

EFFECTS OF POLLEN LOAD AND DONOR DIVERSITY ON SEED AND FRUIT MASS IN THE COLUMNAR CACTUS, *PACHYCEREUS SCHOTTII* (CACTACEAE)

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As seed and fruit size can influence the success of later life history stages, it is important to understand their sources of variation. In this study, we examined the effects of pollen load and donor diversity on variation in seed and fruit mass of outcrossing senita cacti (*Pachycereus schottii*) in the Sonoran Desert. By massing all individual seeds per fruit from pollen supplementation and donor diversity experiments, we were able to examine their effects on seed and fruit mass, compared with intra- and interplant variation. Seed and fruit mass showed up to 13- and 15-fold variations, respectively. Pollen load did statistically increase seed and fruit mass, but it explained <6% of their variation. Pollen donor diversity did not affect seed or fruit mass. Variation in seed and fruit mass was explained by interplant variation (19%), intraplant variation among fruits (30%), and intrafruit variation (50%). These results indicate that intra- and interplant sources, excluding pollen load and donor diversity but possibly including environmental, architectural, and maternal effects, contribute to the substantial variation observed in seed and fruit mass of senita cacti. Such variation may prove useful for plant recruitment under the highly variable water- and nutrient-stressed conditions of desert environments.

Keywords: fruit, mass, maternal effects, pollen donor diversity, pollen load, pollen quality, seed, senita, size.

Introduction

Seed size can span six orders of magnitude, varying more among than within species and more within a plant than among plants within or among populations (Harper et al. 1970; Westoby et al. 1992; Moles et al. 2005). Such variation in seed size can have consequences for later life stages of plants, including seed dispersal and successful establishment, seedling vigor and survival, and adult reproduction (Harper 1977; Crawley 1997; Westoby et al. 2002; Halpern 2005). For example, large-seeded plants are often good competitors with high survival, whereas small-seeded plants are often good colonizers with low survival, leading to a trade-off between seed size and number. Like seed size, fruit size shows considerable variation within and among species, also having consequences for plant demography by influencing seed dispersers (Wheelwright 1985; Mack 1993; Mazer and Wheelwright 1993; Jordano 1987, 1995; Kitamura et al. 2002; Bollen et al. 2004; Lord 2004). For example, fruit size can influence how attractive fruits are to animal dispersers and hence which frugivores eat and disperse seeds given their gape size. Because of their consequences for the ecology and evolution of plants, much attention has been given to sources of variation in seed and fruit size.

In contrast to factors shaping interspecific variation in seed and fruit size, ranging from plant growth form and dispersal mode to biogeography and genome size (Leishman et al. 2000; Westoby et al. 2002; Beaulieu et al. 2007), we have less understanding of some of the sources of intraspecific variation in seed and fruit size. As seed and fruit size can influence later

life history stages of plants, it is important to understand their sources of variation. Such sources of intraspecific variation may include environmental condition among plants; variation in resources within plants; architectural effects within plants; pollen quantity or donor diversity deposited on flowers; and, among others, maternal and paternal effects (Vander Kloet 1984; Galen et al. 1985; Antonovics and Schmitt 1986; Mazer et al. 1986; Nakamura and Stanton 1989; Venable and Burquez 1989; Biere 1991; Wolfe 1992; Schmid and Dolt 1994; Diggle 1995; Waser et al. 1995; Byers et al. 1997; Brown and Kephart 1999; Lipow and Wyatt 1999; Niesenbaum 1999; Dogterom et al. 2000; Galloway 2001; Bañuelos and Obeso 2003; Davis 2004; Halpern 2005). While maternal effects are emerging as a consistent source of variation in seed and fruit size, comparatively less attention has been given to any potential effects arising from pollination. Such pollination effects may well contribute to the extensive within- (and among-) plant variation in seed and fruit mass. Yet few experimental studies have examined pollination effects of pollen load and donor diversity on variation in seed and fruit size in a way that allows for their direct comparison with maternal effects on within- and among-plant variation in seed and fruit size.

