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POPULATION SIZE, POLLINATOR LIMITATION, AND SEED SET IN THE SELF-INCOMPATIBLE HERB *LYTHRUM SALICARIA*¹

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Abstract. In reward-producing animal-pollinated plants, small populations are likely to be less attractive to pollinators than large populations. The likelihood of pollinator limitation of seed production should therefore increase with decreasing population size. I documented the number of flowering plants and plant fecundity in 18 populations of the self-incompatible, tristylous herb *Lythrum salicaria* within an archipelago in northern Sweden in two consecutive years. To test the hypothesis that a positive correlation between population size and seed set is due to a higher degree of pollinator limitation in small than in large populations, I performed supplemental hand-pollinations in eight (1993) and 13 (1994) of the study populations. To test the hypothesis that common mating types are more likely than rare types to experience inadequate pollination, I compared the natural level of seed production and the effect of supplemental pollination in different style morphs in the five populations in which ≥ 10 plants per morph were included in the experiment. There was no significant correlation between population size and plant size in terms of number of floral shoots or number of flower-producing leaf nodes per shoot. However, there was a positive relationship between population size and seed production per flower and between population size and total seed number per plant. In contrast, there was no significant correlation between population size and seed production of flowers that had received supplemental pollination. In both years, the difference in mean seed production per flower between hand-pollinated flowers and controls decreased with increasing population size. In two of five populations, the effect of supplemental pollination differed significantly among morphs. Seed production was more likely to be pollinator limited in long-styled than in short-styled plants, but this difference could not be attributed to a preponderance of the long-styled morph in the studied populations. Results of the supplemental hand-pollinations indicate that the positive correlation between population size and seed production is a function of insufficient pollen transfer in small populations. Additional demographic studies are needed to determine to what extent the reduced level of seed production in small populations limits the growth of young populations, and to what extent it may threaten the local persistence of *L. salicaria*.

Key words: *Lythrum salicaria*; plant–pollinator interaction; pollinator limitation; population size; seed production; self-incompatibility; tristily.

INTRODUCTION

The size of a plant population is expected to affect its demographic and genetic properties for several reasons. With decreasing size, the significance of stochastic processes for the dynamics and genetic composition of a population is expected to increase (e.g., Lande 1988, Barrett and Kohn 1991, Menges 1992, Ellstrand and Elam 1993, Schemske et al. 1994). Moreover, population size may affect interactions between the plant and its flower visitors (Handel 1983, Sih and Baltus 1987), herbivores (Stanton 1983, Kareiva 1985, Bach 1988), and pathogens (Jennersten et al. 1983, Carlsson and Elmquist 1992, Burdon et al. 1995). In particular, it has been suggested that the mutualism between plants and pollinators is likely to be disrupted in small, isolated populations and that this may reduce plant reproductive success and, ultimately, the probability of population persistence (McKey 1989, Rathcke

and Jules 1993, Aizen and Feinsinger 1994a, Olesen and Jain 1994). A positive correlation between population size and plant fecundity has been reported both in animal-pollinated (Lamont et al. 1993, Widén 1993) and in wind-pollinated (Nilsson and Wästljung 1987) species, but there are few experimental studies examining the processes influencing the relationship between population size and plant reproductive output (Jennersten 1988, Heschel and Paige 1995).

Several factors could (in isolation or in combination) produce a positive correlation between population size and plant fecundity. First, small populations of animal-pollinated plants are likely to be less attractive to pollinators than large populations (Sih and Baltus 1987). As a consequence, pollinator visitation may be lower, and the degree to which seed production is limited by pollinators may be higher, in small than in large populations (cf. Jennersten 1988). In this situation, the positive correlation between population size and plant fecundity is expected to disappear if plants are experimentally pollinated by hand. Second, stochastic pro-

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cesses in small populations of self-incompatible plants may result in the loss of mating types from the population, and in skewed relative frequencies of the different mating types (e.g., Heuch 1980, Les et al. 1991, Byers and Meagher 1992). In this case, the availability of compatible pollen may become limiting for seed production for a large fraction of the plants in the population (Thien et al. 1983, Aspinwall and Christian 1992, DeMauro 1993, Reinartz and Les 1994). If the frequencies of different mating types are highly skewed, then insufficient transfer of compatible pollen is expected to have the most pronounced effects on seed production in the most common mating type. Seed production in rare mating types is not expected to suffer from insufficient deposition of compatible pollen, unless pollinator visitation per se is limiting. Third, because the level of inbreeding may be higher in small than in large populations, even under random mating (Falconer 1989, Barrett and Kohn 1991), inbreeding depression could reduce plant fecundity or offspring quality in small populations to a level below that observed in large populations (Menges 1991, Aizen and Feinsinger 1994a, Ouborg and van Treuren 1994, Heschel and Paige 1995). If a positive correlation between population size and plant fecundity is an effect of among-population variation in the level of inbreeding, then this relationship is not expected to disappear if local pollen is used in supplemental hand-pollinations, but could disappear if pollen from other populations is used.

In this study, I document the relationship between population size and plant fecundity in the self-incompatible, tristylous herb *Lythrum salicaria* within an archipelago in northern Sweden in two consecutive years. Like other tristylous species, *L. salicaria* produces three different mating types, the long-styled (L), the mid-styled (M), and the short-styled (S), that can be identified readily in the field based on floral morphology. To test the hypothesis that a positive correlation between population size and seed set is due to a higher degree of pollinator limitation in small than in large populations, supplemental hand-pollinations were performed in eight (1993) and 13 (1994) of the populations studied. In all populations (except two that each had a single flowering plant), the supplemental pollinations were performed using cross pollen from within the population. Thus, if a relationship between population size and seed production is due to differences in the level of inbreeding between populations of different size, then this relationship should not be affected by the supplemental pollination. To test the hypothesis that common mating types are more likely to suffer from inadequate pollination than are rare mating types, I compared the seed production of open-pollinated flowers and the effects of supplemental pollination in different style morphs in the five populations in which at least 10 plants per morph were included in the experiment. All five populations were characterized by a

deficiency of the mid-styled morph (frequency range 0.01 to 0.24). If seed production is limited by the efficiency of compatible pollen transfer, and if this efficiency is determined by the relative frequencies of the three mating types, then seed production should be higher and less affected by supplemental pollination in the M morph than in the other morphs, because the M morph has proportionately more legitimate mates in these populations.

