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PLANT SIZE EFFECTS ON FEMALE AND MALE FUNCTION IN HERMAPHRODITIC *SABATIA ANGULARIS* (GENTIANACEAE)¹

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Abstract. Variation in the contribution of different-sized individuals to female and male function was examined for the extremes of a size-structured population of hermaphroditic *Sabatia angularis* (Gentianaceae). Local populations of *S. angularis* at Miller Dunes, Indiana consisted of 10–15% large plants (> 25 flowers) and ≈ 50% small plants (< 7 flowers). Components of female function studied were (1) pollen grain deposition on stigmas, (2) probability of fruit set, (3) seed production per fruit, (4) average seed mass per fruit, and (5) seed dispersal distributions. Components of male function examined were (1) pollen production on a per flower basis, (2) pollen removal rates, and (3) pollinator observations and fluorescent dye experiments to infer pollen movement.

Large plants contributed disproportionately through female and male function to the production of offspring compared to small plants. In one of the two years examined, the proportion of flowers developing into fruits was significantly greater in large plants than small plants. Seed production per fruit was overall twofold greater for fruits of large plants than small plants. Plant size had no effect on mean seed mass per fruit or the distance of primary and secondary seed dispersal. Flowers of large plants produced significantly more pollen per flower and had significantly more pollen grains deposited on their stigmas than flowers of small plants. However, there was no difference in the proportion of pollen removed from flowers of small and large plants, although the absolute number of pollen grains removed was greater for large plants. Large plants appeared to have the potential for more geitonogamous pollinations than small plants.

Key words: female and male function; geitonogamy; gentian; hermaphrodite; size-structured population.

INTRODUCTION

Plant populations are often size structured with few large and numerous small individuals (Ogden 1970, Harper 1977), resulting in an uneven distribution of reproductive potential among individuals (Obeid et al. 1967, Gottlieb 1977, Leverich and Levin 1979, Crawford 1984). In semelparous species, plant size is correlated with an individual's fitness (Werner 1975, Werner and Caswell 1977, Solbrig 1981, Aker 1982). In particular, plant size is positively related to female function through greater flowering and subsequent fruiting (Van Der Meijden and Van Der Waals-Kooi 1979, Kelly 1984, Lovett Doust et al. 1986), seed production (Van Der Meijden and Van Der Waals-Kooi 1979, Kelly 1984, Weller 1985, Shannon and Wyatt 1986, Devlin 1989), and seed mass (Foster and Janson 1985, Waller 1985, Roach 1986). The limited data at present on the relationship of male function to plant size reflects the difficulty of assessing male function, especially in species producing granular pollen. Individual pollen yield correlates with size when flower

number is the measure of plant size (Devlin 1989). In addition, pollen dispersal to other plants (Webb and Bawa 1983) and within a plant (Hessing 1988) is greater for large plants than small plants. However, stigmatic pollen loads have not been found to differ significantly between small and large plants (Weller 1980, Webb and Bawa 1983, Geber 1985, Hessig 1988).

There are possible genetic implications to the variation in plant size observed among individuals in a local population. A size hierarchy reduces the effective number of individuals because of the production of most progeny by a few members of the population (Wright 1931, 1982, Heywood 1986). If a few individuals contribute the majority of ovules and pollen, this increases the probability of mating between related individuals and the degree of biparental inbreeding in future generations when there is limited gene flow (Uyenoyama 1986). In addition, as plant size increases, more flowers are open simultaneously, which may promote selfing by increasing geitonogamous pollinations (Darwin 1859, Bawa 1974, Arroyo 1976, Hessing 1988).

Plant size may have further consequences on reproductive output besides the obvious production of greater numbers of flowers, fruits, and seeds. Large plants have a potentially greater dispersal range in terms of plant height and the resulting seed shadow (Harper

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1977). As a result, seeds from large plants may act more as colonists of new habitat than seeds from shorter (smaller) plants (Watkinson 1978). A large plant's advantage in seed production may increase the probability of getting some seeds to a "safe site" for germination and overall plant growth (Smith 1980).