In this study, we examined the pollination effects of pollen load and pollen donor diversity on seed and fruit mass of senita cacti (*Pachycereus schottii*) in the Sonoran Desert. Prior studies of senita have shown that its reproductive output in terms of the quantity of seeds and fruit, as measured by fruit-to-flower ratios at the whole-plant level and seed-to-ovules at the individual flower level, is not limited by pollen loads or influenced by pollen donor diversity (Holland and Fleming 2002; Holland et al. 2004; Holland and Chamberlain 2007). Alternatively, effects of pollen load or donor diversity may be manifest in terms of seed and fruit size, as plants may invest more

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or less in seeds and fruit given such aspects of the pollination process. However, variation in seed and fruit mass may arise from intra- and interplant effects, including within-plant variation in resources and among-plant variation in environmental condition. In either case, seed and fruit mass may be particularly important for senita, as dispersal and recruitment may be driven by the successful establishment and vigor of seedlings under the highly variable water- and nutrient-stressed conditions of desert environments (Godínez-Álvarez et al. 2003). This study aims to examine the extent to which variation in seed and fruit size is shaped by pollen load and donor diversity in comparison to intra- and interplant effects. Because mean seed mass per fruit and mean fruit mass per plant mask and prevent intra- and interplant partitioning of variation in them (Thompson 1984; Thompson and Pellmyr 1989; Mitchell 1997; Davis 2004; Herrera 2009), we measured the mass of all individual seeds per fruit and all fruit per plant from our pollen supplementation and donor diversity experiments. In turn, this allowed us to compare the effects of pollen load and donor diversity with intra- and interplant effects on variation in seed and fruit mass.

Material and Methods

Study Site and Study Organisms

This study was conducted at Organ Pipe Cactus National Monument in Arizona during spring and summer flowering seasons of 2005 and 2006. Endemic to the Sonoran Desert, senita (*Pachycereus schottii* [Engelmann] Hunt [Cactaceae]) is a multistemmed columnar cactus attaining heights of 2–4 m and suspected to live for >75 yr. Senita can produce tens to hundreds of flowers per night from April through July (Holland and Fleming 1999). Flowers are hermaphroditic, containing ~100 anthers, one pistil, and an inferior ovary with 200–400 ovules (Holland and Chamberlain 2007). Fruits contain hundreds of seeds, the smallest in size of the *Pachycereus* genus (Arias and Terrazas 2004), more than 95% of which germinate on moistened filter paper (Holland and Fleming 1999). At sunset, flowers open and anthers dehisce; flowers close <12 h later, often before sunrise, thereby excluding diurnal copollinators (Holland and Fleming 2002). Senita rely on a pollinating seed-eating moth (*Upiga virescens* Hulst; Pyralidae) for pollination, as they are self-incompatible and diurnal bees are typically unimportant (Holland and Fleming 2002). Female moths actively pollinate flowers by rubbing their pollen-covered abdomens directly onto stigmas, after which they lay an egg. Moths then collect pollen by rubbing their abdomens among anthers. Low fruit-to-flower ratios (0.50) and fruit set (fraction of flowers initiating fruit) result from trade-offs in resource (water) allocation between flower production and fruit set (Holland 2002; Holland et al. 2004). Resulting fruit abortion and seed production do not vary with pollen load or donor diversity (Holland et al. 2004). Low seed-to-ovule ratios (0.61) do not arise from pollen or resource limitation, donor diversity, or bet hedging (Holland and Chamberlain 2007). Differential resource allocation does not appear to occur among open- and hand-pollinated flowers (see Zimmerman and Pyke 1988).

Natural Variation in Seed and Fruit Mass

We examined intra- and interplant variation in seed and fruit mass by collecting one to seven ripe fruits from each of 26 plants. For these studies and others described later, study plants were selected randomly from among those that were flowering; fruits from those plants were then chosen haphazardly. For each fruit, we measured fruit mass and the mass of each individual seed per fruit (72–242 seeds per fruit). Using these data, we then calculated mean individual seed mass per fruit, total seed mass per fruit, and the coefficient of variation (CV) in individual seed masses per fruit. We weighed fruits immediately after they were collected with a top-loading balance (0.01 g; Ohaus, Pine Brook, NJ). Seeds were then collected and later weighed with an analytical balance (0.001 mg; Denver Instrument, Denver, CO). In total, we weighed ~28,000 seeds.

