Alternative Outcomes of Natural and Experimental High Pollen Loads

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ALTERNATIVE OUTCOMES OF NATURAL AND EXPERIMENTAL HIGH POLLEN LOADS[1]

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Abstract. Seed production is usually assumed to be a positive monotonic function of pollen deposition and/or pollinator visitation. If this assumption were correct, there would be only two outcomes of excess pollen levels: an increase in fruit or seed set, or no increase. However, a substantial minority of the studies reviewed here has found that seed production declines with increased pollen loads, both under experimental and natural conditions. To explain this decrease, we propose the following mechanisms: pollen tube crowding, pollen removal or stigma damage by pollen thieves or pollinators, stigma damage during hand-pollination, application of low-diversity or local pollen, effects of bagging flowers, missed stigma receptivity, and the application of inviable pollen. These mechanisms can be distinguished through more complete and more careful experimental designs and incremental pollen supplementation.

Key words: excess pollen; hand-pollination; overpollination; pollen limitation; pollination; reproductive success.

INTRODUCTION

Hand-pollination experiments are designed to test the sufficiency of natural pollination by resulting in one of two outcomes, either an increase or no change in female reproductive success. However, a growing body of evidence indicates that large increases in pollen deposition may, in some cases, actually decrease female reproductive success. The occurrence of this result has important consequences for our interpretation of pollination experiments. We are not the first to suggest or suspect that excess pollination can result in decreased seed production: Darwin (1876: 25) "remembered that Gärtner thought, though without any direct evidence, that an excess of pollen was perhaps injurious. It was therefore necessary to ascertain whether the fertility of the flowers was affected by applying a rather small and an extremely large quantity of pollen to the stigma." Darwin performed hand-pollination experiments using *Ipomoea purpurea,* applying small pollen loads to 64 flowers and large pollen loads to 64 flowers. "The flowers fertilized with little pollen yielded rather more capsules" (62 vs. 57 for large pollen loads) "and seeds" (5.13 vs. 5.07 for large pollen loads) "than did those fertilized with an excess; but the difference is too slight to be of any significance" (chi-squared test performed by us on his data, fruit set $\chi^2 = 2.98$, $P = .08$; not enough data are presented to perform a statistical test on seed production). Because a reduction in seed production resulting from over- or hand-pollination has not been emphasized in the literature, we sought to determine the relative occurrences of the three possible outcomes (hand-pollinated > natural, hand < natural, and no significant difference between hand and natural).

We reviewed all hand-pollination experiments cited in Bierzychudek (1981) and Zimmerman (1988) and did 10-yr surveys (1980–1989) of all pollination studies published in the *American Journal of Botany, Ecology, Evolution,* and *Oecologia.* If the difference in fruit or seed production between hand-pollinated and naturally pollinated flowers was not tested statistically by the author, we performed the appropriate test whenever possible. For example, many authors compared seed production resulting from three treatments (open-pollinated flowers and flowers hand-pollinated with self- and outcross pollen) and then used an ANOVA to test for treatment effects. We used the data presented in these papers to compare the two treatments (open-pollinated and hand-pollinated with outcross pollen), usually performing a *t* test to test for the difference in seed production between the two treatments. In other cases, data were gleaned from graphical figures, and *t* tests or chi-squared tests were performed.

Of the 99 cases for which there are sufficient data, hand-pollination significantly increased female reproductive success in 42 (42.4%), had no significant effect in 40 (40.4%), and significantly reduced female reproductive success in 17 (17.2%) (Table 1). These results indicate that decreased seed production from hand-pollinations may not be a rare event.

Decreases in seed production with increased pollen deposition were not restricted to experimental polli-

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TABLE 1. Summary of data on reproductive success of hand-pollination compared to natural pollination.

Hand > natural (42 species)

