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Nontarget effects on crepe myrtle by *Galerucella pusilla* and *G. californiensis* (Chrysomelidae), used for biological control of purple loosestrife (*Lythrum salicaria*)

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Field experiments were used to assess how distance mediates the nontarget effect on crepe myrtle by two chrysomelid beetles that were introduced to the United States in 1992 for biological control of purple loosestrife. Previous laboratory tests in Germany and concurrent tests in Oregon showed that although the control organisms can feed on crepe myrtle, they cannot complete development. Therefore, we predicted that negative effects on crepe myrtle would decrease with distance from the purple loosestrife stand. To test this prediction, cohorts of both plant species were transplanted at increasing distances (0, 5, 15, 30, and 50 m) from the colonization source. We found that leaf damage inflicted by the beetles was negatively correlated with increasing distance. Damage was significantly lower at each distance for crepe myrtle plants than for purple loosestrife plants, with a mean difference of 22% and a 95% confidence interval ranging from 12 to 31%. Extensive defoliation of crepe myrtle was limited to within 30 m of the edge of the loosestrife stand. Plant yield was negatively correlated with damage: the closer plants were to the purple loosestrife stand, the greater the suppression of biomass in both plant species. However, loosestrife biomass decreased significantly more quickly than crepe myrtle biomass, with a mean difference in slopes of 0.035 and a 95% confidence interval ranging from 0.022 to 0.048. Our results suggest that release of the *Galerucella* beetles in North America poses little risk to crepe myrtle. Beetles can feed but cannot complete their life cycle on crepe myrtle, and damage to crepe myrtle approaches zero approximately 50 m from the beetle colonization source.

Nomenclature: Crepe myrtle, *Lagerstroemia indica* L. LAGIN; purple loosestrife, *Lythrum salicaria* L. LYTSA; black-margined loosestrife beetle, *Galerucella californiensis* L.; golden loosestrife beetle, *Galerucella pusilla* Duftschmid.

Key words: Leaf beetle, wetland, nontarget effect, field testing of host specificity, biological control.

Host specificity is the primary criterion by which scientists and regulators judge the risks of releasing biological control organisms into new environments (Harley and Forno 1992; McEvoy 1996; Secord and Kareiva 1996; Zwölfer and Harris 1971). The risk to nontarget organisms can be minimized by using control organisms with a narrow host range in environments containing few nontarget organisms (Pemberton 2000). Sources of uncertainty in conventional assessments of host range include the possibility of dispersal, indirect effects, and evolution (McEvoy 1996; Secord and Kareiva 1996). Recent evidence on nontarget effects reinforces confidence in host specificity as a safety criterion. A survey of 117 weed biological control organisms introduced for control of 41 weeds found that only one could complete its life cycle on a native plant whose genus is different from that of the target plant (Pemberton 2000).

Host specificity tests typically use no-choice tests to measure whether a proposed biological control agent can complete its life cycle on a nontarget plant isolated in a closed system (McEvoy 1996). Although a biological control agent may be unable to form self-sustaining populations on a nontarget plant, it may still inflict significant “spill-over” damage on nontarget plants that are located near populations of the target plant. There is no current protocol for assessing this risk. Here, we develop a means to quantify this spatially

dependent risk and use it to assess potential damage to the economically important ornamental plant, crepe myrtle.

In this study we examine the potential nontarget effect on crepe myrtle by two leaf beetles (golden loosestrife beetle and black-margined loosestrife beetle) widely introduced in the United States and Canada for control of purple loosestrife (Malecki et al. 1993). The original host specificity greenhouse studies from Germany reported minimal adult and larval feeding, no oviposition, and no larval maturation on crepe myrtle (Blossey et al. 1994). Subsequent studies done in quarantine facilities at Virginia Polytechnic Institute detected oviposition on cut crepe myrtle stems by both beetle species (Kok et al. 1992). This ambiguous potential for nontarget damage to an economically important nursery plant led the California Department of Food and Agriculture (CDFA) to deny permission for release of the beetles within the state despite the possibility that the purple loosestrife invasion could harm wild rice (*Oryza sativa* L.) production in the Fall River Drainage in Shasta County, CA. In 1996 the CDFA asked us to clarify the nontarget damage potential by (1) verifying that the local population of beetles from which the California releases were to be collected (Baskett Slough NWR, Salem, OR) could not form self-sustaining populations on crepe myrtle, and (2) assessing the effect of distance from a colonization source (i.e., purple loosestrife

