

Lack of Pollinators Limits Fruit Set in the Exotic *Lonicera japonica*

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ABSTRACT.—The nonindigenous invasive, *Lonicera japonica*, is a woody vine with a well-documented capacity for vegetative spread. In contrast, few data exist on its potential for establishment by seed. *Lonicera japonica* is biotically pollinated and xenogamous, requiring pollen from a genetically distinct individual for fruit set. We conducted hand-pollinations to determine if the fruit set of *L. japonica* in Arkansas was pollinator limited. Naturally pollinated control shoots produced fruit from 17.4% of their flowers, but the hand-pollinated flowers had a fruit set of 78.7%. Shoots with pollinators excluded set fruit on only 2.1% of the flowers. To determine geographic patterns in fruit set we surveyed seven different sites along the western edge of the naturalized range of *L. japonica*. Average fruit set on primary shoots was $13 \pm 4.1\%$ (mean \pm SE), whereas the secondary shoots averaged $23 \pm 6.7\%$. These results support our conclusion that sexual reproduction in populations of *L. japonica* along the western edge of its naturalized range is limited by a lack of pollination.

INTRODUCTION

Plants introduced into new geographic ranges may benefit from leaving behind their specialized herbivores (Blossey and Nötzold, 1995), but they may also lose the services of specialized pollinators. Coevolved mutualisms are not expected to be common in invading plants (Orrians, 1986) and broad surveys of plant invaders have concluded that a generalized pollination system, such as wind or self-pollination, is most common among invaders (Baker, 1986). In a recent taxonomic survey Daehler (1998) found families of biotically-pollinated plants to be under-represented as invaders on a global scale, presumably because they are more likely to suffer negative effects when they must interact with a new guild of pollinators.

One notable exception to the above pattern is *Lonicera japonica*, a woody vine that requires biotically transferred pollen from a genetically distinct plant to set seed (xenogamous). *Lonicera japonica* is native to eastern Asia, but is an aggressive invader of natural areas in the eastern and southeastern U.S. The flowers of *L. japonica* have characteristics associated with pollination by hawkmoths (Proctor *et al.*, 1996; Miyake *et al.*, 1998) and within its native range in Japan it is visited by both nocturnal hawkmoths and diurnal bees (Miyake and Yahara, 1998). The capacity of *L. japonica* to produce fruit within its naturalized range in the U.S. depends on its relationships with North American pollinators. Because the plant and the pollinators available in the U.S. have not coevolved, and *L. japonica* is completely dependent on pollinators to produce seed, we expect mismatched phenology or pollinator behavior could negatively impact fruit set.

Within its naturalized range in the U.S. *Lonicera japonica* produces an abundance of flowers and is anecdotally reported to reproduce abundantly from seed (Bruner, 1967; Prine and Starr, 1971; Carter and Teramura, 1988), but unfortunately quantitative data is lacking. In Arkansas, which lies near the western edge of the naturalized distribution of *L. japonica*, we made several observations that suggested a lack of pollinator service: (1) we saw few pollinators visiting the huge floral displays of *L. japonica*, (2) we noted nectar accumulating until it dripped from the narrow corolla tube and (3) we found few ripe fruits. Based on

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these observations we addressed the following questions: (1) is fruit set of *L. japonica* pollinator limited, (2) what is the fruit set of naturalized populations of *L. japonica* in Arkansas and (3) does fruit set on flowers produced early in the season differ from flowers produced later in the season?

METHODS

To determine if lack of pollination limits natural fruit set, we quantified fruit set on hand-pollinated flowers, flowers with all pollinators excluded and control flowers open to natural pollination. The study site was located in central Arkansas (Faulkner County, 92°27'W 35°10'N) where *Lonicera japonica* begins producing primary shoots in early April. Primary shoots begin to produce paired axillary flowers by early May. In April 1999 we haphazardly selected three shoots of similar size and developmental stage on twenty-five clearly separate individual plants. On each shoot we used cloth laundry clip-tags to mark a group of three successive flowering nodes; each node bears two axillary floral shoots containing two flowers each for a total of 12 flowers marked on each shoot. The tags were prelabeled with the following three treatments and then haphazardly chosen and attached to three shoots per plant: (1) control shoots open to natural pollination, (2) hand-pollinated shoots and (3) pollinator exclusion shoots. Hand pollinated and pollinator exclusion shoots were covered with mesh bags to prevent insect pollination; control shoots were simply tagged and monitored.

