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Author(s): Hema Somanathan, Renee M. Borges, V. Srinivasa Chakravarthy
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Does Neighborhood Floral Display Matter? Fruit Set in Carpenter Bee-pollinated *Heterophragma quadriloculare* and Beetle-pollinated *Lasiosiphon eriocephalus*¹

Hema Somanathan, Renee M. Borges²
Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India
and
V. Srinivasa Chakravarthy
Department of Electrical Engineering, Indian Institute of Technology, Chennai 600036, India

ABSTRACT

Fruit set is pollen-limited in the self-incompatible tree *Heterophragma quadriloculare* (Bignoniaceae), pollinated by long-distance flying carpenter bees, and in the self-compatible shrub *Lasiosiphon eriocephalus* (Thymeleaceae), pollinated by weak-flying, sedentary beetles. We studied a single *H. quadriloculare* population over high and low flowering years and found no difference in bee visitation rates between these years. For *H. quadriloculare*, neighborhood floral display did not make a significant contribution to reproductive success. We investigated dense and sparse *L. eriocephalus* populations in the same year. In the low density *L. eriocephalus* population, individual floral displays were higher than in the dense population, yet reproductive success was low, indicating that plant isolation was a major factor influencing fruit set. This result was due to the extremely low number of beetles per plant and per flower in this population. In the dense *L. eriocephalus* population, although the displays of individual neighbors were smaller and plants were closer, neighborhood floral display did not contribute significantly to reproductive success, whereas the effect of individual floral display was ambiguous. Species with self-incompatible rather than self-compatible breeding systems are expected to experience neighborhood effects on reproductive success; however, at the spatial scale and floral display levels of plants in this study, only individual floral display affected fruit set in *H. quadriloculare*, whereas neither individual nor neighborhood display influenced fruit set in *L. eriocephalus*. Therefore, pollinator type, pollinator behavior, and plant population isolation, rather than breeding system alone, will determine if neighborhood floral display affects fruit set.

Key words: cantharophily; India; nearest-neighbor analysis; plant spacing; scale-based clustering; seasonal cloud forest; Western Ghats.

Variation in reproductive success within and across plant populations is largely attributed to differences in pollen limitation (Feinsinger et al. 1986, Kunin 1993, Ågren 1996, Dudash & Fens-ter 1997) and/or resource limitation (Stephenson 1980, Niesenbaum 1993). The spatial distribution of the population can influence reproductive success through the response of pollinators to the density and floral display of conspecific plants (Jennersten 1988; Feinsinger et al. 1991; Meagher 1991; House 1992, 1993; Jennersten & Nilsson 1993; Kunin 1993; Aizen 1997; Cresswell 1997; Kunin 1997; Ghazoul et al. 1998) or of heterospecific plants competing for the same pollinators (McLernon et al. 1996; Chittka & Schurkens 2001, Ghazoul 2002). Reproductive success can vary across species due to differences in the ability of their pollinators to move between plants. Therefore, reproductive success of isolated plants could be jeopardized by reduced pollinator visits (House 1992, Kunin 1993, Lamont et al. 1993), especially if the pollinators are weak-flying rather than long-distance fliers (Law & Lean 1999). The effect of neighborhood floral display on reproductive success will therefore depend on pollinator responses to the density of the display. Furthermore, species with self-incompatible rather than self-compatible breeding systems are more likely to face reproductive constraints imposed by the spatial distribution of conspecifics in the neighborhood because pollen transfer between conspecific plants is not essential for successful mating in the latter (Beattie 1976, Feinsinger et al. 1991). Pollination failure is therefore less likely to occur in self-compatible and autogamous species (Larson & Barrett 2000). Even in self-compatible species, however, there may be a requirement for pollinator visitation to transfer

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² Corresponding author; e-mail: renee@ces.iisc.ernet.in; Fax: 091-080-3601428.
self-pollen (Augspurger 1980, Schuster et al. 1993) and isolated plants may not be able to attract pollinators to perform this function. Impacts of plant spacing are more complex and ambiguous than previously thought (Wilcock & Neilland 2002) and much more empirical evidence is needed to understand both pattern and process.