Species	Reference	Female success criterion*	Test†	*P*
Amianthium muscaetoxicum	Travis 1984	F	*t*	<.01
		S	*t*	<.01
Anchusa officinalis	Andersson 1988	F	*G*	<.001
Aplectrum hyemale (comparing natural and hand self-pollination)	Hogan 1983	F	χ^2	<.05
Arisaema triphyllum	Bierzychudek 1981	S	@	
Ascelpias syriaca	Morse and Fritz 1983	F	χ^2	<.05
Aspasia principissa	Zimmerman and Aide 1989	F	@	
Brassavola nodosa	Schemske 1980	F	χ^2	<.001
Campsis radicans	Bertin 1982			
2 yr		F	χ^2	<.001
2 yr		S	χ^2	<.001
Chilopsis linearis	Peterson et al. 1982	F	SNK	<.05
Eichornia crassipes 4 mo	Barrett 1980	F	χ^2	<.001
Encyclia cordigera	Janzen et al. 1980	F	@	
Epidendrum ciliare 2 yr	Ackerman and Montalvo 1990	F	*G*	<.001
Erythronium americanum	Harder et al. 1985	S	TK	<.05
Espeletia batata	Berry and Calvo 1989	F	*t*	<.002
E. moritziana	Berry and Calvo 1989	F	*t*	<.002
Gaylussacia frondosa 3 sites, 2 yr, 2 dates = 8 tests	Rathcke 1988	F	*t*	<.05
Inga (4 species)	Koptur 1984	F	χ^2	<.01
Ipomopsis aggregata	Hainesworth et al. 1985			
3 dates		F	SNK	<.05
1 date		S	*t*	<.02
Ipomopsis aggregata	Paige and Whitham 1987	F	*t*	<.05
Kalmia latifolia 2 yr, 2 dates = 4 tests	Rathcke 1988	F	*t*	<.001
Lithospermum caroliniense	Weller 1980	S	ANOVA	<.001
Luehea candida	Haber and Frankie 1982	F	χ^2	<.001
		S	*W*	<.02
Lysimachia quadrifolia "Open" site 1982, 1983 "Scrub" site 1984	McCall and Primack 1985	F	SNK	<.05
Melampyrum pratense when hand-pollinated 4 times	Kwak and Jennersten 1991	S	*t*	<.05
Nepeta cataria	Sih and Baltus 1987	F	ANOVA	<.05
		S	χ^2	<.05
Passiflora vitifolia	Snow 1982	F	χ^2	<.001
		S	*t*	<.001
Phlox divaricata	Willson et al. 1979	F	@	
Platanthera stricta	Patt et al. 1989	F	*D*	<.05
		S	*D*	<.05
Platystemon californicus	Hannan 1981	S	*t*	<.01
Polemonium foliosissimum	Zimmerman 1980	S	*t*	<.001
Polemonium foliosissimum (before controlling for whole-plant effect)	Zimmerman and Pyke 1988	S	ANOVA	<.05
Polemonium viscosum 3 elevations, 2 morphs = 5 tests	Galen 1985	S	*t*	<.01
Rhinanthus angustifolius when hand-pollinated 6 times	Kwak and Jennersten 1986	S	*t*	<.05
Solidago canadensis "late"	Gross and Werner 1983	S	*t*	
open vs. overpollinated				<.001
open vs. bagged and pollinated				<.02
Solidago graminifolia "early"	Gross and Werner 1983	S	*t*	
open vs. overpollinated				<.001
open vs. bagged and pollinated				<.001

TABLE 1. Continued.

Hand > natural (42 species)

Species	Reference	Female success criterion*	Test†	P
Solidago juncea "late" open vs. overpollinated	Gross and Werner 1983	S	*t*	<.05
Staphylea trifolia	Garwood and Horvitz 1985	F	χ^2	<.001
Stellaria pubera "early"	Campbell 1985	S	*t*	=.02
Tipularia discolor	Snow and Whigham 1989	F	*t*	<.001
Veronica cusickii 2 yr	Campbell 1987	F	*t*	<.01
Viscaria vulgaris 1986 when hand-pollinated once	Kwak and Jennersten 1991	S	*t*	<.02

Hand < natural (17 species)

Species	Reference	Female success criterion*	Test†	P
Catalpa speciosa	Stephenson 1979	F	*t*	<.05
Costus laevis	Schemske 1983	S	*t*	<.05
C. guanaiensis	Schemske 1983	S	*t*	<.001
Delphinium nelsoni 1976 study, compare Tables 4 and 6	Waser 1978	S	*t*	<.001
Gaylussacia frondosa Maple 1 site, 8 July 1981	Rathcke 1988	F	*t*	<.05
Geranium maculatum Trelease site, 1976	Willson et al. 1979	F	*t*	<.01
Ipomopsis aggregata§ 1976 study, compare Tables 4 and 6	Waser 1978	S	*t*	<.001
Kalmia latifolia 23 August 1981	Rathcke 1988	F	*t*	<.05
Lobelia telekii uncaged only	Young 1982	S	ANOVA	<.01
Luehea seemannii diurnal crosses	Haber and Frankie 1982	F	χ^2	<.01
Melampyrum pratense when hand-pollinated 1 or 3 times	Kwak and Jennersten 1991	S	*t*	<.01
Mertensia ciliata	Geber 1985	S	*t*	<.001
Rhinanthus angustifolius when hand-pollinated once or twice	Kwak and Jennersten 1986	S	*t*	<.01
Solidago juncea "early" open vs. over-pollinated	Gross and Werner 1983	S	*t*	<.05
Solidago graminifolia "late" open vs. bagged and pollinated	Gross and Werner 1983	S	*t*	<.01
Trientalis borealis	Anderson and Beare 1983	S F	ANOVA ANOVA	<.05 <.05
Viscaria vulgaris 13 June 1988 19 June 1988	Kwak and Jennersten 1991	S	TK	<.05