MATERIALS AND METHODS

The species and study site

The purple loosestrife, *Lythrum salicaria* L. (Lythraceae), is a perennial herb with a heteromorphic incompatibility system. It produces three floral morphs that differ in the relative positioning of stigma and anthers in the flowers. In each flower of a given morph, two anther whorls are produced at levels corresponding to the positions of the stigmas in the flowers of the other two morphs (reciprocal herkogamy). Controlled crosses performed on plants from the area of this study (J. Ågren, unpublished data) and from other areas (Darwin 1877, Stout 1923, O'Neil 1994) have shown that full seed set is achieved only if pollen is transferred between different morphs and from an anther level that corresponds to the position of the receiving stigma. The species is native to Eurasia and has been introduced to North America (Hultén and Fries 1986). In the study area, plant establishment is predominantly from seed. Each plant may produce one to several floral shoots. Flower buds develop in leaf nodes (commonly 2–5 flowers per leaf node) in the upper part of the floral shoot. In Fennoscandia, *L. salicaria* flowers for 6–8 wk in July–August. The flowers are visited primarily by bumble bees, but also by honey bees, syrphid flies, and lepidopterans (J. Ågren, unpublished data). The seeds mature 6–8 wk after flowering.

Populations of *L. salicaria* were studied in the Skeppsvik archipelago in the Gulf of Bothnia, ≈17 km east-southeast of Umeå, northern Sweden (63°47' N, 20°37' E). This archipelago is located near the northern range margin of *L. salicaria* in Fennoscandia (Hultén and Fries 1986). The archipelago is characterized by a substantial land uplift (the rate is ≈0.9 m per century; Ericson and Wallentinus 1979). As a result, new islands are continuously formed, while older islands grow larger and eventually merge with the mainland. *L. salicaria* usually colonizes young islands before a closed vegetation has established. On old islands, the species is confined to the open shore vegetation in front of the developing forest. In the Skeppsvik archipelago, there is a positive correlation between island size and *L. salicaria* population size (population size expressed in terms of number of flowering plants; Spearman rank correlation, $r_s = 0.52$, $n = 36$, $P = 0.002$; J. Ågren, unpublished data).

Natural seed production and supplemental hand-pollination

To document the relationship between population size (number of flowering plants) and the number of seeds produced per flower, data on fruit set and seed production were collected in two consecutive years from populations representing a wide size range (the number of flowering plants per population ranged from 1 to 19 100 in 1993, and from 1 to 22 200 in 1994; $n = 18$ in both years). A population was operationally defined as all plants on an island, or, when growing on an island >6 ha (islands ranged in size from ≈ 200 m² to 24 ha), as a group of plants separated from their closest conspecifics by ≥ 300 m. For each population, the total number of flowering plants was estimated during the central part of the flowering period (when all plants were in flower). Style-morph frequencies were determined in all populations as part of a long-term study of *L. salicaria* population dynamics (J. Ågren and L. Ericson, unpublished data). Most of the smallest populations (consisting of up to eight flowering plants) were monomorphic or dimorphic (i.e., included only one or two floral morphs), whereas all populations with nine or more flowering plants were trimorphic (Table 1).

To test if any correlation between population size and plant fecundity was a function of among-population differences in the degree of pollinator limitation, supplemental hand-pollinations were performed in eight populations in 1993, and in 13 populations in 1994 (Table 1). For this experiment, up to 25 plants per morph (depending on availability) were marked in each population. On the experimental plants, pairs of newly opened flowers (one flower in each of two adjacent leaf nodes) were marked and assigned to two different treatments. One of the flowers served as a control and the other received supplemental hand-pollination. At pollination, "legitimate" pollen (produced by another morph in anthers at the same level as the receiving stigma) was transferred by gently brushing newly dehisced anthers across the stigma until it was densely covered with pollen. For each flower to be pollinated, a pollen donor was randomly chosen among plants 5–10 m away from the focal plant. In some of the smallest populations, the latter criterion could not be met and a plant at a shorter (or longer) distance from the focal plant had to be selected as the pollen donor. Except for two populations in which there was a single flowering plant in 1994 (S31 and S34), pollen from a plant within the same population was used in all pollinations. Two to four pairs of flowers were marked on each plant, and all hand-pollinations were performed during the central part of the flowering period. In large populations, rates of pollinator visitation were high; it was thus necessary to bag flowers on non-experimental plants to ensure the availability of pollen for the supplemental pollinations.

TABLE 1. Study populations of *Lythrum salicaria* ordered according to size (number of flowering plants). The morph structure is denoted by letters representing the morphs present in the population (L, long-; M, mid-; S, short-styled morph). Supplemental hand-pollinations were performed in eight populations in 1993, and in 13 populations in 1994 (indicated with an X). Number of plants sampled for quantification of seed production is indicated.