Flowers open and anthers dehisce at dusk in *Lonicera japonica*. The morning after opening flowers are white and anthers still contain most of their pollen (Miyake and Yahara, 1998), but by the next day (40 h after opening) flowers fade to yellow and most pollen is gone. The stigmas swell from 1.32 (± 0.019) mm diameter on the first morning to 1.49 (± 0.019) mm at 40 h after opening (based on a sample of $n = 20$ from plants in Faulkner Co., AR). Based on these observations, we chose white flowers to serve as pollen donors and transferred pollen to stigmas of yellow flowers shortly after dawn. Pollen was applied directly from the dehiscing anthers to the receptive stigmas. Because *L. japonica* is xenogamous (Miyake and Yahara, 1998), we collected all pollen from donors that were distant and distinct from the plant receiving the pollen. The mesh bags were removed when all corollas had withered and fallen.

We quantified fruit set on these experimental shoots 1 mo after pollination. We counted the number of fruits produced on each of the marked nodes and calculated fruit set as the number of fruits/number of flowers. A few flowers were damaged during hand-pollination or by herbivores, and these were marked and excluded from fruit set calculations.

To determine if hawkmoths (Lepidoptera, Sphingidae) were visiting the flowers of *Lonicera japonica*, we observed pollinator visits at night and during the day in 1999 at our main study site in central Arkansas (Faulkner Co.). We captured and identified the common insects visiting the flowers; we did not quantify visitation rates, but simply recorded the presence of visitors. Insect visitors were identified to family.

To determine if the natural level of fruit set we documented in central Arkansas was representative of other geographic locations within the state, we quantified natural levels of fruit set in seven additional populations. Four sites were located along a transect running at approximately 35°30'N. From west to east these sites were: (1) Sequoyah Co., OK, (2) Franklin Co., AR, (3) Pope Co., AR, and (4) Crittenden Co., AR. Three additional sites were located 160–200 km. further south at approximately 34°N. From west to east these sites were: (5) Clark Co., AR, (6) Cleveland Co., AR, and (7) Drew Co., AR.

Because changes in the pollinator community potentially impact fruit set and the pollinator pool will change during the season, we quantified fruit set on flowers that opened in

May with those that opened in late June. *Lonicera japonica* has two distinct flowering periods in Arkansas: one when the primary shoots produce axillary flowers in May and a second period, starting about 3 wk after the first period ends, when secondary lateral shoots begin to produce axillary flowers. Because this architectural difference represented early and late formed flowers, we quantified natural levels of fruit set on both primary and secondary shoots at each site ($n = 30$). We selected shoots haphazardly by walking along a fence covered with *L. japonica* stopping to cut one primary and one secondary shoot every 5 m (or a greater distance if we encountered a gap in plant cover). By spacing the sampling sites at 5 m or greater we reduced our chances of sampling two consecutive primary or secondary shoots from the same individual. The primary and secondary shoot were sampled independently and may or may not have been from the same individual plant, as it is not possible to determine where one individual begins and another ends in these tangled masses of vines.

We calculated fruit set after fruit maturation in November or early December by counting all the dried axillary flower stems and all the fruit produced per shoot. More detailed monitoring of fruit set in an experimental garden indicated that dried axillary flower stems remain on the shoots and that few fruits fall or are removed by birds by December (Fowler, 2000).

The fruit set data from the experimental hand pollinations were analyzed with one-way ANOVA following arcsine transformation to improve normality and reduce heteroscedasticity. We graphically present the data on geographic patterns of fruit set and examine the difference in average fruit set on primary and secondary shoots with a paired t -test (paired by geographic location). Although we originally sampled 30 primary shoots and 30 lateral shoots at each site, some sites have a reduced n for the secondary shoots because some haphazardly chosen shoots produced no flowers.

RESULTS

Hand pollinated flowers produced fruit from 78.7% of their flowers, whereas the naturally pollinated control shoots produced fruit from only 17.4% of their flowers ($F = 126.4$, $df = 68$, $P < 0.001$, Fig. 1). As expected for a plant reported to be biotically pollinated and xenogamous, the shoots with pollinators excluded set fruit on only 2.1% of the flowers (Fig. 1).