The purpose of this field study was to compare the extremes of a size-structured population in terms of an individual's potential contribution to future progeny through female and male function. This study specifically examines female function in terms of (1) pollen grain deposition on stigmas, (2) probability of fruit set, (3) seed production per fruit, (4) average seed mass per fruit, and (5) seed dispersal distributions. Components of male function examined were (1) pollen production per flower, (2) pollen removal rates of flowers of known ages, and (3) pollinator observations and fluorescent dye experiments to infer pollen movement in the study population.

MATERIALS AND METHODS

Study plant and study site

Sabatia angularis L. (Gentianaceae), commonly known as Rose Pink, is a self-compatible, protandrous species which is obligately biennial in the northern portion of its range. Flowering occurs from late July into early September, peaking in August. Fruits mature from early September through October. In contrast to many monocarpic species (Werner 1975, Aker 1982), *S. angularis* exhibits tremendous variability in adult flowering size, since all surviving individuals flower in their 2nd yr, regardless of their size. Adults range in size from 3–80 cm tall with 1–200 flowers per individual in the field.

The anthers of each flower dehisce on the 1st d of anthesis. Stigmas of some flowers become receptive at the end of the 1st d and all are receptive by the 2nd d. Most flowers are pollinated by day 4 of their life-span. The primary pollinators in the field are leaf-cutter bees (Megachilidae) and sweat bees (Halictidae), sand wasps (Sphecidae), and hover flies (Syrphidae). *Sabatia angularis* produces a fragrance but no nectar; the only reward for insect visitors is pollen.

Sabatia angularis was studied at Miller Dunes in Gary, Indiana, which is part of the Indiana Dunes National Lakeshore. *Sabatia angularis* is found in densities ranging from 1–200 individuals/m² in bands surrounding the margins of interdunal ponds.

Small plants were defined as those individuals that produced no more than 6 flowers during their lifetime. Large plants were those individuals that produced a minimum of 25 flowers. Plants in the intermediate size class were examined only during pollinator observations. The population under study consisted of \approx 10–15% "large" plants and 50% "small" plants, with the remaining plants in the intermediate size class.

Statistical analyses

All computer analyses were conducted with the SAS statistical package (SAS 1985) on the University of Illinois at Chicago mainframe computer. All transformations described below were performed to meet the assumptions of analysis of variance (ANOVA). Analysis of variance was performed using the GLM (general linear model) procedure. Type I analysis of variance compared large and small plants unless another statistical test is described below. Temporal variation in components of female and male function was not commonly detected; therefore, the results presented below are from data pooled across the season, unless otherwise noted. Throughout the study, one average value per individual was used in each analysis to prevent pseudoreplication.

Female function

Pollen deposition.—Pollen grain deposition on stigmas was examined by collecting stigmas during the 3rd d of anthesis from flowers of 70 small and 27 large randomly chosen plants throughout the flowering season at Miller Dunes in 1984. The stigmas were imbedded in a semi-permanent mount of fuchsin glycerine jelly on microscope slides in the field (Beattie 1971). Pollen grains were counted at 100 \times and the data were square-root transformed.

Flower/fruit production.—In 1983 and 1984, small and large plants were randomly sampled to follow individual flower production and subsequent fruit production of naturally pollinated flowers. In 1983 the fate of all flowers produced by 105 small and 28 large plants was followed. In 1984, 37 small and 11 large plants were monitored. Individual flower and fruit production was analyzed separately in both years. The data were transformed to natural logs.

Seed production/seed mass.—To assess whether seed production per fruit and average seed mass differed between small and large plants, fruits were collected from individual flowers that opened during the early, middle, and latter portion of the 1983 flowering season. Whenever possible, fruits from all three time periods were collected from the same individual. A total of 30 fruits were collected from 24 small individuals and 30 fruits from 10 large individuals. The seeds from each fruit were counted with a dissecting microscope and weighed en masse to measure total seed mass. Total seed mass was divided by the seed number to estimate mean seed mass. Square-root transformed values of seed production per fruit and natural-log transformed values of mean seed mass were used in the analyses.

In 1984, all the fruits produced by 37 small plants and 11 large plants were collected. The seeds from each fruit were counted and weighed en masse to estimate a mean seed mass as described in the previous paragraph for all the fruits from the small plants and for seven randomly chosen fruits from the large plants.