Population	Morph composition	Total number of flowering plants	Hand-pollination	Number of plants sampled
1993				
S34	L	1		1
S44	L	1		1
S9	LS	2	X	2
S19	MS	2		2
S30	LS	2		2
S31	LM	2	X	1
S28	LS	7	X	5
S10	LMS	9	X	8
S8	LMS	29	X	21
S25	LMS	47	X	19
S41	LMS	49		29
S33	LMS	68		66
S13	LMS	181		137
S23	LMS	183	X	55
S14	LMS	1300		178
S3	LMS	5350	X	75
S1	LMS	9500		180
S2	LMS	19100		179
1994				
S31	L	1	X	1
S34	L	1	X	1
S9	LS	3		1
S22	LS	3	X	2
S30	LS	3	X	1
S19	LMS	4	X	1
S28	LS	8	X	2
S10	LMS	8	X	7
S8	LMS	39	X	16
S25	LMS	53	X	27
S41	LMS	56		35
S33	LMS	95		34
S23	LMS	166	X	22
S13	LMS	209		60
S14	LMS	1790		60
S3	LMS	4850	X	78
S1	LMS	10200	X	75
S2	LMS	22200	X	40

When control flowers and flowers receiving supplemental pollination are located on the same plant, the effect of hand-pollination may be inflated by reallocation of resources from control flowers to flowers that receive a surplus of pollen (Zimmerman and Pyke 1988). The strength of such an effect should increase with decreasing distance between control and experimental flowers (cf. Watson and Casper 1984). However, in a previous experiment with *L. salicaria* (Ågren and Ericson 1996), there was no significant difference in seed production between control flowers in leaf nodes adjacent to leaf nodes with a hand-pollinated flower and open-pollinated flowers on other shoots of the same individual. In this species, hand-pollination of one flower apparently has a negligible effect on seed pro-

duction of open-pollinated flowers in adjacent leaf nodes.

Fruits were collected at maturation (before dehiscence) and were brought to the laboratory. The number of mature seeds was counted for each fruit under a stereomicroscope. For each plant and treatment, the mean number of seeds produced per flower was calculated by multiplying the proportion of flowers producing a fruit by the mean number of seeds per fruit.

To test whether plant size or total seed number per plant was correlated with population size, the number and size of floral shoots were quantified, and total seed production by open-pollinated flowers was estimated for all experimental plants in 1994. The number of floral shoots produced by each experimental plant was recorded at flowering. From each experimental plant, the floral shoot on which most or all experimental pollinations had been performed was collected and brought to the laboratory at fruit maturation. For each of these shoots, the number of leaf nodes producing a flower and the total fruit number (excluding fruits that had developed from hand-pollinated flowers) were recorded. Total seed production was estimated for each plant as number of floral shoots \times number of fruits produced by the sampled shoot \times mean seed number in fruits formed by open-pollinated control flowers.

In the populations in which no supplemental hand-pollinations were performed, a somewhat different method was used to estimate the natural level of fruit set and seed production. In each of these populations, up to 60 plants per style morph were marked during flowering, and the number of flower-producing shoots produced by each of these plants was recorded. At fruit maturation, one floral shoot per plant was sampled and brought to the laboratory. To estimate fruit set (proportion of flowers producing a fruit with mature seeds), I determined the number of mature fruits and the total number of flowers produced in each of five haphazardly chosen flower-producing leaf nodes per shoot. Flower production was determined by adding the number of scars left by aborted flowers and fruits to the number of mature fruits. I counted the number of seeds in five intact (nondehisced) fruits per shoot. For each plant, the mean number of seeds per flower was estimated as mean proportion of flowers producing a fruit \times mean seed production per fruit. In 1994, numbers of flower-producing leaf nodes and total fruits were determined for each of the sampled shoots, and total seed number per plant was estimated as for the experimental plants.

To test if the relationship between population size (\log_{10} [number of flowering plants]) and seed production differed between controls and flowers receiving supplemental pollination, I performed an analysis of covariance on population means of seed number per flower. To test if the effect of supplemental hand-pollination decreased with increasing population size, I further regressed the difference in mean seed output between hand-pollinated and control flowers on num-

ber of flowering plants (\log_{10} -transformed) in the population. To determine if the effects of supplemental hand-pollination on seed number per flower differed among years, a mixed-model ANOVA with four main factors (pollination [fixed], population [random], year [random], and plant [random, nested within population and year]) was applied to data from the five populations in which at least five plants were hand-pollinated in each year. The analysis was performed using the GLM procedure of SAS (SAS Institute 1988); for significance tests, error terms were derived with the RANDOM/TEST statement of this procedure. To examine whether or not the effects of supplemental pollination on seed number per flower differed among style morphs, data from each population with ≥ 10 plants per morph included in the experiment were analyzed as a two-factor split-plot design (Snedecor and Cochran 1967), with morph as the "whole-plot" treatment. To control the Type I error rate when performing multiple tests, the sequential Bonferroni test (Holm 1979) was used to determine if results were significant at the $P \leq 0.05$ table-wide level.

Because rather few flowers of each treatment were scored on each plant included in the hand-pollination experiment, precision of the estimated fruit set of individual plants was low. This may have inflated the estimates of among-plant variation in seed number per flower. To check if this was likely to have affected the conclusions reached, I reanalyzed the data in a different way: For each population, morph, and treatment, I calculated the overall fruit set as the proportion of flowers producing a mature fruit. I then assigned this value to all plants in the group, calculated new estimates of seed number per flower, and reran the analyses. The results were qualitatively similar to those obtained using individual-plant estimates of fruit set, and only the latter will be reported.

To examine if the relationship between population size and plant fecundity was likely to be confounded by differences in location within the archipelago, I calculated the Spearman rank correlations between population size (estimated as number of flowering plants in 1993) and distance to the mainland, distance to the nearest conspecific population, and size of the nearest conspecific population in 1993. Moreover, to test if distance to the mainland, distance to the nearest conspecific population, or size of the nearest conspecific population (\log_{10} [number of flowering plants]) could account for some of the variance in seed output among populations, I entered these variables, together with population size, as independent variables in multiple regressions.