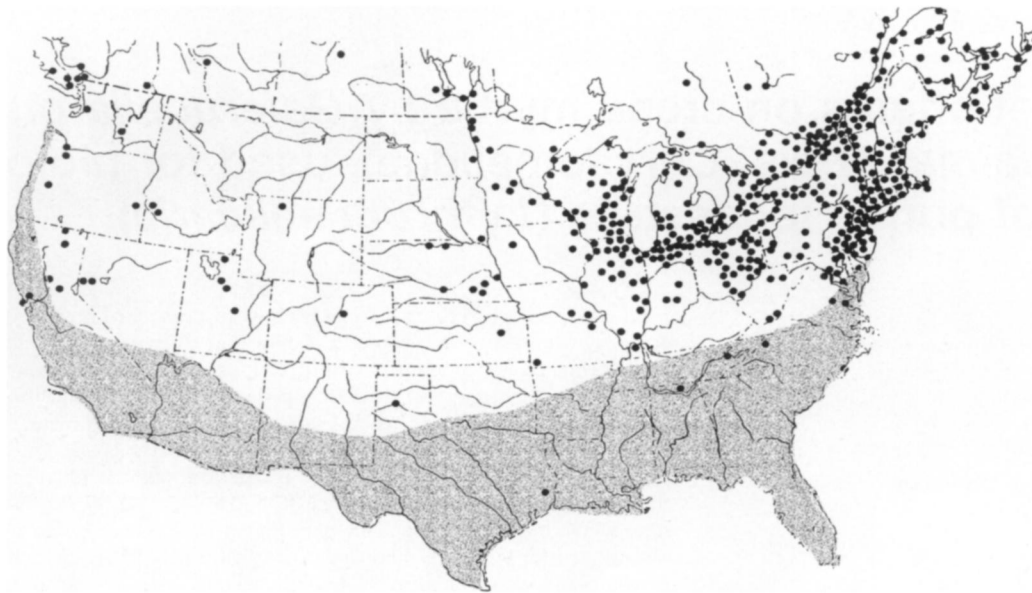


FIGURE 1. Distributions of purple loosestrife (*Lythrum salicaria* L.) (dots) and crepe myrtle (*Lagerstroemia indica* L.) (shaded zone) in the United States show minimal overlap (after Martin 1983; Thompson et al. 1987).

stand) on beetle damage to crepe myrtle plants. It is this spatial approach to ecological host specificity testing that we wish to emphasize.

Prior and concurrent sweep net sampling indicated that the population of beetles waxed and waned in the surrounding fields up to 30 m from the purple loosestrife stand (Schooler 1998), which suggested the potential for local indirect spill-over effects to susceptible nontarget organisms. The three matters of interest were (1) the capacity of the beetles to feed and develop on crepe myrtle, (2) the effect of distance on the ability of the beetles to colonize crepe myrtle under open field conditions, and (3) the influence of insect feeding on crepe myrtle's growth, survivorship, and reproduction.

Target Plant

Purple loosestrife is a tall (2 to 3 m), iteroparous, perennial wetland plant native to Eurasia. It probably arrived on the east coast of the United States before 1830 in ballast deposited by trading ships from northern Europe (Thompson 1991). It has since been spreading across the country, aided more recently by road construction and irrigation channels (Wilcox 1989) as well as through the planting of seeds and potted plants sold by the nursery industry. Although it is most abundant in the northern United States and southern Canada (Thompson et al. 1987; see Figure 1), purple loosestrife has spread throughout the continental United States (Blossey 1999).

Purple loosestrife is an invasive species that displaces native wetland vegetation in riparian areas, often forming dense, single-species stands that degrade habitat quality for waterfowl and other wetland animal species (Balogh and Bookhout 1989; Blossey 1999; Thompson et al. 1987). In the United States, its mean rate of spread since 1940 is estimated to be 645 km² yr⁻¹ (Thompson 1991), and the estimated cost of damage to wildlife and agriculture is \$45 million yr⁻¹ (Thompson et al. 1987). Losses in Oregon dur-

ing 1999 are estimated at \$2.8 million in net personal income (Radtke and Davis 2000).

