THE BOTANICAL REVIEW

VOL. 60 JANUARY–MARCH 1994 NO. 1

Bateman's Principle and Plant Reproduction: The Role of Pollen Limitation in Fruit and Seed Set

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The Botanical Review 60(1): 83–139, Jan.–March 1994

I. Abstract

Bateman's principle states that male fitness is usually limited by the number of matings achieved, while female fitness is usually limited by the resources available for reproduction. When applied to flowering plants this principle leads to the expectation that pollen limitation of fruit and seed set will be uncommon. However, if male searching for mates (including pollen dissemination via external agents) is not sufficiently successful, then the reproductive success of both sexes (or both sex functions in hermaphroditic plants) will be limited by number of matings rather than by resources, and Bateman's principle cannot be expected to apply. Limitation of female success due to inadequate pollen receipt appears to be a common phenomenon in plants. Using published data on 258 species in which fecundity was reported for natural pollination and hand pollination with outcross pollen, I found significant pollen limitation at some times or in some sites in 159 of the 258 species (62%). When experiments were performed multiple times within a growing season, or in multiple sites or years, the statistical significance of pollen limitation commonly varied among times, sites or years, indicating that the pollination environment is not constant. There is some indication that, across species, supplemental pollen leads to increased fruit set more often than increased seed set within fruits, pointing to the importance of gamete packaging strategies in plant reproduction. Species that are highly self-incompatible obtain a greater benefit relative to natural pollination from artificial application of excess outcross pollen than do self-compatible species. This suggests that inadequate pollen receipt is a primary cause of low fecundity rates in perennial plants, which are often self-incompatible. Because flowering plants often allocate considerable resources to pollinator attraction, both export and receipt of pollen could be limited primarily by resource investment in floral advertisement and rewards. But whatever investment is made is attraction, pollinator behavioral stochasticity usually produces wide variation among flowers in reproductive success through both male and female functions. In such circumstances the optimal deployment of resources among megaspores, microspores, and pollinator attraction may often require more flowers or more ovules per flower than will usually be fertilized, in order to benefit from chance fluctuations that bring in large number of pollen grains. Maximizing seed set for the entire plant in a stochastic pollination environment might thus entail a packaging strategy for flower number or ovule number per flower that makes pollen limitation of fruit or seed set likely. Pollen availability may limit female success in individual flowers, entire plants (in a season or over a lifetime), or populations. The appropriate level must be distinguished depending on the nature of the question being addressed.

II. Introduction

An important question in plant reproductive ecology is whether female reproductive success is frequently limited by insufficient receipt of pollen. The adequacy of pollen deposition is expected to affect selection for floral traits relating to male and female function (Bawa & Beach, 1981; Queller, 1987; Waser, 1983; Willson, 1979), the potential for microgametophyte competition (Snow, 1986; Walsh & Charlesworth, 1992), the evolution of breeding systems (Jain, 1976; Stebbins, 1957), the potential for plant-animal coevolution (Feinsinger, 1983), the packaging strategy for ovules (Burd, 1994), and the demography of plant populations.

It is sometimes thought that flowering plants commonly receive sufficient pollen to fertilize all ovules, and only the availability of resources for flower production and for fruit and seed maturation limits female reproductive success. Bateman's (1948) principle is often invoked as the theoretical basis for this supposition. A strict dichotomy between resource and pollen limitation may seldom occur (Haig & Westoby, 1988; Campbell & Halama, 1993), but the assumption that pollen limitation is infrequent appears often in theoretical and empirical work on plant reproduction (Burd & Head, 1992; Charnov, 1979; Kunin, 1992; Stanton & Preston, 1988b; Willson & Burley 1983). In this article I wish to reconsider Bateman's principle and examine the empirical evidence for pollen limitation of fruit and seed set.

There is no doubt that resources are sometimes insufficient to mature all fertilized ovules, while in other cases resources are adequate but pollen deposition is not (and that in other cases seed set is limited by predation or damage from weather). The question of pollen limitation is one of relative frequency. I suggest in this article that pollen limitation of female reproductive success is common, and that we should expect this as the outcome of optimal resource investment strategies in a stochastically fluctuating pollination environment. Insufficient fertilization may affect individual ovules, flowers or inflorescences on a plant, the whole plant (in a single season or during a lifetime), or enire populations (that is, different sites may differ in pollinator activity). The modular gamete packaging characteristic of plants leads to different consequences of pollinator limitation at the different levels. No single scale is the true scale, and the appropriate level or levels depend on the question being asked.

Support for a revised understanding of pollen limitation comes from a compilation of published data comparing reproductive performance under natural pollination and artificial selfing and outcrossing. The data come from 258 species in 77 families. Although it is difficult to assess how representative this sample is of angiosperms in general, the large sample size and the taxonomic, morphological, and habitat diversity of the species in the sample provide confidence that pollen limitation is not an occasional phenomenon of unusual circumstances.

I will review Bateman's (1948) paper on sexual selection and argue that resource limitation of female success does not follow necessarily from Bateman's principle, because males may not find all available females or female gametes. I then consider how Bateman's principle applies to plants, and argue that it may not be a safe assumption that male and female gametes are highly effective in locating each other.

Next I describe the compilation of published data on female reproduction under natural and artificial pollination. I then analyse these data to extract the among-species patterns of overall pollen limitation, the variability of pollen limitation from site to site or year to year, and the differences between fruits and seeds in the degree of pollen limitation. By using data on self-compatibility I consider the hypothesis that low rates of ovule success in some plants may be due to high mutational or recombinational load.

Finally, I consider the implications of the trends identified in the analysis. When pollen receipt is highly variable, the fitness-maximizing allocation of resources may be one that involves an over-stocking of flowers, or ovules within flowers, relative to the average levels of pollination. As a result, we would expect that fitness through both sex functions would often be limited by mating success. Pollen limitation may occur at many levels, and has been well demonstrated at some but not at other levels.

III. Theoretical Considerations

A. BATEMAN'S PRINCIPLE

Bateman's principle has been restated often, in ways that give emphasis to different features of the argument. Bateman himself provided two summaries of his main point. He first gives what might be called the "resources *versus* access" argument: "In most animals the fertility of the female is limited by egg production which causes a severe strain on their nutrition . . . In the male, however, fertility is seldom likely to be limited by sperm production but rather by the number of inseminations or the number of females available to him" (Bateman, 1948, p. 364). He also states a "numerical excess" principle: "The primary cause of intra-masculine selection would thus seem to be that females produce much fewer gametes than males. Consequently there is competition between male *gametes* for the fertilisation of the female *gametes*" (Bateman, 1948, pp. 364–365, italics in original).

These two components of Bateman's principle coincide particularly well in animal species in which the male invests little beyond sperm in the production of offspring. Nonetheless, the differences between the two components reflect genuinely separate features of sexual reproduction, and these differences are important for interpreting the nature of sexual reproduction in plants.

Bateman was interested in showing that mating systems resulted from intra-masculine sexual selection, rather than, as Darwin supposed, that sexual selection occurred because of the mating system. Bateman sought a cause of sexual selection acting on males that was "independent of mating system and probably inherent in the mechanics of sexual reproduction" (1948, p. 352). The numerical superiority of small, usually motile sperm relative to larger eggs is a matter of common observation. Then in sexually reproducing species some males could, in principle, achieve vastly more fertilizations than any female. Only access to eggs limits the success a male realizes, and competition and high variance in success among males follows readily. Anisogamy provided the inherent cause of sexual competition that Bateman sought.

Anisogamy is not a guarantee that female fitness will be limited by resources, however. Competition of three different kinds may occur among males: (1) to locate receptive females, (2) to exclude other males from access to mates, and (3) to be accepted by choosy females. Resources can limit female success only if available female sex cells are found by the searching males. The "resources versus access" argument depends on the outcome of this first kind of competition. Bateman recognized that the motility of male gametes and the searching behavior of males may be due to competition among males (1948, p. 365), but did not consider the potential for failure in searching. If the densities of males and females are chronically low, or if the searching is inefficient for other reasons, then some female gametes may remain unfertilized for want of being found. Fewer than sufficient encounters between eggs and sperm makes the fertility of each sex limited by availability of the other sex (cf. Queller, 1987). It is important to note that availability refers to "effective" or "functional" access, since the numerical difference argument still holds, in principle.

The failure to locate available females or female gametes might be rare in animals, which are usually mobile and can respond behaviorally to sensory cues concerning female location (but see Levitan, 1993). It would also be unusual in animals for only a portion of a female's eggs to be fertilized for want of sperm once she has accepted a male and copulation has occurred. But flowering plants are sessile organisms that ordinarily rely on external agents for export and receipt of pollen from many, often multi-ovulate flowers. Thus some flowers might remain unpollinated, or underpollinated. In plants the adequacy of male "search" for females is not certain. This is an indication that additional nuance may be required when applying Bateman's principle, and particularly the resources-access argument, to plants.

Bateman's principle was extended and modified in an influential paper by Trivers (1972) in which he considered the effect of parental investment on sexual selection. Ecological circumstances may provide greater ultimate reproductive success to males if they invest in parental care of offspring rather than invest in additional matings. Male parental care may even become a limiting resource for female reproductive success in some species (Clutton-Brock, 1991), accompanied by the evolution of competitive mating behaviors on the part of females and discrimination by males among potential mates (Gwynne, 1991).

Male parental care does not obviate the numerical excess principle, which is based on anisogamy, but it can clearly moderate or eliminate the resources-access argument. Likewise in many flowering plants, the need to invest resources in pollinator attraction (and the imperfect control over pollen transfer that such investment brings) may require a modification of the resources-access component of Bateman's principle.

B. THE TRANSFER OF BATEMAN'S PRINCIPLE TO PLANTS

Bateman worked with *Drosophila* but suggested that his argument would apply to plants as well. He noted the tendency for microspores to far outnumber megaspores, and suggested that the brightly colored male catkins and inconspicuous female catkins of insect-pollinated *Salix caprea* resulted from sexual selection (1948, p. 366).

An enormous amount of data indicates that pollen donors compete to fertilize ovules, and there seems little reason not to attribute this to Bateman's numerical excess principle. As noted above, three types of competition can occur among males: competition to locate females, to exclude other males, and to be accepted by females. Bateman's principle does not provide that all three mechanisms of competition are equally likely to occur, however.

Seed abortion or style-pollen tube interactions can result in differential success of individual pollen donors (Bertin, 1988a; Cruzan, 1990; Marshall & Ellstrand, 1988; Stephenson & Winsor, 1986), and this corresponds in some ways to female choice of mates in animals (Willson, 1990) [although Queller (1987) has pointed out the limits to the analogy]. But sometimes ovule fertilization seems to be random with respect to pollen donors (Sork & Schemske, 1992).

Similarly, faster growth of pollen tubes may give some males access to ovules while others are excluded (Snow & Spira, 1991), an analogy to male behavioral contests in animals. However, differences in pollen tube growth rate need not have a genetic basis (Young & Stanton, 1990) or at least need not be heritable (Snow & Mazer, 1988), and the evolutionary interpretation of pollen tube competition is unclear at present (Queller, 1987; Walsh & Charlesworth, 1992).

Competition for pollinator service is analogous to mate searching in animals. Numerous reproductive traits have been interpreted as evidence of male competition to export pollen, including the size of floral displays (Sutherland & Delph, 1984; Queller, 1983; Willson & Price, 1977; Wyatt, 1982; but see Broyles & Wyatt, 1990), duration and floral rewards of male flowers or staminate phases of perfect flowers

Table I

Variation in stigmatic pollen loads reported in the literature

Species	Stigmatic Pollen		Reference
	$\bar{x} \pm s$	Range	
Besleria triflora	3375 ± 7807[a]	(0, 78000[a]	Feinsinger et al. 1986
Cassia reticulata		(0, 300)	Snow & Roubik 1987
Daphne kamtchatica		(0, 40)	Kikuzawa 1989
Drymonia rubra	1366 ± 3361[a]	(0, 22500[a]	Feinsinger et al. 1986
Hansteinia blepharorachis	11.1 ± 18.6[a]	(0, 140)[a]	Feinsinger et al. 1986
Ipomoea trichocarpa	90.7 ± 51.8	(8, 292)	Murcia 1990
Jepsonia heterandra	215.6[b]	(73, 503)[b]	Ornduff 1971
Passiflora vitifolia		(<25, > 1000	Snow 1982
Pavonia dasypetala		(1, 104)	McDade & Davidar 1984
Psiguria warscewiczii	1029[c]	(20, 5000)[c]	Murawski 1987
Razisea spicata	5.9 ± 12.6[a]	(0, 83)[a]	Feinsinger et al. 1986
Staberoha banksii	18.3 ± 22.6	(0, 196)	Honig et al. 1992
Trichanthera gigantea		(0, > 8)	McDade 1983

[a] Conspecific pollen only.
[b] Pin pollen on thrum stigmas.
[c] Pollen tetrads.