RESULTS

Population size and seed production

There was no significant correlation between population size and plant size in terms of number of floral

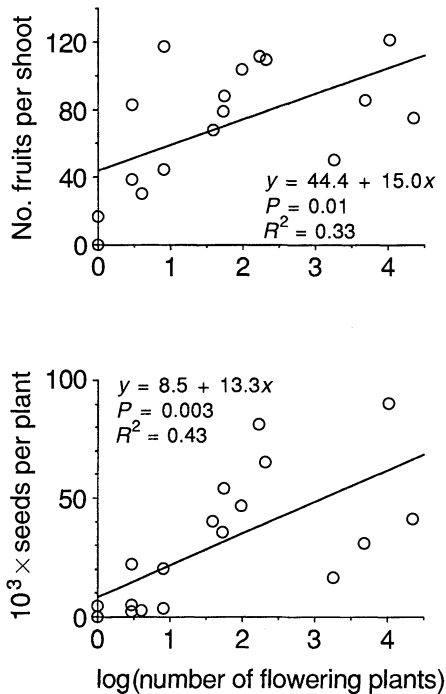


FIG. 1. Relation between the log of population size (number of flowering plants) and number of fruits per floral shoot, and between the log of population size and total seed production per plant in *Lythrum salicaria* in 1994 ($n = 18$ populations). Least square linear regressions are indicated. See Table 1 for number of plants sampled in each population.

shoots (Spearman rank correlation, $r_s = 0.12$, $n = 18$, $P = 0.62$) or number of flower-producing leaf nodes per floral shoot ($r_s = 0.38$, $n = 18$, $P = 0.12$). However, population size was positively correlated with number of fruits per shoot ($r_s = 0.66$, $n = 18$, $P = 0.007$) and with total seed production per plant ($r_s = 0.75$, $n = 18$, $P = 0.002$; Fig. 1).

The analysis of covariance indicated a significant interaction between population size and effects of the pollination treatment on seed number per flower in both years (Table 2). In the control group, there was a significant positive relationship between population size and seed production per flower (Fig. 2). In the 2nd yr, this relationship appeared to flatten out at a population size of ≈ 100 – 200 flowering plants (Fig. 2), but the curvature was only marginally significant (partial regression coefficient of squared term in second-order polynomial regression, $c = -4.2$, $t = 2.0$, $P = 0.06$).

In contrast to the controls, seed production per flower did not increase with population size for flowers that had received supplemental pollination (least square linear regressions; 1993: $P = 0.46$, $R^2 = 0.10$; 1994: $P = 0.67$, $R^2 = 0.02$; Fig. 2). The difference between hand-pollinated flowers and controls in mean seed number per flower decreased with increasing population size, indicating that seed production was more strongly limited by insufficient pollen transfer in small

than in large populations (1993: regression coefficient, $b = -15.7$, $n = 8$, $P = 0.04$, $R^2 = 0.53$; 1994: $b = -12.9$, $n = 13$, $P = 0.0004$, $R^2 = 0.68$). Despite this trend, supplemental hand-pollination also significantly increased seed production in several large populations (Table 3).

Variation in population size was not confounded with degree of isolation from the mainland or from other conspecific populations. There was no significant correlation between population size and distance to the mainland ($r_s = 0.24$, $n = 18$, $P = 0.34$), distance to the nearest conspecific population ($r_s = -0.16$, $n = 18$, $P = 0.45$), or the size of the nearest conspecific population ($r_s = 0.25$, $n = 18$, $P = 0.30$). Multiple regressions indicated a strong effect of population size (partial regression coefficient, 1993: $P < 0.0001$; 1994: $P = 0.004$), but no significant effect of distance to the mainland, distance to the nearest conspecific population, or size of the nearest conspecific population on the mean seed number per flower ($P > 0.3$, except for distance to the mainland in 1993, for which $P = 0.08$; 1993: $P = 0.0001$, $R^2 = 0.81$; 1994: $P = 0.009$, $R^2 = 0.62$; $n = 18$ in both years).

Among-year variation

Seed production was lower and more strongly pollinator-limited in 1993 than in 1994. In the 17 populations that were sampled in both years, production was 26.0 ± 4.5 seeds per open-pollinated flower (mean ± 1 SE, based on population means) in 1993, and 41.4 ± 5.8 seeds in 1994 (paired test, $t = 4.3$, $P = 0.0005$). There was no significant difference between years in seed production by hand-pollinated flowers (73.7 ± 6.6 vs. 79.7 ± 3.4 seeds per flower, $n = 7$; paired test, $t = 1.7$, $P = 0.14$). Significant variation among years in the magnitude of the effect of hand-pollination on seed number per flower is indicated by a significant pollination \times year interaction term in the mixed-model ANOVA that included the five populations in which

TABLE 2. Analysis of covariance of the effects of pollination treatment (control vs. supplemental pollination) and population size (\log_{10} [number of flowering plants]) on mean seed number per flower in *Lythrum salicaria* (Type III sums of squares). Hand-pollinations were performed in eight (1993) and 13 (1994) of a total of 18 study populations. Single-test significance values are indicated with asterisks. F values significant at the $P \leq 0.05$ table-wide level (sequential Bonferroni test) are indicated in boldface.