The quantitative evidence supporting the negative ecological effects of purple loosestrife has been questioned (Anderson 1995; Hager and McCoy 1998). In two recent articles Blossey (1999, 2001) summarizes the "suspected" and "documented" environmental effects of purple loosestrife.

Nontarget Plant

Crepe myrtle is an ornamental plant economically important to the California nursery industry, with total California sales estimated to be \$5 million and total national sales, \$34 million (USDA, 1998 Census of Horticultural Specialties). It is typically a large shrub or small tree, although there are also dwarf varieties (Martin 1983) such as the variety studied here. Crepe myrtle was originally introduced from the Indian subcontinent (Bailey 1951; Dunmire 1979) and needs hot summers and well-drained soil to flower. It is therefore cultivated mainly in the southern portion (Agricultural climate zone 7) of the United States (Martin 1983; see Figure 1).

Biological Control Agents

The release of golden loosestrife beetle and black-margined loosestrife beetle for biological control of purple loosestrife was approved by the Animal and Plant Health Inspection Service (USDA—APHIS) in 1992 (Malecki et al. 1993). The two beetle species live sympatrically in similar ecological niches on purple loosestrife (Blossey 1995). Larvae proceed through three instars before pupation. Experimental study of movement between purple loosestrife patches using a target-centered mark-recapture method indicated that black-margined loosestrife beetle adults can detect the host up to 50 m and are capable of flying at least 850 m within 1 wk (Grevstad and Herzig 1997). The study also documented that black-margined loosestrife beetle individ-

uals are strongly attracted to one another, leading to aggregated distribution patterns. We documented migration patterns of the beetles into the fields surrounding the purple loosestrife stand in 1995 and 1996. The beetles were detected up to 30 m within the range of observations 0 to 50 m from the edge of the stand, and this migration coincided with the emergence of overwintering and teneral adults during early spring and summer, respectively (Schooler 1998).

Study Site

Field work was conducted at Morgan Lake in the Baskett Slough National Wildlife Refuge, western Oregon (Polk County, 44°59'N, 123°16'W). The two beetles, golden loosestrife beetle and black-margined loosestrife beetle, were introduced together (total of 1,050 adults) along the southern shore of Morgan Lake in 1992. The beetles were imported from Germany and proceeded through quarantine facilities at Virginia Polytechnic Institute before being released at our site. By 1996 the beetles had increased in abundance to levels that caused nearly 100% leaf damage to purple loosestrife near the initial release site and reduced purple loosestrife biomass by 91% in 1997 (Schooler 1998). This high density of herbivores gave us the opportunity to test a "worst-case" scenario of negative effects on nontarget vegetation along a gradient of distance from the colonization source.

Materials and Methods

Larval Development Studies

We began by testing whether the beetle larvae were able to complete development on crepe myrtle. Beetles used in the greenhouse feeding trials were collected from the local population at Morgan Lake in April 1996. Approximately 40 individuals of each species were placed on separately caged purple loosestrife and crepe myrtle plants and allowed to oviposit for 3 d. Five newly emerged larvae of the golden loosestrife beetle were transferred using a fine paintbrush on each of five randomly selected potted purple loosestrife plants and each of five potted crepe myrtle plants. This procedure was repeated for the black-margined loosestrife beetle larvae. Larvae placed on crepe myrtle were reared from eggs oviposited on crepe myrtle, whereas larvae placed on purple loosestrife were reared from eggs oviposited on purple loosestrife.

The 10 potted purple loosestrife plants and the 10 potted crepe myrtle plants (approximately 1 yr old and 30 cm tall) were placed in a shallow pool with 5 cm of water. The water moat discouraged larval movement between plants. The greenhouse was kept at 24 C with a natural photoperiod of approximately 16:8 (light-dark). Surviving larvae were counted at 4-d intervals until they reached their third instar. Because first-instar larvae tend to move into the tender tissue of the apical meristem, we examined the tissue for damage and carefully opened the buds to count the number of individuals when damage was found. Third-instar larvae were placed in transparent plastic containers with fresh leaf material of their respective host plants and left to pupate. The numbers of pupae and the resulting teneral adults were recorded.

