

COMPETITION FOR POLLINATION BETWEEN AN INVASIVE SPECIES (PURPLE LOOSESTRIFE) AND A NATIVE CONGENER

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Abstract. Invasive species are frequently regarded as superlative competitors that can vegetatively crowd out natives, but little is known about whether invasives can compete for pollination services with native plants. We hypothesized that, when the showy invasive species *Lythrum salicaria* (purple loosestrife) was present, pollinator visitation and seed set would be reduced in a native congener, *L. alatum* (winged loosestrife). To test this hypothesis, we constructed mixed and monospecific plots of the two species. Over two years of study, we found that *L. salicaria* significantly reduced both pollinator visitation and seed set in *L. alatum*. Furthermore, pollinators moved frequently between the two plant species, which may cause heterospecific pollen transfer. Thus, reductions in both pollen quantity and pollen quality may reduce *L. alatum* seed set. If similar patterns occur in the field, invasive plants may be an even greater threat to natives than previously thought.

Key words: competition; invasive species; *Lythrum alatum*; *Lythrum salicaria*; pollination; pollinator visitation; purple loosestrife; seed set; winged loosestrife.

INTRODUCTION

Invasive alien species are frequently considered superlative competitors that can impact native species in many ways including competition for nutrients (Wardle et al. 1994), water (Delph 1986), light (Grace and Wetzel 1981, 1982, Weihe and Neely 1997), and space (Ågren and Fagerström 1980, Newsome and Noble 1986). Such competition may reduce the ability of native species to maintain or increase population size (Huenneke and Thomson 1995). Beyond such vegetative competition, competition for pollinator services by invasive plants may also reduce the reproductive capacity of native plants.

Although the impact of invasives is of increasing global concern, to date there have been few studies on competition for pollinator services between invasives and other species (but see Robertson 1895, Free 1968, Grabas and Laverty 1999). Yet invaders have the potential to affect two important aspects of pollination service for native flora: quantity and quality (Waser 1978a, Rathcke 1983). The quantity of pollination service refers to the number of visits or amount of pollen received. Showy invasive species may draw pollinators away from native species, decreasing visit quantity (Free 1968, Waser 1978a, Gross and Werner 1983, Rathcke 1983, Armbruster and Herzig 1984), or they might increase visitation rate to natives by attracting pollinators which otherwise would not visit the native species as often (facilitation; Thomson 1978, Brown

and Kodric-Brown 1979, Rathcke 1983, 1988, Campbell and Motten 1985). Such changes in visit quantity may affect plant reproduction by altering the amount of pollen arriving on stigmas, which can affect seed and fruit production (Burd 1994). The quality of pollination service refers to the effects of pollinator sharing on interspecific pollen transfer. Shared pollinators affect pollination in two main ways. First, from the female perspective, pollinators that move between species will deposit mixed loads of pollen. Mixed pollen loads may reduce seed set in a variety of ways, including stigma clogging (Waser 1978b, Kohn and Waser 1985, Waser and Fugate 1986), stylar clogging (Shore and Barrett 1984, Galen and Gregory 1989), stigma closing (Waser and Fugate 1986), and pollen allelopathy (Char 1977, Sukhada and Jayachandra 1980, Thomson et al. 1981, Murphy and Aarssen 1995a, b, c, d). Second, from the male perspective, pollinators that move between species may waste and lose pollen (Waser 1983, Campbell and Motten 1985, Murcia and Feinsinger 1996).

We examined the impact of the invasive plant *Lythrum salicaria* L. (purple loosestrife) on seed set in the native congener *L. alatum* Pursh (winged loosestrife). These species serve as an excellent system for study given that they have overlapping ranges throughout the northern United States, have similar floral structure, have a prolonged period of overlapping blooming times, and share pollinators. We hypothesized that the native *L. alatum* would receive fewer visits and produce fewer seeds in the presence of *L. salicaria* for two reasons. First, *L. salicaria* is likely to be more attractive to pollinators (reducing quantity of pollination service to *L. alatum*). Second, our previous work in this system

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PLATE 1. (a) Pollinator visiting *Lythrum salicaria*. (b) Typical display for a *Lythrum alatum* plant.

(Brown and Mitchell 2001) indicates that mixed pollen loads reduce *L. alatum* seed set.

