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(Gentianaceae)**



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**VARIATION IN POLLEN LIMITATION
 AMONG INDIVIDUALS OF
 SABATIA ANGULARIS
 (GENTIANACEAE)**

Michele R. Dudash^{1,2}

Pollen limitation is unambiguously demonstrated when hand-supplementation of outcrossed pollen to all flowers on an individual results in a significant increase in seed and/or fruit set per plant compared to naturally pollinated plants (e.g., Johnston 1991a, and references therein, Young and Young 1992, and references therein). The degree of pollen limitation can vary among years (e.g., Campbell 1987, Lubbers and Lechowicz 1989), within a season (e.g., Hainsworth et al. 1985, Zimmerman and Aide 1989), among sites within a season (e.g., Campbell 1987, Johnston 1991a), and among plants flowering synchronously within a site (e.g., Snow 1986). Individual variation in pollen limitation may have direct consequences on an individual's fitness. However, we know little about the factors responsible for variation in pollen limitation among individuals within a population.

Plant populations are often size structured, consisting of many small individuals and relatively few large ones (e.g., Harper 1977). If a taxon is semelparous, adult size structuring can have direct effects on an individual's reproductive fitness in terms of potential female (seeds and fruits) and male (pollen production) function (e.g., Dudash 1991). The interactions among plant size, pollinator attraction, and pollen limitation may influence an individual's fitness. Flowering phenology may vary as a function of plant size and differentially influence reproductive output. Selection on floral traits associated with pollinator attraction may vary among individuals in different size classes. Larger inflorescences often have greater probability of maturing fruit (Ackerman and Montalvo 1983, Paton and Turner 1985) and attracting visually cued pollinators (Inoue 1985) than smaller ones. Additionally, significantly greater pollen loads are found on stigmas of large plants compared to small plants (Dudash 1991, but see Weller 1980, Webb and Bawa 1983), differentially in-

fluencing seed production per plant as a function of plant size.

The primary objective of this study was to determine if plant size affects the magnitude of pollen limitation on fruit and seed production throughout the flowering season of monocarpic *Sabatia angularis*. I have demonstrated previously that plant size disproportionately influenced male and female function in the size-structured population of *S. angularis* (Dudash 1991). Larger plants in the population matured on average twice the number of seed per fruit, produced significantly more pollen per flower, and had significantly more pollen grains deposited on their stigmas compared to smaller plants. This study investigates the role of pollen limitation in contributing to the observed differential seed and fruit production among individuals.

Materials and Methods

Study plant and study site. *Sabatia angularis* L. (Gentianaceae) is self-compatible, protandrous, and obligately biennial. In contrast to many monocarpic species (e.g., Werner 1975), *S. angularis* exhibits tremendous variability in size at flowering. Adults range from 3 to 80 cm in height and have 1–200 flowers per individual. Flowering densities of *Sabatia angularis* range from 1 to 100 individuals per square metre in bands surrounding the margins of large permanent and small temporary interdunal ponds at Miller Dunes, Indiana (Dudash 1987). The primary visitors to *S. angularis* are leaf-cutter bees (Megachilidae), 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.

To determine whether the degree of pollen limitation experienced by an individual was a function of plant size, I chose to study the extremes of the size distribution of my study population. Large plants were defined as those individuals expected to produce >25 flowers ($\bar{X} \pm 1 \text{ SE} = 27.5 \pm 3.6$ flowers), and small plants were defined as those individuals that produced <7 flowers (2.6 ± 0.2 flowers) representing 10–15% and 50% of the population, respectively (Dudash 1991).

Flowering phenology. A phenological study was performed where I monitored total flower production of 74 small and 22 large randomly chosen plants in close proximity to one another. The flowering data could not be normalized, prompting the use of nonparametric tests of significance. A Kolmogorov–Smirnov two-sample test was performed to determine if the distribution of flowering over time (phenology) differed between small and large plants (Hollander and Wolfe 1973). A Wilcoxon rank two-sample test (SAS 1985) was used to compare date of first flowering between small and large plants.

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TABLE 1. Comparison of the control (no treatment) and experimental (all flowers pollinated by hand-outcrossing) pollination treatments in large and small plants of *Sabatia angularis*, where n = the number of plants per treatment. (a) Average fruit production per individual, (b) percentage of flowers developing into fruits, and (c) mean seed number per fruit per plant. Plant means \pm 1 SE are presented.