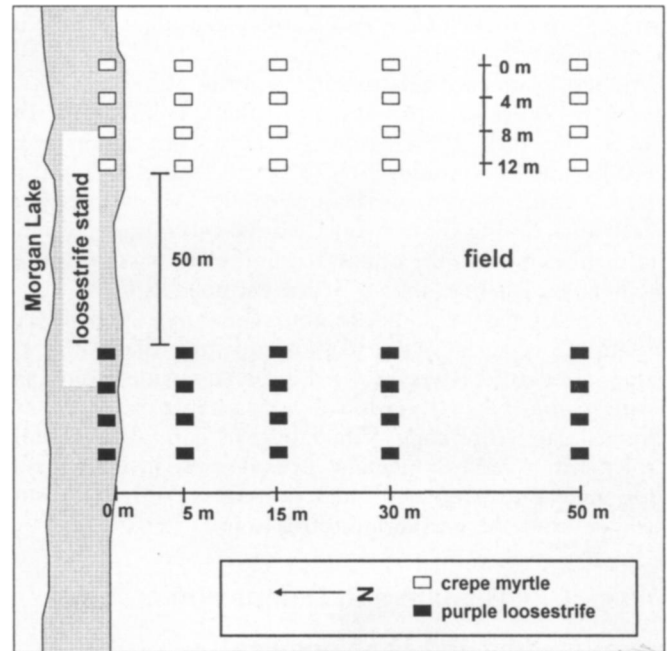


FIGURE 2. Experimental design of the nontarget field study involving two plant species at five distances from the source of herbivore colonization. Four plants of each species were located at each distance for a total of 40 experimental units.

Colonization and Effect Studies

To study the colonization potential of the beetles on crepe myrtle, four nursery-grown crepe myrtle plants were transplanted at each of five distances (0, 5, 15, 30, and 50 m) from the edge of a heavily beetle-infested stand of purple loosestrife on the southern side of Morgan Lake. A cohort of greenhouse-grown purple loosestrife plants were transplanted 50 m to the east at the same distances from the edge of the purple loosestrife stand (Figure 2). The ground slope and aspect were the same for the two blocks of plant species.

Colonizing ability may be influenced by plant cues or by intraspecific pheromones (Grevstad and Herzig 1997; Visser 1986), so the two plant species were planted in separate locations to reduce any influence of purple loosestrife in attracting the beetles to crepe myrtle. Therefore, our block design did not allow for interspersed plant species, although each individual plant was randomly assigned a location within its block. All plants were watered once a week.

From initial transplanting to the end of the second generation of adult beetles, each plant was examined weekly to determine (1) percent leaf damage, (2) number of adults, (3) presence of eggs, (4) presence of larvae, and (5) plant condition. Approximately 1 min was spent in searching for each beetle stage on each plant. We visually assessed percentage of leaf damage by subjectively choosing an average leaf, comparing it with a precalculated leaf damage chart, and assigning it a damage level. Plant condition indicated whether the plant was alive or dead. Plants were considered alive if green tissue was present or if there was evidence of new buds. Because of heavy defoliation, some plants may be subjectively considered dead and may subsequently resprout. Final plant condition was objectively assessed by ex-

aming root tissue at the end of the experiment, when the plants were harvested.

All test plants were harvested to estimate biomass after the adult beetles had moved off the plants to overwintering sites at the end of the growing season. The plants were carefully washed through a mesh sieve (2-mm² cell size) to retain as much root material as possible. The samples were placed in a drying oven at 60 C, dried to constant weight, and then weighed to the nearest 0.1 g. If plant material existed but weighed less than 0.05 g, it was recorded as 0.1 g.

We integrated adult beetle abundance over time as cumulative “beetle days” per plant to quantify the plant’s exposure (Hull and Beers 1990). Linear regressions were performed using S-plus (version 4.5; MathSoft, 1999). Plant biomass data were transformed by the natural log before implementing regression analyses because variation increased with increasing biomass values correlated with increasing distance from the purple loosestrife stand.

Results and Discussion

Larval Feeding and Development

Larvae reared in the greenhouse failed to develop on crepe myrtle but readily developed on purple loosestrife. None of the 50 beetle larvae placed on crepe myrtle survived longer than 8 d in the greenhouse trials, and none survived to the third instar. Control larvae reared on purple loosestrife showed a 78% survival rate to the third instar, and 74% reached the adult stage. The results from our laboratory feeding trials support the earlier finding that the *Galerucella* beetles are unable to complete their life cycle on crepe myrtle (Blossey et al. 1994).