METHODS

Study species

Lythrum salicaria is a tristylous plant with a showy floral display, frequently growing as high as 2 m and producing hundreds of brilliant magenta flowers (Thompson et al. 1987, Mal et al. 1992). The flowers are relatively large (~17 mm in diameter) and presented in whorls at the nodes to form a spike-like inflorescence (Levin and Kerster 1973, Graham 1975, Mal et al. 1992; see Plate 1a). *Lythrum salicaria* is self-incompatible and exhibits many characteristics associated with trimorphic heterostyly (Darwin 1877, Nicholls 1987). It prefers very moist soil or standing water and can withstand prolonged periods of water logging (B. J. Brown, *personal observation*). Plants are perennial and grow as individual clumps. Although cuttings from *L. salicaria* root quickly and show significant viability (Brown and Wickstrom 1997), its primary reproductive strategy involves production of prodigious quantities of seeds (Thompson et al. 1987).

Lythrum salicaria is a native of Eurasia and a notorious wetland and riverbank invader in North America (Thompson et al. 1987, Mal et al. 1992). It has moved across North America over the last hundred years (Stuckey 1980) creating severe problems for land managers and those concerned with biological conservation (Thompson et al. 1987, Mal et al. 1992, Piper 1996). *Lythrum salicaria* can rapidly move into a mesic area and create a near monoculture (Thompson et al.

1987) and has drastically altered wetlands across North America (Thompson et al. 1987, Balogh and Bookhout 1989, Anderson and Ascher 1993). Monotypic stands of the species are not well utilized by native fauna (McKeon 1959, Thompson et al. 1987, Piper 1996; but see Whitt et al. 1999).

Lythrum alatum is the most widespread species of *Lythrum* in the United States (Graham 1975). It grows ~0.5–1 m high in the wild and is generally found in moist mesophytic, but not necessarily inundated sites (Graham 1975, Cody 1978, Anderson and Ascher 1993). Flowers are distylous (two style morphs), generally smaller (4–13 mm in diameter) than those of *L. salicaria*, and are paired in axils rather than in whorls (Levin and Kerster 1973, Graham 1975; see Plate 1b). Most distylous plants are self-incompatible, but the extent of self-incompatibility is currently unknown in *L. alatum*. Flower and seed production per plant are generally lower than in *L. salicaria* (B. J. Brown, *unpublished data*). Pollen production per flower is roughly half that of *L. salicaria*, regardless of morph (Brown and Mitchell 2001), and the pollen is morphologically indistinguishable from that of *L. salicaria*. In addition to sexual reproduction, *L. alatum* reproduces vegetatively through adventitious roots. One plant may consist of >100 stems and cover one square meter or more, but plants frequently are smaller (3–15 stems).

Experimental procedure

For this study we used potted plants placed in field plots. We initially grew *L. salicaria* and *L. alatum* in the greenhouse using seeds collected in 1996 from the

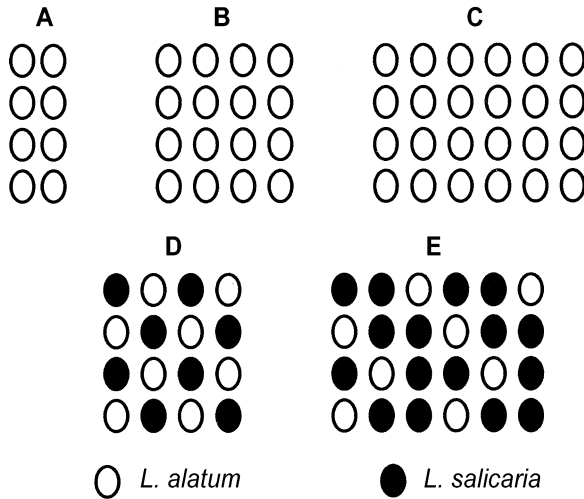


FIG. 1. Design for the five experimental treatments. The five plots diagrammed represent one complete block. A = 8 *Lythrum alatum*; B = 16 *L. alatum*; C = 24 *L. alatum*; D = 8 *L. alatum* and 8 *L. salicaria*; and E = 8 *L. alatum*, and 16 *L. salicaria*.