The average seed number per fruit and mean seed mass of the fruit sampled for each individual were used in the analysis when more than one fruit was sampled per plant. Natural-log transformed values of seed number per fruit and reciprocal square-root transformed values of mean seed mass were used in the analyses.

Seed dispersal.—Primary seed dispersal of small and large plants was compared in a garden plot at the University of Illinois at Chicago. Each group was composed of three plants and manipulated to produce a total of 100 fruits. Average height for the small plants was 24 cm, and for the large plants, 54 cm.

Seed traps of plastic petri dishes, 9 cm in diameter, and sprayed with Tanglefoot sticky resin were arranged by the N, S, E, and W directional coordinates. The same proportion of area was sampled (33% of the area of an annulus) at the 12 distances monitored for each group of source plants out to a 2.15 m radius. The seed distributions of the small and large source plants were compared using a Kolmogorov-Smirnov two-sample test (Siegel 1956). The average seed dispersal distance between small and large plants was compared.

The seed dispersal experiment performed in the garden was replicated twice in the field by locating two areas with clumps of small and large plants in the center of an area with a 5 m radius, otherwise free of *S. angularis*. The first replicate had a group of 8 small plants with an average height of 12 cm and a group of 3 large plants with an average height of 39 cm, and each group was manipulated to produce 79 fruits. The second replicate's groups were composed of 17 small plants with an average height of 15 cm, and a group of 3 large plants with an average height of 38 cm; each of these groups was manipulated to produce 100 fruits.

Because it was impossible to see *S. angularis* seeds on the surface of the sand, rosette formation was monitored as an indication of primary and secondary seed dispersal in the field experiments. Primary dispersal for *S. angularis* is the passive dehiscence of seeds from fruits onto the ground. Secondary dispersal is the additional movement of seeds along the ground with the blowing sand. The rosette distribution of small and large plants in an area with a 3 m radius was monitored; a 2-m buffer zone prevented contamination from other seed sources. The rosette distributions were compared with a Kolmogorov-Smirnov two-sample test. The average rosette distance from the small and large source plants was also compared.

Male function

Pollen production.—In 1983, preliminary analyses suggested that flowers of large plants produced more pollen on a per flower basis than small plants. Future analyses were only performed on viable pollen grains, because no significant difference was found between inviable pollen grain production of small and large plants (Dudash 1987).

Pollen production was quantified on a per flower basis in 1984 for 111 flowers on 98 small plants and 72 flowers on 27 large plants. Flowers were collected throughout the flowering season. Whenever possible the same individual was sampled at different times during the season to determine if variation within a season could be detected. Two of the five anthers produced from an unopened (but almost fully mature) flower bud were placed in 0.5 mL lactophenol solution with 0.1% aniline blue. In the laboratory, anthers were finely chopped, spun on a vortex mixer, and the pollen grains counted on hemacytometer grids. Ten replicates per individual sample were counted and their average value was used in the analysis.

Pollen removal.—In 1984 flowers of different ages were tagged on small and large plants in the field to determine the rate of pollen removal. The terminology was as follows: flower buds = day 0, male-only phase = day 1, primarily female phase = day 2, day 3, and day 4. All flowers are normally pollinated by day 4 in the field. For large plants the full sequence of anthers was collected when possible from the same plant three times during the flowering season. Small plants had fewer flowers, so anthers could not be collected from any one individual throughout the flowering season. Pollen removal rates were estimated by comparing pollen remaining to pollen production on different flowers from the same individual. The pollen-counting procedure was the same used to measure pollen production. In total, pollen removal data were collected from 287 flowers on 101 small plants and 306 flowers on 27 large plants.

Pollinator observations.—Pollinators were identified and monitored as they visited flowers in 1984 and 1985 to determine overall pollinator flight patterns within local patches of flowering plants. I quantified whether pollinators visited more than one flower within an individual, flew <1 m between individuals, or flew >1 m to the next individual.

To determine the effect of plant size on the likelihood of geitonogamous pollinations, pollinator visitation rate was quantified as a function of plant size in 1985. The three plant size classes were small, large, and medium, with the medium plants ranging in size from 7 to 24 flowers per plant. The data were analyzed using chi-square tests with Bonferroni simultaneous confidence intervals to account for the multiple chi-square tests performed (Snedecor and Cochran 1980).