Plant size	n	Pollination treatment		P
		Control	Experimental	
a) No. fruits* per plant				
Small	37	2.6 \pm 0.2	2.5 \pm 0.2	NS
Large	11	28.0 \pm 3.8	26.7 \pm 3.4	NS
b) % fruit set†				
Small	37	93.0 \pm 2.3	99.0 \pm 0.7	<.01
Large	11	92.0 \pm 3.6	98.0 \pm 0.6	<.05
c) Seed set/fruit*				
Small	37	405.6 \pm 29.5	431.8 \pm 25.2	NS
Large	11	610.7 \pm 57.0	810.3 \pm 44.2	<.05

* Analyzed with two-way Model I ANOVA.

† Analyzed with two-sample rank test.

Pollen limitation experiment. I examined pollen limitation for the same small and large plants used in the phenological study. The control plants were unmanipulated and were allowed to undergo open-pollination. All flowers on experimental plants were hand-pollinated with pollen from single donors located > 1 m away to minimize the likelihood of performing matings between closely related individuals and the subsequent expression of inbreeding depression (Dudash 1990). Thirty-seven small plants and eleven large plants were randomly assigned to each pollination treatment. The fates of all flowers on each plant were monitored. Wilcoxon rank two-sample tests (SAS 1985) were performed separately for the small and large plants to compare the percentage of flowers developing into fruits (arcsine transformed) following the two pollination treatments when the data could not be normalized after being transformed.

The seeds from each fruit were counted and weighed en masse for all fruits produced by the small plants (\bar{X} = 2.5 fruits per plant) and seven randomly chosen fruits from each large plant (see Table 1 for the ANOVA results and range in total fruit production). The fruits chosen from the large plants represented the 1st d of flowering and were sampled evenly throughout the duration of flowering for each large plant. When more than one flower opened on any given day, the fruit sampled was randomly chosen. Total seed mass of each fruit was divided by its seed number to estimate average seed mass. Two-way ANOVAs (SAS 1985) were used to determine the effect of plant size and pollination treatment on seed production and average seed mass. I attempted an ANOVA (SAS 1985) to factor out flowering date as a covariate of seed production,

in addition to determining the effect of plant size and pollination treatment. In order to prevent pseudoreplication on a per plant basis I had to lump all the flowering data from each individual and calculate an average or use date of first flower for each plant. Neither approach was useful in interpreting my data. Additionally, because small and large plants flowered at significantly different times in the season, sample sizes on a given date were insufficient to examine the effects of plant size and flowering date (as a main effect) on fecundity in the ANOVAs. Thus, to examine the effects of flowering date on the small and large treatment groups, I performed a series of regressions (SAS 1985) of flowering date on seed production per fruit.

Results

Flowering phenology. No significant difference in flowering phenology was detected between the treatment groups within a size class. Flowering phenology differed significantly between small and large plants (Kolmogorov-Smirnov two-sample test: $D_{\max} = 3.07$, $P < .0001$). Peak flowering occurred an average of 6 d earlier in large plants than small plants in a 6-wk flowering season. Average date of first flowering differed by 10 d for the small and large plants (Wilcoxon rank two-sample test: $s = 429.0$, $P < .0001$).

Pollen limitation experiment. Significantly more flowers developed into fruits in the pollen supplementation treatment than the control treatment for both small and large plants (Wilcoxon rank two-sample test; Table 1). Hand-outcrossed flowers of large plants produced significantly more seed per fruit compared to the control group. In contrast, there was no significant difference in seed production per fruit between the control and experimental pollination treatments for small plants (Table 1). Overall, the ANOVA showed that large plants produced significantly more seeds per fruit than small plants, regardless of the pollination treatment ($F_{1,92} = 51.5$, $P < .0001$). The variable effect of pollen supplementation depending on plant size is indicated by the significant interaction term in the ANOVA ($F_{1,92} = 4.5$, $P < .05$). I detected no significant effect of pollination treatment ($F_{1,92} = 0.1$, $P = .7$) or plant size ($F_{1,92} = 3.03$, $P = .1$) on average seed mass.

Significant negative regressions of seed number per fruit on flowering date were found for the control (small: $r^2 = 0.06$, B [slope] = -8.8 , $P < .05$; large: $r^2 = 0.19$, $B = -23.6$, $P < .0001$) and experimental (small: $r^2 = 0.15$, $B = -16.6$, $P < .001$; large: $r^2 = 0.41$, $B = -37.4$, $P < .0001$) pollination groups. A homogeneity of slopes test revealed no significant difference between the two pollination treatment groups within a size class (small: $F = 1.8$, $P = .2$; large: $F = 3.13$, $P = .1$). There were, however, significant differences in the slopes of the regressions between small and large plants (pollination

treatment data pooled within a size class, $F = 16.39$, $P < .0001$). Large plants' seed production per fruit decreased more rapidly as the flowering season progressed for both the control and experimental group compared to small plants.