Ottawa National Wildlife Refuge (Ottawa County, Ohio, USA). When seedlings were 10–15 cm in height, we transplanted them to three-gallon (~11.4-L) pots for transfer to the field.

At the beginning of the 1997 field season, we selected 84 *L. salicaria* and 256 *L. alatum* plants and moved them to a fenced area near a natural wetland on the Kent State University campus. We randomly assigned these plants to five treatments: three monospecific and two competitive. The three monospecific treatments (A–C) (included only *L. alatum* in plots of 8, 16, or 24 plants, respectively). The two competitive treatments included eight *L. alatum* and eight *L. salicaria* (treatment D), or eight *L. alatum* and 16 *L. salicaria* (treatment E). For all treatments the morph representation was equal within *L. alatum*. Since *L. salicaria* is tristylous and the experimental design precludes equal numbers of morphs in trimorphic species, we randomly chose which morphs of *L. salicaria* would be more abundant within each replicate of each of the competitive treatments. The spatial arrangement of morphs within each species and plot were also random.

During the first week of July 1997, when all plants were blooming, we arranged them as depicted in Fig. 1, with pots directly adjacent to one another within a plot. The treatments were repeated four times, with each group of five treatments considered a block. Thus, there was a total of four blocks (20 test plots of plants). Plots ranged from a minimum of 1.0 × 0.5 m to 1.6 × 1.15 m and were located 3.2–3.5 m from the nearest adjacent plot. Blocks were run simultaneously throughout the summer, and were located 3.2–3.5 m from the nearest block. We maintained these treatments until more than one plant of either species in a plot ceased to bloom and then discontinued observations of that

plot. Within a species, all plants tended to cease blooming within a week of each other, with *L. alatum* persisting about one week longer than *L. salicaria*. By midsummer, *L. alatum* plants which started as single stems had 12–15 stems and were quite bushy. Plant height ranged from 0.72 to 0.84 m for *L. alatum* and from 1.2 to 1.3 m for *L. salicaria*. There was no effect of treatment on these characters (data not shown).

In 1998, we modified the procedure outlined above. Plants for the second field season were randomly selected from plants that overwintered outside (i.e., second-year plants). We also trimmed individual *L. alatum* plants to one stem to more closely mimic natural growth under field conditions. *Lythrum salicaria* plants were not trimmed since their growth in the previous year was similar to field conditions. By midsummer *L. alatum* plants had 8–10 stems and were less bushy than the previous year. Plant height ranged from 0.86 to 0.96 m for *L. alatum* and from 1.3 to 1.4 m for *L. salicaria*. There was no effect of treatment on plant size (data not shown).

Seed set

When fruits matured (late September and early October), we determined seed set in 15 fruits per *L. alatum* plant (5 representative spikes × 3 fruits per spike from low, middle, and high positions on the spike). We used a dissecting scope at 6× to determine seed set per fruit. Because flowers that do not produce fruit tend to abscise without leaving a mark on the stem, we were unable to determine proportion fruit set.

Insect visitation

We observed insect visitation during three four-day periods across the flowering season (July–August) in both 1997 and 1998. Each block was observed for one day during each period, with each of the five plots within the block observed for 15 min for three to five periods during the day. Blocks were observed on separate days, but within one week of each other. We followed individual visitors and recorded the type of visitor, the plant species visited, and number of flowers visited. In 1997, we counted the number of flowers open on each plant in the morning and because we were unable to observe visitation to all of the flowers on these bushy plants, before each observation period we estimated the percentage of the total plant that we were able to observe. From the total floral display and the proportion of flowers that were visible we calculated the number of flowers observed. In 1998, we determined the number of flowers observed (floral display) just before each observation period. In both years we counted all sequential flower visits by a single pollinator within the observed portion of a plot as one bout. We randomized the order of observation for blocks and plots within blocks. This resulted in a total of ~120 h of observations conducted on 24 d in 1997 and 1998.

Statistical methods

Except where noted, we used SAS procedure GLM with Type III sums of squares (SAS Institute 1996) for all analyses. We tested the assumption of normality by visually inspecting distributions of residuals. The ANOVA for mean seed number per fruit per plant for *L. alatum* included effects of treatment, block, morph (long- vs. short-styled morphs) and their pairwise and three-way interactions. Because we applied treatments to entire plots, we used plot means for each morph as the fundamental experimental unit in analysis (therefore, the 256 *L. alatum* plants contributed 4 blocks \times 5 treatments \times 2 morphs = 40 observations). To determine if the monospecific treatments differed from the competitive treatments we used a priori multiple contrasts (contrast statement in SAS), comparing the performance of the three monospecific treatments with that of the two mixed treatments.