Source of variation	1993			1994		
	df	MS	F	df	MS	F
Pollination	1	11 741.1	69.6***	1	12 287.3	57.4***
Size	1	329.6	2.0	1	2 138.3	10.0**
Pollination \times Size	1	2 030.5	12.0**	1	2 951.6	13.8***
Error	22	168.7		27	214.0	

** $P = 0.01$; *** $P < 0.001$.

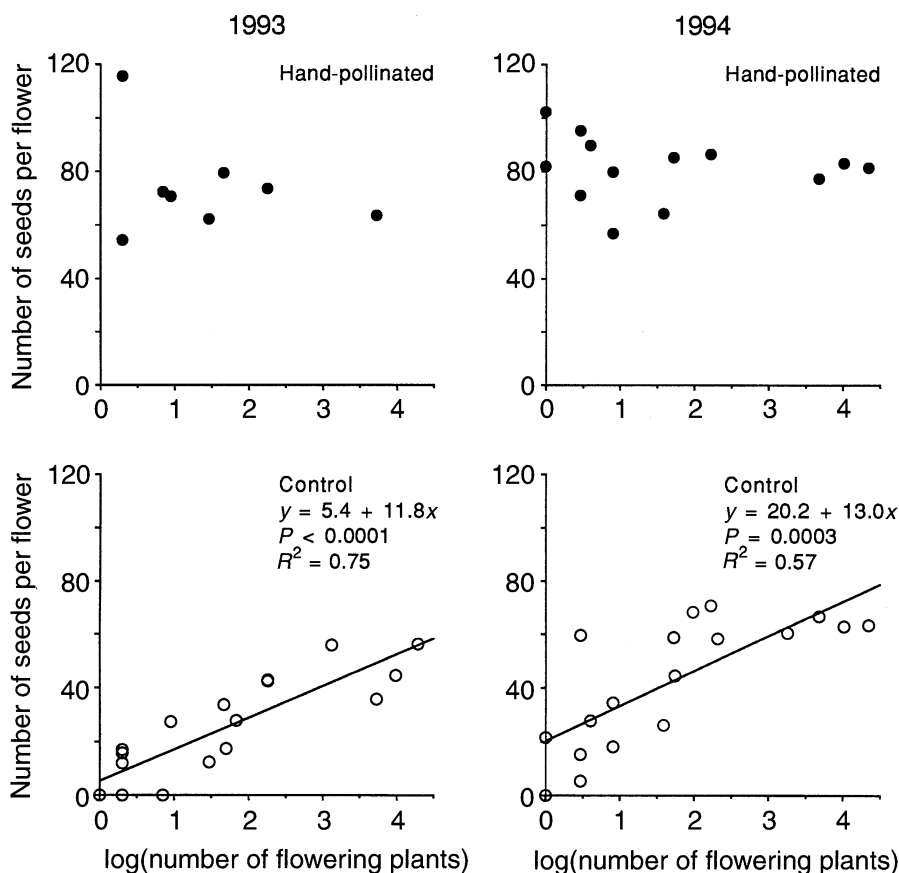


FIG. 2. Relation between the log of *Lythrum salicaria* population size (number of flowering plants) and mean number of seeds produced per flower. Data are given for control flowers receiving only natural pollination (open symbols, $n = 18$ populations) and for flowers receiving supplemental pollination (solid symbols; 1993: $n = 8$ populations; 1994: $n = 13$ populations). Least-square linear regressions are indicated in those cases where the slope of the regression line was significantly different from zero. See Table 1 for number of plants sampled in each population.

eight or more plants were hand-pollinated in each year (S3, S8, S10, S23, and S25; Table 4). In all five populations, the mean increase in seed number per flower after supplemental hand-pollination was greater in 1993 than in 1994 (Table 3). There was no significant pollination \times population \times year interaction (Table 4), indicating that the relative strength of pollen limitation in the five populations was consistent among years.

Style morph and seed production

In five populations, sample sizes were large enough to allow a comparison of style morphs in terms of seed production in open-pollinated flowers and the effect of hand-pollination. All five populations were characterized by a marked deficiency of the mid-styled morph (Fig. 3). In all five populations, supplemental hand-pollination significantly increased seed number per flower; in one population (S23), seed number per flower differed consistently among morphs (Table 5). In two populations (S2 and S25), the effect of hand-pollination differed among style morphs as indicated by a significant pollination \times style morph interaction term (Table 5).

The differences among style morphs in seed production and in the effects of supplemental pollination were not correlated with their relative frequencies in a straightforward way. In population S23, the L morph produced fewer seeds per open-pollinated control flower than did the rare M morph, but it also produced fewer seeds than did the S morph, which was as frequent as the L morph (S23: $F_{2,52} = 13.9$, $P < 0.0001$; Tukey-Kramer multiple comparison, $L < M = S$; Fig. 3). Similarly, in populations S2 and S25, frequencies of the L and S morphs were roughly equal (Fig. 3), but seed production by control flowers in both populations tended to be lower in the L than in the S morph (S2: $t = 1.7$, $df = 38$, $P = 0.10$; S25: $t = 4.3$, $df = 23$, $P = 0.0003$). Moreover, in these two populations, seed number per flower was significantly increased by supplemental hand-pollination in the L but not in the S morph (Fig. 3).

DISCUSSION

This study has documented a significant positive correlation between population size and both seed production per flower and seed production per plant in the

TABLE 3. Mean difference in seed production between flowers receiving supplemental pollination and flowers receiving only natural pollination in *Lythrum salicaria* populations with at least five experimental plants (based on plant means; n = number of experimental plants). Populations are ordered according to size (number of flowering plants; see Table 1). Deviations from the null hypothesis of no difference were examined with one-tailed, paired t tests (Sokal and Rohlf 1981). Single-test significance values are indicated with asterisks. Differences significant at the table-wide $P \leq 0.05$ level (sequential Bonferroni test calculated for each year separately) are indicated in boldface.