Beetle Colonization

Adult beetles from the first generation were found on all crepe myrtle and purple loosestrife plants within 30 m of the purple loosestrife stand. Two of the four purple loosestrife plants at 50 m were colonized, and one of the four crepe myrtle plants was colonized. Mean beetle exposure per plant varied between 0 and 17.4 beetles per day for crepe myrtle and between 0 and 9.7 beetles per day for purple loosestrife (Figure 3).

Eggs were present on all plants of both species that were colonized by the beetles. During the first beetle generation six separate crepe myrtle plants were found with larvae (30%), whereas 14 purple loosestrife plants were found hosting larvae (70%). In a previous host specificity study of crepe myrtle under greenhouse conditions, Blossey et al. (1994) reported no oviposition on plants outside the genus *Lythrum*. Subsequent studies conducted in quarantine facilities at Virginia Polytechnic Institute detected oviposition on cut crepe myrtle stems by both beetle species (Kok 1992).

Close to the source, within 30 m of a high-density beetle population, the colonization potential on crepe myrtle was identical to that on purple loosestrife (100%). At 50 m, beetle colonization dropped to 25% for crepe myrtle and to 50% for purple loosestrife. This ability to locate new plants may be due to diffusive movement away from the stand and taxis response to cues (visual, chemical, etc.) associated with the host plant (Visser 1986). The study by Grevstad and

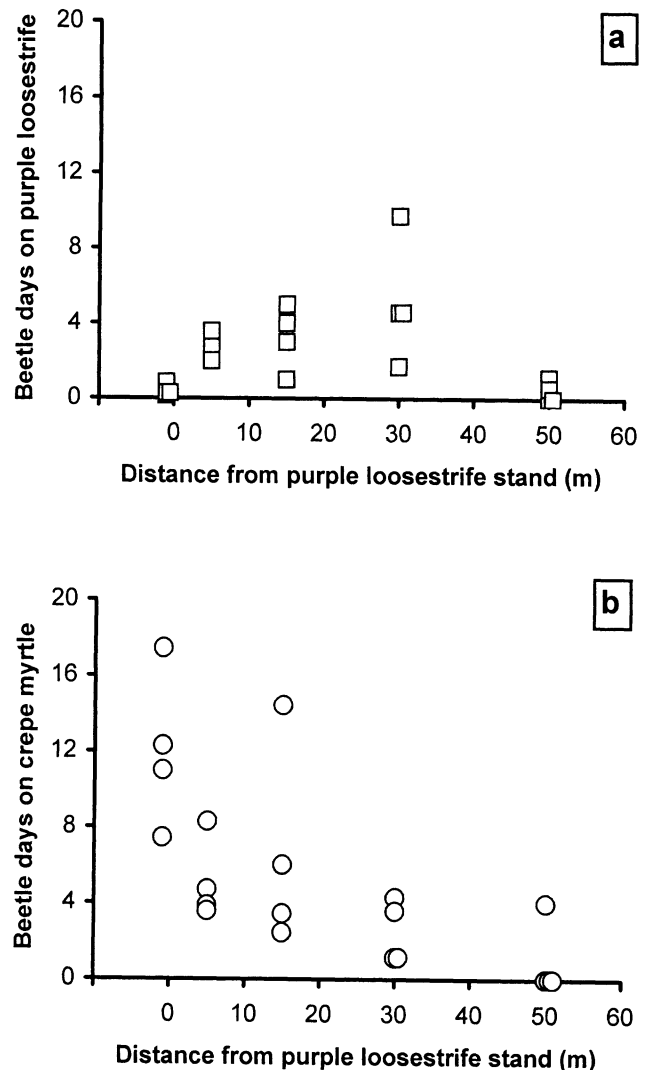


FIGURE 3. Beetle duration (mean adult beetles per day) calculated for (a) purple loosestrife (*Lythrum salicaria* L.) and (b) crepe myrtle (*Lagerstroemia indica* L.) plotted against distance from the purple loosestrife stand.