To test for effects on visitation rate, we used fixed effects ANOVA, which included treatment, season, morph, and block, and all interactions as independent factors. Season is defined here as the three four-day periods of observation per year during the six-week period when both species were flowering. We considered both season and block as fixed factors because we could not ensure random samples of all possible levels of these factors (see Newman et al. 1997). Response variables in this analysis were visits per plant and visits per open flower. For both response variables we used mean visit rate per 15-min period for each morph in each plot in each season (therefore, in each year we used 3 seasons \times 5 treatments \times 4 blocks \times 2 morphs = 120 observations in analysis). We did not compare years due to differences in methods of observation.

We tested interspecific movement of pollinators for goodness of fit with the *G* test using seasons as a replicated measure (Sokal and Rohlf 1981). Plant ratios were used as predictors of expected frequencies of movement.

RESULTS

Floral display

Total floral display was much greater for *L. salicaria* than for *L. alatum*. *Lythrum salicaria* had 77.8 ± 4.7 open flowers in 1997 (mean \pm 1 SE, $N = 95$) and 115.0 ± 4.8 open flowers in 1998 ($N = 96$), while *L. alatum* had 59.3 ± 2.1 open flowers in 1997 ($N = 257$) and 31.8 ± 1.0 open flowers in 1998 ($N = 256$). Because of these differences in floral display between species, plant ratios (*L. alatum*:*L. salicaria*; treatment D = 1 and treatment E = 0.5; treatment letters as in Fig. 1) overestimated the relative abundance of *L. alatum* flowers in all cases (flower ratios *L. alatum*:*L. salicaria*; 1997, D = 0.64, E = 0.47; 1998, D = 0.25, E = 0.15), although treatment E in 1997 had an unusually low number of *L. salicaria* flowers.

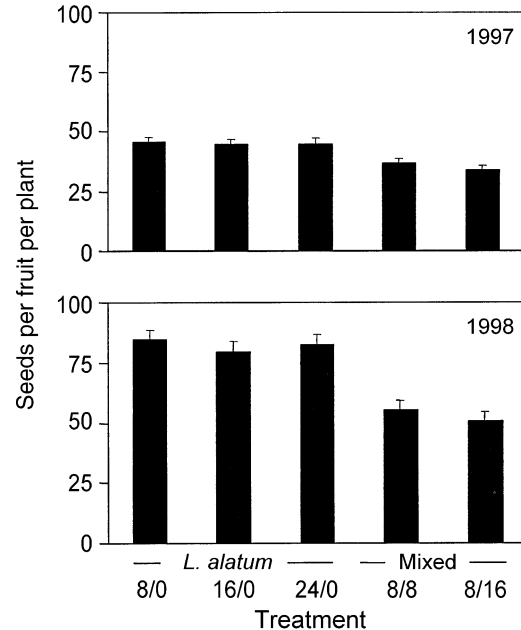


FIG. 2. Seed set (number of seeds per fruit per plant, least-squares means \pm 1 SE) for *Lythrum alatum* for 1997 and 1998. $N = 8$ plot \times morph means for each bar. Treatment numbers on the x-axis refer to the number of *L. alatum* plants per number of *L. salicaria* plants in each plot.