Fluorescent dye as a pollen analog.—Pollen carry-over experiments using hand-manipulated dead pollinators demonstrated a significant relationship between fluorescent dye and pollen movement (Dudash 1987; Spearman rank $r = 0.62$, $P < .001$, $n = 348$) that allowed me to perform the following experiments in the field using dye to infer pollen movement. In the field, six areas were identified where a pair of small and large plants were located in the center of a circle within a radius of 1 m. Plant size and location were

TABLE 1. Characters associated with female and male function of small and large plants (means \pm 2 SE). Data are untransformed.*

Character	Plant size	
	Small	Large
Female function		
Pollen grains on stigmas	336.03 \pm 46.59	496.22 \pm 76.80
Proportion of flowers developing into fruits 1983	0.70 \pm 0.08	0.89 \pm 0.03
Proportion of flowers developing into fruits 1984	0.93 \pm 0.05	0.92 \pm 0.07
1983 flower production	2.70 \pm 0.35	37.50 \pm 6.78
1984 flower production	2.57 \pm 0.47	35.43 \pm 5.10
1983 fruit production	1.98 \pm 0.34	33.77 \pm 6.73
1984 fruit production	2.32 \pm 0.42	34.29 \pm 4.92
1983 seed no./fruit	261.92 \pm 80.96	540.50 \pm 132.13
1984 seed no./fruit	405.56 \pm 59.02	610.68 \pm 113.92
1983 mean seed mass (mg)	0.0163 \pm 0.0038	0.0178 \pm 0.0066
1984 mean seed mass (mg)	0.0131 \pm 0.0010	0.0123 \pm 0.0017
Primary seed dispersal in the garden plot (cm)	80.50 \pm 6.27	86.43 \pm 6.89
Primary and secondary dispersal in the field (cm)	142.3 \pm 17.06	139.1 \pm 16.22
Male function		
1984 pollen production per flower	155,555 \pm 6,942	220,835 \pm 16,508

* For sample sizes, see *Materials and methods: Female function, and Male function.*

noted for every individual within the 1 m radius of the center "donor" plants. All individuals occurring 2 m away from the center donor plants were also mapped and measured and referred to as "perimeter" plants. Either green or pink dye was placed using a flat tooth-

TABLE 2. Significant analyses of variance of characters associated with female and male function of small and large plants.

Source of variation	df	MS	F	P
Female function				
a. Pollen grains on stigmas				
Plant size	1	377.32	13.97	<.0003
Error	95	27.02		
b. 1983 flower production				
Plant size	1	115.82	594.71	<.0001
Error	131	0.19		
c. 1983 fruit production				
Plant size	1	132.36	425.02	<.0001
Error	131	0.31		
d. 1984 flower production				
Plant size	1	36.44	194.92	<.0001
Error	46	0.19		
e. 1984 fruit production				
Plant size	1	35.53	193.35	<.0001
Error	46	0.18		
f. 1983 seed number per fruit				
Plant size	1	547 825.93	13.51	<.0009
Error	32	40 537.82		
g. 1984 seed number per fruit				
Plant size	1	1.30	5.42	.0239
Error	46	0.24		
Male function				
h. 1984 pollen production per flower				
Plant size	1	58 788.42	87.79	<.0001
Error	123	669.63		

pick on two of the five anthers of a single day 1 (male-only) flower of the small and large donor plants. White dye was placed in the same fashion on perimeter plants that also had newly opened male flowers. Two days later, all stigmas receptive during the experimental period were collected within the 1 m radius of the circle and from the perimeter plants. The color of the dye used for the small and large donor plants was alternated because earlier experiments indicated that pollinators remove green more readily than pink or white (M. R. Dudash, *unpublished data*). The experiment was repeated in all six areas four times during the flowering season. Because of the difficulty in estimating the dye quantities on stigmas collected from the field, the results used in the analyses are all presence/absence data.

A paired *t* test was performed to compare the donor small and large plant's distribution of dye on stigmas excluding the donor flower. A Kolmogorov-Smirnov two-sample test was used to compare the dye distributions of small and large donor plants within the 1 m radius. Chi-square analysis was used to determine if the dye movement among the plants within the 1 m radius showed any directionality. To do this each site was initially divided into eight equal portions coinciding with the directional coordinates N, NE, E, SE, S, SW, W, and NW. Initially each run was analyzed separately for the presence of dye from both small and large donor plants on stigmas of the surrounding plants. Chi-square analysis was also used to compare the presence of dye loads on stigmas throughout the season.