TABLE 1. Continued.

No significant difference between hand and natural‡ (40 species)

Species	Reference	Female success criterion	Hand	Natural	Test	*P*
Amelanchier arborea	Gorchov 1988	F	0.46	0.38	*G*	=.36
		S	7.2	7.5	MW	=.44
Aplectrum hyemale open vs. bagged with outcrossed pollen	Hogan 1983	F	0.86	0.82	χ^2	=.53
Aquilegia caerulea	J. Brunet (*personal communication*)	F	0.23	0.31	ANOVA	=.07
		S	1.7	2.8	ANOVA	=.07
Argyroxiphium sandwicense	Carr et al. 1986	F	0.30	0.12	*t*	=.09
Calathea ovandensis	Horvitz and Schemske 1988	F	0.081	0.074	*W*	>.05
Cassia fasciculata	Lee and Bazzaz 1982	F	0.82	0.80	ANOVA	=.36
Costus allenii	Schemske 1983	S	45	47	*t*	=.32
Epidendrum ciliare 2 yr	Ackerman and Montalvo 1990	F	0.071	0.070	*G*	=.47
		F	0.15	0.12	*G*	=.29
Espeletia neriifolia	Berry and Calvo 1989	F	0.34	0.52	*t*	=.17
E. lindenii	Berry and Calvo 1989	F	0.50	0.42	*t*	=.60
E. schultzii	Berry and Calvo 1989	F	0.70	0.41	*t*	=.13
E. floccosa	Berry and Calvo 1989	F	0.43	0.47	*t*	=.88
E. semiglobulata	Berry and Calvo 1989	F	0.36	0.08	*t*	=.06
E. spicata	Berry and Calvo 1989	F	0.71	0.59	*t*	=.10
E. timotensis	Berry and Calvo 1989	F	0.85	0.79	*t*	=.45
Erythronium umbilicatum	Motten 1983	F	0.89	0.89	χ^2	>.9
		S	16.2	16.5	ANOVA	=.38
Gaylussacia frondosa	Rathcke 1988	F				
Field 1, 8 July			0.40	0.32	*t*	=.25
Field 2, 8 July			0.48	0.47	*t*	=.83
2 August			0.46	0.46	*t*	>.9
Oak 1, 8 July			0.08	0.05	*t*	>.9
2 August			0.04	0.03	*t*	=.53
Oak 2, 8 July			0.80	0.81	*t*	=.83
2 August			0.30	0.38	*t*	=.16
Maple 3, 8 July			0.26	0.16	*t*	=.37
2 August			0.06	0.07	*t*	=.77
Hepatica americana	Motten 1982	F	0.90	0.95	ANOVA	=.22
Inga oerstediana	Koptur 1984	F	0.12	0.05	χ^2	=.61
I. quarternata	Koptur 1984	F	0.00	0.03	χ^2	=.46
Ipomopsis aggregata, 2 wk	Hainesworth et al. 1985	S	6.4	4.0	*t*	=.19
		S	4.5	3.4	*t*	=.21
Kalmia angustifolia	Rathcke 1988	F	0.90	0.89	*t*	=.88
Kalmia latifolia	Rathcke 1988	F				
9 July 1981			0.68	0.69	*t*	=.60
9 July 1982			0.89	0.92	*t*	=.12
23 August 1982			0.69	0.68	*t*	=.75
Leptospermum scoparium	Primack and Lloyd 1980	F	0.40	0.33	χ^2	=.75
Lobelia telekii (after controlling for bird visitation)	Young 1982	S	310	232	*t*	=.30
Lysimachia quadrifolia "Scrub" site, 1983	McCall and Primack 1985	F	0.44	0.36	SNK	=.70
Melampyrum pratense when hand-pollinated 5 times	Kwak and Jennersten 1991	S	2.3	1.8	*t*	=.10
Polemonium foliosissimum	Zimmerman and Pyke 1988	S	15.4	16.4	MW	>.17
Polemonium viscosum 3640 m elevation, skunky morph	Galen 1985	S	4.37	3.72	*S*	>.05
Raphanus sativus	Stanton 1987	F				
early			0.68	0.72	LL, treatment χ^2	=.93
late			0.44	0.39		
Solidago canadensis	Gross and Werner 1983					
"early"						
open vs. overpollinated		S	30.6	20.3	*t*	=.17
open vs. bagged and pollinated		S	26.6	20.3	*t*	=.49