Seed set

Seed set for *L. alatum* decreased by \sim 22% in 1997 and 34% in 1998 in the presence of the invasive *L. salicaria* (Fig. 2). In 1997, only treatment and block effects were significant (Table 1), and a priori contrasts clearly showed a significant difference between monospecific and competitive treatments ($F_{1,12} = 32.16$, $P = 0.0001$). In 1998, treatment and morph effects were significant, but block effects were not (Table 1). Seed number per fruit was significantly higher in the short-styled morph (77.6 ± 1.9 , $N = 20$ plot means for each morph) than in the long-styled morph (63.6 ± 1.9 , $N = 20$). A priori contrasts again indicated that seed set in monospecific treatments was significantly higher than in mixed treatments ($F_{1,12} = 63.42$, $P = 0.0001$). Seed set for *L. alatum* was lower in 1997 than in 1998 (Fig. 2), perhaps reflecting changes in plant culture conditions. There was no effect of conspecific abundance on seed set for *L. alatum* in either year (ANOVA of only the three monospecific treatments; 1997, $F_{2,6} = 0.07$, $P > 0.9$; 1998, $F_{2,6} = 0.4$, $P > 0.6$). For the mixed treatments, although seed set declined slightly as *L. salicaria* abundance increased, this was not statistically significant (ANOVA of only the two mixed treatments: 1997, $F_{2,3} = 2.23$, $P > 0.2$; 1998, $F_{2,3} = 0.4$, $P > 0.5$).

Visitation

Honeybees (*Apis mellifera*) and bumble bees (*Bombus* sp.) together accounted for more than half of all

TABLE 1. ANOVA for seed set of *Lythrum alatum* in 1997 and 1998.

Source	df	1997			1998		
		MS	F	P	MS	F	P
Treatment	4	263.2	8.38	0.002	2140	16.23	0.0001
Block	3	226.4	7.21	0.005	147	1.12	0.38
Morph	1	19.5	0.62	0.45	1947	14.77	0.002
Treatment × block	12	83.2	2.65	0.052	95	0.72	0.71
Treatment × morph	4	56.8	1.81	0.19	85	0.65	0.64
Morph × block	3	66.0	2.10	0.15	70	0.53	0.67
Error	12	31.4			132		

Notes: Treatment refers to the effect of competition treatment (presence and abundance of *L. alatum* and *L. salicaria*), block refers to the effect of the four experimental blocks, and morph refers to the effect of floral morph (short- or long-styled). The analysis used Type III sums of Squares with the means for each plot–morph combination as the unit of observation.

recorded visitation sequences to both plant species. However, there was substantial variation between years in the taxonomic composition of visitors. In particular, for 1997 the number of foraging bouts made by visitors in the “other” category (including syrphid flies, moths, butterflies, and miscellaneous flies) was roughly equal (50.0%) to the combined number of foraging bouts made by *A. mellifera* (27.3%) and *Bombus* sp. (22.8%), while in 1998 it was much lower (other 5.0%, *A. mellifera* 42.9%, and *Bombus* sp. 52.2%). Overall, we recorded a total of 19 050 flower visits in 1997 and 28 617 in 1998.

Pollinator visitation to *L. alatum* was often reduced in the presence of *L. salicaria*. In 1997, the number of visits per plant per 15-min period was significantly affected by all main effects and interactions except treatment × morph and treatment × season × morph (Fig. 3, Table 2). Although many interactions were significant, the ranking of the different treatments was generally consistent across seasons, blocks, and morphs. Despite a significant overall treatment effect

in this year, a priori contrasts indicated no significant difference between competitive and monospecific treatments ($F_{1,117} = 3.32$, $P = 0.11$). However, the number of visits per plant per 15-min period did decrease with increased abundance of conspecifics (ANOVA of treatments A, B, C; $F_{2,12} = 7.2$, $P < 0.01$; Fig. 3). Visits per flower followed a similar pattern except that the treatment × block × season interaction was not significant (Fig. 3, Table 3). However, in this case, a priori contrasts clearly show that competitive treatments experience a significant reduction in per flower visitation rate compared to monospecific treatments ($F_{1,21} = 16.9$, $P = 0.0098$). ANOVA of only the monospecific treatments indicates no significant effect of the abundance of conspecifics on the rate of flower visitation ($F_{2,12} = 0.8$, $P > 0.4$).