We used the Pearson product-moment statistic to test for correlations among mean seed mass per fruit, total seed mass per fruit, CV in individual seed masses per fruit, seed number per fruit, and fruit mass. We do not address seed number beyond these correlation analyses as pollen load and donor diversity do not limit seed production (Holland et al. 2004; Holland and Chamberlain 2007). We used nested ANOVAs (with REML estimates of variance) to examine the effects of plant and fruit within plant on natural variation in individual seed masses per fruit, mean seed mass per fruit, total seed mass per fruit, CV in individual seed masses per fruit, and fruit mass. For analyses of individual seed masses per fruit, the unit of observation was seed, with seed nested within fruit and fruit nested within plant. For analyses of mean seed mass per fruit, total seed mass per fruit, CV in individual seed masses per fruit, and fruit mass, the unit of observation was fruit, with fruit nested with plant. In accord, *F*-tests were conducted by changing denominator (error) terms as appropriate for the particular test of the nested ANOVAs (Littell et al. 2002). We also used PROC VARCOMP of the nested ANOVAs to partition variation in seed and fruit mass among plants, fruits within plant, and seeds within fruit (SAS Institute 2000). We used appropriate transformations as necessary to meet normality assumptions and homogeneity of variance. Statistics were conducted using SAS 9.1 and JMP 5.1 (SAS Institute 2000, 2004).

Pollen Load

We conducted two studies to examine the effect of pollen load on seed mass. First, we examined whether seed and fruit mass varied with natural pollen loads deposited by senita moths. On each of 20 plants, we haphazardly selected one to seven moth-pollinated flowers. The same night as moth pollination we emasculated the flowers to avoid any confounding effect of within-flower pollen transfer to stigmas during flower closing and corolla wilting. Two days later, we clipped the top 15 mm of wilting corollas to collect the stigmas (Holland and Chamberlain 2007). Pollen loads of stigmas were estimated by staining (Calberla's fluid) and counting pollen grains with a microscope (Kearns and Inouye 1993). We collected mature fruit ~25 d later and then measured seed and fruit mass variables as described earlier. We used regression analyses to examine whether mean seed mass per fruit, total seed mass per

fruit, CV in individual seed masses per fruit, and fruit mass varied with natural pollen loads. We used fruits rather than plants as replicates, as most variation in seed and fruit mass occurred within rather than among plants. Averaging fruits within plants would have masked relationships between response variables and pollen load of individual flowers. Second, we examined whether pollen supplementation affects seed and fruit mass by comparing hand-pollinated (HP) flowers with control open-pollinated (OP) flowers. HP flowers were given an excess of pollen from ~50 anthers of a fresh flower from another plant. We treated 6–15 HP and 8–15 OP flowers on each of 20 plants, but only one to eight fruits were available per plant as not all flowers set fruit. We used nested ANOVAs and PROC VARCOMP, with appropriate *F*-tests and REML variance estimates, as described earlier, to examine the effect of pollen supplementation on individual seed masses per fruit, mean seed mass per fruit, total seed mass per fruit, CV in individual seed masses per fruit, and fruit mass, with fruit nested within plant and seeds nested within fruit, as appropriate.

Pollen Donor Diversity

We conducted a pollen donor diversity experiment to examine effects of the number of pollen donors on seed and fruit mass. We manipulated the number of outcross pollen donors while holding pollen quantity constant. We used a randomized design in which each of 26 plants was assigned to one of four pollen donor diversity treatments (1, 2, 3, 4 donors). Five flowers were treated per plant, but not all flowers set fruit, resulting in one to five fruits per plant. We applied pollen from ~100 anthers to stigmas while varying pollen donor diversity. Identities of specific pollen donors varied haphazardly among replicate plants and pollen donor treatment. We used nested ANOVAs and PROC VARCOMP, with appropriate *F*-tests and REML variance estimates, as described earlier, to examine the effect of pollen donor diversity on individual seed masses per fruit, mean seed mass per fruit, total seed mass per fruit, CV in individual seed masses per fruit, and fruit mass, with plant nested within treatment, fruit nested within plant, and seeds nested within fruit, as appropriate.