Population	Differences (no. seeds per flower, mean \pm 1 SE)	n
1993		
S28	72.2 \pm 21.9*	5
S10	42.8 \pm 11.8**	8
S8	49.3 \pm 9.9***	20
S25	43.6 \pm 10.9***	18
S23	30.1 \pm 6.7***	55
S3	27.6 \pm 5.2***	75
1994		
S10	38.6 \pm 8.9**	7
S8	36.1 \pm 13.3**	12
S25	26.2 \pm 8.5**	27
S23	13.8 \pm 7.8*	21
S3	8.3 \pm 4.2*	71
S1	19.4 \pm 3.4***	73
S2	16.6 \pm 4.9***	39

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

self-incompatible herb *Lythrum salicaria*. The correlation between population size and seed production per flower was significant in each of two years, which differed substantially (1.6 times) in mean seed production of open-pollinated flowers. In contrast, the seed production of flowers receiving supplemental hand-pollination did not increase with increasing population size. This is one of the first studies to verify experimentally that variation in the efficiency of pollen transfer may produce a significant positive relationship between population size and plant fecundity within a local system of plant populations.

There are a few observational studies indicating that pollination efficiency and seed production may be reduced in small populations of animal-pollinated plants. In *Banksia goodii*, for example, total seed production of the population tended to increase disproportionately with the number of plants in the population (Lamont et al. 1993). Widén (1993) documented a positive correlation between number of flowering stems and seed set when data collected in six populations of *Senecio integrifolius* in two to four different years were pooled. Seed set was lower in two isolated patches of *Dianthus deltoides*, located in a large agricultural field, than in a large population surrounded by natural vegetation (Jennersten 1988). A hand-pollination experiment indicated that this difference was due to a difference in the degree of pollinator limitation between the two sites (Jennersten 1988). Aizen and Feinsinger (1994b) found that fragmentation of a subtropical dry forest in Ar-

gentina resulted in substantial changes in the pollinator fauna; they further documented (Aizen and Feinsinger 1994a) that, in some of the 16 plant species investigated, these changes were associated with declines in pollination level and seed production in small habitat fragments.

The relationship between population size and pollination intensity may differ for rewarding vs. nonrewarding animal-pollinated plants. In species pollinated by deceit, a large population does not represent a greater food resource to flower visitors than a small population. Instead, the likelihood that pollinators learn to avoid the nonrewarding flowers may increase with increasing population size. In a study of three nonrewarding orchid species, pooling three years of data (Fritz and Nilsson 1994), there was no correlation between population size and fruit set in *Orchis palustris* and *O. spitzelii*, and a negative correlation between these two variables in *Anacamptis pyramidalis*. The proportion of the pollinia removed by flower visitors was negatively correlated with population size in all three species. Similarly, no correlation between population size and fruit set was detected in a study of the bumble bee-pollinated, nonrewarding orchid *Calypso bulbosa* (Alexandersson and Ågren 1996).

Further experiments are required to establish whether or not the positive relationship between population size and pollination intensity in *L. salicaria* represents a causal relationship. In populations of reward-producing, animal-pollinated plants, several factors in addition to size are likely to influence the attractiveness of a population to pollinators. These include plant density (Feinsinger et al. 1991, Kunin 1993) and the degree of isolation from other conspecific populations. In island populations, composition of the pollinator fauna and pollination intensity could further be influenced by the distance to the mainland (Feinsinger et al. 1982, Spears 1987).

There is a strong correlation between population size and plant density (measured as median distance to clos-

TABLE 4. Effects of pollination treatment (control vs. supplemental pollination), population, and year on seed number per flower in *Lythrum salicaria*, analyzed with a mixed-model ANOVA (Type III sums of squares). The analysis included the five populations in which eight or more plants received supplemental pollination in each of the two years of study (populations S3, S8, S10, S23, and S25).

Source of variation	df	MS	F
Pollination	1	84829.3	13.6
Population	4	8863.4	1.6
Year	1	10894.9	1.8
Plant (Population \times Year)	303	1761.8	1.9***
Pollination \times Population	4	3114.9	27.5**
Pollination \times Year	1	4210.6	11.5**
Population \times Year	4	2426.4	2.5
Pollination \times Population \times Year	4	113.3	0.1
Error	303	907.8	