Herzig (1997) found that when cohorts of black-margined loosestrife beetles were released within 50 m of a host patch, the proportion of beetles reaching that patch was greater than that expected at random. This suggests that the beetles use host plant cues to locate host plant patches, but it is not known whether olfactory, visual, or other cues are involved. The similarity we found in colonization ability between purple loosestrife and crepe myrtle suggests that the beetles may use similar cues to locate both purple loosestrife and crepe myrtle plants. However, using sweep net sampling we found that the beetle population expanded and contracted in the fields surrounding the purple loosestrife population and was detectable at distances of up to 30 m from the purple loosestrife stand (Schooler 1998). Therefore, rather than following chemical cues, the colonization of plants outside the purple loosestrife stand may be due to diffusive movements of the beetles as they haphazardly search for higher-quality host plants.

Crepe myrtle plants at the edge of the purple loosestrife stand tended to harbor more beetles over time than did the transplanted purple loosestrife plants (Figure 3). A possible explanation is that the herbivores moved on to “greener pas-

tures” after completely defoliating the purple loosestrife transplants (mean 87% leaf damage) at the edge of the stand by the fifth week of exposure, thus leaving the plants uninhabited. The crepe myrtle within the stand exhibited 42% leaf damage by the fifth week and did not show 87% damage until the ninth week of exposure. This suggests that because beetle abundance on the host plant is affected by the defoliation status, counts of beetles on host plants may lead to inaccurate measurement of the current beetle density at a location. Beetles may instead leave the damaged low-quality host to search for higher-quality host plants in the surrounding vegetation. Therefore, indicators of beetle abundance that integrate density over time, such as leaf damage, or methods that sample the surrounding vegetation, such as vacuum sampling, may be better predictors of local beetle density.

To determine the probability of crepe myrtle being adjacent to populations of purple loosestrife, we overlaid a map of recorded purple loosestrife populations (Thompson et al. 1987) with the recommended cultivation zone of crepe myrtle (Martin 1983). We found that the distribution of purple loosestrife and the recommended range of crepe myrtle in the United States and Canada exhibited minimal overlap (Figure 1). Crepe myrtle is mainly cultivated in the southern United States (Zone 7) owing to the hot, dry summers necessary for flowering (Martin 1983), whereas purple loosestrife is mainly distributed across the northern United States (Thompson et al. 1987). However, more recent estimates of purple loosestrife abundance (Blossey 1999) suggest that the plant is currently spreading into more southern states and therefore into areas of crepe myrtle cultivation.

Beetle Effect

Percent leaf damage decreased with distance from the purple loosestrife stand for both plant species (Figure 4). We used multiple linear regression to determine the difference in damage effected by the beetles on the two plant species while controlling for the effect of distance. The interaction term in a full regression model generated a two-sided P-value of 0.23, supporting the reduced model that the two slopes were not significantly different. The reduced model of equal slopes but separate intercepts was then fit, and the low P-value (> 0.001) indicated that the intercepts were significantly different. The mean difference was 21.6%, with a 95% confidence interval extending from 12.2 to 31.1%. This means that at a given distance, the beetles caused approximately 22% less leaf damage to crepe myrtle than to purple loosestrife.

Plant biomass increased with increasing distance from the purple loosestrife stand for both plant species (Figure 5). Purple loosestrife increased from a mean biomass of 6.3 to 56.3 g, whereas mean crepe myrtle biomass increased from 44.3 to 68.3 g. The relationship between biomass and distance was similar for total plant biomass and for biomass of the separate plant parts (roots, stems, leaves). We used multiple linear regression to determine the difference in biomass loss caused by the beetles on the two plant species while controlling for the effect of distance. The interaction term in a full model generated a low two-sided P-value (> 0.001), indicating that the two slopes were significantly different. The mean difference in slopes was 0.035, with a 95% confidence interval ranging from 0.022 to 0.049. Therefore,