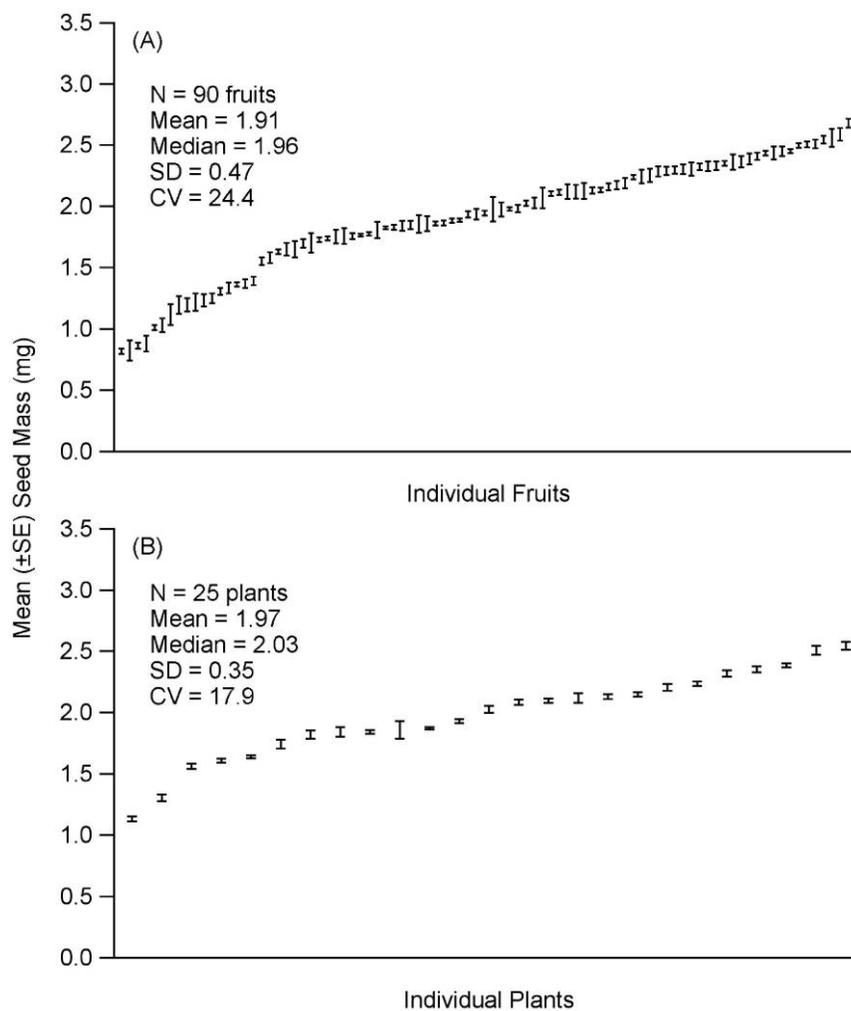


Fig. 1 Mean (\pm SE) seed mass for fruits (A) and plants (B) of senita cacti, ordered by increasing seed mass from left to right. Summary statistics for the distribution of seed mass are presented within each part of the figure.

Results

Natural Variation in Seed and Fruit Mass

Seed and fruit mass showed up to 13- and 15-fold variation, respectively (fig. 1). Significant correlations did occur among seed and fruit mass variables (table 1). Positive correlations among fruits were detected among mean seed mass per fruit, total seed mass per fruit, and fruit mass (table 1). No correlation among fruits occurred between mean seed mass per fruit and seed number, but a positive correlation occurred between total seed mass per fruit and seed number (table 1). Negative correlations among fruits occurred between CV in individual seed masses per fruit and each of mean seed mass per fruit, total seed mass per fruit, fruit mass, and seed number, suggesting that variation in seed mass per fruit decreases with increases in seed mass. These correlations at the level of fruits did not change at the plant level, with the exception of those between CV in individual seed masses per fruit and each of total seed mass per fruit, seed number per fruit, and fruit mass becoming insignificant (table 1). Thus, averaging seed and fruit mass at the plant level can mask their intraplant variation.

Both plant and fruits within plant had significant effects on individual seed masses per fruit, with 15% of variation in individual seed masses explained by plant and 85% of variation explained by fruits within plant and seeds within fruit (table 2). Plant had a significant effect on mean seed mass per fruit and fruit mass, with 24% of their variation explained by plant and 76% explained by fruits within plant (table 2). Plant did not have a significant effect on total seed mass per fruit or CV in individual seed masses per fruit, with most variation (>87%) in them, like that of other seed and fruit mass variables, explained by fruits within plant.