RESULTS

Female function

Pollen deposition.—Pollen grain deposition on stigmas of large plants was \approx 1.5-fold greater than on stigmas of small plants ($P < .0003$, Tables 1 and 2).

Flower/fruit/seed production.—In 1983 a significantly greater proportion of flowers on large plants developed into fruits than on small plants ($t = 2.5$, $df = 131$, $P < .01$; Table 1). In 1984, however, there was no significant difference between small and large plants in the proportion of flowers developing into fruits ($t = 1.28$, $df = 20$, $P > .22$; Table 1). Large plants also produced significantly more seed per fruit than small plants in 1983 and 1984 (Tables 1 and 2). There was no significant difference in mean seed mass between small and large plants in either year (1983: $F = 0.22$, $df = 1, 32$, $P = .64$; 1984: $F = 1.39$, $df = 1, 46$, $P = .25$; Table 1).

Seed dispersal.—Primary seed dispersal in the garden plot of small and large plants was not significantly different (Kolmogorov-Smirnov two-sample test: $D_{max} = 0.134$, $D_{crit} = 0.18$, $P > .05$; Fig. 1A). There was a trend for seeds from the shorter group of plants to fall closer to the seed source than seeds from the taller group of plants. ANOVA also showed there was no significant difference in the mean seed dispersal distance of the small and large groups of plants ($F = 0.56$, $df = 1, 266$, $P = .45$; Table 1). Rosette distribution surrounding the small and large groups of plants in the field was not significantly different (Kolmogorov-Smirnov two-sample test: $D_{max} = 0.044$, $D_{crit} = 0.048$, $P > .05$; Fig. 1B). The average dispersal distance assessed by rosette formation from the small and large plants was also not significantly different ($F = 1.2$, $df = 1, 3418$, $P = .27$; Table 1).

Male function

Pollen production and removal.—Flowers of large plants produced significantly more pollen per flower than flowers of small plants in 1984 ($F = 87.79$, $df = 1, 123$, $P < .001$; Tables 1 and 2). The pollen removal curves of flowers of small and large plants were not significantly different from one another throughout the life-span of flowers in the field (Fig. 2; Kolmogorov-Smirnov two-sample test: $D_{max} = 0.03$, $D_{crit} = 0.116$, $P > .05$).

Pollinator observations.—During the flowering seasons of 1984 and 1985 a total of 1016 pollinator flights were monitored. In both years, 95% of all pollinator flights were between flowers on the same plant or between individuals < 1 m apart. Only 5% of the observed pollinator flights were > 1 m (Dudash 1987).

In 1985, more pollinator flights occurred within large vs. small plants (Fig. 3). All three pairwise chi-square tests were significantly different at the .01 level using the Bonferroni correction factor (small and medium $\chi^2 = 22.62$, $df = 1$; medium and large $\chi^2 = 64.37$, $df = 1$; small and large $\chi^2 = 70.61$, $df = 1$).

Fluorescent dye as a pollen analog.—The distribution of dye on stigmas excluding the donor flower differed significantly within the small and large donor plants ($t = 5.37$, $df = 23$, $P < .0001$). Fifty-four percent of the stigmas from the small donor plants contained

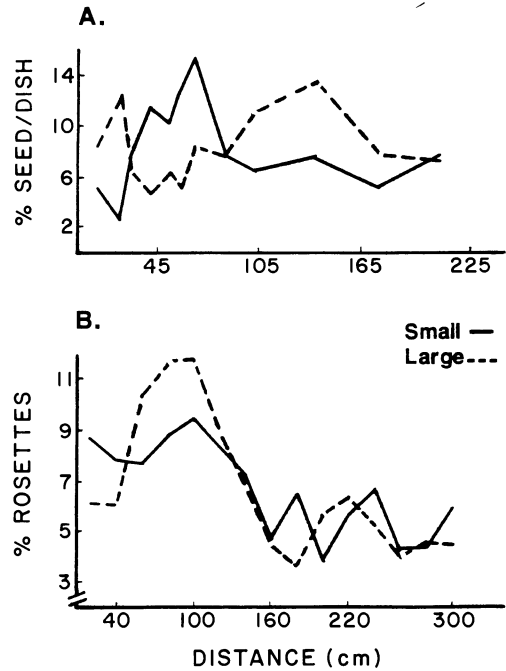


FIG. 1. Seed dispersal distributions of small and large plants in the (A) garden plot and (B) field. In the field, rosette formation was used to indicate seed dispersal. — = small plants, --- = large plants.