In this study, we examined the effects of (1) distance to nearest neighbor and (2) neighborhood floral display on pollinator visitation and reproductive success of plants within natural populations for two plant species with different breeding systems and pollinator flight abilities. Heterophragma quadriloculare (Bignoniaceae) is an obligately self-compatible tree pollinated by the strong-flying nocturnal carpenter bee Xylocopa teniscapa (Somanathan & Borges 2001), whereas Lasiosiphon eriocephalus (Thymeleaceae) is a self-compatible shrub pollinated by weak-flying sedentary nitidulid beetles (see Results). The effect of individual floral display on fruit set in H. quadriloculare has been reported previously (Somanathan & Borges 2001). Here, we examined the role of neighborhood floral display on fruit set in H. quadriloculare, whereas in L. eriocephalus we examined the effect of both individual floral display and of neighborhood floral display on fruit set. We investigated the effect of neighborhood floral display on reproductive success at different spatial scales using a novel scale-based clustering approach. We compared fruit set of H. quadriloculare in high and low flowering years and of L. eriocephalus in a high- and low-density population.

METHODS

STUDY SITE AND SPECIES.—This study was conducted in the Bhimashankar Wildlife Sanctuary (19°21’–19°11’N, 73°31’–73°37’E; 900 m elev.) situated in the Western Ghats of Maharashtra, India. Heterophragma quadriloculare and L. eriocephalus are common along the edges of the mountain crest seasonal cloud forest and in open grassy patches. Heterophragma quadriloculare flowers are bisexual, white, large, fragrant, occur in terminal panicles, open at night, and last ca 12 hours. Flowering is from February to early April. Fruits are capsules and seeds are wind-dispersed and vary in number from 200 to 250/capsule. We studied this species in 1995 and 1996. Lasiosiphon eriocephalus flowers from early December to March. The flowers are yellow, produced in terminal inflorescences, and last four days. Flowers are protandrous, open in the evenings, and are sweetly fragrant, with the stigma enclosed in the corolla tube and anthers nearly exerted. Pollination is by relatively sedentary nitidulid beetles that remain inside the flowers for extended durations. During the day, the beetles feed on pollen from anthers and at night they move to the base of the corolla during which time they pollinate flowers. The fruit is single-seeded and wind-dispersed. Lasiosiphon eriocephalus was studied during a single flowering season from December 1995 to March 1996.

Heterophragma quadriloculare is known to be obligately self-incompatible (Somanathan & Borges 2001). To examine the breeding system of L. eriocephalus, we performed hand-pollination experiments to compare fruit set following self- and cross-pollination (see sample sizes later). To examine the effect of beetles on fruit set in L. eriocephalus, we added beetles to inflorescences, which were then enclosed in paper bags.

MAPPING STUDY POPULATIONS.—Within an area of 4.5 km², we mapped the spatial locations of plants for both species to the nearest centimeter. Only H. quadriloculare trees greater than 30 cm GBH (girth at breast height; N = 175) were mapped, since trees with lower girths did not flower. Using the spatial coordinates for plant positions, we calculated the distances to the nearest flowering neighbor for all individuals of both species. Individual trees could be separated by a few meters or by as much as 406 m from their nearest neighbor. In L. eriocephalus, we studied a high-density (HD; N = 131) and a low-density (LD; N = 37) population located ca 0.5 km apart, within the same contiguous area of crest forest. In the LD site, which was close to human habitation, plants were relatively more isolated due to selective harvesting (for fish poisons prepared from their roots) while the HD site was relatively undisturbed. For both species, population spatial dispersion was characterized using a nearest-neighbor index (Clark & Evans 1954).

FLOWERING PHENOLOGY, POLLINATION, AND FRUIT SET.—In H. quadriloculare, we monitored flower production every fourth day for all focal flowering trees (N = 175 trees, 1995; N = 167, 1996) and counted the total number of open flowers and buds that were large enough to open before the next sampling date. At the end of flowering, we counted the absolute number of immature fruits for each focal tree and estimated fruit set as the percentage of flowers setting fruit. We observed nightly carpenter bee visits to H. quadriloculare (N = 10 trees, 1995; N = 11 trees, 1996) throughout the flow-
ering season (for details see Somanathan & Borges 2001).

In *L. eriocephalus*, at the start of the flowering season, for each plant in both populations (*N* = 131, HD; *N* = 37, LD), we counted the number of inflorescences on a few branches and multiplied the mean number of inflorescences/branch by the total number of branches on the plant to estimate the total number of inflorescences on a plant. We estimated the total number of flowers for each plant by calculating the mean number of flowers and buds/inflorescence at four-day intervals throughout the flowering season for a sample of inflorescences chosen randomly (*N* ≥ 30) and by multiplying this by the estimated total number of inflorescences. We refer to the total number of flowers produced during the flowering season as the number of flowers/plant. At the end of flowering, we harvested inflorescences (*N* ≥ 35) from each plant and estimated fruit set/inflorescence as the percentage of flowers setting fruit. We estimated fruit set for entire plants by multiplying fruit set/inflorescence by the total number of inflorescences/plant. At the time of quantifying flower production, we also estimated beetle numbers/inflorescence on plants in both sites at four-day intervals by looking into inflorescences (flowers were readily accessible) and counting the number of beetles in flowers. We recorded the time beetles spent on a plant by making them (*N* = 15) with paint and periodically checking for their presence.