Pollen Load

Mean seed mass per fruit and CV in individual seed masses per fruit did not vary significantly with natural pollen loads deposited by senita moths (fig. 2A, 2C). There was not quite a significant increase in total seed mass per fruit (fig. 2B) and a significant increase in fruit mass (fig. 2D) with natural pollen loads, but pollen load explained <18% of variation in total seed mass per fruit and fruit mass. HP fruit did have statistically greater individual seed masses per fruit over OP fruit, but pollen supplementation explained <3% of variation in individual seed masses per fruit, whereas plant explained 21% and fruits within plant and seeds within fruit explained >76% (table 3). Pollen supplementation did lead to a significant increase in mean seed mass per fruit and fruit mass and a not quite significant increase in total seed mass per fruit (table 3). In each case, pollen supplementation explained <6% of variation, while plant and fruits within plant explained the remaining variation (table 3). Pollen supplementation had no effect on CV in individual seed masses per fruit (table 3).

Pollen Donor Diversity

The number of pollen donors did not affect individual seed masses per fruit, but plant and fruits within plant did have significant effects (table 4). Plant explained 23% of variation in individual seed masses per fruit, whereas fruits within plant and seeds within fruit explained 30% and 48% of their variation, respectively. Pollen donor diversity did not affect mean seed mass per fruit, total seed mass per fruit, CV in individual seed masses per fruit, or fruit mass, but in each case, plant did have a significant effect (table 4). Plant and fruits within plant each explained ~50% of variation in seed and fruit mass.

Table 1

Mean (\pm SE) and Pearson Product-Moment Correlations

	Mean \pm SE	Correlations among variables			
		Mean seed mass	Seed no.	Fruit mass	CV seed mass
Total seed mass (mg):					
Fruits	272 \pm 14	.55 ^{***}	.87 ^{***}	.75 ^{***}	-.51 ^{***}
Plants	281 \pm 23	.55 [*]	.89 ^{***}	.72 ^{**}	-.27 ^{ns}
Mean seed mass (mg):					
Fruits	1.9 \pm .1		.11 ^{ns}	.49 ^{***}	-.60 ^{***}
Plants	1.9 \pm .1		.12 ^{ns}	.53 [*]	-.44 [*]
Seed number:					
Fruits	139 \pm 6			.56 ^{***}	-.36 ^{**}
Plants	141 \pm 10			.56 [*]	-.17 ^{ns}
Fruit mass (g):					
Fruits	5.4 \pm .3				-.22 [*]
Plants	5.4 \pm .5				-.12 ^{ns}
CV seed mass:					
Fruits	24.1 \pm 1.5				
Plants	22.5 \pm 1.7				

Note. Mean seed mass per fruit, total seed mass per fruit, coefficient of variation (CV) in individual seed masses per fruit, seed number per fruit, and fruit mass of senita cacti. For fruits, $n = 91$; for plants, $n = 25$. ns = an insignificant correlation.

* $P < 0.05$.

** $P < 0.001$.

*** $P < 0.0001$.

Table 2**Statistical Results for the Effects of Plant, Fruits within Plant, and Seeds within Fruit**

Source	df	F	P	%Var
Individual seed mass:				
Plant	24	2.4	.0034	14.9
Fruit (plant)	58	98.2	.0001	36.8
Seeds (fruit)	12,570	48.3
Mean seed mass:				
Plant	24	2.08	.010	23.4
Fruit (plant)	65	76.6
Total seed mass:				
Plant	24	1.51	.098	11.7
Fruit (plant)	65	88.3
CV seed mass:				
Plant	24	1.40	.142	12.2
Fruit (plant)	65	87.8
Fruit mass:				
Plant	24	2.38	.003	25.4
Fruit (plant)	65	74.6

Note. Effects on natural variation in individual seed masses per fruit, mean seed mass per fruit, total seed mass per fruit, coefficient of variation (CV) in individual seed masses per fruit, and fruit mass, and the percentage contribution of each source to their total variance (%Var).