(Bell et al., 1984; Delph & Lively, 1992), corolla size (Bell, 1985; Stanton & Preston, 1988a) and other aspects of floral morphology (Campbell et al., 1991; Cruzan et al., 1988; Galen & Stanton, 1989; Harder & Thomson, 1989; Stanton et. al., 1986; Young & Stanton, 1990) (but see Wilson et al., 1994, for an interpretation of floral traits based on selection for female function).

The numerical excess principle seems to explain why competition to locate ovules (through a pollen vector) occurs, but Bateman's principle is silent concerning the outcome of this competition. In a particular population pollinators may deposit a superfluity of pollen grains on stigmas or they may not (or, most likely, there will be variation among flowers and plants such that some have adequate pollen and others not, and the pattern may vary from year to year).

Table I presents distributional statistics for stigmatic pollen loads in species having a variety of pollination vectors. Variation over several orders of magnitude is common within populations (see also Bertin & Sholes, 1993; Cruzan et al., 1988; Elam & Linhart, 1988; Garwood & Horvitz, 1985; Koptur, 1984). These data, especially the regular occurrence of stigmatic loads of zero, reveal the difficulties and inefficiencies in the search for mates. Whether resource limitation of female reproduction occurs depends, of course, on the outcome of male competition to locate ovules through pollen vectors.

IV. Compilation of Data

Artificial pollination is frequently used to assess self-compatibility or other aspects of the mating system as well as to examine pollen limitation. Thus a large literature involving a wide variety of plants, habitats, and geographical locations is available. Hand pollination experiments are not the only means by which pollen limitation might be assessed. Low stigmatic pollen loads relative to ovule number (Snow, 1986), or correlations of seed set with number of pollinator visits (Real & Rathcke, 1991) may indicate pollen limitation. However, in order to compile a cohesive data set obtained by similar methods, I relied solely on studies using hand pollination.

To locate relevant studies, I consulted initially my own collection of literature on plant reproduction and the studies used by Young and Young (1992). I also surveyed the titles of articles appearing from 1980 through 1992 in *American Journal of Botany, Bulletin of the Torrey Botanical Club, Ecology, Plant Species Biology,* and *Plant Systematics and Evolution,* and checked all articles that seemed likely, judging from the title, to involve hand pollination as an experimental technique. When authors in the sample cited other studies involving hand pollination, I consulted the cited articles.

I located articles containing usable data on 258 species in 77 families. The complete data set is presented in Appendix I. It is impossible to know how well this sample represents angiosperm populations in general. Young and Young (1992) suggest that experiments in which hand pollination had no significant effect on fecundity often go unreported in the literature. However, Wilson et al. (1994) suggest that most tests occur in the plant populations least likely to experience pollinator limitation, so that non-significant effects of hand pollination would be over-represented in the literature. Many of the studies cited in Appendix I were investigations of self-compatibility rather than pollen limitation per se, which would tend to ease any reporting bias.

Objectives of the various studies and their techniques and manner of reporting data differed. I excluded from consideration data on cultivated plants or on greenhouse experiments. I required that data be presented from unmanipulated control flowers and from artificial outcrossings with (at least ostensibly) excess pollen addition to receptive stigmas. Although I did not require it for inclusion of a study, I recorded data from artificial self-pollinations or the authors' indications that a plant was self-compatible, self-incompatible, or dioecious. The data used were the mean effects of each treatment.

When hand outcross pollinations were made to both open flowers (supplemental pollination) and bagged flowers in a single experiment, I used the data from open flowers (e.g., Gross & Werner, 1983). However, in some studies only bagged outcrosses were employed, so among the various studies contributing to the data set, I did not distinguish between bagged and open flowers. Bagging is, nonetheless, an additional difference between experimental and control flowers that may affect reproductive performance.

Data from outcrossings among patches were preferred over "outcrossings" within a patch, especially in clonal species for which intra-patch pollinations may actuallly be selfings within a genet (e.g., Anderson & Beare, 1983). When multiple outcross treatments were used, I took the results from the least manipulative [e.g., treatments not involving emasculation were preferred over emasculation (Kevan, 1972)], or from the one corresponding most closely to natural pollination [e.g., nocturnal hand pollinations were preferred in the nocturnally moth-pollinated trees *Luehea candida* and *L. seemannii* (Haber & Frankie, 1982)].

Various measures of female success were reported. The most common was percent fruit set, followed by seed number per fruit. Other commonly used measures were percent seed set (the fraction of ovules maturing to seeds) and number of seeds per flower (similar to seed number per fruit but accounting for aborted flowers as well). Multiple measures were sometimes given for a single experiment. In such cases the data provide an indication of how supplemental pollen affects fruit set vs. seed number within fruits. In total I identified nine standard types of data, along with some ideosyncratic measures (see Appendix I). Even within a standard type there may exist variation. For example, percent fruit set may refer to the fraction of all flowers in a treatment setting fruit (taking each flower as a replicate of the experiment), or to the mean of fruit set from several plants (taking plants as replicates). Distinctions such as this were not always made clear (even implicitly, as by the inclusion of standard deviations), so I have not attempted to further divide the categories. When initial fruit development was distinguished from final maturation (e.g., Rathcke, 1988), I used only the data for final fruit set.

When multiple sites, years, or other samples were used, I preserved the subsets of the authors. This provides a valuable indication of the variability of pollen limitation. Most studies reported data from samples of entire populations for entire growing seasons. For seven species in Appendix I percent fruit set data were given for individual plants or population subsets such as morphs in a way that allowed totalling for the entire population. For these seven species I calculated the totals [*Argyroxiphium sandwicense* (Compositae), *Raphanus sativus* (Cruciferae), *Andira inermis* (Leguminosae), *Leptospermum scoparium* (Myrtaceae), *Oncidium variegatum* (Orchidaceae), *Eichornia crassipes* (Pontederiaceae), *Mitchella repens* (Rubiaceae)]. Thus, to the extent possible the data in Appendix I are population samples for a reproductive season. Where data represent my totalling, this is indicated.

I employed the taxonomic nomenclature of the authors, and I have largely preserved the format in which data were given in the original references.

Appendix I indicates the results of statistical tests contrasting female success from natural pollination and hand outcrossing treatments. When the authors of a study performed a test, I used their result. When no test was made, but data were presented as percent fruit based on individual flowers as replicates, I performed a χ^2 test of independence between treatment (natural vs. hand outcrossing) and outcome (fruit vs. no fruit), using a continuity correction due to a single degree of freedom in the test (Steel & Torrie, 1960). Often no statistical test was performed and the reported data were not appropriate for my test of independence, but the author(s) concluded that pollen limitation did or did not occur based on the magnitude of the difference between natural and hand pollination. Results based on these conclusions or on my test are distinguished in the Appendix and in all figures.

V. Analysis

A. PATTERNS AMONG SPECIES

A breakdown of results by type of data reported is presented in Table II. For all measures of female performance, pollen limitation seems common, involving at least a third of the species in the sample. Pollen limitation is especially apparent in the overall sample and in the percent fruit set data (which make up most of the overall data).

Of 258 species in the sample, 159 (62%) were significantly pollen limited in female reproductive success at some times or sites. Nine of the 159 species showing some pollen limitation presented data for morphs within a population or periods within a

Table II

Summary of the data in Appendix I. Entries give the number of species showing each pattern of natural pollination vs. hand outcrossing, categorized by the type of data reported.

Type of Data[b]	No. of Species	No. of Families	Outcome of Treatments[a]		
			Outcross < Nat.	NS	Outcross > Nat.
All data	258	77	10[c] (4%)	90 (35%)	159 (62%)
%f	207	70	5 (2%)	79 (38%)	123 (59%)
%s	29	16	0	16 (55%)	13 (45%)
s/fl	17	12	1 (6%)	6 (35%)	10 (58%)
s/fr	86	39	5 (6%)	57 (66%)	24 (28%)
s/pl	8	7	0	1 (12%)	7 (88%)
f/pl	4	4	0	1 (25%)	3 (75%)
%i	6	3	0	0	6 (100%)

[a] NS indicates a non-significant difference between natural pollination and hand outcrossing. The other two categories are for significant differences in the direction indicated. Species contributing to the "Outcross > Natural" category showed significant pollen limitation at some times or sites, but not necessarily in every experimental test performed.

[b] Notation is the same as that used in Appendix I.

[c] Includes *Allium tricoccum* (Liliaceae), which also contributes to the "Outcross > Natural" category from results in a second year (see data in the Appendix).

growing season (e.g., Copeland & Whelan, 1989; Dudash, 1993) for which I could not calculate results for the whole population or season from the data given. This does not imply that the combined data would not indicate pollen limitation, merely that the data, as presented, could not be directly totalled to give results for the whole season or whole population. Nonetheless, even if one excludes all nine ambiguous species, there still remain 150 species, or 58% of the total sample, having pollen-limited fruit or seed set at the whole-population level in some sites or years.

The magnitude of differences between natural and hand pollination is displayed in Figs. 1–3. In each figure, the result of natural pollination is given on the abscissa and of hand outcrossing on the ordinate. Each plotted symbol represents the outcome for a population in a growing season. Symbols in the upper left indicate that supplemental outcross pollen increased female reproduction over natural levels, while symbols in the lower right indicate the opposite.

The fruit set data in Fig. 1 reveal that the magnitude of pollen limitation is often large. Not only is fruit set enhanced by hand outcrossing in the great majority of cases, the output is often many times greater than that obtained under natural pollination. Data for percent seed set or seed number per fruit in Figs. 2 and 3 are less dramatic, but still show occasional large effects of supplemental pollen.

Hand outcrossing resulted in significantly reduced female performance relative to controls in 11 species in the sample. [*Clintonia borealis* (Lileaceae) is not included in this category in Table II because percent fruit set increased (significantly) by 41% even though seed number per fruit declined (significantly) by 23%, relative to controls.] For some species the data showing a decline are ambiguous. *Clintonia borealis* seems to benefit overall from extra pollen, even though seed number per fruit

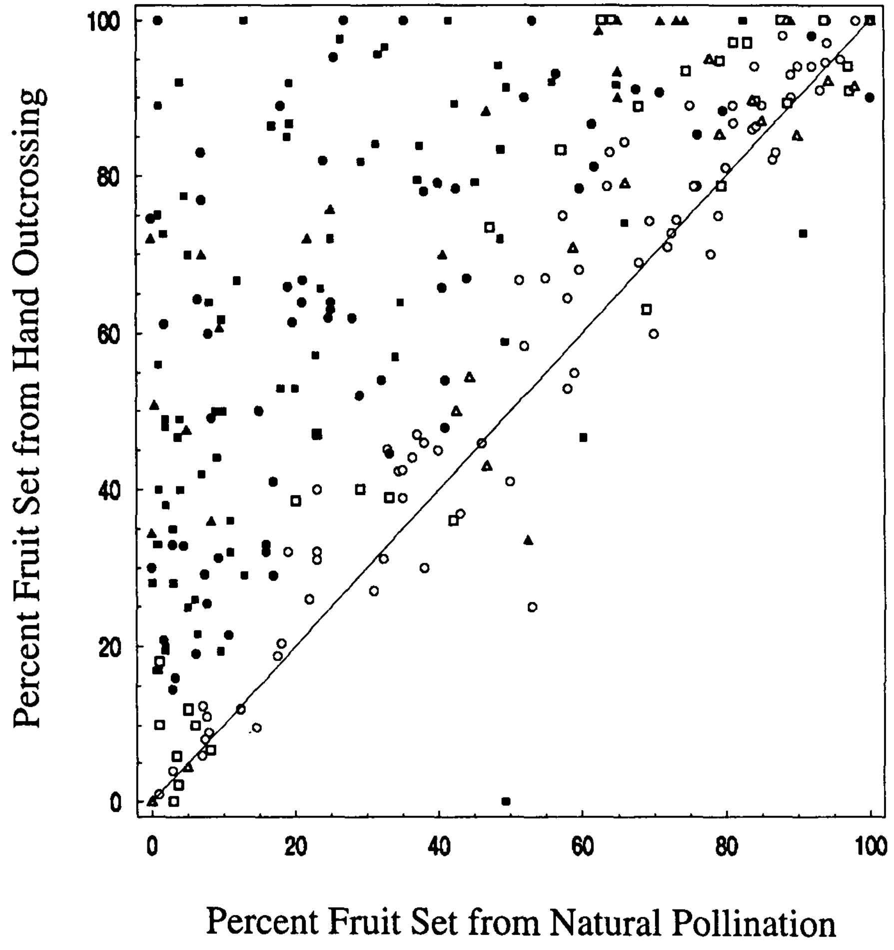

Fig. 1. Comparison of natural pollination and hand outcrossing for 207 species in 70 families with data reported as percent fruit set. Each plotted symbol (N = 278) represents the outcome of an experiment for a population in a single growing season. The x = y line is given for reference. Points above the line indicate that hand outcrossing yielded higher fruit set than natural pollination. Points below the line indicate the opposite. Open symbols indicate statistically non-significant differences; filled symbols indicate statistically significant differences. *Circles*: statistical test given by author(s) of study. *Squares*: tests of independence calculated when appropriate data were given and authors(s) do not provide a test (see Compilation of Data for further explanation). *Triangles*: author(s) did not perform a test and data are not appropriate for a test of independence, but pollen limitation (filled triangles) or absence of pollen limitation (open triangles) is assumed based on the magnitude of the difference between natural and hand pollination treatments.