During 1998, both visits per plant per 15-min period, and visits per flower per 15-min period varied significantly with treatment, block, and season (Fig. 3, Tables 2 and 3). A priori contrasts for both visits per plant and visits per flower indicate significant reductions in

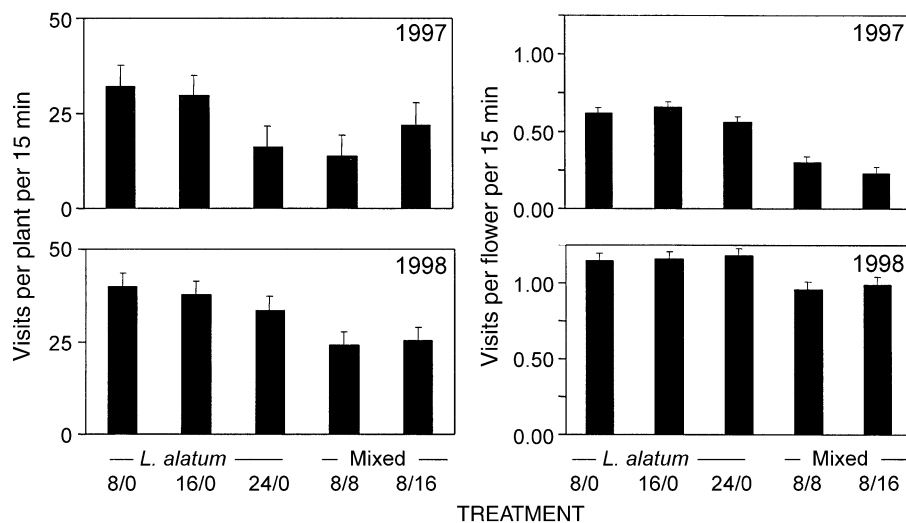


FIG. 3. Visits per *Lythrum alatum* plant and flower per 15 min (least squares means + 1 SE) in 1997 and 1998. $N = 24$ plot × season × morph means for each bar. Treatment numbers on the x-axis refer to the number of *L. alatum* plants per number of *L. salicaria* plants in each plot.

TABLE 2. ANOVA for visits per plant to *Lythrum alatum* during 15-min observation periods in 1997 and 1998.

Source	df	1997			1998		
		MS	F	P	MS	F	P
Treatment	4	1626	6.34	0.0015	1769	5.38	0.0038
Season	2	37 305	145.46	0.0001	1624	4.94	0.0174
Block	3	3169	12.36	0.0001	2331	7.09	0.0018
Morph	1	3633	14.17	0.0011	133	0.41	0.5311
Treatment × block	12	1122	4.38	0.0014	336	1.02	0.4644
Treatment × morph	4	206	0.80	0.5366	681	2.07	0.1207
Block × morph	3	2613	10.19	0.0002	305	0.93	0.4448
Season × treatment	8	830	3.24	0.0137	552	1.68	0.1627
Season × block	6	3577	13.95	0.0001	561	1.71	0.1691
Season × morph	2	2300	8.97	0.0014	89	0.27	0.7655
Season × block × morph	6	2058	8.03	0.0001	276	0.84	0.5527
Treatment × block × morph	12	346	1.35	0.2616	350	1.06	0.4334
Treatment × season × morph	8	185	0.72	0.6697	342	1.04	0.4379
Treatment × block × season	24	827	3.22	0.0037	262	0.80	0.7068
Error	22	256			329		

Notes: Treatment refers to the effect of competition treatment (presence and abundance of *L. alatum* and *L. salicaria*), season refers to the effect of early, mid-, or late summer, block refers to the effect of the four experimental blocks, and morph refers to the effect of floral morph (short- or long-styled). The analysis used Type III sums of squares with means for each plot-morph combination as the unit of observation.

visitation rates when *L. salicaria* was present ($F_{1,21} = 17.9$, $P = 0.0004$; $F_{1,21} = 10.9$, $P = 0.0034$, respectively). In 1998, the abundance of *L. alatum* did not significantly affect visitation rate per plant (ANOVA of treatments A, B, C; $F_{2,12} = 1.5$, $P > 0.2$), or per flower ($F_{2,12} = 0.0$, $P > 0.9$; Fig. 3).

Pollinator movement

Pollinators moved frequently between the two species in mixed plots (Table 4), with 33–65% of all interplant moves being between species. In all treatment-year combinations, *L. alatum* to *L. alatum* moves were less common than expected based on a null model of

random movements between plants, and in three of four treatment-year combinations *L. salicaria* to *L. salicaria* moves were more common than expected (interspecific movements did not show any clear pattern). Movements of pollinators were significantly different from random in all treatment-year combinations (G_p [pooled heterogeneity] > 41.5 , critical value $\chi^2_{0.05[3]} = 7.8$). For most seasons within treatment-year combinations pollinators showed the pattern above (*L. alatum* to *L. alatum* moves were less common than expected in nine of 12 seasons; *L. salicaria* to *L. salicaria* moves were more common in nine of 12 seasons). However, seasonal heterogeneity was significant in all treatment-

TABLE 3. ANOVA for visits per flower to *Lythrum alatum* during 15-min observation periods in 1997 and 1998.