Discussion

In addition to variation among species, greater recognition is being made of the causes and consequences of intra- and interplant variation in traits, and their consequences for plant fitness and plant-animal interactions (Herrera 2009). While progress is being made through the study of variation in mean seed mass, this response variable can mask variation in seed mass and prevent the partitioning of variation attributable to plants, fruits within plant, and seeds within fruit (table 1; Thompson 1984; Thompson and Pellmyr 1989; Mitchell 1997; Davis 2004). By massing all individual seeds of each sampled fruit (~28,000 seeds, 180 fruits), we were able to examine the pollination effects of pollen load and donor diversity on variation in seed and fruit mass, compared with intra- and interplant effects. Prior studies of senita have shown that pollen load and donor diversity do not influence their consistently low seed-to-ovule and fruit-to-flower ratios (Holland et al. 2004; Holland and Chamberlain 2007). For this reason, we predicted that pollen load and donor diversity may manifest instead in seed and fruit mass. Contrary to our speculation, and despite extensive variation in seed and fruit mass (fig. 1), pollen load and donor diversity explained little of their variation. Instead, most variation was attributable to intra- and interplant effects. We discuss these results in terms of understanding the role of pollination in shaping intra- and interplant variation in seed and fruit mass.

Pollen load did statistically increase some seed and fruit mass variables, but in no case did it explain more than 6% of variation (table 3). Rather, it was intra- and interplant effects that explained most (95%) variation within and among plants (table 3). Of 21 studies reviewed by Knight et al. (2005), three reported no effect of pollen supplementation on seed mass,

nine reported a negative effect, and nine reported a positive effect, suggesting that any effect of pollen load on seed size may be contingent on other factors. For example, greater pollen loads may increase seed number and seed mass per fruit if plants are pollen limited (Ashman et al. 2004; Knight et al. 2005, 2006), but they may also reduce seed mass if a trade-off occurs between seed size and number. Neither scenario is likely to explain the lack of effect of pollen load on seed mass in senita, as their low seed-to-ovule and fruit-to-flower ratios do not result from pollen limitation (Holland et al. 2004; Holland and Chamberlain 2007), and the lack of a significant negative correlation between seed mass and number suggests no such trade-off (table 1). More studies are needed that assess trade-offs between seed size and number in relation to pollen

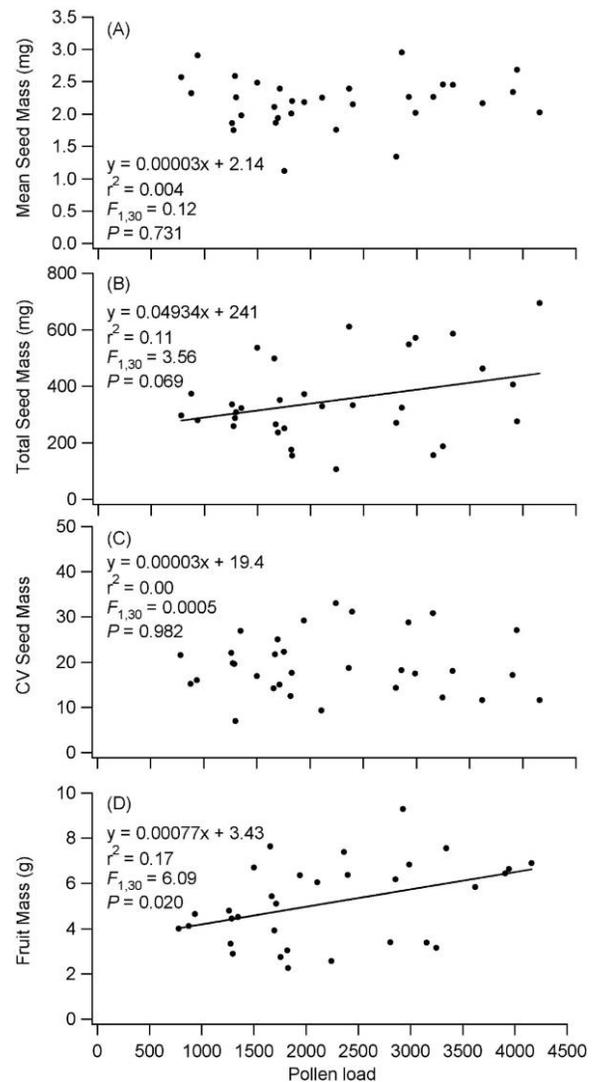


Fig. 2 Linear regression analyses of mean seed mass per fruit, total seed mass per fruit, coefficient of variation (CV) in individual seed masses per fruit, and fruit mass with naturally measured pollen loads (number of pollen grains) deposited by senita moths on stigmas of senita cactus flowers.