**Scale-based clustering.**—The relationship between fruit set and neighborhood floral display was determined using a scale-based clustering approach (Chakravarthy & Ghosh 1996) in which neighborhoods of different spatial scales were examined around individual plants. This approach was applied to avoid the problems of nonindependence of data points and pseudo-replication inherent in scale analysis by generating nonoverlapping neighborhoods for individual focal plants in the population. The difference between scale-based clustering and other clustering techniques is the use of an explicit scale parameter, σ. In traditional approaches, the number of clusters in the data is arbitrarily chosen beforehand. In scale-based clustering, however, the data are clustered at a given scale, σ, which determines the number of clusters. The scale parameter σ (also referred to as neighborhood size after this section) is taken to be of the order of the minimum distance between conspecific plants in the population. Accordingly, a large value of σ results in a small number of clusters and a small σ yields a large set of clusters. We begin by randomly assigning a large number of cluster centers or centroids in the population. The algorithm that is used in the iterations is:

\[
\Delta m_j = \eta \exp(-\|x_p - m_j\|^2/(\sigma^2))(x_p - m_j) \tag{1}
\]

where *x*<sub>p</sub> is the location of individual plants, *m*<sub>j</sub> is the cluster center, Δ*m*<sub>j</sub> is the location of the *j*th centroid, and η is the step size for iterations of equation (1). This algorithm is iterated on all the centroids. Each centroid is adjusted according to equation (1) by presenting all data points, *x*<sub>p</sub>. Note that due to the exponential term, only points that are close (relative to a scale of σ) to a given centroid have significant influence on the centroid. In this process, nearby (relative to a scale of σ) centroids may merge; duplicate centroids are eliminated when they merge. Only a few clusters remain as the iterations progress. This final number of clusters depends on the scale parameter and the data set. The iterations are repeated with increasing values of the scale parameter σ. As σ is increased, neighboring centroids tend to merge and yield fewer clusters. The relationships are perceived to be salient if they are stable over a range of scale values (σ). For *H. quadriloculare*, we used σ values that ranged from 10 to 300 m. For the high-density *L. eriocephalus* population, we used σ values from 2 to 13 m and for the low-density population, we used σ values from 8 to 40 m since this population was very isolated and we obtained a reasonable number of clusters (at least three) using these scales. Larger values of σ yielded less than three clusters and these were avoided since the parameters of interest were bound to be correlated at these levels. Using partial correlation coefficients, the mean values of fruit set of focal plants in each cluster at each neighborhood size were related to the mean floral display of all neighbors within the cluster while controlling for the effect of mean individual floral display of focal plants. Since member plants in each cluster are not identical for different values of σ, the data sets at each cluster or neighborhood size can be considered independent of each other.

**RESULTS**

**Breeding system and pollen limitation in *L. eriocephalus.**—**Fruits were not produced in bagged inflorescences from which pollinators were excluded (*N* = 35). Hand-pollination using self-pollen and cross-pollen yielded similar fruit set in both sites (selfing—HD site: \(x \pm SD = 69.83\% \pm 9.79\%\), *N*
TABLE 1. Comparison of key population characters between years in Heterophragma quadriloculare and between populations in Lasiosiphon eriocephalus.