Source	df	1997			1998		
		MS	F	P	MS	F	P
Treatment	4	0.11	4.07	0.0135	0.26	2.74	0.0560
Season	2	3.07	110.34	0.0001	0.54	5.79	0.0099
Block	3	0.49	17.58	0.0001	0.81	8.66	0.0006
Morph	1	0.24	8.5	0.0084	0.06	0.62	0.44
Treatment × block	12	0.07	2.37	0.0404	0.17	1.77	0.12
Treatment × morph	4	0.03	1.17	0.3539	0.14	1.53	0.23
Block × morph	3	0.16	5.62	0.0054	0.09	0.93	0.44
Season × treatment	8	0.06	2.27	0.0633	0.09	0.99	0.47
Season × block	6	0.53	19.02	0.0001	0.20	2.13	0.09
Season × morph	2	0.21	7.57	0.0033	0.22	2.32	0.13
Season × block × morph	6	0.14	4.93	0.0027	0.04	0.38	0.88
Treatment × block × morph	12	0.02	0.87	0.5844	0.16	1.76	0.12
Treatment × season × morph	8	0.18	0.66	0.7189	0.17	1.88	0.12
Treatment × block × season	24	0.05	1.67	0.1187	0.17	1.83	0.08
Error	21	0.03			0.09		

Notes: Treatment refers to the effect of competition treatment (presence and abundance of *L. alatum* and *L. salicaria*), season refers to the effect of early, mid-, or late summer, block refers to the effect of the four experimental blocks, and morph refers to the effect of floral morph (short- or long-styled). The analysis used Type III sums of squares with means for each plot-morph combination as the unit of observation.

TABLE 4. Visitor transitions between species for 1997 and 1998 in mixed-species treatments.

	Initial species	Subsequent species			
		Treatment D		Treatment E	
		<i>L. alatum</i>	<i>L. salicaria</i>	<i>L. alatum</i>	<i>L. salicaria</i>
1997	<i>L. alatum</i>	24	51	24	73
	<i>L. salicaria</i>	50	104	71	266
1998	<i>L. alatum</i>	86	158	32	140
	<i>L. salicaria</i>	158	212	158	126

Note: Treatment D is eight *Lythrum alatum* and eight *L. salicaria*; Treatment E is eight *L. alatum* and 16 *L. salicaria*.

year combinations (G_H [heterogeneity] > 38.2, critical value $\chi^2_{0.05[6]} = 12.6$) except in treatment D in 1997.

DISCUSSION

Our results indicate that the showy, invasive herb *Lythrum salicaria* can harm reproduction of the native congener *L. alatum* by significantly reducing seed set. Part of this impact probably occurs because *L. salicaria* siphons pollinators away from *L. alatum*, a reduction in the quantity of pollination service due to pollinator preference. Reduction in the quality of pollination services may also contribute to the reduction in seed set since we frequently observed movement of pollinators between species.

Seed set and pollinator visitation

In both years of our study, *L. alatum* seed set was significantly reduced in the presence of *L. salicaria* (Fig. 2), consistent with the proposition that competition from *L. salicaria* reduces pollination of *L. alatum*. Competition for pollination services and its impact on seed set have been investigated in a variety of systems, and outcomes range from reduced seed set (Waser 1978a, Armbruster and Herzig 1984, Campbell 1985), to no impact (Schemske et al. 1974, Rathcke 1988, Armbruster and McGuire 1991, McGuire and Armbruster 1991, Kunin 1997, Caruso 1999), to increased seed set (Rathcke 1988, Gross 1996). Thus, our results contribute to a growing literature showing that plant–plant interactions can significantly influence pollinator visitation and plant reproductive success. Furthermore, we have demonstrated that an invasive species can potentially have important competitive effects on natives (see also Grabas and Laverly 1999).