declined. In *Allium tricoccum* (Liliaceae), a significant decrease in fecundity from hand outcrossing in 1984 was followed by a significant increase in 1985 (Nault & Gagnon, 1987). In *Saxifraga oppositifolia* (Saxifragaceae), an emasculation, outcross treatment (not reported in Appendix I) did not produce lower fruit set, even though the non-emasculation treatment did (Kevan, 1972). In *Espeletia neriifolia* (Com-

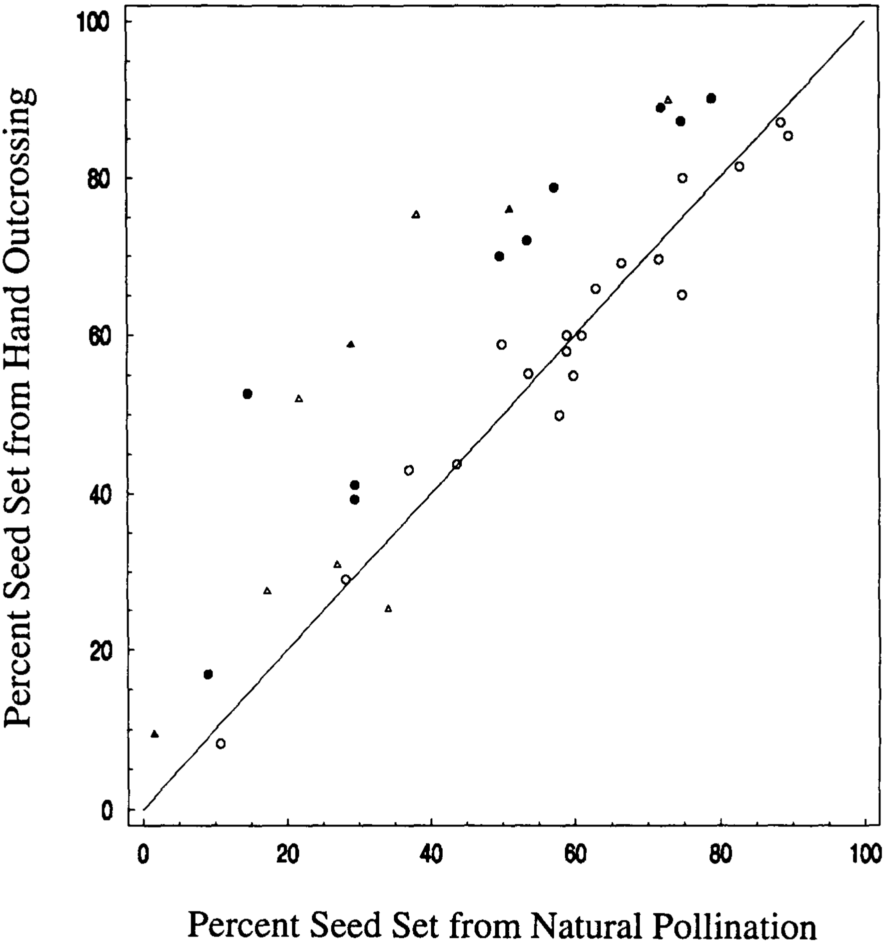

Fig. 2. Comparison of natural pollination and hand outcrossing for 29 species in 16 families with data reported as percent seed set. Interpretation of symbols (N = 38) is as in Figure 1.

positae), the significance of the decrease is surmised, and the reported values are medians from distributions the authors describe as highly skewed (Berry & Calvo, 1989). It is not clear that the appropriate non-parametric test would indicate a significant decline.

A potential explanation of apparently detrimental effects of extra pollen is statistical Type I error. Even with the ambiguous cases noted above, only 4% of the species show significant declines in fecundity from pollen addition. Spurious significance may be expected by chance in 5% of all experiments when a 5% significance level is used. This generalization does not demonstrate that any particular result is erroneous, but Appendix I does not support the idea that detrimental effects from pollen addition are common.

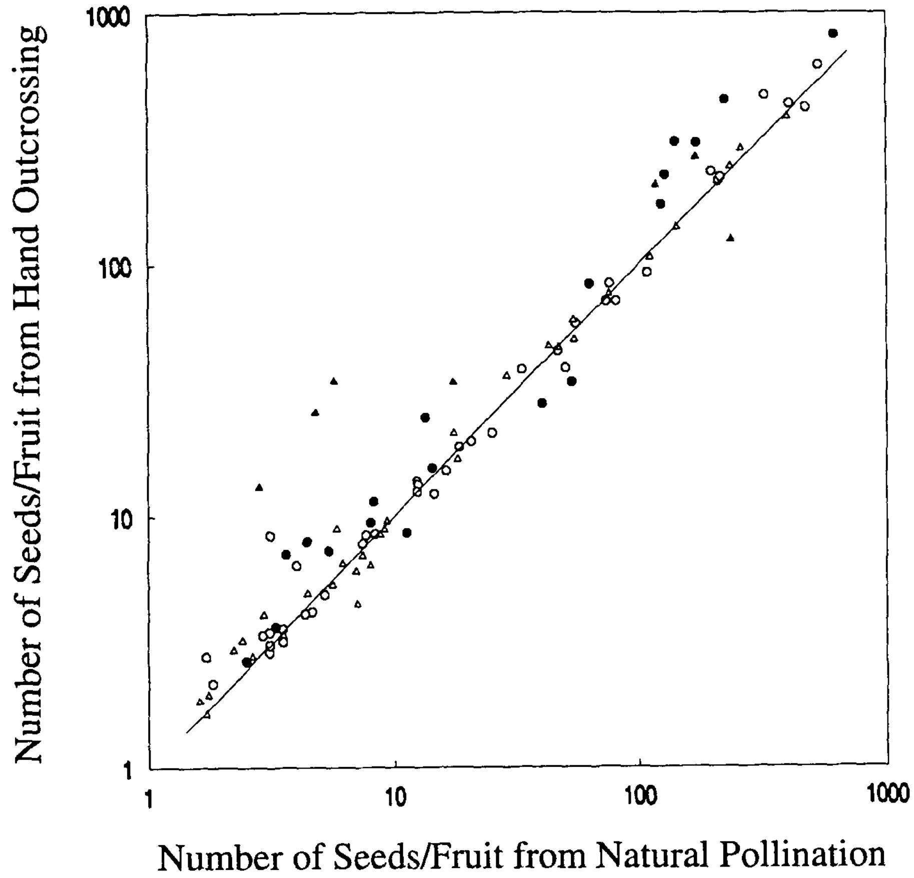

Fig. 3. Comparison of natural pollination and hand outcrossing for 84 species in 36 families with data reported as number of seeds per fruit. Note the logarithmic scale on both axes. Interpretation of symbols (N = 110) is as in Figure 1.

This conclusion differs from that of Young and Young (1992), who suggest that maximal reproductive success might frequently occur at intermediate pollination levels (although two examples of a detrimental effect of hand pollination in that paper, *Kalmia latifolia* and *Viscaria vulgaris*, were misclassified, H. Young pers. comm.). The discrepancy stems in part from different criteria for incorporating data. For example, many studies employ statistical techniques that control experiment-wide Type I error when analysing, say, comparisons from multiple dates (e.g., Gross & Werner, 1983), and I use these original results in Appendix I. Post-hoc selection and statistical testing of individual comparisons isolated from larger tables of data, as in Young and Young (1992), can draw attention to patterns overlooked by the original authors, but may inflate the statistical significance because of selection bias. More thorough experimental techniques of the sort recommended by Young and Young (1992) are necessary to determine experimentally whether adverse effects of high pollen loads are common in nature.

Table III

Variation in pollen limitation within a season and among sites or years. Each entry indicates the number of species with the corresponding pattern of pollen limitation

	Difference between Natural Pollinationand Hand Outcrossing		
	Consistently Pollen-Limited	Consistently Not Pollen-Limited	Variable
Tested Multiple Times within Growing Season	1	2	10
Tested in Multiple Sites or Years	15	6	17

B. PATTERNS WITHIN AND AMONG SEASONS AND SITES

Thirteen species in the sample were explicitly tested at multiple times within a growing season. Table III shows that most species experienced fluctuating levels of pollen limitation within a season.

Thirty-eight species had data from more than one site or year. Of these, 15 species showed consistent pollen limitation in all sites and years, 6 showed consistently non-significant differences between natural and hand pollination, and 17 species showed both significant and non-significant results among years or sites (Table III). In addition, one species not included in Table III, *Allium triccocum*, had a significant increase one year and a significant decrease the following year, as previously noted.

C. PATTERNS OF FRUIT AND SEED MATURATION

Fruit abortion has received more attention than seed abortion within fruits (Stephenson, 1981; Sutherland & Delph, 1984). This may reflect a genuine biological effect of modular gamete packaging in plants. Seed maturation requires fruit maturation, and the most efficient use of reproductive resources in a multi-ovulate fruit may be to mature as full a complement of seeds as possible. Thus, ovules might usually be matured or aborted as packages. If this is true, we would expect pollen limitation to show more strongly in patterns of fruit set than in number of seeds per fruit.

Seventy-three species had data on both percent fruit and seed number per fruit from the same experiment. With these data the effect of additional pollen on fruits set can be compared with the effect on seed set. Table IV shows the pattern of effects on fruit and seed production of hand outcrossing. Each entry in this table represents the results for a population in a growing season. A single species can be represented multiple times if multiple sites or years were used, and, inasmuch as results sometimes varied among sites and years, a single species may contribute to more than one cell of the table.

In only seven cases did hand pollination produce any significant increase in seed number per fruit without an increase in the rate of fruit set. In contrast, four times as many cases occurred in which fruit set increased significantly but seed set per fruit did not. Eleven instances in which both fruit set and seed number per fruit increased significantly occurred, while the most common outcome was to have no significant change in either measure. The data in Table IV suggest that variation in fecundity in

Table IV

Effect of hand outcrossing on fruit vs. seed maturation for experiments reporting both fruit and seed data. Each entry in the table is the number of experiments having the results for that cell. A species may contribute more than once (and to more than one cell) if experiments occured in multiple sites or years (multiple tests within a season were not used).

	Fruit Production[a]		
Seed Production[a]	Outcross < Nat.	NS	Outcross > Nat.
Outcross < Natural	1	0	1
NS	1	38	28
Outcross > Natural	0	7	11

[a] Data for some species could not be totalled to give results for a whole population. These cases are resolved as follows: *Agalinis strictifolia* (Scrophulariaceae): FM 1985 is entered as "NS" for fruit production and "Outcross > Natural" for seed set, because four of the five weeks showed this result; all other site-year combinations are entered as "NS" for both fruit and seed set. *Ipomopsis aggregata* (Polemoniaceae): entered as "Outcross > Natural" for fruit production and "NS" for seed set, because 2 of the three test periods showed this result. *Physalis longifolia* (Solanaceae) and *Sabatia angularis* (Gentianaceae): small and large plants are entered separately because they showed different patterns.

most species is more often due to maturation or abortion of whole fruits rather than of individual seeds within fruits.

Using only those studies containing data on both fruit and seed maturation could involve a reporting bias. However, a bias is likely to underrepresent the importance of fruit set relative to seed set within fruits. Fruit set may commonly be the only type of data reported because it is the "obvious" or "natural" measure (i.e., because variance of fruit set or the effect on fruit set from experimental treatments is many times larger than that of seeds per fruit). Nonetheless, effects of pollen loads on seed number occur with reasonable frequency, and are not to be discounted.

D. GENETIC LOAD HYPOTHESIS

It has been noted that percent seed set tends to be higher in annuals than perennials, and in selfing than in outcrossing species (Wiens, 1984). There is considerable overlap in these categories, with perennials commonly being outcrossers and annuals often selfing.

Genetic load in outcrossers has been suggested as a source of these low fertility rates (Wiens, 1984; Wiens et al., 1987, 1989; cf. Charlesworth, 1989). A higher genetic load in perennials might arise from the maintenance of genetic polymorphisms under the selective pressure imposed by parasites and pathogens, and from less frequent purging of harmful recessive mutations than occurs in self-fertilizing plants (but see Dole & Ritland, 1993). The zygotes of outcrossers would more frequently suffer the lethal selective effects of genetic load, leading to low rates of seed set.