Fruit set varied geographically, with sites in the southern part of the state (sites 5, 6 and 7 in Fig. 2) having higher fruit set than the more northern sites (sites 1, 2, 3 and 4 in Fig. 2). Fruit set was higher on the secondary shoots produced in June and July than on primary shoots produced in May at every site but one, where they were equal. Average primary shoot fruit set for the seven sites was only $13 \pm 4.1\%$ (mean \pm SE), significantly less than the average for secondary shoots of $23 \pm 6.7\%$ (paired t -test, $t = 3.4$, $df = 6$, $P = 0.014$).

During May we observed insects of three families, Vespidae, Xylocopidae and Syrphidae, feeding from flowers of *Lonicera japonica*; no hawkmoths (Sphingidae) were observed. Carpenter bees (Xylocopidae) were observed taking nectar from corolla tubes and robbing from the base of the corolla, whereas wasps (Vespidae) were only observed cutting longitudinal slits at the base of the corolla tubes and collecting the nectar leaking out. Hover flies (Syrphidae) were observed on stigmas and anthers. During the flowering period of the secondary shoots (late June and July), we observed the same three families of insects as we did in May, with the addition of nocturnal hawkmoths (Sphingidae). Other insect pollinators were seen, but more rarely, and were not captured and identified.

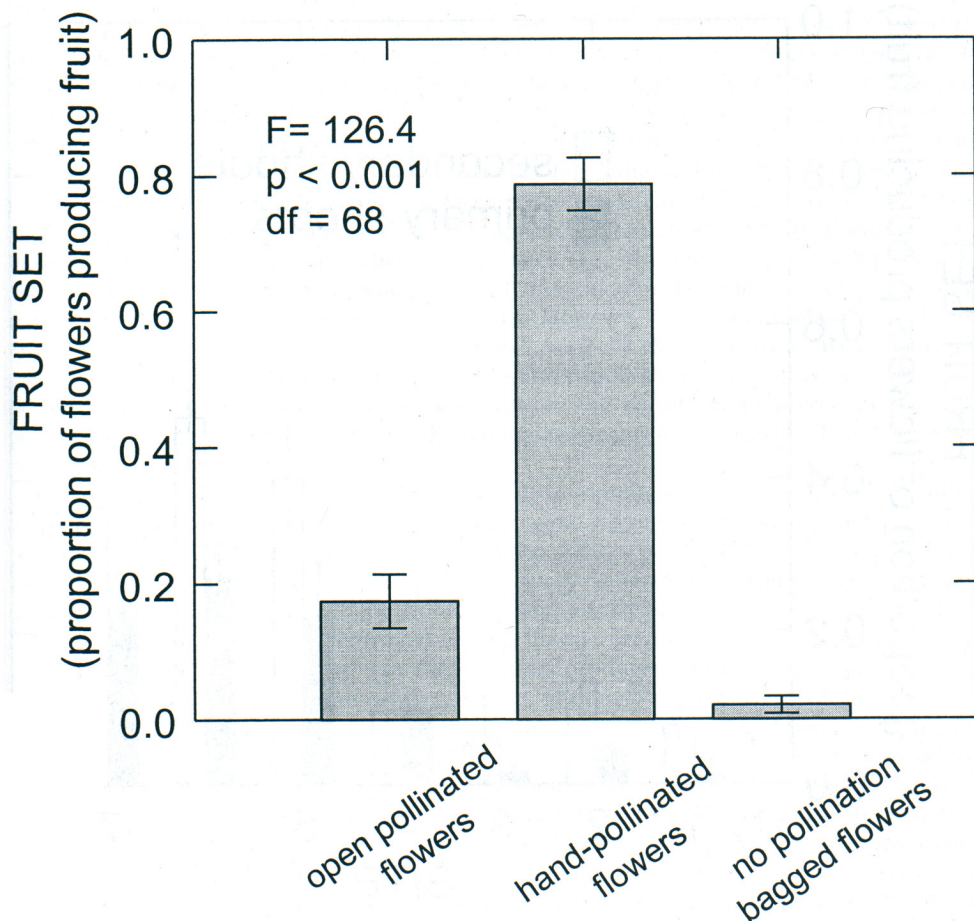


FIG. 1.—The impact of pollination treatment on average fruit set (mean \pm SE, $n = 25$) of *Lonicera japonica*. Each bar represents the average fruit set of 12 flowers per shoot for 25 replicated plants of *L. japonica*.