Table 3
Statistical Results for the Effects of Pollen Quantity
(Pollen Supplementation vs. Open Pollination)

Source	df	F	P	%Var
Individual seed mass:				
Pollen quantity	1	134.4	.0001	2.8
Plant	18	5.76	.0001	21.4
Fruit (plant)	74	46.1	.0001	20.4
Seeds [fruit (plant)]	15,819	55.4
Mean seed mass:				
Pollen quantity	1	8.35	.005	6.4
Plant	18	4.86	.0001	41.9
Fruit (plant)	92	51.7
Total seed mass:				
Pollen quantity	1	3.30	.072	1.3
Plant	18	4.15	.0001	34.2
Fruit (plant)	92	64.5
CV seed mass:				
Pollen quantity	1	.24	.625	.6
Plant	18	1.39	.156	7.5
Fruit (plant)	92	91.9
Fruit mass:				
Pollen quantity	1	5.76	.018	2.5
Plant	18	6.69	.0001	52.8
Fruit (plant)	92	44.7

Note. Effect on individual seed masses per fruit, mean seed mass per fruit, total seed mass per fruit, coefficient of variation (CV) in individual seed masses per fruit, and fruit mass, and the percentage contribution of each source to their total variance (%Var).

load, as few studies have experimentally tested the effects of pollen load in the context of such a trade-off, and both insignificant and significant relationships have been observed between seed size and number (see Vaughton and Ramsey 1998; Halpern 2005). Alternatively, any effect of pollen load on variation in seed and fruit size may be mediated by stigma clogging or pollen tube competition (Waser 1978; Herrera 2004). Though not directly examined, such factors may be important in senita, as their stigmas receive thousands more pollen grains than there are ovules (Holland and Chamberlain 2007). Despite these and other potential issues, our results indicate that pollen load is not central to or a key biological source of intra- or interplant variation in seed and fruit mass of senita, which is consistent with some findings for other plants (Mitchell 1997; Brown and Kephart 1999; Niesenbaum 1999; Bañuelos and Obeso 2003; Davis 2004).

Like pollen load, pollen donor diversity was not an important source of intra- or interplant variation in seed and fruit size of senita cacti (table 4), which is also consistent with some findings for other plants (Wolfe 1995; Niesenbaum 1999). Nevertheless, pollen donor diversity has been reported to have an effect on seed size and later life stages of other plants, including, for example, germination and seedling vigor and survival (Schemske and Paulter 1984; Vander Kloet 1984; Nakamura 1988; Bañuelos and Obeso 2003). Although pollen donor diversity is not a source of variation in seed and fruit size for senita, it may still affect their later life stages; however, this is not always the case (Mitchell 1997; Niesenbaum 1999; Davis 2004). The lack of an effect of pollen donor diversity in senita may be mediated by other factors such as maternal

choice, sibling rivalry, and parent-offspring conflict (Marshall 1988; Uma Shaanker et al. 1988). If sibling rivalry was occurring among seeds of flowers with different pollen donor diversities, that is, lower relatedness among seeds within and among fruit, then pollen donor diversity should affect seed mass, seed number, seed-to-ovule ratios, or fruit-to-flower ratios, which it has not in senita (table 4; Holland et al. 2004; Holland and Chamberlain 2007).

Although aspects of the pollination process can, in some cases, influence variation in seed or fruit size (Waser 1978; Biere 1991; Dogterom et al. 2000; Herrera 2004), results of our studies indicate that, rather than pollen load and donor diversity, intra- and interplant effects are the dominant source of variation in seed and fruit mass of senita. In the pollen supplementation experiment, 94% of variation in seed and fruit mass was explained by intra- and interplant effects (table 3). In the pollen donor diversity experiment, 93% and 80% of variation in seed and fruit mass, respectively, were explained by intra- and interplant effects (table 4). Averaging among our studies (tables 2–4), 19%, 30%, and 50% of variation in seed mass were explained by plant, fruits within plant, and seeds within fruit. Likewise, 37% and 56% of variation in fruit mass were explained by plant and fruits within plant (tables 2–4). Moreover, variation in seed mass of senita was due more to variation within (80%) than among (19%) plants, which is consistent with the intra- and interplant contributions to variation in seed size of some other plants (Pitelka et al. 1983; Thompson 1984; Thompson and Pellmyr 1989; Vaughton and Ramsey 1998).