dye compared to 84% of the stigmas from the large donor plants.

In the field there was no significant difference in dye movement either within a run or between runs, so the data were pooled from all four runs conducted on different dates. Overall, there was no significant difference in the distributions of dye away from the small and large donor plants (Kolmogorov-Smirnov two-sample test: $D_{max} = 0.056$, $D_{crit} = 0.112$, $P > .05$). As the flowering season progressed and plant density decreased, a significantly greater proportion of stigmas had dye deposited on them than earlier in the season. Further chi-square analysis (pink $\chi^2 = 130.0$; green $\chi^2 = 200.9$; white $\chi^2 = 164.0$; $df = 1$ and $P < .0001$ in all cases) showed that the flowering season could be broken into two parts, with runs 1 and 2 composing the first half, and runs 3 and 4 composing the second half of the season when more stigmas received dye.

Chi-square analysis showed the direction of dye movement away from both small and large donor plants was not significantly different from random for each run. Each run was analyzed separately owing to variation in plant density among the sampling dates.

To quantify dye movement from the perimeter plants to the center donor plants, I examined the ratio of stigmas with white dye divided by total stigmas collected from the small and large donor plants. There was no significant difference between the ratio for small donor plants (0.14) and large donor plants (0.11; chi-square analysis: $\chi^2 = 0.29$, $df = 1$).

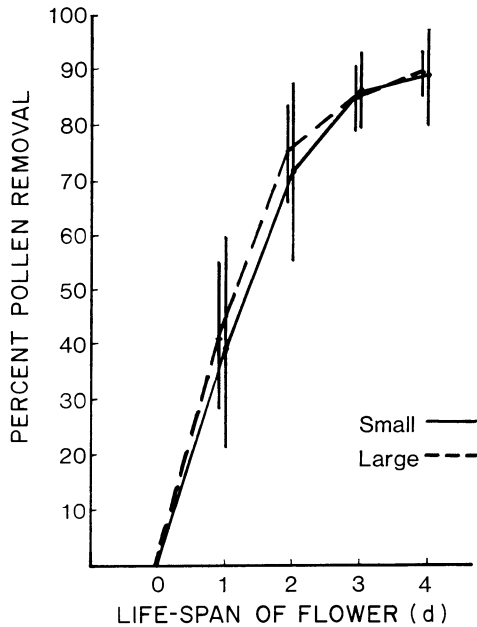


FIG. 2. Percent pollen removal by insects from flowers of small and large plants in the field. Day 0 = flower bud, day 1 = male flower, day 2–4 = female-dominant phase. — small plants, --- large plants. Vertical lines are 95% confidence intervals.

DISCUSSION

In the size-structured population of *S. angularis*, large plants contributed disproportionately through both female and male function to production of offspring compared to small plants. Female and male potential contributions to production of offspring were in agreement and in part a function of the total number of flowers produced by an individual. In contrast, Scheiner (1987) did not find plant size a good predictor of potential fecundity inequalities in the perennial grass *Danthonia spicata*. A semelparous species like *S. angularis* may be more likely to show a positive relationship between plant size and fecundity than an iteroparous species that experiences winter die-back and whose repeated growth and reproduction varies in response to previous and current yearly environmental conditions (Zimmerman and Aide 1989). Therefore, for iteroparous species, any one year's reproductive output may not be indicative of total reproductive output by an individual.