** $P < 0.01$; *** $P < 0.001$.

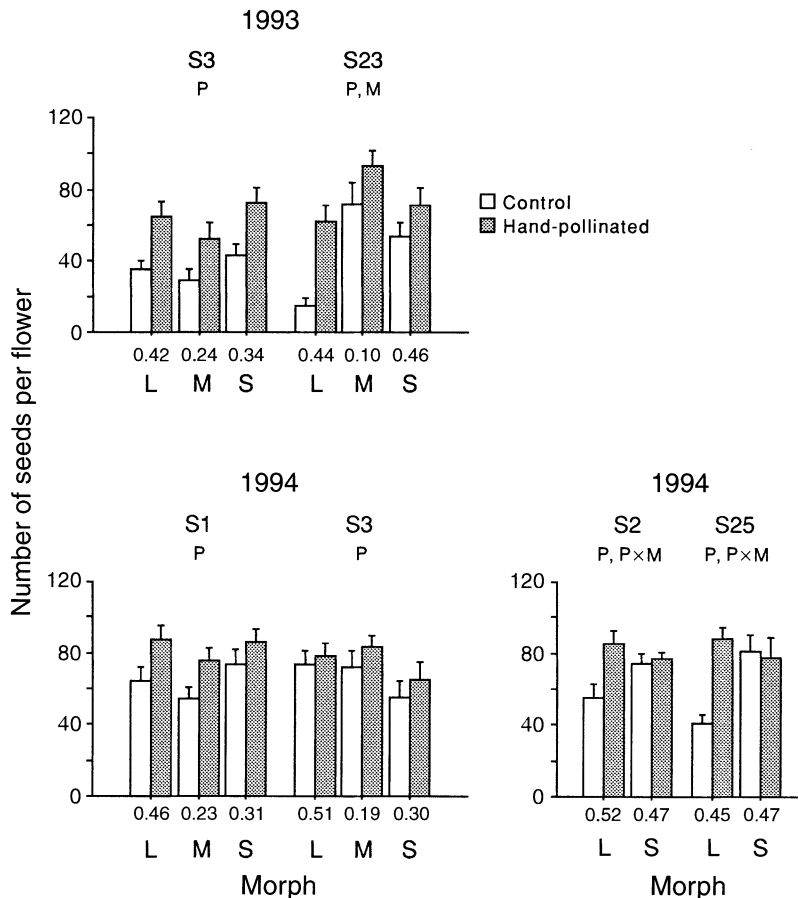


FIG. 3. Number of seeds (mean + 1 SE) produced by open-pollinated control flowers (open bars) and by hand-pollinated flowers (solid bars) in five *Lythrum salicaria* populations (S1, S2, S3, S23, and S25; L, long-; M, mid-; S, short-styled morph). Data are based on plant means, with sample sizes (n) for each morph in parentheses. For 1993, S3: L (25), M (25), S (25); S23: L (21), M (13), S (21). For 1994, S1: L (25), M (24), S (25); S2: L (20), S (20), M (27), S (21); S25: L (14), S (11). Relative frequencies of the three style morphs in the study populations are given below the bars (in populations S23 and S25, all plants were scored for morph type; 206–488 plants were scored in each of the other populations). Significant effects of pollination (P), style morph (M), and their interaction (P \times M), detected in a mixed-model ANOVA, are indicated above the bars. In most populations, there was also a significant effect of plant (nested within morph) on seed number per flower (see Table 5).

est flowering plant) in this system of *L. salicaria* populations (Spearman rank correlation, $r_s = -0.91$, $n = 18$, $P = 0.0002$; J. Ågren and A. Reimer, unpublished data). Experimental manipulations will, therefore, be necessary to separate the effects of these two factors on pollination intensity and seed production. It seems likely that both the difference in size and the difference in density will contribute to making large *L. salicaria* populations more attractive to pollinators than small populations. Differences in the degree of isolation are not likely to have produced the correlation between population size and seed production in the current study. There was no significant correlation between population size and distance to the mainland, distance to the nearest conspecific population, or the size of the nearest conspecific population (Spearman rank correlations ranged from -0.16 to 0.25 , single-test significance values $P \geq 0.3$). Moreover, in multiple regres-

sions, no significant relationship was detected between the three latter variables and seed output in *L. salicaria*.

Differences in seed set between open-pollinated flowers in small and large populations may be a function of differences in both the amount and the quality of pollen deposited on receptive stigmas. Rates of pollinator visitation and pollen deposition were not quantified in this study, but several observations indicate that the amount of pollen transferred was lower in small than in large populations. First, although flower visitors (mainly bumble bees) were regularly observed foraging on *L. salicaria* in the large populations, they were only occasionally seen in populations with fewer than ≈ 50 flowering plants. Second, it was necessary to bag flowers in large populations to ensure the availability of pollen for the experimental pollinations, whereas finding open flowers with dehiscing anthers rich in pollen was never a problem in populations with < 50 flowering

TABLE 5. Effects of style morph and pollination treatment (control vs. supplemental pollination) on seed number per flower in *Lythrum salicaria*, analyzed as a two-factor split-plot design (Type III sums of squares). Single-test significance levels are indicated with asterisks. *F* values significant at the $P \leq 0.05$ table-wide level (sequential Bonferroni test calculated for each factor separately) are indicated in boldface.

Population and year	Source of variation	df	MS	<i>F</i>
S3, 1993	Morph	2	3733.2	2.1
	Plant (Morph)	72	1748.7	1.7*
	Pollination	1	28510.8	27.1***
	Pollination × Morph	2	210.0	0.2
	Error	72	1050.5	
S23, 1993	Morph	2	15931.4	10.4***
	Plant (Morph)	52	1536.4	1.3
	Pollination	1	21944.4	18.9***
	Pollination × Morph	2	2581.7	2.2
	Error	52	1163.6	
S1, 1994	Morph	2	2921.3	1.4
	Plant (Morph)	70	2102.2	5.0***
	Pollination	1	13620.4	32.7***
	Pollination × Morph	2	379.6	0.9
	Error	70	416.7	
S2, 1994	Morph	1	514.2	0.5
	Plant (Morph)	37	1102.5	2.9***
	Pollination	1	5142.7	13.4***
	Pollination × Morph	1	3653.5	9.6**
	Error	37	382.4	
S3, 1994	Morph	2	3994.6	1.6
	Plant (Morph)	68	2455.3	3.9***
	Pollination	1	2455.3	3.9*
	Pollination × Morph	2	155.5	0.3
	Error	68	631.1	
S25, 1994	Morph	1	2758.3	3.7
	Plant (Morph)	23	744.3	1.0
	Pollination	1	5720.4	7.8*
	Pollination × Morph	1	7856.4	10.8**
	Error	23	730.6	

* $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$.

plants. Finally, pollen was usually observed on the stigmatic surface of most of the open flowers in large populations, whereas a large proportion of the stigmas typically lacked pollen in the smallest populations (J. Ågren, *personal observation*).

If small *L. salicaria* populations consist of closely related plants, then the low seed set in these populations could reflect inbreeding depression, even if there were considerable pollen transfer among plants within the population (cf. Menges 1991, Ouborg and van Treuren 1994). However, this explanation seems less likely, because the supplemental pollinations that produced marked increases in seed production in small populations used local pollen (from the same population) in all populations with at least two flowering plants.

