of 300 stems/m² in the absence of *L. salicaria* (Figure 3) were seedling flushes of *Polygonum hydropiperoides* and *Rubus alleghaniensis* at Southbury and Hamden, re-



Figure 4. Relationship between biomass of *Lythrum* stems and the total biomass of all other species harvested from quadrats at four sites: "Wethersfield" (\blacklozenge), "Hamden" (\blacktriangledown), "Bloomfield" (\blacklozenge), and "Southbury"(\blacktriangle).

spectively. As above, stem density was inspected separately for each of four functional groups (Treberg and Husband 1999), but no significant correlations were detected.

The total biomass of species other than L. salicaria was significantly, negatively correlated with the total biomass of L. salicaria stems at each site surveyed (b =-0.37, P = 0.005, N = 32). A linear relationship explained approximately 24% of the variance in the data (Figure 4). When one anomalously high biomass (from a quadrat with one large sapling at Wethersfield) was excluded from the analysis, the r^2 increased to 0.36. Regression analyses at each site all showed similar patterns. Further, these analyses indicated that high-density L. salicaria stands had a higher biomass per m² than un-invaded stands of the other vegetation. Stands of L. salicaria without other vegetation showed standing crops of up to 800-900 g/m², whereas stands of non-L. salicaria species with only low densities of L. salicaria weighed only up to 550 g/m² (excluding the anomalous quadrat with a sapling, Figure 4). The biomass per stem of L. salicaria was negatively correlated with the density of L. salicaria stems (r^2 = 0.142; b = 0.142), and the highest total standing crops of L. salicaria were observed in quadrats of intermediate L. salicaria stem density (25-48 stems/m² in a range of 5-69 harvested stems/m², $r^2 = 0.76$ for a Gaussian 3-parameter peak equation fitting the data).

DISCUSSION

We sought to collect data relevant to developing hypotheses about the ecological impacts of *Lythrum salicaria* on other plant species in a ubiquitous, wet meadow wetland type. Because previous correlative studies have disagreed on whether *L. salicaria* poses a significant threat to the richness and composition of diverse wetland plant communities, we sampled at multiple sites, employing greater numbers of quadrats per site than have been used previously in other published studies. We also used a range of ecological metrics to describe the dominance of *L. salicaria* and the structure of the invaded community.

The present study had several limitations and operated under many of the constraints that most land managers may face when evaluating the threat posed by L. salicaria. For example, as in many other L. salicaria studies (Table 1), we were able only to sample at one time and at only five sites. Our chosen sites and the corresponding biomass (standing crop and weight per stem), densities, and percent covers of L. salicaria were, however, highly comparable to figures reported elsewhere (Shamsi and Whitehead 1977, Emery and Perry 1995, Twolan-Strutt and Keddy 1996, Weihe and Neely 1997). Consequently, we consider our sites to be typical of many wetlands in the northeast sector of continental North America where L. salicaria invasion is well underway (Table 1). These sites spanned Connecticut and, despite similar species composition, physiognomy, and physical setting, they likely differed in disturbance and land-management regimes, as well as age since establishment. Differences in the species composition and standing biomass of these wetlands may reflect different ecological histories and vulnerability to invasion as much as they do differences in L. salicaria dominance. Indeed, L. salicaria invasion may be as much a symptom as a cause of factors that influence species shifts in wetland assemblages-an hypothesis worthy of more intensive study.

Like Treberg and Husband (1999), we found little correlation between the density or cover of *L. salicaria* stems and any changes in density, richness, or diversity of other plant stems (Figures 2 and 3). Frequently, the presence of *L. salicaria* was loosely associated with increasing numbers of other species (Table 3). This observation may indicate that the same site factors encouraging *L. salicaria* expansion also facilitate the growth of other plants, especially those of similar physiognomy (multi-stemmed herbaceous perennials *sensu* Treberg and Husband 1999).