<table>
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<td>( \bar{x} \pm SD )</td>
<td>( \bar{x} \pm SD )</td>
<td>( z )</td>
<td>( z )</td>
</tr>
<tr>
<td><strong>Heterophragma quadriloculare</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Percent fruit set</td>
<td>11.89 ± 12.27</td>
<td>13.85 ± 16.48</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Beetles/plant</td>
<td>0.02 ± 0.01</td>
<td>0.02 ± 0.03</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Flowers/tree</td>
<td>714.04 ± 64.53</td>
<td>307.14 ± 26.16</td>
<td>-7.40***</td>
<td>-7.40***</td>
</tr>
<tr>
<td>Nearest-neighbor distance (m)</td>
<td>26.53 ± 51.41</td>
<td>25.09 ± 44.20</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>Index of dispersion, ( R )</td>
<td>0.32**</td>
<td>0.32**</td>
<td></td>
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<tr>
<td><strong>Lasiosiphon eriocephalus</strong></td>
<td>Low density site</td>
<td>High density site</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent fruit set</td>
<td>1.38 ± 1.01</td>
<td>10.33 ± 6.59</td>
<td>-7.94***</td>
<td>-7.94***</td>
</tr>
<tr>
<td>Beetles/plant</td>
<td>46.34 ± 65.23</td>
<td>796.85 ± 1454.90</td>
<td>-4.36***</td>
<td>-4.36***</td>
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<tr>
<td>Beetles/flower</td>
<td>0.001 ± 0.0001</td>
<td>0.05 ± 0.035</td>
<td>-9.53***</td>
<td>-9.53***</td>
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<tr>
<td>Flowers/plant</td>
<td>32.899 ± 40.930</td>
<td>13,864 ± 18,142</td>
<td>-9.07***</td>
<td>-9.07***</td>
</tr>
<tr>
<td>Nearest-neighbor distance (m)</td>
<td>11.56 ± 13.53</td>
<td>2.29 ± 1.38</td>
<td>-7.17**</td>
<td>-7.17**</td>
</tr>
<tr>
<td>Index of dispersion, ( R )</td>
<td>0.62**</td>
<td>0.35**</td>
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** \( P \leq 0.001, *** \( P \leq 0.0001, z \) = \text{Mann–Whitney} \ U\text{-test statistic}; \ R = \text{Clark and Evans index of dispersion}; a N = 208 bouts on 10 trees in 1995, 149 bouts on 11 trees in 1996.

= 4 plants [133 flowers], LD site: 76.42% ± 7.97, \( N = 3 \) plants [133 flowers], \( t = -0.95 \), df = 5, \( P > 0.05 \); outcrossing—HD site: 58.71% ± 10.64, \( N = 4 \) plants [110 flowers], LD site: 54.40% ± 3.04, \( N = 3 \) plants [110 flowers], \( t = 0.66 \), df = 5, \( P > 0.05 \). Selfing rather than outcrossing, however, produced higher fruit set for unknown reasons (selfing—72.65% ± 9.03, \( N = 7 \) plants pooled across sites [266 flowers]; outcrossing—56.87% ± 8.06, \( N = 7 \) plants pooled across sites [220 flowers], \( t = 3.45 \), df = 12, \( P < 0.005 \). Similar results were obtained in a comparison of selfing and outcrossing within each site. The fruit set following hand-pollination was markedly higher than fruit set following natural pollination on marked flowers (HD site: 4.44%, LD site: 0%, \( N = 45 \) marked flowers in each site), indicating pollinator limitation. Similar low values of fruit set were obtained following natural pollination on unmarked flowers (Table 1). When the number of beetles/inflor russcence was enhanced to 8 from the ratio observed naturally, which always was less than 4, and the inflorescences were bagged, fruit set was much higher in these inflorescences than in control inflorescences that were left open for natural pollination on the same plant (Mann–Whitney U-test, \( z = -5.20 \), \( P < 0.0001 \), \( N = 18 \)). Nine of the 15 marked beetles were relocated after 24 hours on the same plant, while on the fourth day, 3 of the marked beetles remained on the plant, indicating that beetles remained on individual plants for extremely long durations.

**Population spatial distributions.**—In *H. quadriloculare*, the mean distance to nearest flowering neighbor was similar in both years and the population was significantly clumped (Table 1). The density of *L. eriocephalus* in the LD site was lower than the density in the HD site by a factor of 59. Plants were clumped in both sites, but were more clumped in the HD site (Table 1). In the LD site, neighbors were more isolated and the nearest flowering neighbor was on average five times more distant in the LD site than in the HD site (Table 1).