Another explanation of patterns of low seed set involves pollen limitation. A self-incompatible (SI) plant cannot make use of pollen transfers inside a single flower or among flowers on the same plant, while a self-compatible (SC) plant can benefit from such pollinator visits, since geitonogamous pollen will produce zygotes. Thus SC plants might have higher rates of seed set largely because they receive pollen from an additional source—themselves—not available to SI plants. Indeed, any incompatibility system reduces the pool of potential pollen donors, and this should increase the probability of inadequate fertilization. Incompatible pollen might also clog stigmas or trigger stigmatic reactions that further reduce the chances of ovule fertilization (Ockendon & Currah, 1977; Shore & Barrett, 1984).

Both genetic load and pollen limitation might simultaneously reduce a plant's fertility and, as with pollen limitation generally, the question is one of relative importance. The question can be addressed with the data in Appendix I, because the two explanations make different predictions about the effect of supplemental outcross pollen. If receipt of compatible pollen is the main limit on seed set, then supplemental outcrossing should increase female success (relative to natural pollination) far more in SI than in SC species. However, if genetic load is the more important cause of low fertility, addition of outcross pollen should have similar (and small) effects relative to natural pollination for both SI and SC species. If anything, SC species would tend to benefit somewhat more than SI species if a past history of selfing means that outcross pollen carries fewer deleterious alleles as a result of purging the mutational load.

I compared the effect of hand outcrossing in SI and SC species using percent fruit set data, because that is the most common measure of fecundity. In the studies I consulted, authors sometimes performed experimental selfings, which provides a quantitative measure of compatibility, but in other cases reported only a classification of a species as SI or SC. I created three different measures of compatibility: (1) When experimental self-pollinations were performed, I used percent fruit set to provide a continuous metric of compatibility. (2) Using the same data, I designated populations as SI if female success was zero upon hand selfing, and as SC otherwise. This converts measure 1 to a categorical measure of compatibility. (3) Still using the same data, I created a broader definition of incompatibility by categorizing a species as SI if fruit set was 0–5% in selfing experiments, and as SC if fruit set was greater than 5%. That is, a species could be labelled SI if it showed some, but slight, fruit set upon selfing. To these data I then added species that were designated SI or SC in studies that did not employ experimental selfings.

The relative benefit from addition of outcross pollen was measured by the ratio of mean success from hand outcrossing to mean success from natural pollination. Thus, when natural rates of ovule fertilization are high, additional pollen can provide only a small relative benefit. Relative benefit of hand outcrossing is plotted against percent fruit set from selfing (compatibility definition 1 above) in Fig. 4. The pattern conforms more closely with the expectations of a pollen limitation hypothesis than of the genetic load hypothesis. Highly self-incompatible species sometimes improved female reproductive success more than 10-fold upon hand outcrossing, while more compatible species seldom benefited so greatly from pollen additions. The Spearman rank correlation for these data is negative and highly significant ($R = -0.38$; $p < 0.001$).

When compatibility is classified by the second criterion above (zero or non-zero reproductive success from selfing) the relative benefit from supplemental outcross pollen can be compared between SI and SC species using the *U*-test of Mann and Whitney (1947). Self-incompatible species tend to receive a greater relative benefit from hand outcrossing ($U = 1687$; $N_{SI} = 46$, $N_{SC} = 117$; $p < 0.001$). Using the third criterion above to classify compatibility also shows that SI species benefit more from additional outcross pollen than SC species ($U = 5159.5$; $N_{SI} = 111$, $N_{SC} = 117$; $p < 0.01$).

These patterns cast doubt on the overriding importance of genetic load for low rates

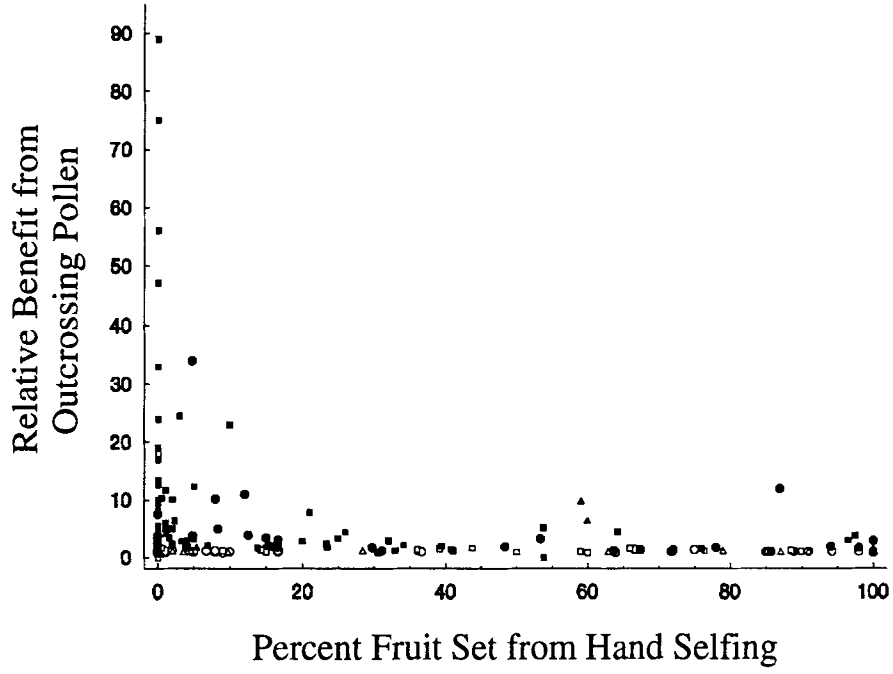

Fig. 4. Test of the genetic load vs. pollen limitation hypotheses for low female fecundity in outcrossers. Compatibility is measured by the percent fruit set from hand selfing. Plotted points on the left-hand side of the graph represent more self-incompatible species, while points on the right-hand side represent more self-compatible species. Ordinate values represent the ratio of fruit set under hand outcrossing to fruit set from natural pollination, that is, the relative benefit of additional outcross pollen. The Spearman rank correlation for the plotted data is negative and highly significant (R = -0.38; p 0.001), supporting the pollen limitation hypothesis. Interpretation of symbols is as in Figure 1.

of ovule success. Difficulties in the pollen limitation hypothesis remain, however. For species having more than about 15% fruit set from selfing the relative benefit of hand outcrossing is low (Fig. 4). One might expect the decline to be more linear with increasing self-compatibility if higher levels of self-compatibility produce equivalently higher rates of natural ovule fertilization. Much would depend on the frequency of geitonogamous pollinations in any population. An additional difficulty is that neither genetic load nor actual selfing rates (as distinct from self-compatibility) were measured. Only detailed information of this sort can resolve the issue.

VI. Discussion

The prevalence of pollen limitation among the species in Appendix I might seem surprising, if, following Bateman, we expect female reproduction to be limited by resources and not by access to males. For flowering plants, however, the search component implicit in Bateman's argument seems frequently to be unsatisisfied, due to the vagaries of pollen dissemination and pollen receipt using external agents.

Investments in pollinator attraction are frequently a large fraction of a flower's biomass investment (Pleasants & Chaplin, 1983; Southwick, 1984), an indication, perhaps, of the difficulty in acquiring adequate pollinator service. Even large floral rewards provide incomplete control over pollinators, and considerable resource expenditure on male competition to locate ovules frequently results in incomplete success (Table I). This evidence reinforces the impression that lack of success in "searching" for each sex by the other is a factor that frequently obviates Bateman's resource limitation argument in flowering plants.

Chronic pollen limitation is expected to create selective pressures that would alter resource allocations and other features of reproduction (Charnov & Bull, 1986; Stanton & Preston, 1988b), leading to a reduction in pollen limitation. Why, then, is pollen limitation so common? Can pollen limitation represent a selective equilibrium? I suggest that pollen limitation may often be the consequence of adaptive resource allocation strategies in a pollination enviroment characterized by large stochastic variation in pollen delivery and ovule fertilization.

A. ALLOCATION STRATEGIES AND POLLEN LIMITATION

Haig and Westoby (1988) presented a graphical model proposing that at an evolutionary equilibrium female fecundity would be limited by both pollen and resources. When pollen limits seed set, selection would favor increased allocation to pollinator attraction at the expense of ovule investment, but in species receiving excess pollen, a shift from attractive investment to ovules would be favored. An equilibrium is achieved when both pollinator attraction and ovule investment limit seed output to the same degree.

The argument of Haig and Westoby implicitly divides a plant's mating effort into what may be called spore investment (pollen and ovule production) and pollination investment. Evolutionary stable strategy models (cf. Maynard Smith, 1982) of allocation involving a trade-off between male, female, and attractive investments have been well studied (e.g., Charlesworth & Charlesworth, 1987; Lloyd, 1987; Lloyd & Venable, 1992). In general, these models make predictions corresponding to the Haig and Westoby argument: at equilibrium, any benefit from small shifts in allocation that increase, say, the number of pollinator visits are balanced by a decrement in some other component of fitness—number of ovules available to be fertilized, for example.

Viewing mating effort as both spore investment and pollination investment makes clear why some nuance is required in any botanical application of statements like "male fitness should be limited by access to females and not by resources." Since access to females requires the investment of resources in pollinator attraction, male fitness could be limited by resource investment even when microspores vastly outnumber megaspores. At an evolutionary stable equilibrium, increased investment in pollinator visitation might be expected to require a loss in fitness from having fewer pollen grains to export when the pollinators arrive (cf. Lloyd, 1987; Lloyd & Venable, 1992).

The argument thus far suggests only that a plant should produce just enough ovules and invest just enough in pollinator attraction so that all ovules are fertilized (Haig & Westoby, 1988). Chronic or even frequent pollen limitation of seed output is not predicted by this view. However, if the effect of attractive investment on fertilization is stochastic, a plant cannot adjust the complement of zygotes each flower will have with such precision. In a random pollination environment one expects pollen limitation to occur often. Haig and Westoby (1988) made this suggestion, and models of stochastic pollination confirm it. Cohen and Dukas (1990) model a situation in which greater floral investment produces an increase (but with diminishing marginal effect) in the probability that a flower will be pollinated. Given a trade-off between attractive investment in individual flowers and the total number of flowers that can be made, the fitness-maximizing strategy occurs with fewer than all flowers being pollinated.

The model of Cohen and Dukas (1990) assumes that individual flowers are unpollinated or completely pollinated. I have modelled pollination intensity as a stochastic variable that allows partial fertilization of multi-ovulate flowers (Burd, 1994). This model suggests that the optimal ovule number per flower will often be above the mean number of successful pollen tubes per flower. This counter-intuitive result occurs because of variance among flowers in pollination intensity. Flowers that are "over-supplied" with ovules have a non-zero probability of achieving very high seed set because they may, by chance, fall in the upper end of natural variation in pollen receipt. The greater the variance, the more likely some flowers are to achieve very high seed set, although a plant cannot predict which of its flowers will be successful. In such circumstances, the expected number of ovule fertilizations on a plant is greater if many ovules are present in each flower than if additional costly flowers must be produced with fewer ovules in each.

These arguments suggest that pollen limitation of female success should be common. Many other components of plant reproduction may obviate the selective pressures assumed above. For example, the need to disperse seeds effectively may favor low ovule numbers (and therefore infrequent pollen limitation) in order to maintain a low seed-to-pulp ratio or low wing loading in the fruits (cf. Augspurger & Hogan, 1983; Lee, 1984). Thus, "excess" flowers and "excess" ovules need not be universal among angiosperm species. But the prevalence of pollen limitation in the data set suggests that among-flower variance in pollination might frequently shape floral strategies in a way that results in chronic pollen limitation.

B. MULTIPLE SCALES OF POLLEN LIMITATION

Explicit consideration of the scale of ecological entitites and processes is becoming common (e.g., Allen & Hoekstra, 1992; O'Neil, 1989), and it is useful to apply this perspective to pollen limitation.

1. Individual Ovules

At the most fundamental level, pollen limitation occurs when individual ovules go unfertilized. Packaging of ovules in flowers may make the individual ovule an unrewarding level of analysis in most cases, but ovule position effects are known (Mazer et al., 1986; Rocha & Stephenson, 1991) and serve as a reminder that interesting phenomena may be associated with differences among ovules within a flower.

2. Individual Flowers

As noted above, among-flower variation in stigmatic pollen deposition can be great, and from this we can infer that inadequate pollination at the level of individual flowers is even more common than Table I would suggest. That is, the least pollinated flowers tend to be the ones aborted when abortion occurs (Stephenson, 1981), so that end-of-season measures of reproductive success may not reveal the low end of the among-flower distribution in pollen receipt.