Table 4
Statistical Results for the Effects of Pollen Donor Diversity

Source	df	F	P	%Var
Individual seed mass:				
Pollen quality	3	.39	.763	.0
Plant (TRT)	22	2.71	.005	22.7
Fruit (plant)	31	81.0	.0001	29.7
Seeds [fruit (plant)]	7924	47.6
Mean seed mass:				
Pollen quality	3	.40	.755	.0
Plant (TRT)	22	2.84	.001	51.5
Fruit (plant)	30	48.5
Total seed mass:				
Pollen quality	3	1.25	.317	7.4
Plant (TRT)	22	3.14	.002	48.7
Fruit (plant)	31	43.9
CV seed mass:				
Pollen quality	3	.51	.682	.0
Plant (TRT)	22	3.00	.003	49.2
Fruit (plant)	31	50.8
Fruit mass:				
Pollen quality	3	2.25	.111	20.4
Plant (TRT)	22	2.38	.013	32.0
Fruit (plant)	31	47.6

Note. Effect on individual seed masses per fruit, mean seed mass per fruit, total seed mass per fruit, coefficient of variation (CV) in individual seed masses per fruit, and fruit mass, and the percentage contribution of each source to their total variance (%Var). TRT = number of genotypic pollen donors.

Some factors that may contribute to intra- and interplant effects on variation in seed and fruit size include, for example, environmental condition among plants, variation in resource levels within a plant, architectural effects within a plant, maternal genotypic effects, and environmental effects during seed and fruit development (Galen et al. 1985; Biere 1991; Wolfe 1992; Diggle 1995; Lacey 1996; Byers et al. 1997; Vaughton and Ramsey 1998; Galloway 2001; Westoby et al. 2002; Halpern 2005). If interplant variation reflects environmental condition or maternal genotypic effects, then at most 15%–22% of variation in seed mass and 25%–53% of variation in fruit mass are attributable to such sources (tables 2–4). Likewise, if intraplant variation reflects within-plant resource, architectural effects, or environmental effects during development, then 75%–85% of variation in seed mass and 47%–75% of variation in fruit mass are attributable to such sources (tables 2–4). In this way, intraplant (environmental, resource, architectural) effects contributed as much as or more than interplant genetic effects of maternal plants did to variation in seed and fruit size of senita (Mazer 1987; Westoby et al. 2002; cf. Byers et al. 1997). Indeed, seed and fruit size can be influenced by variation in resources within plants (e.g., different stems or branches) and by competition for resources among seeds within fruit and among closely positioned fruit (e.g., Galen et al. 1985; Vaughton and Ramsey 1998). Although variation in resource levels and architectural effects are leading hypotheses, further study is necessary to evaluate their roles in shaping intraplant variation of seed and fruit mass of senita.

In conclusion, our results are consistent with other studies in that pollen load and donor diversity contributed little to seed and fruit size, and intraplant effects contributed more than interplant effects on intraspecific variation in seed and fruit size (Biere 1991; Waser et al. 1995; Mitchell 1997; Niesenbaum 1999; Westoby et al. 2002; Davis 2004). Instead of pollen load and donor diversity, genetic differences among maternal plants and environmental effects within maternal

plants accounted for most of the variation in seed and fruit size of senita cacti. Of these maternal effects, environmental effects within maternal plant contributed more to variation in seed and fruit size than differences among maternal genotypes. Thus, we can surmise that maternal effects are greater than the nearly absent pollination effects, and environmental effects appear greater than differences among maternal genotypes. Nonetheless, further studies of senita cacti, and angiosperms more generally, are needed to address the causes of intra- and interplant variation in seed and fruit size, including quantitative genetic analyses of the relative roles of maternal genotype and environmental effects of within-plant resource levels; tests of interactions between pollen load or pollen donor diversity and the seed size/number trade-off; tests of paternal effects of stigma clogging and pollen tube competition; and among others, tests of interactions between pollen load and donor diversity on germination and seedling performance with seed size. Despite such further research needs, results of this study are consistent with the emerging view that maternal rather than pollination effects explain most intraspecific variation in seed and fruit size (Biere 1991; Waser et al. 1995; Mitchell 1997; Niesenbaum 1999; Westoby et al. 2002; Davis 2004).

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