**Individual floral display and pollinator visitation.**—In *H. quadriloculare*, flower production was significantly higher in 1995 than in 1996, yet carpenter bee visitation rates and fruit set were similar (Table 1). *Lasiosiphon eriocephalus* plants in the LD site produced more than twice the number of flowers than plants in the HD site (Table 1); however, plants in the HD site had considerably more fruit set (7.8 times), mean number of beetles/plant (17.9 times), and mean number of beetles/flower (48 times) than plants in the LD site (Table 1). For *L. eriocephalus*, individual fruit set and floral displays were positively correlated in the HD site (\( N = 131 \) plants), but not in the LD site (\( N = 37 \) plants; HD site: Spearman's rank correlation coefficient \( r_s = 0.27, P < 0.0001 \); LD site: \( r_s = 0.19, P > 0.05 \; \text{but see later} \). Beetles/flower and flower number were positively correlated only in the HD site (HD site: Spearman's rank correlation coefficient \( r_s = 0.27, P < 0.0001 \); LD site: \( r_s = 0.19, P > 0.05 \; \text{but see later} \).
0.30, \( P < 0.001, N = 131; \) LD site: \( r_i = 0.02, P > 0.05, N = 37 \). In both sites, however, beetles/flower and fruit set were positively correlated (HD site: Spearman’s rank correlation coefficient \( r_i = 0.71, P < 0.001, N = 131; \) LD site: \( r_i = 0.52, P < 0.001, N = 37 \)), indicating that beetle numbers translate directly to fruit set.

**Fruit set, distance to nearest neighbor, and floral display.**—We examined the influence of the floral display of the nearest neighbor to individual focal plants on fruit set of the focal plants. To avoid pseudo-replication, we chose a subset of focal plants such that their nearest neighbors were not shared by other focal plants (H. quadriloculare: \( N = 119, 107 \) [1995, 1996]; L. eriocephalus: \( N = 93, 29 \) [HD, LD]). In H. quadriloculare, individual floral display explained a significant amount of variation in fruit set in both years, but when floral display of the nearest neighbor was included into the regression analysis, their combined effect on fruit set was not significant. In L. eriocephalus, individual floral display combined with nearest neighbor floral display was not significantly related to fruit set in both HD and LD sites. The lack of a significant relationship between fruit set and individual floral display differs from the positive relationship that was seen when all plants were included (see earlier results).

Since nearest neighbors could be located at any distance from focal plants, we also examined the relationship between fruit set and distance to nearest neighbor using the same subset of focal plants. We found no relationship between these parameters for either L. eriocephalus or H. quadriloculare in either 1995 or 1996.

**Scale-based clustering in H. quadriloculare.**—Fruit set in H. quadriloculare was unrelated to floral display on neighbors after controlling for individual floral display for all neighborhood sizes. The average fruit set/plant/cluster for each neighborhood size did not show any pattern with increasing values of neighborhood size (Fig. 1a, b); however, the mean sum of flowers/cluster increased monotonically with increasing neighborhood size (Fig. 1a, b).

**Scale-based clustering in L. eriocephalus.**—In the HD site, for all increments in neighborhood size there was no correlation between fruit set of focal plants and floral display of neighbors after controlling for individual floral display. We did not proceed with larger neighborhood sizes because they yielded extremely low numbers of clusters. In both populations of L. eriocephalus, the average fruit set/cluster for different neighborhood sizes did not show any pattern, although the mean sum of flowers/cluster increased monotonically with increments in neighborhood size (Fig. 1c, d).

**DISCUSSION**

Earlier studies demonstrated that hand-pollination with a pure load of outcrossed pollen resulted in almost 100 percent fruit set in H. quadriloculare, indicating pollen limitation in the species (Somnathan & Borges 2001). Individual floral display was negatively related to fruit set in H. quadriloculare because carpenter bees visited a greater number of flowers on trees with a large floral display which resulted in the transfer of incompatible self-pollen to stigmas (Somnathan & Borges 2001). In the present study, we also found that hand-pollination significantly increased fruit set in L. eriocephalus compared to natural pollination, as did artificially enhancing the number of beetles inside bagged inflorescences, again indicating pollen limitation. The strong positive correlation between fruit set and beetles/flower coupled with the low numbers of beetles on plants at the low density site indicate that plants were even more pollen-limited than at the high density site. In L. eriocephalus, individual floral display at the high density population had a variable influence on fruit set depending on whether all or a subset of plants were analyzed (positive results were obtained when all plants were considered; this result was nonsignificant when only a subset of plants with nonoverlapping nearest neighbors were analyzed). In the low density site, we did not detect any association between fruit set and individual display. This lack of a relationship between fruit set and individual floral display may be because L. eriocephalus is a mass-flowering species that produces several thousand flowers on individual plants, which can result in saturation of available pollinators visiting these plants. Unlike H. quadriloculare, for which floral longevity is only 24 hours (Somnathan & Borges 2001), the floral longevity of L. eriocephalus is four days. The large floral display and greater floral longevity of L. eriocephalus may result from a strategy to compensate for reduced pollinator availability in this seasonal cloud forest, as has been found for several high elevation and cloud forest plants (Seres & Ramirez 1995, Blionis et al. 2001, Medan 2003).