If a plant must abort some fertilized ovaries, the total female success of an entire plant need not be affected by having some flowers less thoroughly pollinated. The whole plant is often the level of greatest interest to pollination ecologists because of the evolutionary significance of individual fitness. But variation among individual flowers is nonetheless of evolutionary importance because it can affect whole plant fitness by affecting such things as the optimal ovule packaging (Burd, 1994). Variation among flowers in pollen limitation could also be relevant for microgametophyte competition in styles. Even when overall seed output is pollen limited in a plant, some proportion of flowers may have unusually heavy stigmatic pollen loads and selection among pollen tubes could occur (Snow, 1986). If these seeds are of higher quality than in fruits where no competition occurred, flowers from the upper end of a pollination distribution may contribute disproportionately to fitness.

3. Whole Plants

Pollen limitation of whole plant fitness has been difficult to assess. Zimmerman and Pyke (1988) argue that the methods typically used to test for pollen limitation are inadequate at the whole plant level. Improved performance by experimentally pollinated flowers may come at the expense of other flowers, due to reallocation of resources for fruit and seed maturation. Total female success may not increase even if additional pollen increases seed set in any flower receiving it.

Zimmerman and Pyke (1988) found just such an effect in *Polemonium foliosissimum*. However, observing this effect is not sufficient to establish that whole plant female success was not pollen limited: the decrease in unmanipulated flowers must be greater than the increase brought about in hand pollinated flowers. In *P. foliosissimum* whole-plant seed set averaged about 7% higher on experimental plants than on unmanipulated, naturally pollinated plants, despite the reduced performance of some flowers on the experimental plants. This increase was statistically significant.

Zimmerman and Pyke then estimated the seed contribution of flowers that had opened and whithered before, between, or after experimental pollinations, and for which seed set was not directly counted. Including these estimates, experimental plants had about 9% higher seed set, although now the increase was not statistically significant. Although their experiment is not conclusive, as Zimmerman and Pyke (1988) note, their data tend to suggest some degree of pollen limitation in *P. foliosissimum* (even though they conclude that resources probably limit female output, an indication, perhaps, of the common expectation of resource limitation.)

4. Lifetime Fitness

A similar problem confronts investigators over the effect of pollen limitation on lifetime fitness in iteroparous plants. Female reproductive output may increase dramatically upon supplemental pollination, but years of high reproductive investment are frequently followed by reduced vegetative and reproductive performance in subsequent seasons (e.g., Snow & Whigham, 1989, and references therein). A reduced output in following years does not itself establish that lifetime reproductive output is resource limited. The fitness decrease must be greater than the benefit provided by additional pollen in the initial season for pollen limitation of lifetime fitness to be ruled out (Calvo, 1993).

Primack and Hall (1990) compared hand-pollinated plants with unmanipulated controls of the orchid *Cypripedium acaule*. Supplemental pollen produced fruit set from 8496%, compared with 06% in controls, but imposed a growth and flowering cost over the four years of the study. However, the 64 experimental plants in one site produced 158 fruits in four years, while an equal number of control plants produced 7 fruits, and similar results occurred in a second site (Primack & Hall, 1990, Table 7). It seems possible that hand-pollinated plants had higher average fitness than controls, despite the apparent low growth rates and possibly higher mortality that ensued.

Calvo (1993) used a matrix stage model with data on growth and reproduction in the orchid *Tolumnia variegata* to assess the fitness consequences of increased pollination. His analysis suggests that the benefit of high fruit set from additional pollen receipt (about 88 times higher than natural rates of fruit set) would outweigh the cost to future growth and reproduction.

Thus, although pollen limitation may not be conclusively demonstrated in any study using iteroparous plants, it is equally true that resource limitation has not been demonstrated. Both empirical and theoretical work in this direction would be useful.

VII. Conclusion

The very showiness of flowers might suggest that pollinator service is not obtained easily. If it were, advertising resources would be better spent on microspores and megaspores, or on fruit and seed maturation. Even with a large investment in pollinator attraction, it is not surprising that the vagaries of the environment or natural behavioral stochasticity of the pollinators themselves often produce pollen-limited seed set.

Even when resources are not sufficient to mature all flowers, it is likely that many aborted flowers are incompletely pollinated (Stephenson, 1981). Thus, inadequate pollinator service to individual flowers is probably more common than indicated by the data in Appendix I, which represent post-abortion female success.

Our theoretical understanding of plant reproductive strategies probably should not rely on the assumption that only resource investment limits female success. Incorporating randomness into models of female mating success (e.g., Cohen & Dukas, 1990) is likely to describe more fully the pollination environment of flowering plants. Long-term experiments are needed to fully assess the role of pollen limitation on lifetime reproductive success, including attention to the magnitude of immediate gains from additional pollen vs. the magnitude of costs in subsequent years.

VIII. Acknowledgments

I thank T. F. H. Allen and the University of Wisconsin Botany Department for their hospitality during my stay. I received many helpful comments on the manuscript and the ideas presented in it from H. Callahan, M. Johnston, A. Snow, P. Wilson, and H. Young. Jules Archer kindly helped prepare the figures.

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Appendix I

Compilation of published data on female reproductive output from natural and artificial pollination

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Agavaceae							
Agave mckelveyana		%f	18.07	20.35	SI	ns	Sutherland 1987
		s/fr	33.48	38.45	SI	ns	
Amaryllidaceae							
Alstroemeria ligtu		%f	48.49	94.12	39.47	(**)	Arroyo & Uslar 1993
		s/fr	17.60	21.47	10.08	◇	
Alstroemeria pallida		%f	64.87	91.67	40.82	(**)	Arroyo & Uslar 1993
		s/fr	9.30	9.64	8.94	◇	
Crinum erubescens		%f	44.3	54.4	28.4	◇	Manasse & Pinney 1991
		s/fr	2.909	4.106	1.429	◇	
Hippeastrum bicolor		%f	31.35	84.09	0	(**)	Arroyo & Uslar 1993
		s/fr	46.78	46.76	0	◇	
Zephyranthus atamasco		s/fr	13.4	24.7	19.4	*	Broyles & Wyatt 1991
Anacardiaceae							
Spondias mombin		%f	1	89	0	(**)	Bawa 1974
Annonaceae							
Asimina parviflora	BS 1984	%f	3.2	16	8.3	*	Norman et al. 1992
	BS 1987	%f	1.7	20.8		**	
	DL 1987	%f	7.4	29.2	12.5	*	
	Both sites	s/fl	0.46	4.2	0.9	**	
Asimina triloba	1978	%f	0.63	17		(**)	Willson & Schemske 1980
Asimina obovata		%f	16	32	4	**	Norman & Clayton 1986
Asimina pygmaea		%f	8	60	0	**	Norman & Clayton 1986
Sapranthus palanga		%f	1	75	0	(**)	Bawa 1974

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Apocynaceae							
Nerium oleander	El Garrobo 1987	%f	4.9	47.7	59	◆	Herrera 1991
	El Garrobo 1988	%f	0.5	50.8	59	◆	
	Grazalema 1988	%f	0.1	34.4	59	◆	
Aquifoliaceae							
Ilex opaca		%f	69.5	74.3	D	ns	Carr 1991
Araceae							
Arisaema triphyllum	Medium-sized	s/pl	1.0	43.2		◆	Bierzychudek 1981
Dieffenbachia longispatha		%f	40.54	65.86	29.72	**	Young 1986
Araliaceae							
Aralia nudicaulis	1983	s/fl	1.91	2.15	D	ns	Flanagan & Moser 1985
	1983	s/pl	105.5	109.9	D	ns	
	1984	s/fl	1.69	2.52	D	*	
	1984	s/pl	90.5	132.6	D	*	
		%f	70.9	90.7		***	Barrett & Helenurm 1987
Panax quinquefolium		%s	27	31	43	◇	Schlessman 1985
Aristolochiaceae							
Heterotropa tamaensis	Total	%f	57.1	83.3	66.0	(ns)	Sugawara 1988
Asclepiadaceae							
Asclepias syriaca		f/pl	2.2	3.5	SI	**	Morse & Fritz 1983

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Balsaminaceae							
Impatiens capensis	Alone	%f	70.9	100	SC	◆	Rust 1977
	Mixed	%f	74.3	100	SC	◆	
Impatiens pallida	Alone	%f	73.2	100	SC	◆	Rust 1977
	Mixed	%f	89.1	100	SC	◆	
Begoniaceae							
Begonia involucrata		%f	76.0	78.7		ns	Ågren & Schemske 1991
		%s	57.3	78.8		***	
Berberidaceae							
Berberis sp.		%f	5.20	70.00	0	(**)	Arroyo & Uslar 1993
		s/fr	3.50	3.43	0	◇	
Podophyllum peltatum	Population I	s/fr	4.75	26	0	◆	Swanson & Sohmer 1976
	Population II	s/fr	0	19.4	0	◆	
	Population III	s/fr	0.59	8.3	0	◆	
	Population IV	s/fr	0	7.4	0	◆	
		%f	9.4	31.3	0	*	Motten 1986
	1989	%f	7	77		***	Whisler & Snow 1992
	1990	%f	21	64		***	
	1990 Site 1	s/fr	13.8	26.7		**	
	1990 Site 2	s/fr	21.5	31.1		*	
	1990 Site 3	s/fr	16.4	30.0		ns	
	1990 Site 4	s/fr	16.8	39.2		**	
	1990 Site 5	s/fr	20.9	37.3		**	
	1990 Site 6	s/fr	17.8	34.5		*	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Betulaceae							
Alnus firma		%s	34.0	25.3	0.3	◇	Murakami & Maki 1992
Bignoniaceae							
Campsis radicans	1978	%f	4	49	5	(**)	Bertin 1982a
	1979	%f	11	36	5	(**)	
	PT	%s	51	76		◆	
Catalpa speciosa		fr/i	2.68	2.35	SI	*	Stephenson 1979
Chilopsis linearis		fr/i	1.07	3.97		*	Petersen et al. 1982
Eccremocarpus scaber		%f	37.14	79.48	34.09	(**)	Arroyo & Uslar 1993
		s/fr	234.27	245.31	193.13	◇	
Tabebouia neochrysantha		%f	2	48	0	(**)	Bawa 1974
Tabebouia palmeri		%f	4	40	0	(**)	Bawa 1974
Tabebouia rosea		%f	1	56	0	(**)	Bawa 1974
Bombacaceae							
Eriotheca gracilipes		%f	9.62	19.40	0.00	(**)	Oliveira et al. 1992
Eriotheca pubescens		%f	6	10	15	(ns)	Oliveira et al. 1992
Ochroma pyramidale		%f	97	94	15	(ns)	Bawa 1974
Boraginaceae							
Anchusa officinalis	Lockarp	%f	61.7	81.2	SI	***	Andersson 1988
	Käglinge	%f	59.6	78.4	SI	***	
Bourreria quirosii		%f	18	53	4	(**)	Bawa 1974
Cordia alliodora		%f	23.6	65.7	3.3	(**)	Opler et al. 1975

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Cordia dentata	Long style	%f	22.9	57.2	0	(**)	Opler et al. 1975
	Short style	%f	20.7	50	0	(**)	
Cryptantha flava	Pin morph	s/fl	0.83	0.46^{j}	SI	◇	Casper 1983
	Thrum morph	s/fl	0.72	0.82^{j}	SI	◇	
Cryptantha flavoculata	Pin morph	s/fl	2.15	0.92^{j}	SI	◇	Casper 1983
	Thrum morph	s/fl	2.66	1.48^{j}	SI	◇	
Lithospermum caroliniense		%s	9	17	SI	***	Weller 1980
Mertensia ciliata		s/fl	2.045	0.723	0.393	***	Geber 1985
Cactaceae							
Echinocereus coccineus	Jornada A	%f	88.5	100	0	◇	Hoffman 1992
Echinomastus erectrocentrus		%f	94.2	92.2	4	◇	Johnson 1992
Opuntia phaeacantha		s/fr	50.2	38.6	40.3	ns	Osborn et al. 1988
Opuntia polyacantha		s/fr	25.1	21.3	0.6	ns	Osborn et al. 1988
Opuntia stricta	Near island 1983	%f	85	89	71.8	ns	Spears 1987
	Near island 1983	s/fr	73.1	1.5	66.2	ns	
	Far island 1983	%f	89	90	85.7	ns	
	Far island 1983	s/fr	75.9	84.2	61.3	ns	
Caprifoliaceae							
Diervilla lonicera		%f	81.0	97.1	0	(ns)	Schoen 1977
Linnaea borealis		%f	51.3	66.7	66.7	ns	Barrett & Helenurm 1987
Caryophyllaceae							
Dianthus deltoides	Site A	%s	50^{i}	59^{i}		ns	Jennersten 1988
	Site B; early July	%s	29^{i}	59^{i}		◆	
	Site B; late July	%s	15^{i}	63^{i}		◆	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means: Natural	Outcross	Self[c]	Stat. Test[d]	Reference
Silene alba	Entire summer	%f	28	62	D	***	Alexander 1987
	Entire summer	s/fr	140	307	D	***	
Silene vulgaris		s/fr	55.2	58.2		ns	Pettersson 1991
Stellaria pubera	Early	s/fl	3.16	3.77	SC	*	Campbell 1985
	Late	s/fl	1.54	1.56	SC	ns	
		%f	86.5	82.1		ns	Motten 1986
		%s	28.2	29.0		ns	
		s/fr	3.5	3.2		ns	
Viscaria vulgaris	18 June 1985	%s	60^{i}	69^{i}	SC	ns	Jennersten et al. 1988
	25 June 1985	%s	4^{i}	33^{i}	SC	*	
	14 June 1986	%s	74^{i}	79^{i}	SC	ns	
	18 June 1986	%s	59^{i}	75^{i}	SC	*	
	24 June 1986	%s	47^{i}	41^{i}	SC	ns	
	1987	%s	78.9	90.2	SC	*	
		%f	97.9	91.5	SC	◇	Kwak & Jennersten 1986
		s/fr	209.6	212.6	SC	ns	
	16 June 1986	s/fl	180^{g}	252^{g}	SC	ns	
	14 June 1986	%s	57.43	71.83	SC	ns	
	14 June 1988	%s	56.87	67.22	SC	ns	
	8 June 1988	%s	72^{h}	63^{h}	SC	ns	
	13 June 1988	%s	56^{h}	66^{h}	SC	*	
	19 June 1988	%s	26^{h}	60^{h}	SC	*	
Chrysobalanaceae							
Hirtella racemosa		%f	1	18	0	(ns)	Bawa 1974