We did find, however, that increasing *L. salicaria* biomass was associated with lower biomass of other species (Figure 4). This correlation explained less than 25% of the variance in biomass, however, so other factors may complicate this relationship (below-ground biomass, for example, could not be harvested in this study but should be investigated further in other sites). We also found that *L. salicaria* in pure, dense stands maintains a higher above-ground standing biomass on invaded sites than does un-invaded vegetation

of similar physiognomy. These observations suggest that L. salicaria competes with other herbaceous perennials and may be more efficient at translating available resources, especially mineral nutrients, into above-ground biomass. Lythrum salicaria tolerates a broad range of nutrient (N and P) levels (Shamsi and Whitehead 1974, 1977) and is a strong competitor relative to other wetland species across resource gradients in a variety of wetland types (Keddy et al. 1994, Gaudet and Keddy 1995). Emery and Perry (1995) noted that L. salicaria showed high tissue phosphorus contents compared to its frequent competitors, Typha spp. Templer et al. (1998) also observed a capacity for L. salicaria to sequester nitrogen and phosphorus in above-ground biomass. Such abilities, potentially mediated by novel mycorrhizal associations (e.g., Marler et al. 1999), may be a general feature of many invasive plant species. It would be of interest to know whether maximal standing biomass attained by L. salicaria at a site is correlated with the age of invasion; Figure 3 is suggestive of this trend, but the precise ages of L. salicaria colonization are unknown.

Lythrum salicaria biomass per stem decreased as L. salicaria densities increased, and total L. salicaria standing crop peaked at intermediate stem densities and decreased as stems became more numerous (data not shown). Intraspecific competition is strong in L. salicaria (Rawinski 1982, Gaudet and Keddy 1988, Weihe and Neely 1997) and, over the course of an invasion, a few large ramets may prevail rather than a mass of smaller stems. This finding may explain why L. salicaria density alone is not a reliable metric for measuring ecological impacts on communities. Truly monospecific stands of L. salicaria may be relatively uncommon, as other species appear to coexist with even dense stands of small stems. Once large plants with the capacity to monopolize resources gain a foothold, however, the growth of other wetland species may be suppressed.

A more comprehensive review of the ecological impacts of *L. salicaria*, and indeed any invasive plant species, must necessarily incorporate longer-term data from a range of natural communities that have undergone a variety of invasion histories and management regimes. A fuller understanding of the effects of *L. salicaria* on ecosystems will also explore its influences on associated fauna, including pollinators (e.g., Brown 1999). Where time and scientific resources are limiting, however, our study suggests that multiple, simple metrics should be examined and one—namely, biomass—may be indicate the stage and level of threat of the invasion.

Our study does not lay to rest the controversy over the effects of this ubiquitous species (nor does it address the impacts of *L. salicaria* on animal assemblag-

es), but it does suggest that a range of parameters must be measured in the field. Lythrum salicaria does not appear to threaten the diversity or density of other wet meadow species, at least at the range of stem densities and ramet sizes examined in this study. However, L. salicaria may come to predominate in these systems by attaining a larger size. We propose that the standing biomass of L. salicaria may be a reliable indicator of the potential for the population to outcompete other plant species. We recommend that at least the biomass of L. salicaria and other co-occurring plant species should be determined from harvest plots, using a sample size that is appropriate to capture variability in L. salicaria dominance. At the same time, the identity of other species present in the harvest can be recorded, as a means to detect correlations between L. salicaria biomass and the richness of other plant taxa in the wetland. Thus, at least two metrics illustrating the distribution of L. salicaria and its relationship with other plant species can be simultaneously quantified.

If, as Mal et al. (1997) suggest, L. salicaria takes several years to reach a threshold biomass and become a long-term wetland dominant, an effective management strategy would eradicate early invasions or at least arrest or suppress the growth of L. salicaria (e.g., Wilcox et al. 1988, Malecki et al. 1993). The costs of such efforts must be weighed against the certainty of threat, the stage of the invasion, and the urgency of managing other, more destructive invasive species (Anderson 1995, Hager and McCoy 1998). To determine the generality of our findings and to tease apart the reasons for and consequences of L. salicaria invasion, a wider range of sites, wetland types, and L. salicaria stem densities must be surveyed in a consistent way. Moreover, as Mack (1996), Parker et al. (1999), and others have suggested, careful field experimentation must augment correlative studies where possible (e.g., Twolan-Strutt and Keddy 1996, Weiher et al. 1996, Rachich and Reader 1999 for L. salicaria). Researchers hypothesizing about the effects of L. salicaria in the field should also make reference to the published, controlled studies already completed on this species; citation lists in recent reports seem to almost completely ignore this literature, and repeatedly cite a small subset of studies. Finally, the responses of wetlands to invasion and to the process of removing L. salicaria through various control measures must be monitored in the long term and the findings from these studies shared widely (Blossey 1999, Parker et al. 1999, Blossey et al. in press).

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