There was a 20–40 fold advantage in female reproductive output of large over small plants in both years. Large plants produced 10–20 fold more fruits than small plants, and their fruits had on average twice the number of seeds. Stanton (1985) has also observed a positive relationship between flower number and fecundity in the annual *Raphanus raphanistrum*. The same positive relationship that *S. angularis* exhibited between fruit production and seeds per fruit was observed in five species of annuals and biennials studied by Kelly (1984). Thus, this relationship between size inequalities and

female function in semelparous species may be fairly common and should be considered more fully when addressing questions to understand a population's ability to persist over time.

Most fruits of *S. angularis* are matured regardless of their seed number. Mature fruits have been collected from the field with as few as 9 seeds (M. R. Dudash, *personal observation*), though fruits more typically contain hundreds of seeds (see Table 1). Because *S. angularis* is a monocarpic species, there are probably strong selective pressures for fruit development. Extreme temperatures during the 1983 season (Dudash 1987) appear to have significantly lowered the probability of fruit development on small plants compared to large plants. However, in 1984 the probability of fruit formation was the same for small and large plants. Lovett Doust et al. (1986) also observed that the largest female plants of *Arisaema triphyllum* produced more flowers that developed into fruits than smaller female plants, although seasonal variation was not noted.

The average seed mass per fruit of *S. angularis* differed between flowering seasons but did not vary among plants of different sizes within a season. These results suggest that within a given season, ecological factors influence seed mass for both small and large plants in a similar fashion. Furthermore, large plants appear to be internally regulated because they were not able to accrue more resources on a per-seed basis, although they do mature significantly more seeds per plant. The initial investment in a large ovule number per pistil of *S. angularis* may dictate how resources are utilized if a sufficient number of pollen grains is deposited on the stigmas.

The rosette distributions away from small and large plants in the field were very similar. These distributional patterns reflect primary and secondary seed dispersal in the field. The seeds of *S. angularis* are the size of sand grains and are likely to be carried by wind on the sand surface, contributing to the similar dis-

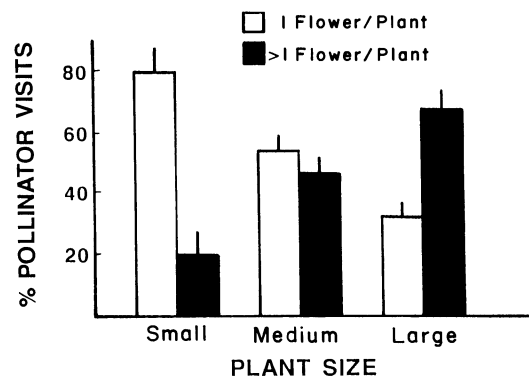


FIG. 3. Percent pollinator flight distances as a function of plant size, with upper half of 95% confidence intervals. □ pollinator visited only one flower before flying to another individual, ■ pollinator visited more than one flower on an individual before flying to another plant.

persal distributions in the field of small and large plants. However, the disproportionate seed production by large plants of *S. angularis* may increase the likelihood (over a small plant) of some seeds reaching a favorable microhabitat for establishment, as Smith (1980) has found for fruits from larger plants of *Espeletia schultzii*.

There was a 14–28 fold difference in potential male reproductive output between individual large and small plants. Large plants produced 10–20 fold more flowers per individual and their flowers produced about 1.4 times the absolute number of pollen grains per flower compared to small plants. In contrast, there was no difference in the proportion of pollen removed between flowers of small and large plants. In *S. angularis*, it appeared either that pollinators were picking up the same proportion of pollen whether they visited a flower of a small or large plant, or that they were revisiting flowers more often on large plants. Once a pollinator landed on a small or large plant, the average number of flowers visited was 1.08 and 1.80, respectively. Pollinator observations and fluorescent dye studies revealed that pollinators appeared to visit all individuals regardless of their size and/or location within the study plots. However, to address conclusively whether large plants are visited more frequently, one would need to know arrival rates of pollinators to plants of different sizes. In contrast to these results, Webb and Bawa (1983) found that total pollen removal differed significantly between flowers on small and large bushes of *Malvaviscus arboreus*. Nakamura et al. (1989) assumed in a hypothetical population example that potential male reproductive success was proportional to flower number, and that pollen production and pollen export were also equal among flowers in a fully self-compatible species exhibiting a size hierarchy. The variation observed in pollen production and the absolute number of pollen grains removed from the small and large plants of *S. angularis* were not in agreement with the assumptions of their model. However, the proportion of pollen removed on a per-flower basis was consistent and similar between the small and large plants. The variation documented in this study is probably more the rule than the exception in the field. Therefore, we need more complex models to predict accurately what may be occurring in nature.