Appendix I
Continued

Species	Subset^{a}	Type of Data^{b}	Treatment Means			Stat. Test^{d}	Reference
			Natural	Outcross	Self^{c}		
Cistaceae							
Cistus albidus		%f	19	85	0	(**)	Bosch 1992
		s/fr	42.84	47.7	0	◇	
Cistus monspeliensis		%f	13	100	21	(**)	Bosch 1992
		s/fr	2.8	13.27	1.37	◆	
Cistus salvifolius		%f	4	92	10	(**)	Bosch 1992
		s/fr	5.67	34.95	28.00	◆	
Cochlospermaceae							
Cochlospermum vitifolium		%f	11	32	0	(*)	Bawa 1974
Commelinaceae							
Tinantia anomala	CMTI 1983 vs. upper anthers	s/fr	4.66	4.60	4.24	◇	Simpson et al. 1986
Compositae							
Argyroxiphium sandwicense	(Total)	%f	12.9	29.0	1.9	(**)	Carr et al. 1986
Crepis tectorum	Runmarö	%f	93.9	94.5	94.3	ns	Andersson 1989
	Österby	%f	67.5	91.1	67.4	**	
	Stavsklint	%f	42.5	78.4	48.4	***	
	Möckleby	%f	6.4	64.4	8.0	***	
	Kalkstad	%f	0	74.6	0.6	***	
	Vickleby	%f	1.8	61.2	4.7	***	
Espeletia batata		%f	25.0^{k}	75.8^{k}	0.0^{k}	◆	Berry & Calvo 1989
Espeletia floccosa		%f	46.7^{k}	43.1^{k}	3.5^{k}	◇	Berry & Calvo 1989
Espeletia lindenii		%f	42.5^{k}	50.0^{k}	0.0^{k}	◇	Berry & Calvo 1989
Espeletia moritziana		%f	46.7^{k}	88.3^{k}	5.3^{k}	◆	Berry & Calvo 1989

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Espeletia neriifolia		%f	52.5^{k}	33.7^{k}	0.0^{k}	◆	Berry & Calvo 1989
Espeletia schultzi		%f	40.6^{k}	70.1^{k}	0.0^{k}	◆	Berry & Calvo 1989
Espeletia semiglobulata		%f	8.3^{k}	36.0^{k}	1.1^{k}	◆	Berry & Calvo 1989
Espeletia spicata		%f	58.8^{k}	70.8^{k}	4.6^{k}	◇	Berry & Calvo 1989
Espeletia timotensis		%f	79.2^{k}	85.3^{k}	9.7^{k}	◇	Berry & Calvo 1989
Solidago canadensis	Early	%f	20.32	30.64		ns	Gross & Werner 1983
	Intermediate	%f	37.14	44.69		ns	
	Late	%f	41.03	60.18		*	
	All	%f	33.24	44.68	4.47	**	
Solidago graminifolia	Early	%f	21.71	50.39		**	Gross & Werner 1983
	Late	%f	39.56	27.06		ns	
	All	%f	34.46	42.34	3.26	ns	
Solidago juncea	Early	%f	19.32	8.58		ns	Gross & Werner 1983
	Intermediate	%f	12.86	14.03		ns	
	Late	%f	5.77	15.68		ns	
	All	%f	12.39	12.06		ns	
Cornaceae							
Cornus canadensis		%f	10.7	21.5	0	***	Barrett & Helenurm 1987
Cruciferae							
Cardamine angustata		%f	17.5	18.8	8	ns	Motten 1986
Raphanus sativus	1983	%f	73.2	74.4	4.9	ns	Stanton 1987
	1983	s/fr	m	m		*	
	1984 (All colors)	%f	58	53		(ns)	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means: Natural	Outcross	Self[c]	Stat. Test[d]	Reference
Dilleniaceae							
Curatella americana		%f	42	36	60	(ns)	Bawa 1974
Ericaceae							
Gaylussacia frondosa	Maple 1 1981	%f	17	29	0	*	Rathcke 1988
	Maple 2 1981	%f	17	41	0	*	
	Maple 3 1981	%f	7	6	0	ns	
	Field 1 1981	%f	19	32		ns	
	Field 1 1982	%f	41	54		**	
	Field 2 1981	%f	46	46		ns	
	Field 2 1982	%f	3	33	12	*	
	Oak 1 1981	%f	3	4		ns	
	Oak 2 1981	%f	38	30	9	ns	
Kalmia angustifolia	1981	%f	75	89	72	ns	Rathcke 1988
Kalmia latifolia	Maple 1980	%f	24	82		***	Rathcke 1988
	Maple 1981	%f	19	66	15	***	
	Field 1981	%f	59	55		ns	
	Field 1982	%f	68	69		ns	
Gentianaceae							
Frasera caroliniensis		%f	60.2	46.7	30.5	(**)	Threadgill et al. 1981
		s/fr	7.0	6.1	5.3	◇	
Schultesia brachyptera		%f	100.00	100.00	100.00	(ns)	Ramirez & Brito 1990
Sabatia angularis	Small plants	%f	93.0	99.0		**	Dudash 1993
	Small plants	s/fr	405.6	431.8		ns	
	Large plants	%f	92.0	98.0		*	
	Large plants	s/fr	610.7	810.3		*	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Geraniaceae							
Geranium berterianum		%f	88.46	89.28	90.00	(ns)	Arroyo & Uslar 1993
		s/fr	4.41	4.96	4.42	◇	
Geranium maculatum	1982	%f	1	1		ns	McCall & Primack 1987
	1983	%f	8	9		ns	
	1984	%f	53	25		ns	
	Hart	%f	37.1	47.0	SC	ns	Ågren & Willson 1992
	Hart	s/fr	3.1	3.5	SC	ns	
	Hart	s/pl	12.6	18.4	SC	**	
	Trelease	%f	32.9	45.1	SC	ns	
	Trelease	s/fr	2.9	3.4	SC	ns	
	Trelease	s/pl	7.2	11.3	SC	*	
Guttiferae							
Kielmeyera coriacea	var. *coriacea*	%f	9.8	61.8	2.3	(**)	De Oliveira & Sazima 1990
	var. *intermedia*	%f	9.1	44.1	0	(**)	
	var. *glabripes*	%f	20.0	38.5	4.1	(ns)	
Kielmeyera speciosa		%f	6.4	21.6	1.6	(*)	De Oliveira & Sazima 1990
Hippocastanaceae							
Aesculus californica		%f	5	4.5	SC	◇	Benseler 1975
Aesculus pavia		%f	3.6[n]	2.1		(ns)	Bertin 1982b
Hippocrataceae							
Hemiangium excelsum		%f	1	17	0	(**)	Bawa 1974

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Iridaceae							
Iris cristata		%f	56.5	93.1	78	*	Motten 1986
		%s	10.7	8.2		ns	
		s/fr	7.4	7.8	6.9	ns	
Sisyrinchium arenarium		%f	42.29	89.29	6.90	(**)	Arroyo & Uslar 1993
		s/fr	9.05	8.96	0	◇	
Sisyrinchium philippii		%f	45.16	79.17	23.53	(**)	Arroyo & Uslar 1993
		s/fr	7.07	4.53	4.75	◇	
Labiatae							
Hyptis suaveolens		%f	79	75	85	ns	Aluri 1990
Nepeta cataria		%f	76.1	85.3	63.7	*	Sih & Baltus 1987
		s/fl	3.13	2.50	1.83	◇	
		s/fr	3.28	3.67	2.88	*	
Stachys albicaulis		%f	82.44	100.00	85.71	(**)	Arroyo & Uslar 1993
		s/fr	2.63	2.83	2.73	◇	
Leguminosae							
Adesmia montana		%f	64.15	100.00	39.21	(ns)	Arroyo & Uslar 1993
		s/fr	2.21	3.00	1.40	◇	
Adesmia mucronata		%f	62.71	100.00	43.75	(ns)	Arroyo & Uslar 1993
		s/fr	2.39	3.25	2.14	◇	
Andira inermis	(Total)	%f	0.7	33	0	(*)	Frankie et al. 1976
Bauhinia pauletia		%f	21.1	66.7	53.4	*	Heithaus et al. 1974
Bauhinia ungulata		%f	23	47	4	(ns)	Bawa 1974
Caesalpina eriostachys		%f	0.98	40.00		(**)	Bawa & Webb 1984
		%f	1	10	0	(ns)	Bawa 1974

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Cassia fasciculata		fr/i	0.80	0.82	SC	ns	Lee & Bazzaz 1982
Cassia nictitans		%f	50	41	64	ns	Lee 1989
		%s	72	89	90	*	
		s/fr	5.4	7.3	7.3	**	
Centrosema virginianum	Mainland 1981	%f	55	67	6.7	ns	Spears 1987
	Near island 1981	%f	40	45	16.7	ns	
	Far island 1981	%f	0	30	23.3	*	
	Mainland 1982	%f	23	40		ns	
	Near island 1982	%f	43	37		ns	
	Far island 1982	%f	23	32		ns	
Dalbergia retusa		%f	8	64	0	(**)	Bawa 1974
Enterolobium cyclocarpum		%f	0.1	28	0	(**)	Bawa 1974
Hymenaea courbaril		%f	2	38	0	(**)	Bawa 1974
Inga brenesii		%f	3	35	1	(**)	Koptur 1984
Inga densiflora		%f	5	25	1	(**)	Koptur 1984
Inga mortoniana		%f	2	49	3	(**)	Koptur 1984
Inga oerstediana		%f	5	12	2	(ns)	Koptur 1984
Inga punctata		%f	2	20	2	(**)	Koptur 1984
Inga quaternata		%f	3	0	0	(ns)	Koptur 1984
Lathyrus vernus	1988	%f	3.0	14.6	SC	**	Ehrlén 1992
	1989	%f	7.7	11.1	SC	ns	
		%s	29.4	39.3	SC	*	
Lonchocarpus costaricensis		%f	1	33	0	(**)	Bawa 1974
Lonchocarpus eriocarinalis		%f	3	28	0	(**)	Bawa 1974
Lupinus nanus	Site 1	f/pl	4.9	5.5	SC	ns	Karoly 1992
	Site 1	s/pl	13.8	13.0	SC	ns	
	Site 2	f/pl	5.5	6.7	SC	ns	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
L. nanus (contd.)	Site 2	s/pl	10.1	18.6	SC	**	
Myrospermum fructescens		%f	3.40	5.86	0.58	(ns)	Bawa & Webb 1984
Piscidia carthagenensis		%f	20	53	0	(**)	Bawa 1974
Pithecolobium saman		%f	9	50	0	(**)	Bawa 1974
Pterocarpus rohrii		%f	7	42	1	(**)	Bawa 1974
Liliaceae							
Allium tricoccum	1984	%f	52.1	58.4	36.2	ns	Nault & Gagnon 1987
	1984	s/i	17.8	10.9		*	
	1985	%f	14.6	9.7		ns	
	1985	s/i	1.9	3.5		*	
Amianthum muscaetoxicum		%f	29	52	16	**	Travis 1984
Blandfordia grandiflora	Tableland	%s	53.4	72.1	39.4	*	Ramsey et al. 1993
	Coastal	%s	14.6	52.7	4.3	*	
Calochortus leichtlinii	Sage	s/pl	40^{e}	35^{e}		ns	Holtsford 1985
	Forest	s/pl	23^{e}	28^{e}	23^{e}	ns	
Clintonia borealis		%f	61.5	86.6	72.0	***	Barrett & Helenurm 1987
		s/fr	11.2	8.6	3.7	***	
Erythronium albidum		%f	69	63	50	(ns)	Banks 1980
		s/fr	5.8	9.0		◇	
Erythronium americanum		%sp	29.4	41.2	10.5	*	Harder et al. 1985
Erythronium propullans		%f	0	0	0	◇	Banks 1980
Erythronium umbilicatum	1977	%f	94	97		ns	Motten 1983
	1977	%s	59	60		ns	
	1977	s/fr	20.6	19.7		ns	
	RB 1978	%f	78	70		ns	
	Gate 24 1978	%f	96	95		ns	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
E. umbilicatum (contd.)	Gate 24 1979	%f	92	94		ns	
	Gate 24 1979	%s	61	60		ns	
	Gate 24 1979	s/fr	18.4	18.9		ns	
	Gate 24 1980	%f	89	93		ns	
	Gate 24 1980	%s	37	43		ns	
	Gate 24 1980	s/fr	12.4	13.8		ns	
	NA 1979	%f	93	91		ns	
	NA 1979	%s	59	58		ns	
	NA 1979	s/fr	14.6	12.3		ns	
	NA 1980	%f	72	71		ns	
		%f	89.0	93.0	10	ns	Motten 1986
		%s	53.7	55.2		ns	
		s/fr	16.3	15.1		ns	
Leucocoryne ixioides		%f	55.93	92.00	16.67	(**)	Arroyo & Uslar 1993
		s/fr	18.24	16.94	5.25	◇	
Maianthemum canadense	CQ1	%i	56	74	SI	*	Worthen & Stiles 1988
	CQ2	%i	42	67	SI	**	
	CQ3	%i	60	61	SI	ns	
	T1	%i	40	65	SI	**	
	T2	%i	65	79	SI	*	
	K1	%i	51	35	SI	ns	
	FS1	%i	33	67	SI	***	
	1982	%f	22	26	1	ns	McCall & Primack 1987
	1983	%f	31	27	1	ns	
	1984	%f	35	39	1	ns	
		%f	7.1	12.5	0	ns	Barrett & Helenurm 1987