Discussion

The extent of pollen limitation differed between small and large plants. While large plants were pollen limited at both the fruit and seed level, small plants exhibited pollen limitation only at the fruit level. Significantly more pollen grains were deposited on stigmas of large plants, but were still more pollen limited than small plants (Dudash 1991, this study). Large plants also have more ovules per pistil to fertilize than small plants (M. R. Dudash, *personal observation*). Thus, pollen limitation is more severe in large plants affecting both fruit and seed set, especially early in the flowering season when pollinators are initially being attracted to the early-flowering, large plants of *S. angularis*. Selection on floral traits associated with pollinator attraction may vary among individuals in different size classes.

The delayed flowering phenology of small plants compared to large plants makes them more susceptible to seasonal depletion of soil moisture and other resources (Dudash 1987). Small and large basal rosettes of *S. angularis* initiate inflorescences synchronously, but subsequent growth and flowering is slower for small individuals (M. R. Dudash, *unpublished data*). Large plants also flower earlier than small ones in the desert annual, *Eriogonum abertianum* (e.g., Fox 1989) and in two short-lived perennial *Lobelia* species (Johnston 1991b). Therefore, resources other than pollen may be limiting reproductive output (e.g., Zimmerman and Aide 1989).

The effect of flowering date on seed production per fruit was greater for the large plants than the small plants. However, the large plants' overall reproductive success was still far greater than the small plants. From mid-August, the potential seed production per fruit of the late-flowering small plants was greater than that for the earlier flowering large plants. The duration of flowering was staggered over a longer period of time in large plants, because large plants had on average 10 times the number of flowers as small plants (Dudash 1991). A correlation between plant size and flowering duration has also been found in *Linanthus androsaceus* (Schmitt 1983) and in two *Lobelia* species (Johnston 1991b).

A monocarpic species should be under strong selective pressure for flowers to develop into fruits, regardless of seed number. Even if some flowers function solely as males (no pollen limitation) there is still a much greater chance of failure to contribute towards the production of offspring than if one is also capable

of seed production. For the majority of the 1983 flowering season >80% of all flowers developed into fruits on 450 randomly chosen individuals of *S. angularis* (Dudash 1987). Seed production in the field ranged from 9 to 1600 seeds per fruit, but very low seed set was rare (Dudash 1987). The ability of *S. angularis* to set a fruit containing very few seeds parallels observations on the perennial *Oxalis magnifica* (Guth and Weller 1986), and differs from results in other perennial species where a minimum pollen load is required to promote fruit formation (e.g., Bertin 1982, Schemske and Fenster 1983, Snow 1986). Because *S. angularis* is a monocarp, any reduction in potential seed and/or fruit production among individuals of different sizes may directly promote fitness differences among those individuals.

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INFERRING EXTINCTION FROM SIGHTING DATA

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The existence of certain rare species of animal is known only through occasional chance sightings. If the species is endangered, then it is possible to infer its extinction from the time of the most recent sighting. For example, the conclusion by LeBoeuf et al. (1986) that the Caribbean monk seal is extinct was based in part on the fact that it has not been sighted since 1952. The purpose of this note is to describe two simple methods for statistical inference about extinction from a record of sightings.

The methods described in this note assume that, prior to extinction, sightings follow a stationary Poisson process. The first method is based on classical sta-

tistical inference, while the second method takes a Bayesian approach. Classical methods of inference in Poisson process are discussed in Cox and Lewis (1966). The Bayesian approach is similar to that developed by Raftery and Akman (1986), which contains additional references.

Methods

Suppose that during the period of observation (0, T) sightings occur at ordered times $\mathbf{t} = (t_1, t_2, \dots, t_n)$. These sightings are assumed to represent a realization of a Poisson process with rate function:

$$m(s) = \begin{cases} m & 0 \leq s \leq T_E \\ 0 & s > T_E \end{cases} \quad (1)$$

The pre-extinction sighting rate m and the time of extinction T_E are unknown. The Poisson process and its properties are discussed in most elementary texts on stochastic processes (e.g., Taylor and Karlin 1984).

Interest centers on testing the null hypothesis that extinction has not occurred (i.e., $H_0: T_E = T$ (or equivalently, $T_E > T$)) against the alternative hypothesis that it has (i.e., $H_1: T_E < T$). Let T_i be the random variable of which t_i is a realization. A natural statistic for testing H_0 against H_1 is the time of the most recent sighting

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