TABLE 1. Continued.

No significant difference between hand and natural‡ (40 species)

Species	Reference	Female success criterion	Hand	Natural	Test	P
"intermediate"						
open vs. overpollinated		S	44.7	37.1	*t*	=.24
open vs. bagged and pollinated		S	52.7	37.1	*t*	=.06
Solidago juncea "intermediate"	Gross and Werner 1983					
open vs. overpollinated		S	14.0	12.9	*t*	=.90
Solidago graminifolia "late"	Gross and Werner 1983					
open vs. overpollinated		S	27.1	39.6	*t*	=.17
Spathiphyllum friedrichsthalii	Montalvo and Ackerman 1986	F	1.0	0.78	χ^2	=.75
Staphylea trifolia	Garwood and Horvitz 1985	S	2.2	1.8	*G*	=.40
Stellaria pubera "late"	Campbell 1985	S	1.54	1.56	*t*	=.95
Telopea speciosissima	Pyke 1981	F				
Brisbane			0.75	0.96	*t*	=.32
Floralands			1.12	1.21	*t*	=.87
Trientalis borealis (inter-patch pollination)	Anderson and Beare 1983	F	0.84	0.66	ANOVA	>.05
		S	8.5	8.3	ANOVA	>.05
Veronica cusickii	Campbell 1987	F				
site EM, 1981			0.92	0.90	*t*	=.78
site EM, 1982			0.90	0.87	*t*	=.67
site BV, 1981			0.86	0.54	*t*	=.27
Viscaria vulgaris 8 June 1988	Kwak and Jennersten 1991	S	0.61	0.70	TK	>.05

* Female success was measured as fruit set (F = proportion of flowers maturing fruits, except in Pyke [1981] where F = mean number of fruits matured per inflorescence), or as seed set (S = number of seeds per fruit).

† Notes on statistical tests: @ = data were not presented to perform a test for significant differences, significance was assumed from the magnitude of the difference in means between the treatments; *D* = Duncan's multiple-range test; *G* = *G* test; LL = log-linear contingency test (SAS Proc CATMOD); MW = Mann-Whitney *U* test; *S* = Scheffé test for orthogonal contrast; SNK = Student-Newman-Keuls test; *t* = *t* test; TK = Tukey Kramer test; *W* = Wilcoxon test; χ^2 = chi-squared test.

‡ Mean reproductive values are presented for the case of no significant difference between hand and natural, for visual comparison; where possible, precise *P* values are given. If author does not give test value or precise *P* value, *P* is stated as *P* > .05.

§ Waser (1978:936) compared the fruit sets of naturally pollinated plants and plants in the greenhouse, where he pollinated only 60% of the flowers because "this technique approximates the within-plant intensity . . . of hummingbird visitation."

nations. Young (1988) showed a peak in seed production of *Dieffenbachia* at intermediate levels of pollinator (beetle) visitation, with a decrease in seed production at higher visitation levels. She suggested that visitation by large numbers of beetles resulted in the removal of previously deposited pollen on the stigmas (i.e., Gori 1983). A similar pattern also occurs in beetle-pollinated *Astrocaryum mexicanum* (Burquez et al. 1987) and wasp-pollinated figs (Herre 1990). Seed production in *Passiflora vitifolia* showed a nonlinear relationship with the number of pollen grains deposited naturally by hummingbirds: pollen loads between ≈500 and 725 grains resulted in fewer seeds than did smaller pollen loads (Snow 1982: Fig. 5).