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means: Natural	Outcross	Self[c]	Stat. Test[d]	Reference
Mediola virginiana		%f	25.6	95.2	4.8	***	Barrett & Helenurm 1987
		s/fr	3.6	7.1	3.0	***	
Tricyrtis affinis	Control vs. 2nd day	%f	83.8	86.0	85.2	ns	Takahashi 1989
	Control vs. 2nd day	s/fr	54.5	50.7	48.2	◇	
Tricyrtis flava	Control vs. 2nd day	%f	89.9	85.2	62.9	◇	Takahashi 1987
	Control vs. 2nd day	s/fr	75.2	76.8	62.6	◇	
Tricyrtis latifolia	Control vs. 2nd day	%f	79.4	78.7	59.0	(ns)	Takahashi 1984
Tricyrtis nana		%f	83.7	89.7	87.1	◇	Takahashi 1987
		s/fr	54.0	60.9	58.7	◇	
Trillium apetalon		%s	75[f]	80[f]	80[f]	ns	Ohara et al. 1990
Trillium catesbaei		%f	79.6	88.3	31	*	Motten 1986
		%s	43.7	43.9		ns	
		s/fr	7.6	8.4	2.0	ns	
Trillium kamtschaticum		%s	63[f]	66[f]	59[f]	ns	Ohara et al. 1990
Trillium smallii		%s	58[f]	50[f]	58[f]	ns	Ohara et al. 1990
Trillium tschonoskii		%s	60[f]	55[f]	53[f]	ns	Ohara et al. 1990
Trillium undulatum		%f	100.0	90.0	100.0	***	Barrett & Helenurm 1987
		s/fr	40.2	28.0	29.2	**	
Uvularia sessilifolia	1982	%f	88	98	0	ns	McCall & Primack 1987
	1982	s/fr	3.1	3.1	0	ns	
	1983	%f	87	83	0	ns	
	1983	s/fr	3.1	2.9	0	ns	
		%f	58.0	64.5	8	ns	Motten 1986
		%s	74.9	65.2		ns	
		s/fr	4.6	4.2	1.0	ns	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Loasaceae							
Loasa heterophylla		%f	67.80	88.89	14.29	(ns)	Arroyo & Uslar 1993
		s/fr	5.58	5.38	1.00	◇	
Lobeliaceae							
Lobelia cardinalis	1980, Top ⅓	s/fr	334	382	SC	ns	Devlin & Stephenson 1987
	1908, Middle ⅓	s/fr	324	466	SC	ns	
	1980, Bottom ⅓	s/fr	209	530	SC	ns	
	1982, Top ⅓	s/fr	355	316	SC	ns	
	1982, Middle ⅓	s/fr	472	418	SC	ns	
	1982, Bottom ⅓	s/fr	591	476	SC	ns	
	Wintergreen Lake	%f	64	83		ns	Johnston 1991
	Wintergreen Lake	s/fl	139	329		**	
	Wintergreen Lake	s/fr	223	450		*	
	Wintergreen Lake	s/pl	1550	4626		**	
	Glass Creek	%f	38	78		***	
	Glass Creek	s/fl	206	504		***	
	Glass Creek	s/fr	532	619		ns	
	Glass Creek	s/pl	3663	7935		**	
Lobelia deckenii		s/fr	693	1249	1314	**	M. Burd (unpubl. data)
Lobelia keniensis	Uncaged, Intact	s/fr	395^{f}	385^{f}	155^{f}	◇	Young 1982
Lobelia siphilitica		%f	32	54	SC	*	Johnston 1991
		s/fl	62	176	SC	***	
		s/fr	170	304	SC	**	
		s/pl	612	2318	SC	***	
Lobelia telekii	Uncaged, Intact	s/fr	235^{f}	125^{f}	125^{f}	◆	Young 1982

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means Natural	Outcross	Self[c]	Stat. Test[d]	Reference
Magnoliaceae							
Magnolia hypoleuca		%f	25	63		***	Kikuzawa & Mizui 1990
		s/fr	29	36		◇	
Malpighiaceae							
Byrsonima crassifolia		%f	25	72	32	(**)	Bawa 1974
Malpighia glabra		%f	15	50	25	(**)	Bawa 1974
Malvaceae							
Cristaria dissecta		%f	87.67	100.00	88.57	(ns)	Arroyo & Uslar 1993
		s/fr	6.17	6.57	6.16	◇	
Marantaceae							
Calathea ovandansis		%f	7.4	8.1		ns	Horvitz & Schemske 1988
		s/fr	2.5	2.7		*	
Melastomataceae							
Clidemia capitellata		%f	74.53	93.33	100.00	(ns)	Ramirez & Brito 1990
Miconia stephananthera		%f	48.67	72.00	76.00	(*)	Ramirez & Brito 1990
Pterolepis glomerata		%f	84.00	89.47	88.89	(ns)	Ramirez & Brito 1990
Monimiaceae							
Siparuna neglecta		%f	4.6	77.5	D	(**)	Feil 1992
Myrsinaceae							
Ardisia revoluta		%f	66	74	33	(*)	Bawa 1974

Appendix I
Continued

Species	Subset^{a}	Type of Data^{b}	Treatment Means: Natural	Outcross	Self^{c}	Stat. Test^{d}	Reference
Myrtaceae							
Leptospermum scoparium	(Total)	%f	33	39	36	(ns)	Primack & LLoyd 1980
Syzygium cormiflorum		%f	72.6	72.7	36.6	ns	Crome & Irvine 1986
Orchidaceae							
Aplectrum hyemale		%f	81.1	86.7	100.0	ns	Hogan 1983
Aspasia principissa		%f	9.5	60.8	60	◆	Zimmerman & Aide 1989
Brassavola nodosa		%f	12.0	66.7	SC	(**)	Schemske 1980
Calopogon tuberosus		%f	7	83	87	*	Firmage & Cole 1988
Comparettia falcata	1989	%f	16.9	86.4	53.8	(**)	Rodríguez-Robles et al. 1992
	1990	%f	19.4	86.7	64.2	(**)	
Cyclopogon cranichoides	1986	%f	32.6	96.5		(**)	Calvo 1990
	1987	%f	26.4	97.5		(**)	
Cypripedium acaule		%f	1.0	100.0	100.0	***	Barrett & Helenurm 1987
Encyclia cordigera		%f	7	70	SC	◆	Janzen et al. 1980
Encyclia krugii		%f	3.7	46.7	0	(**)	Ackerman 1989
Epidendrum cilare	1982-83	%f	8.3	49.2	SC	**	Ackerman & Montalvo 1990
	1983-84	%f	4.5	32.9	SC	**	
Ionopsis utricularioides		%f	6.1	19.1	SC	**	Montalvo & Ackerman 1987
Myrosmodes cochleare	1983	%f	29	40	36	(ns)	Berry & Calvo 1991
Oncidium variegatum	(Total)	%f	1.8	72.6		(**)	Ackerman & Montero O. 1985
Platanthera blephariglottis		%f	62.4	98.6	100	◆	Cole & Firmage 1984
Platanthera ciliaris	Mountains	%f	85	87	91	◇	Robertson & Wyatt 1990
	Coastal Plain	%f	66	79	79	◇	
Platanthera stricta		%f	52	90	98	*	Patt et al. 1989
Tipularia discolor	Site 1 1986	%f	18	89	SC	***	Snow & Whigham 1989
	Site 1 1987	%f	25	64	SC	***	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
T. discolor (contd.)	Site 2 1987	%f	23	47	SC	***	
Tolumnia variegata		%f	0	72	SI	***	Calvo 1993
Oxalidaceae							
Oxalis montana		%f	35.2	100.0	100.0	**	Barrett & Helenurm 1987
		s/fr	3.5	3.6	3.1	ns	
Paeoniaceae							
Paeonia californica		x	0.3	4.5	1.4	***	Schlising 1976
Papaveraceae							
Argemone aurantiaca	Control vs. 1st day	s/fr	117	206	187	◆	Schneider & Nichols 1984
Platystemon californicus	Hastings	%s	73	90	1	◇	Hannan 1981
Sanguinaria canadensis		%f	96.9	94.1	89	ns	Motten 1986
		%s	66.6	69.1		ns	
		s/fr	12.6	13.4	15.7	ns	
Passifloraceae							
Passiflora vitifolia	Vine #2	%f	34	57	0	(*)	Snow 1982
	Vine #4	%f	9	70	0	(**)	
Polemoniaceae							
Ipomopsis aggregata	Period 1	%f	36	83	SI	*	Hainsworth et al. 1985
	Period 1	s/fr	4.37	7.93	SI	*	
	Period 2	%f	40	79	SI	*	
	Period 2	s/fr	4.00	6.36	SI	ns	
	Period 3	%f	36	71	SI	*	

Appendix I
Continued

Species	Subset^{a}	Type of Data^{b}	Treatment Means: Natural	Outcross	Self^{c}	Stat. Test^{d}	Reference
I. aggregata (contd.)	Period 3	s/fr	3.42	4.50	SI	ns	
		s/fl	0.63	1.95	SI	***	Campbell 1991
Polemonium foliosissimum	22 July, CC vs. EP	s/fl	12.7^{f}	14.3^{f}	SI	*	Zimmerman & Pyke 1988
	28 July, CC vs. EP	s/fl	15.8^{f}	16.9^{f}	SI	ns	
	3 Aug., CC vs. EP	s/fl	11.4^{f}	13.4^{f}	SI	*	
	9 Aug., CC vs. EP	s/fl	11.0^{f}	13.2^{f}	SI	*	
Polemonium viscosum	3528 m, sweet	s/fl	1.37	4.47	SI	***	Galen 1985
	3528 m, skunky	s/fl	2.67	4.86	SI	**	
	3640 m, sweet	s/fl	3.12	5.82	SI	***	
	3640 m, skunky	s/fl	3.72	4.37	SI	ns	
	4025 m, sweet	s/fl	2.73	5.03	SI	**	
	4025 m, skunky	s/fl	1.84	4.69	SI	***	
Polygalaceae							
Monnina angustifolia		%f	47.13	73.33	0	(ns)	Arroyo & Uslar 1993
		s/fr	1.00	1.00	0	◇	
Pontederiaceae							
Eichhornia crassipes	(All months)	%f	31.7	95.6	SC	(**)	Barrett 1980
	June	s/fl	3.1	74.1	SC	◆	
	July	s/fl	6.0	168.1	SC	◆	
	August	s/fl	31.2	163.1	SC	◆	
	Sept	s/fl	40.8	188.7	SC	◆	
	October	s/fl	32.9	159.1	SC	◆	
Portulacaceae							
Calandrina grandiflora		%f	93.58	100.00	76.47	(ns)	Arroyo & Uslar 1993