A higher level of self-pollination in small than in large populations may contribute to the low seed set in small populations. Because of an overall lower visitation rate, the average amount of nectar and pollen available per flower may be higher in small than in large populations. As a result, the number of flowers visited per plant (e.g., Pyke 1978, Heinrich 1979,

Hodges 1985, Harder 1990; see also Klinkhamer and de Jong 1990) and, thereby, the opportunities for geitonogamous self-pollination (de Jong et al. 1993, Barrett et al. 1994, Hodges 1995), should be higher in small than in large populations. Self-pollination prior to the deposition of legitimate outcross pollen may negatively affect seed production in self-incompatible, tristylous plants (Nicholls 1987, Scribailo and Barrett 1994). To determine the relative importance of differences in the size and quality of the stigmatic pollen load for among-population differences in fecundity, it would be of interest to quantify how population size affects the different components of pollen deposition, i.e., how it affects the rates of autogamous self-pollination, geitonogamous self-pollination, illegitimate outcross, and legitimate outcross pollen deposition. In principle, this could be done using floral manipulations similar to those outlined by Schoen and Lloyd (1992), combined with manipulations of the morph composition of the population (cf. Lloyd and Webb 1992). In *L. salicaria*, the long-level anthers produce larger pollen grains than anthers at the other two levels in the flower (Mulcahy and Caporello 1970). This facilitates the quantification of patterns of pollen deposition in *L. salicaria*, although conditions are not as favorable for this kind of study as in tristylous species that display a discrete pollen trimorphism (e.g., Barrett and Glover 1985, Harder and Barrett 1993).

The present results did not support the hypothesis that insufficient pollen deposition should limit seed production more strongly in common than in rare mating types. The effect of supplemental hand-pollination on seed number per flower was compared among style morphs in five populations with strongly skewed morph ratios. Supplemental hand-pollination increased seed production in all populations, but only in two (S2, S25) did the effect of supplemental pollination vary among morphs. Moreover, the differences detected among morphs could *not* be attributed to differences in their relative frequencies. In both the S2 and S25 populations, frequencies of the L and S morphs were roughly equal (0.52 vs. 0.47, and 0.45 vs. 0.47, respectively), but only in the L morph was seed production increased by supplemental hand-pollination (Fig. 3).

Results of the present study and of a previous hand-pollination experiment in two *L. salicaria* populations in the same archipelago (Ågren and Ericson 1996) suggest that seed production is more likely to be pollinator limited in the L morph than in the other two morphs, and that this difference at least partly may explain why long-styled plants tend to produce fewer seeds than mid- and short-styled plants. In tristylous species, the morph-specific differences in flower morphology could affect the efficiency with which pollen is picked up and deposited by flower visitors (Barrett and Glover 1985, Kohn and Barrett 1992, Harder and Barrett 1993), and may potentially explain differences among style morphs in the likelihood of pollinator limitation

(O'Neil 1992, Eckert and Barrett 1995, Ågren and Ericson 1996). Interestingly, in contrast to results obtained in the present study area, O'Neil (1992) found that seed production was more strongly pollinator-limited in the S than in the L morph in two *L. salicaria* populations in northeastern USA, where the species is introduced. The contrasting results may be related to differences in the morphology and behavior of the dominant pollinators in the two areas, and deserve further study. Differences among morphs in the strength of the self-incompatibility reaction (Barrett and Anderson 1985, O'Neil 1994) and in the effects of self-pollination on seed production (Scribailo and Barrett 1994) could potentially also contribute to among-morph differences in seed production in tristylous species. In *L. salicaria*, the self-incompatibility is somewhat weaker in the M morph than in the other morphs (Darwin 1877, Stout 1923, O'Neil 1994, J. Ågren, *unpublished data*), but this cannot by itself explain why the L morph tends to produce fewer seed than the other morphs. We are currently investigating whether or not differences in the effects of self-pollination may contribute to among-morph differences in seed production in *L. salicaria*. Nicholls (1987) found that deposition of self pollen prior to the deposition of legitimate outcross pollen reduced seed production in long-styled *L. salicaria* plants, but did not perform the corresponding experiment with mid- and short-styled plants.

A relationship between population size and plant fecundity due to among-population variation in pollinator visitation may not only be found in obligately outcrossing plant species. In self-compatible species, variation in pollinator visitation may affect the number of seeds produced, the outcrossing rate, or both (e.g., Karoly 1992). The effects on seed output should depend on how variation in pollinator visitation affects the deposition of outcross and self pollen, respectively, and the effects of self-pollination on seed number and quality. A reduced deposition of outcross pollen may, in some situations, be compensated by pollinator-mediated self-pollination (Feinsinger et al. 1991), and, in facultatively autogamous plants, by autonomous self-pollination (Lloyd and Schoen 1992). However, in several species, pollination with self pollen has been found to result in a lower seed production than pollination with outcross pollen (see review in Johnston 1992), and autogamous selfing need not fully compensate for a reduction in pollinator visitation in facultatively autogamous plants (Jennersten 1988, Karoly 1992). These observations suggest that if there is a relationship between population size and pollinator visitation, then this may cause seed output to vary with population size in self-compatible as well as self-incompatible plants.

To summarize, this study has documented a positive correlation between population size and seed production per flower within a local system of *Lythrum salicaria* populations, and it has experimentally demonstrated that this positive relationship is due to insuf-

ficient pollen transfer in small populations. The reduced level of seed production in small populations (with <100–200 flowering individuals) may have both genetic and demographic consequences for this system of populations. Because of the relationship between population size and plant fecundity, large populations are expected to contribute disproportionately to the seed pool, and this should influence the genetic composition of the founders of new populations. Furthermore, the relationship between population size and plant fecundity may affect population dynamics. In small populations, the low seed production could potentially limit population growth and may also threaten the local persistence of *L. salicaria* at particular sites. The effects of different levels of seed production on population dynamics can be evaluated if they are combined with additional demographic information in matrix projection models (e.g., Menges 1992, Schemske et al. 1994, Ehrlén and Eriksson 1995). Demographic studies are underway to assess the consequences of low seed production for the dynamics of *L. salicaria* populations in this area.

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