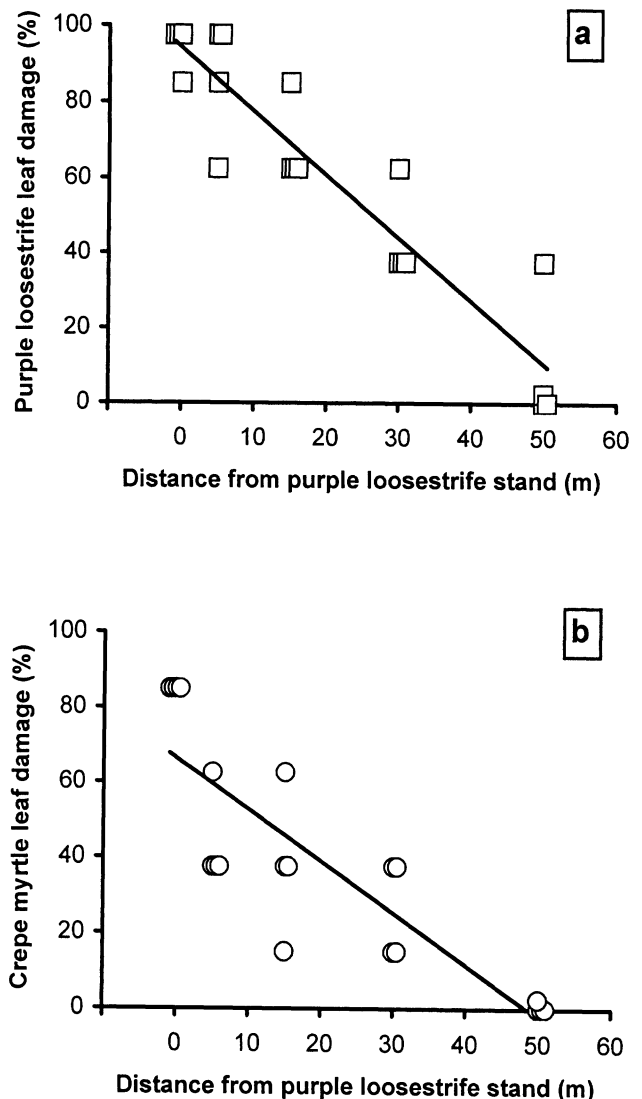


FIGURE 4. Mean percentage leaf defoliation decreased with distance from the colonization source (purple loosestrife stand [*Lythrum salicaria* L.]) for both (a) purple loosestrife and (b) crepe myrtle (*Lagerstroemia indica* L.). Solid lines were determined by linear regression. Regression results—purple loosestrife: $n = 20$, $R^2 = 0.87$, $y = -1.68x + 94.01$, $P < 0.001$; crepe myrtle: $n = 20$, $R^2 = 0.72$, $y = -1.37x + 66.21$, $P < 0.001$.

yield loss near the source was greater for purple loosestrife than for crepe myrtle and diminished, approaching 0 at approximately 50 m from the herbivore colonization source.

The insects had negative effects on plant biomass but no detectable effect on mortality (no plants died) or flowering (only two purple loosestrife plants flowered, one at 50 m and one at 30 m) in this experiment. Biomass of both plant species increased with increasing distance from the source of colonizing herbivores and increasing beetle damage (Figures 4 and 5). This indicates that these biological control agents have negative effects on both plant species. The significantly greater slope of the regression line for purple loosestrife suggests that beetles exert a greater effect on their intended target plant. This is likely due to the greater defoliation of purple loosestrife that we found in our visual estimates of beetle damage (Figure 4).

A weak point of our study was the lack of interspersion of the plant-by-distance treatment arrays. Spatial constraints and beetle distributions limited our ability to replicate and