DISCUSSION

Fruit set on naturalized populations of *Lonicera japonica* is limited by lack of pollination in Arkansas. Fruit set averaged only 13% on primary shoots in seven naturalized populations along the western edge of the region where *L. japonica* has become a pest. The hand-pollination experiment indicated that the plants were capable of increasing fruit set over four fold when flowers were supplied with an abundance of xenogamous pollen. Hand-pollination studies must be interpreted carefully, as it is possible for hand-pollination of a few flowers on a plant to draw on a limited resource pool, resulting in increased fruit set on experimental flowers being offset by lower ovule development on other flowers (Stephenson, 1981). This does not appear to be the case in *L. japonica*. The abundance of flowers produced on the secondary shoots at approximately the same time ovules would be developing on the primary shoots suggests that lack of resources does not contribute to low

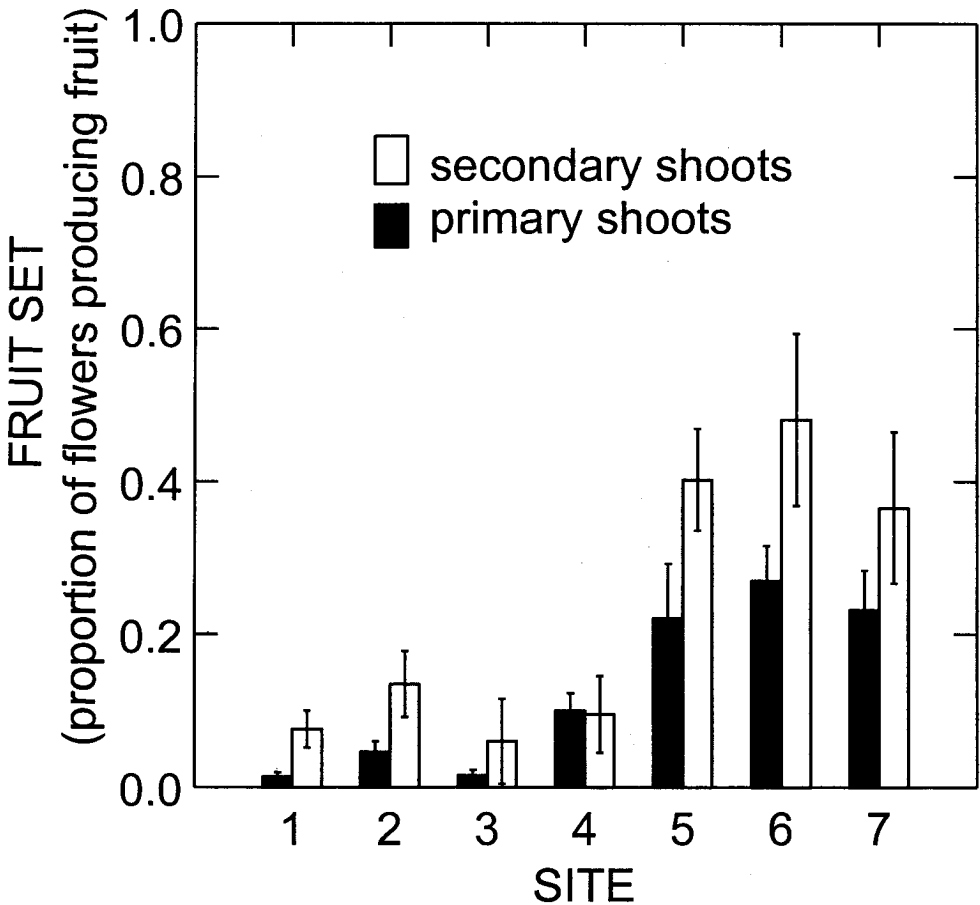


FIG. 2.—Geographic variation in fruit set of flowers produced on primary and lateral shoots (mean \pm SE, $n = 30$). Sites 1 through 4 were located along a transect running at approximately $35^{\circ}30'N$. From west to east these sites are listed here by county and nearest city: (1) Sequoyah Co., Sallisaw, OK, (2) Franklin Co., Ft. Smith, AR, (3) Pope Co., Russellville, AR, (4) Crittenden Co., Village Creek, AR. Three additional sites were located 160–200 km. farther south at approximately $34^{\circ}N$. From west to east these sites were: (5) Clark Co., Arkadelphia, AR, (6) Cleveland Co., Kingsland, AR, and (7) Drew Co., Moticello, AR

fruit set in *L. japonica*. Further, if fertilized ovules were competing for limited resources for development, we would expect the first flowers produced to have the greatest fruit set; we found the opposite pattern.