Although fruit set is apparently pollen-limited
in both species, proximity to nearest neighbor did not influence fruit set in either species, at least at the scale of this study. Since most trees in the H. quadriloculare population (all except six) flowered in both years, population size and nearest neighbor distances did not vary much between the two years. For this reason, we could not test the effect of increased spatial isolation on fruit set in this species; however, low flowering of H. quadriloculare in 1996 provided an opportunity to examine the effect of natural variation in floral density on fruit set. The absence of an effect of floral neighborhood density during the low flowering year shows that at this level of a natural reduction in floral display size, fruit set did not decline proportionally in this species. The lack of a neighborhood effect in H. quadriloculare is probably because carpenter bees are strong-flying insects capable of long-distance flight; at least two Indian xylocopids are known to fly up to 20 km (Kapil & Daliwahl 1969). Furthermore, they are probably trapliners that are able to remember locations of foraging points (Janzen 1971, Thomson 1996). They are therefore capable of making the mandatory inter-tree pollinating flights at the scale of spatial separation of trees in this population. One tree in our study population was naturally isolated from the nearest pollen source by ca 330 m, but set fruit in both years. Hence in H. quadriloculare, we expect that although cross-pollination is essential for fruit set,
the species can cope with some degree of spatial isolation because of the long-distance movement potential of its pollinator.

_Lasioisiphon eriocephalus_, on the other hand, is pollinated by a relatively weak-flying beetle with a poor capacity for between-plant movement. Pollination is therefore expected to increase when inter-plant distances are small and/or densities of flowers in the neighborhood are high. We, however, found no evidence of a neighborhood effect on fruit set in either the high- or the low-density population of _L. eriocephalus_ at all spatial scales investigated. Even though beetles fly only small distances between plants, this lack of a neighborhood effect may be attributed to self-compatibility and/or the response of the pollinators to the specificity of a signal despite its low density (Borges et al. 2003); however, other studies on beetle-pollinated plants (e.g., _Asclepias syriaca_) have shown that beetle densities are positively related to patch size and are primarily a function of beetle movement between host plants (Englund 1993, Matter 1997). Although plants at our low-density site had a larger floral display, the greater isolation between plants at this site probably resulted in extremely low beetle numbers and low fruit set compared to the high-density site. Extreme pollination failure has been reported in isolated populations (Lamont et al. 1993, Groom 1998) and other studies have shown that reproductive success can decline at low population densities (Feinsinger et al. 1991, Ghazoul et al. 1998). The high- and low-density sites in _L. eriocephalus_ are part of the same contiguous crest forest separated by a distance of just 0.5 km, and thus the differences in fruit set are not likely to be due to environmental variables not accounted for in this study.

Does breeding system influence the effect of plant spacing on fruit set? Effects of neighbor density or neighborhood floral density on reproductive success due to variation in pollinator visitation have been largely demonstrated in obligately self-incompatible species, including dioecious species (Silander 1978; Thomson 1981; Feinsinger et al. 1986; House 1992; Kunin 1992, 1993; Fritz & Nilsson 1994; Ágren 1996; Ghazoul et al. 1998; Hendrix & Kyhl 2000; Somanathan & Borges 2000; Knight 2003). In our study, we found fruit set in the self-incompatible species _H. quadriloculare_ to be influenced by individual floral display while neighborhood floral display had a negligible effect if any. Low-density plant populations that did not show reduced pollination success were nearly all populations of self-compatible species (Schmitt 1983; Feinsinger et al. 1986, 1991; Klinkhamer & de Jong 1990; Kunin 1997). Declines in fruit set following fragmentation, however, affected both self-compatible and self-incompatible species, indicating that breeding system alone does not account for the effects of spacing of plants on reproductive success (Aizen & Feinsinger 1994). Our study shows marked decline in fruit set due to spatial isolation of _L. eriocephalus_ plants in the low-density site and pollinator number and visitation rates are implicated in this decline even though the species is self-compatible. Despite self-incompatibility, however, _H. quadriloculare_ can tolerate some level of spatial isolation primarily because its pollinators are carpenter bees that can negotiate large distances between pollen sources. Therefore, the scale of individual plant isolation, the scale of population isolation, pollinator type, pollinator behavior, floral display intensity, and breeding system need to be considered together to determine the degree to which neighborhood influences reproductive success.

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**LITERATURE CITED**


Special Section


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