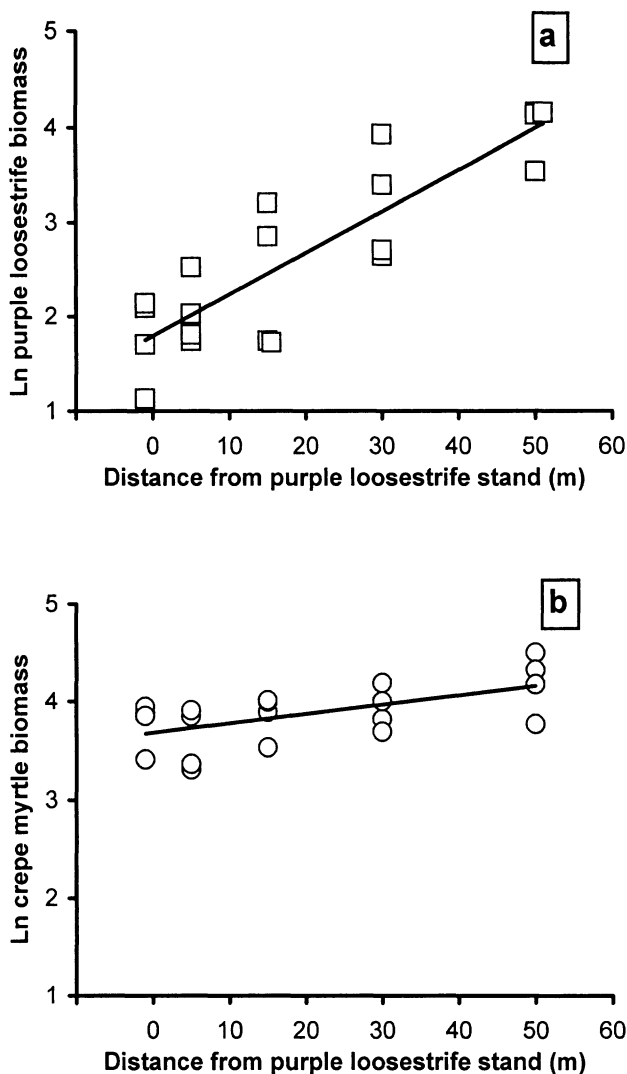


FIGURE 5. Natural log of total dry weight of (a) purple loosestrife (*Lythrum salicaria* L.) and (b) crepe myrtle (*Lagerstroemia indica* L.) at five distances from a stand of purple loosestrife densely populated by golden loosestrife beetle (*Galerucella pusilla* Dufschmid) and black-margined loosestrife beetle (*Galerucella californiensis* L.). Solid lines were determined by linear regression. Regression results—purple loosestrife: $n = 20$, $R^2 = 0.76$, $y = 0.05x + 1.77$, $P < 0.001$; crepe myrtle: $n = 20$, $R^2 = 0.35$, $y = 0.01x + 3.67$, $P = 0.006$.

intersperse our distance transects. Therefore, the arrays were grouped, with 50 m between the two potential host plant species, to limit the effect of the alternate host plant on beetle colonization behavior (see Figure 2). Nonetheless, it seems clear that the beetles caused more damage to purple loosestrife than to crepe myrtle plants at equal distances from the colonization source and that the risk of severe nontarget defoliation is limited to within 30 m of a population of the herbivores at high beetle densities.

Our results suggest that these biological agents, golden loosestrife beetle and black-margined loosestrife beetle, will have temporary minimal effects on populations of crepe myrtle based on (1) unsuitability of crepe myrtle for beetle development, (2) evidence of low overlap in geographic distributions of the two plant species, and (3) decrease in the effect on crepe myrtle with increasing distance from purple loosestrife stands inhabited by the beetles. Larvae of golden loosestrife beetle and black-margined loosestrife beetle could

not completely develop on crepe myrtle in either the greenhouse or the field, further confirming that the beetles are unable to develop self-sustaining isolated populations on the nontarget host. Therefore, damage to crepe myrtle in the field by black-margined loosestrife beetle and golden loosestrife beetle is restricted to adult beetles colonizing from local stands of purple loosestrife.

Host specificity tests typically determine whether a proposed biological control agent can complete its life cycle on a nontarget plant in a laboratory. Some investigators argue that laboratory host specificity testing may be unreliable for assessing safety, principally because they neglect dispersal, evolution, and indirect effects (McEvoy 1996; Secord and Kareiva 1996). In addition, plants grown under artificial conditions may be physiologically different from plants grown in the field (Blossey et al. 1994). Here, we have presented a procedure for extending host specificity evaluations into the field and have included the effects of biological control agent dispersal on local nontarget hosts. This procedure is time-consuming and will be most useful in checking the validity of prerelease screening procedures and addressing specific concerns of cautious land managers. By quantifying the risks to nontarget organisms accurately, we can make more informed decisions regarding the safety of releases of biological control organisms and thereby increase predictability and build public support.

After receiving this report the CDEA approved the release of golden loosestrife beetles and black-margined loosestrife beetles for control of purple loosestrife populations within the state.

Acknowledgments

We dedicate this manuscript to the memory of Richard Guadagno of the USFWS, who generously supported this study on the Baskett Slough National Wildlife Refuge and died a hero on Flight 93 during the events of September 11, 2001. We also thank D. Joley and B. Villegas of the CDEA for the supply of crepe myrtle plants. Finally, we thank the two anonymous reviewers who greatly enhanced the clarity of this manuscript. The opinions expressed are solely ours and do not necessarily represent the views of the reviewers or the sponsoring agencies. This is Oregon State University Experiment Station Technical Paper 11760.

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