The field fluorescent dye experiments and pollinator observations suggested that the potential for geitonogamous pollinations was greater within a large plant than a small plant. The studies focusing on dye movement within and into the donor plants suggest that the significantly greater numbers of pollen grains deposited on stigmas of large plants was probably due to geitonogamous pollination events. Hessing (1988) has also demonstrated that geitonogamy increases with increasing plant size for *Geranium caespitosum*. In contrast, Weller (1980), Webb and Bawa (1983), and Geber (1985) found no significant difference in compatible pollen loads on stigmas of small and large plants of

self-incompatible *Lithospermum caroliniense*, self-compatible *Malvaviscus arboreus*, and self-compatible *Mertensia ciliata*, respectively. The difference in pollen loads between small and large plants is surprising in protandrous *S. angularis* and suggests that protandry may be effective within a flower but not between flowers on an individual.

Another field study of *S. angularis* found a greater than twofold increase in relative fitness of progeny derived from hand-outcrossing plants no more than 5 m apart compared to progeny derived from selfing (Dudash 1990). The dramatic 50% decrease in progeny fitness following self-pollination would be a great disadvantage for a large plant, if in fact geitonogamous fertilizations are as common as suggested from the data presented here. The 20–40 fold advantage of large plants over small plants in terms of quantity of progeny contributed to could be reduced to a 10–20 fold advantage if on average half the seeds were a result of self-pollinations. Fruit production of progeny of naturally pollinated small and large plants grown in the greenhouse was found to be essentially identical to fruit production of greenhouse-grown progeny derived from outcrossing plants originally separated by no more than 5 m in the field (Dudash 1987). These results are supported by an additional analysis of the field study mentioned above that revealed no increase in the incidence of inbreeding depression with increasing plant size (Dudash 1987). One explanation may be selection against self seeds to germinate under unpredictable field conditions because self seeds under benign greenhouse conditions were found to be at a disadvantage compared to seeds from outcrossing (Dudash 1990). Geber (1985) also found no evidence of increased inbreeding depression with increased plant size in *Mertensia ciliata*. However, Hessing (1988) has collected some data that suggests the expression of inbreeding depression increases with increasing plant size. Although large plants may experience many more geitonogamous pollinations than small plants, if they result in geitonogamous progeny that fail to reproduce, the increase in geitonogamy could have no measurable effect on the stability of the mating system and the local population dynamics.

The role of an increased floral display (plant size) in determining male and female function can be compared to an increase in inflorescence size if one considers both as a means of packaging and presenting flowers. In *S. angularis*, larger floral displays increased female function 20–40 fold. Pollen receipt per flower on large plants was 1.5–2 times greater than on small plants. Another study revealed that small plants had lower seed production per fruit than large plants even when supplemented with outcross pollen (M. R. Dudash, unpublished manuscript). Thus the advantage of large plants in seed production is probably attributable both to increased pollen deposition on stigmas (this study) and more ovules per fruit and/or more resources to develop fertilized ovules. Male function also in-

creased 14–28 fold with a larger floral display. Pollen donation per flower of large plants was 1.4 times greater than small plants owing to the higher pollen production per flower and similar pollen removal curves. Therefore, selection for increasing floral display may be slightly stronger on female function or equally strong on both male and female function. Campbell (1989) has shown at the level of the inflorescence that female function benefitted more than male function when inflorescence size increased in *Ipomopsis aggregata*.

The disproportionate production of pollen and seeds by a few large individuals may have long-term evolutionary consequences. Since drift is dependent on the number of individuals in a local population contributing to the mating pool, the presence of a size hierarchy decreases the effective number of individuals in a local mating population (Gottlieb 1977, Heywood 1986, Scheiner 1987), and increases the chances of biparental inbreeding. The size distribution of *S. angularis* is leptokurtic because only 10–15% of all plants are defined as large. Weighting large plants in terms of their disproportionate reproductive output through female and male function further increases the kurtosis in the size distribution, demonstrating how important a few large individuals can be in local population dynamics.

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