Most pollination studies do not measure the effect of varying pollinator visits on seed production, and they use experimental hand-pollinations to determine whether the abundance of pollen or pollinators limits seed production. Below we outline explanations for each of the three possible results of hand-pollinations.

SIGNIFICANT INCREASE IN FEMALE REPRODUCTIVE SUCCESS

Increases in female reproductive success associated with increased pollination are usually considered evidence of pollen and/or pollinator limitation. Application of heavy pollen loads and the resulting increases in seed production suggest that natural pollination levels result in the fertilization of only a fraction of the ovules available. In addition, any time a null hypothesis (of no difference in seed production between hand-pollinated and naturally pollinated flowers) is rejected, there is a possibility of a Type I error. This is especially true when multiple comparisons are made (see Gross and Werner 1983).

SIGNIFICANT DECREASE IN FEMALE REPRODUCTIVE SUCCESS

Current pollination theory makes no allowance for this result. We suspect that this result is under-reported

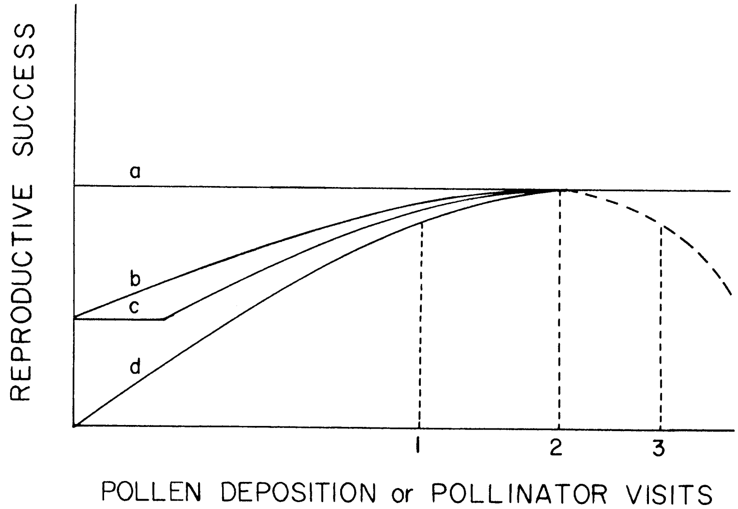

FIG. 1. Solid lines: hypothetical asymptotic relationships between pollen deposition or pollinator visits and female reproductive success. (a) complete self-pollination or apomixis; (b and c) partial self-pollination or apomixis; (d) obligate outcrosser. Dashed line: the effect of high pollen loads decreasing female reproductive success.

(as is the result of no significant difference between hand- and natural pollination). For most of the studies, it is not known what aspect of the experimental procedure caused reduced reproductive success. We suggest several possible explanations for the occurrence of hand-pollination reducing fruit or seed set.

1) At high densities, pollen grains or pollen tubes may interfere with each other to such a degree that fertilization is reduced (suggested by Feinsinger 1987). Negative effects of large pollen loads on pollen tube growth have been documented (Schemske and Fenster 1983, Cruzan 1986).

2) High pollen loads may attract pollen thieves (visitors that do not serve as pollinators) that damage stigmatic surfaces or other female reproductive organs (McDade and Kinsman 1980, Grant and Grant 1981).

TABLE 2. Proposed mechanisms for reduced fruit/seed production of (A) naturally pollinated flowers with increasing pollinator visitation; (B) hand-pollination of naturally pollinated flowers ("overpollination") compared to fruit/seed production of naturally pollinated flowers; and (C) hand-pollination of bagged flowers compared to fruit/seed production of naturally pollinated flowers.

	A	B	C
1. Pollen crowding	X	X	X
2. Pollen thieves remove pollen from stigmas	X	X	
3. Pollinators remove pollen from stigmas	X	X	
4. Stigma damaged from hand-pollination		X	X
5. Low-diversity pollen used		X	X
6. Bagging			X
7. Stigma receptivity missed			X
8. Inviable pollen used			X
9. Insufficient quantity of pollen applied			X

3) Pollinators may indirectly damage female reproductive organs or remove the supplemental pollen from stigmas. Young (1982) found that decreased seed set of hand-pollinated flowers occurred only in inflorescences open to pollinators; he suggested that pollinating sunbirds damaged overpollinated stigmas of *Lobelia* while feeding on the unusually high quantity of pollen there.

4) The stigma may be damaged by the hand-pollination process.