Pollination could be limited by low visitation rates, visitation by inappropriate insects, or for the xenogamous *Lonicera japonica*, high levels of pollen movement within a clone (geitonogamy). Our observations of insect visitors to *L. japonica* indicate that both low visitation and visitation by inefficient pollinators could be important. Insect activity at *L. japonica* was far below the level observed at the simultaneously flowering exotic Chinese privet (*Ligustrum sinense*) and the native common persimmon (*Diospyros virginiana*) (K. Larson, pers. obs.).

The loss of a specialized pollinator could result in inefficient pollen transfer even when flowers of exotic species are visited by generalized pollinators. The flowers of *Lonicera japonica* are adapted for nocturnal hawkmoth pollination (e.g., anthers dehisce at dusk, corolla tubes are long and narrowly tubular and flowers are pale with a heavy-sweet fragrance), but they remain receptive to pollination during the following day and receive pollen deposited by diurnal bees (Roberts, 1979; Miyake and Yahara, 1998). Miyake and Yahara (1998) found that within *L. japonica*'s native range in Japan both nocturnal hawkmoths and diurnal bees moved pollen to receptive stigmas. However, nocturnal hawkmoths carried pollen farther and were more efficient than bees (i.e., the ratio of pollen deposited to pollen removed was greater for hawkmoths). Unfortunately, they did not include data on fruit set, so we cannot compare results directly. However, our observation that no hawkmoths visited the primary flowers of *L. japonica*, suggests that, in central Arkansas, *L. japonica* is limited to the services of more generalized pollinators during its May flowering period. Our observation of nectar accumulating in the corolla tubes is consistent with a lack of hawkmoth services, as hawkmoths are mainly nectar foragers, while bees forage for pollen only or both nectar and pollen.

The lack of hawkmoth pollination could result in a reduction in pollen transfer leading to pollen limitation, but it could also increase geitonogamy. Bees that carried pollen to receptive *Lonicera japonica* stigmas in Japan did not carry pollen as far as hawkmoths (Miyake and Yahara, 1998). Lack of xenogamous pollen exchange is a strong possibility in our study areas because a single genetic clone can be quite large.

Nocturnal hawkmoths were observed visiting flowers produced on the secondary shoots in late June and July. We found that these flowers produced significantly more fruit than flowers produced earlier on the primary shoots, although still relatively low at only 23%. This suggests that at least part of the problem for *Lonicera japonica* in Arkansas is a matter of timing, with flowers on the primary simply opening before efficient pollinators are active.

We found only two other studies that have examined the relationship established between invasive exotics and the native pollinator community. Parker (1997) also found low visitation rates by native insects in her study on scotch broom (*Cytisus scoparius*), an invasive exotic in the Pacific Northwest. Scotch Broom is self-incompatible and dependent on insects for pollen transfer and, like *Lonicera japonica*, significantly increased fruit set when hand-pollinated. In contrast, Brown and Mitchell (2001) found that the exotic purple loosestrife (*Lythrum salicaria*) is heavily visited by insect pollinators and shares and potentially competes for pollinators with a native congener. Purple loosestrife poses a threat to the native *Lythrum alatum* through the transfer of interspecific pollen that can clog stigmas or styles and, thus, reduce fruit set.

For biotically pollinated invasives, the relationship established with native pollinators can impact the rate at which they spread through seedling establishment. For example, simulation models indicated that the rate of spread of the invasive scotch broom could be increased with increased pollination (Parker, 1997). In addition, Rejmánek and Richardson (1996) found that species of pine with large consistent seed crops were more likely to be invasive than those with smaller more variable seed crops. It seems clear that seed production can impact invasiveness, and even though self-incompatible biotically pollinated species are underrepresented as invaders (Daehler, 1998), they do occur; their relationships with native pollinators need more thorough investigation.

Lonicera japonica's capacity for colonization of space through morphologically plastic and rapid vegetative growth is well documented (Nuzzo, 1997; Schweitzer and Larson, 1999; Larson, 2000), but to develop effective management plans it is also critical to understand its potential for establishment through seeds (Hiebert, 1997). We found fruit set ranging

from 0% to 36% at different geographic sites in Arkansas and Oklahoma, and only one other empirical study which documented *L. japonica* fruit set. Leatherman (1955) found a fruit set of 56% in eastern Tennessee. With so few studies, it is not clear if there are predictable geographic patterns of *L. japonica* fruit set or simply high site to site and/or year to year variation. Until more data are available, management of *L. japonica* populations must proceed without information on seed production and establishment that would allow better predictions of its capacity for colonization and reinfestation following removals.

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