Reduced seed set in competitive plots probably resulted in part from a significantly lower quantity of visits to *L. alatum* in the presence of *L. salicaria* (Fig. 3); visitation was reduced by 14–54% compared to control plots. Such strong reductions in visitation in response to competition are rarely documented (see Waser 1983). In our system the greater nectar and pollen rewards and larger floral display of *L. salicaria* probably explain why pollinators prefer this attractive invader.

Another probable cause of reduced seed set in competitive plots is interspecific pollen transfer and an associated decline in visit quality. Pollinators often moved between the two species, with interspecific movements constituting 33–65% of movements between plants in mixed treatments. Such movements can generate mixed-species pollen loads (Brown and Mitchell 2001), and the presence of *L. salicaria* pollen on stigmas significantly reduces *L. alatum* seed set (Brown and Mitchell 2001). Note that in the mixed treatments, much more *L. salicaria* than *L. alatum* pollen was available to pollinators because *L. salicaria* produced up to four times more flowers per plant and twice as much pollen per flower (Brown and Mitchell 2001). A reduced quality of pollinator service has been implicated as a cause of reduced seed set in many other studies, primarily of native species (Waser 1978b, Sukhada and Jayachandra 1980, Thomson et al. 1981, Campbell and Motten 1985, Kohn and Waser 1985, Waser and Fugate 1986, Galen and Gregory 1989, Murphy and Aarssen 1995a, b, c, d, Murcia and Feinsinger 1996).

Together, these results suggest that the invader can decrease both visit quantity and quality for this native plant species. Most studies to date have found evidence supporting only competition through reductions in visit quality (but see Waser 1978a, Armbruster and Herzig 1984), but few studies of competition for pollinator services have tested for both mechanisms (e.g., Campbell 1985, Campbell and Motten 1985, Armbruster and McGuire 1991, Jennersten and Kwak 1991). The evolutionary responses to competitors and the ecological situations that might ameliorate competition depend strongly on which mechanisms are involved (see also Waser 1983, Caruso 1999). For example, if effects were only due to reduced visitation, increased attractiveness or self-compatibility might be likely evolutionary outcomes, but these adaptations would have little effect on interspecific pollen transfer. Likewise, divergence in floral form or in habitat preferences might reduce interspecific pollen transfer, but have no effect on visitation rate. Because both mechanisms appear to be involved in our system, plants have few options to escape competition. The threat posed by *L. salicaria* thus may be even larger than if only a single mechanism were involved.

Floral display

Lythrum salicaria is much showier than *L. alatum*, having larger and more numerous flowers, and this probably accounts for much of the observed reduction in visitation rate and seed production in *L. alatum*. Yet the *L. alatum* in our experiment had much larger floral displays than the 7–16 flowers typically found in field populations (B. J. Brown, unpublished data), and the *L. salicaria* had substantially fewer than the 120–155 open flowers found in typical field populations (B. J. Brown, unpublished data). Furthermore, aside from

having a larger floral display, *L. salicaria* produces substantially more nectar and pollen per flower (Brown and Mitchell 2001; B. J. Brown, unpublished data), potentially increasing its attractiveness to pollinators. If *L. alatum* experiences reduced seed set in our plots, where its floral display is two to three times normal, and the *L. salicaria* floral display is reduced, the effect of *L. salicaria* on a natural population could be even greater than shown in this experiment.

Conclusions

Our research shows that one native species suffers significantly reduced seed set in the presence of an aggressive invading congener when the species share the same kind of pollinators. Work by Grabas and Laverty (1999) indicates that *L. salicaria* may also affect other sympatric native species. The present studies set the stage for additional work on a variety of topics, including the importance of interspecific movement of flower visitors in field populations, the movement of pollen in the field, heterospecific pollen loads in the field, and the role of nectar production and standing crop in pollinator choice. Furthermore, our work to date has exclusively addressed effects on female function. Male function may be affected through pollen wastage and other means (Waser 1978b, Armbruster and Herzig 1984, Campbell 1985) and deserves further study.

Many invasive plant species around the globe have showy flowers and are pollinated by animal visitors (B. J. Brown, unpublished data). Such attractive species may have negative effects on pollination of neighboring plants similar to those we document here between two species of *Lythrum*. This insidious threat to the native flora has rarely been considered, but should be taken into account when an alien species threatens the continued existence of a native.

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