5) Because hand-pollinations frequently use pollen from only one donor, a large amount of low-diversity pollen may swamp a more varied natural pollen diversity and reduce reproductive success relative to natural pollination (cf. Schemske and Pautler 1984, Vander Kloet and Tosh 1984, Ellstrand and Marshall 1986, Marshall and Ellstrand 1986).

6) The bagging process itself may reduce seed set. Gross and Werner (1983) found that hand-pollination reduced seed production in *Solidago graminifolia* late in the season only when the hand-pollinated flowers were bagged.

7) Peak stigma receptivity may be missed by the experimenter.

8) The pollen used may be inviable (Hall and Brown 1977; J. Thomson, *personal communication*) or incompatible (Anderson and Beare 1983). Galen et al. (1989) found that self-pollen applied before outcross pollen resulted in reduced pollen germination and reduced seed production in self-incompatible *Polemonium viscosum*.

9) An insufficient quantity of pollen may be used in hand-pollinations, resulting in reduced seed set (Kwak and Jennersten 1986, 1991).

10) Type I error (the rejection of a true null hypothesis).

Complete and careful experimental designs can help distinguish among many of these possibilities (Table

2). An example follows from *Lobelia telekii* (Young 1982): overpollination of flowers produced fewer seeds than natural levels of pollination (B in Table 2), and hand-pollination of bagged flowers (C) had no distinguishably different effect on seed production than natural pollination. Therefore, any mechanism in common between B and C (1, 4, 5) could not explain the reduction in seed production resulting from overpollination relative to natural pollination. In addition, because hand-pollination of bagged flowers did not reduce seed production (treatment C), mechanisms 1, 4, 5, 6, 7, and 8 could not explain the effects of overpollination. Therefore, only mechanisms 2 (pollen thieves) and 3 (pollinators themselves remove the extra pollen and/or damage stigmas) are left to explain the results of overpollination, and these mechanisms can be distinguished through observation of floral visitors. If pollen thieves or pollinators are suspected of removing the pollen applied by hand, permutations of the experimental treatments can be done: apply the "extra" pollen to flowers that are unlikely to be visited by thieves or pollinators. For example, perform the hand-pollinations at night for species pollinated by diurnal pollinators (see Haber and Frankie 1982).

No Significant Increase in Female Reproductive Success

There are several possible interpretations of the failure to find significant differences in seed or fruit set between hand and natural pollination:

1) The standard interpretation of this result is that natural pollination levels are sufficient for full seed set.

2) In some cases, the failure to find significant differences may be due to Type II error. For several cases in Table 1, moderate increases in sample size (or reductions in experimental error) would likely result in significant differences between hand- and natural pollination treatments. Fifteen of the 56 studies in this category in Table 1 resulted in statistical tests with $.05 < P < .20$. This is nearly twice as many as would be expected by chance ($\chi^2 = 5.22$, $P < .02$).

3) If excess pollination can sometimes reduce fruit or seed set, then a result of no change could occur in pollen-limited situations if pollen loads sufficiently surpass (level 3 in Fig. 1) the optimal level (level 2) to bring fruit or seed set back to natural levels (level 1). Overpollination using small increments of pollen will detect the presence of an optimal pollen load (Haig and Westoby 1988).

Conclusion

We suggest three factors to consider to minimize the likelihood of making incorrect deductions from pollination experiments. First, more complete experimental designs are appropriate: they can reveal details of the relationships between pollen density, pollinator visitation, experimental manipulation, and reproductive success. Complete experimental designs (cf. Young 1982) were rare among the papers we reviewed. Second, if reductions in reproductive success come only at very high pollen or pollinator levels, then a marginal artificial increase in pollen deposition (i.e., an increase in pollen load from level 1 to level 2 in Fig. 1) may be more appropriate to test for pollen limitation than the more usual massive dose (see Haig and Westoby 1988). Although maximal pollen loads would be valid for testing pollinator limitation if an asymptotic relationship between pollen level and reproductive success exists, such a relationship cannot be assumed a priori. Third, control and treatment flowers should be appropriately chosen (data collected simultaneously and from the same area; both control and treatment flowers should be chosen so that reallocation within the plant will not make the data uninterpretable [Zimmerman and Pyke 1988]).

The reductions in seed number with increased pollinator visitation noted by Burquez et al. (1987), Young (1988), and Herre (1990) give rise to a terminological question. If maximal reproductive success occurs at intermediate pollination levels, pollinators can certainly be limiting if they are too few, but might pollinators also be considered limiting if they are too many?

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