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means: Natural	Treatment Means: Outcross	Treatment Means: Self[c]	Stat. Test[d]	Reference
C. grandiflora (contd.)		s/fr	141.77	141.50	129.08	◇	
Calandrina prostrata		%f	100.00	100.00	100.00	(ns)	Arroyo & Uslar 1993
		s/fr	8.73	8.50	8.43	◇	
Claytonia virginica		%f	84.4	86.4	91	ns	Motten 1986
		%s	71.7	69.7		ns	
		s/fr	4.3	4.1		ns	
Primulaceae							
Lysimachia quadrifolia	Open 1982	%f	19.7	61.5	16.6	*	McCall & Primack 1985
	Open 1983	%f	16.0	33.0	16.6	*	
	Open 1983	s/fl	0.26	0.63		ns	
	Scrub 1982	%f	32.4	31.1	16.6	ns	
	Scrub 1983	%f	36.3	44.1	16.6	ns	
	Scrub 1983	s/fl	1.34	1.92		ns	
	Scrub 1984	%f	24.7	62.0	16.6	*	
	Scrub 1984	s/fl	0.60	1.80		*	
Trientalis borealis	All patches	%f	66.1	84.3	2.0	ns	Anderson & Beare 1983
	All patches	s/fr	8.3	8.5		ns	
		%f	27.0	100.0	0	***	Barrett & Helenurm 1987
		s/fr	3.1	8.4		ns	
Trientalis europaea		%f	6.00	26.00	26.00	(**)	Hiirsalmi 1969
		s/fr	8.00	6.44	6.23	◇	
Proteaceae							
Banksia ericifolia	1984 Peak	%i	68.4	79.1		ns	Copland & Whelan 1989
	1985 Early	%i	50.9	52.0		ns	
	1985 Peak	%i	32.8	55.2		*	

Appendix I
Continued

Species	Subset^{a}	Type of Data^{b}	Treatment Means Natural	Outcross	Self^{c}	Stat. Test^{d}	Reference
B. ericifolia (contd.)	1985 Late	%i	12.1	3.7		ns	
	1986 Early	%i	32.1	18.5		ns	
	1986 Peak	%i	57.1	58.6		ns	
	1986 Late	%i	41.4	20.7		ns	
Banksia paludosa	1985 Early	%i	23.0	43.4		*	Copland & Whelan 1989
	1985 Peak	%i	42.9	48.3		ns	
		f/pl	35.9	64.6	2.3	*	Goldingay & Whelan 1990
		%i	15	30	6	*	
Banksia spinulosa		%i	13	22	0	ns	Goldingay & Whelan 1990
	1985 Peak	%i	10.7	43.3		***	Copland & Whelan 1989
Telopea speciosissima		s/fr	14.3	15.5	0	***	Whelan & Goldingay 1989
		s/pl	133.0	352.0	0	***	
		f/pl	9.5	22.3	0	*	
		%i	52	91	0	***	
Pyrolaceae							
Chimaphila umbellata		%f	57.4	75.0	75.0	ns	Barrett & Helenurm 1987
Pyrola secunda		%f	53.2	100.0	94.1	***	Barrett & Helenurm 1987
Ranunculaceae							
Aquilegia caerulea		%f	23	31		ns	J. Brunet in Young & Young 1992
		s/fr	1.7	2.8		ns	
Hepatica americana		%f	98.0	100	100	ns	Motten 1986
		%s	88.5	87.1		ns	
		s/fr	12.5	12.5	13.5	ns	
Thalictrum thalictroides		%f	98.0	100	98	ns	Motten 1986
		%s	82.8	81.5		ns	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
T. thalictroides (contd.)		s/fr	5.2	4.9	4.8	ns	
	Week 1	%s	89.4	85.4	79	ns	Lubbers & Christensen 1986
	Week 2	%s	74.7	87.3	79	*	
Rhamnaceae							
Talquena quinquenervia		%f	48.80	83.33	13.85	(*)	Arroyo & Uslar 1993
		s/fr	1.00	1.00	1.00	◇	
Rosaceae							
Amelanchier arborea		%f	38	46	SI	ns	Gorchov 1988
Crataegus crus-galli	S1	y	3.7	27.2	24.3	◆	Dickinson & Phipps 1986
	S2	y	15.3	21.3	11.0	◇	
	S3	y	1.7	5.8	1.0	◇	
	S4	y	0.7	0.9	5.0	◇	
	S10	y	5.4	19.1	17.2	◆	
Crataegus fontanesiana	S1	y	0.9	0	0.2	◇	Dickinson & Phipps 1986
	S2	y	1.0	4.1	0	◇	
	S2	y	6.8	1.4	24.8	◇	
Crataegus prunifolia	S6	y	8.6	11.1	17.7	◇	Dickinson & Phipps 1986
Crataegus punctata		y	14.6	24.5	0	◇	Dickinson & Phipps 1986
Dryas integrifolia	Total	%f	79.2	94.7		(ns)	Kevan 1972
Potentilla anserina	1985	s/fl	16.8	20.0	SI	ns	Eriksson 1987
	1986	s/fl	9.5	24.3	SI	***	
Rubus chamaemorus		%f	75.6	78.6		ns	Ågren 1989
		%s	49.7	70.0		**	
		s/fr	8.2	11.4		*	

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means: Natural	Treatment Means: Outcross	Treatment Means: Self[c]	Stat. Test[d]	Reference
Rubiaceae							
Houstonia caerulea	Heterogeneous vs. Total	%f	77.81	95	2	◇	Wyatt & Hellwig 1979
Mitchella repens	(All morphs)	%f	83	97	9	(ns)	Ganders 1975
Relbunium hypocarpium		%f	100.00	100.00	100.00	(ns)	Arroyo & Uslar 1993
		s/fr	1.74	2.00	1.76	◇	
Rutaceae							
Phellodendron amurense	1987	%f	15^f	50^f	D	***	Mizui & Kikuzawa 1991
	1988	%f	70^f	60^f	D	ns	
	1989	%f	80^f	81^f	D	ns	
Salicaceae							
Salix alaxensis		s/fr	8.0	9.5	D	*	Fox 1992
	1985	z	0	$+36^e$	D	*	
	1986	z	0	$+3^e$	D	ns	
Salix arctica	Total	%i	80.6	100	D	(*)	Kevan 1972
Salix novae-angliae		z	0	$+37^e$	D	*	Fox 1992
Salix planifolia		z	0	$+13^e$	D	ns	Fox 1992
Saxifragaceae							
Saxifraga granulata	Hermaphrodites	%s	38.1	75.3	38.4	◇	Stevens 1988
	Females	%s	21.7	52.2		◇	
Saxifraga oppositifolia	Total	%f	90.8	72.7		(*)	Kevan 1972
Tiarella cordifolia		%f	59.7	68.1	4	ns	Motten 1986

Appendix I
Continued

Species	Subset^{a}	Type of Data^{b}	Treatment Means			Stat. Test^{d}	Reference
			Natural	Outcross	Self^{c}		
Scrophulariaceae							
Agalinis strictifolia	FM, 1985 week 3^{q}	%f	90	94		ns	Dieringer 1992
	FM, 1985 week 3^{r}	s/fr	122.5	172.4		**	
	FM, 1987 week 3^{q}	%f	94	100		ns	
	FM, 1987 week 3^{q}	s/fr	196.8	231.4		ns	
	WH, 1984 week 3^{q}	%f	81	89		ns	
	WH, 1984 week 4^{e}	s/fr	127.6	226.3		**	
	WH, 1987 week 3^{q}	%f	84	94		ns	
	WH, 1987 week 3^{q}	s/fr	213.3	220.7		ns	
Angelonia bisaccata		%f	65^{t}	90	0	◆	Vogel & Machado 1991
Angelonia hirta		%f	65^{t}	100	0	◆	Vogel & Machado 1991
Angelonia hookeriana		%f	65^{t}	93.3	0	◆	Vogel & Machado 1991
Angelonia pubescens		%f	100	100	100	◇	Vogel & Machado 1991
Calceolaria purpurea		%f	29.29	81.81	20.00	(**)	Arroyo & Uslar 1993
		s/fr	111.48	106.56	21.33	◇	
Calceolaria sp.		%f	37.45	83.33	15.22	(**)	Arroyo & Uslar 1993
		s/fr	257.92	289.78		◇	
Hebe stricta		%f	63.6	78.7	SC	ns	Delph & Lively 1992
Linaria vulgaris		%s	1.6	9.5	0	◆	Arnold 1982
Mazus miquelii		%f	97.1	90.9	85.3	(ns)	Kimata 1978
Melampyrum pratense	8 June 1988	%f	36^{f}	54^{f}		$*^{u}$	Kwak & Jennersten 1991
	8 June 1988	s/fr	1.5^{f}	2.0^{f}		$*^{u}$	
	13 June 1988	%f	41^{f}	48^{f}		$*^{u}$	
	13 June 1988	s/fr	1.6^{f}	1.9^{f}		◇	
	19 June 1988	%f	22^{f}	28^{f}		◇	
	19 June 1988	s/fr	0.9^{f}	1.1^{f}		◇	
Rhinanthus angustifolius	Control vs. Trt. F	s/fl	5.3g	6.0g	SC	◇	Kwak & Jennersten 1986

Appendix I
Continued

Species	Subset[a]	Type of Data[b]	Treatment Means			Stat. Test[d]	Reference
			Natural	Outcross	Self[c]		
Solanaceae							
Physalis longifolia	Small plants	%f	7.6	25.4	SI	**	Lawrence 1993
	Small plants	s/fl	5.5	18.1	SI	ns	
	Small plants	s/fr	71.0	65.8	SI	ns	
	Large plants	%f	35.0	42.5	SI	ns	
	Large plants	s/fl	28.0	28.7	SI	ns	
	Large plants	s/fr	80.6	71.2	SI	ns	
Salpiglossis sinuata		%f	41.51	100.00	23.33	(**)	Arroyo & Uslar 1993
		s/fr	169.62	268.82	136.71	◇	
Solanum ligustrinum		%f	49.54	91.30	0	(**)	Arroyo & Uslar 1993
		s/fr	7.39	7.05	0	◇	
Solanum marginatum		%f	8.14	6.59	48	(ns)	Dulberger et al. 1981
Staphyleaceae							
Staphylea trifolia		%f	1.9	19.5	0.5	(**)	Garwood & Horvitz 1985
		s/fr	1.8	2.2		ns	
Sterculiaceae							
Gauzuma tomentosa		%f	1	89	0	(**)	Bawa 1974
Thymeliaceae							
Daphne kamtschatica	Female flowers	%f	44	67		**	Kikuzawa 1989
Tiliaceae							
Luehea candida	Cntrl. vs. Nocturnal	%f	19.3	91.9	0	(**)	Haber & Frankie 1982
	Cntrl. vs. Nocturnal	s/fr	62.9	82.8		*	
Luehea seemannii	Cntrl. vs. Nocturnal	%f	49.3	58.9	41.1	(*)	Haber & Frankie 1982
	Cntrl. vs. Nocturnal	s/fr	17.5	34.3	24.6	◆	

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Continued

Species	Subset[a]	Type of Data[b]	Treatment Means: Natural	Outcross	Self[c]	Stat. Test[d]	Reference
Luehea speciosa		%f	10	50	2	(**)	Bawa 1974
Tropaeolaceae							
Tropaeolum tricolor		%f	49.35	0	53.8	(**)	Arroyo & Uslar 1993
		s/fr	2.92	0	3.00	◆	
Vivianaceae							
Viviana marifolia		%f	34.67	64.00	0	(**)	Arroyo & Uslar 1993
		s/fr	1.70	1.69	0	◇	
Winteraceae							
Pseudowintera colorata		%f	21.8	72	0	◆	Lloyd & Wells 1992
Zingiberaceae							
Costus allenii		s/fr	46.7	45.1	30.5	ns	Schemske 1983
Costus guanaiensis		s/fr	107.9	92.5	81.2	ns	Schemske 1983
Costus laevis		s/fr	52.9	34.2	26.2	*	Schemske 1983

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[a] Site, time, morph, and treatment notation correspond to the usage of the authors. Parentheses indicate my summary when data were presented in a manner that allowed totalling.

[b] %f = percent fruit set; %s = percent seed set; %i = percent of inflorescences setting fruit; s/fl = number of seeds per original flower; s/fr = number of seeds per mature fruit; s/pl = number of seeds per plant; f/pl = number of fruits per plant; fr/i = number of fruits per inflorescence; s/i = number of seeds per inflorescence;

[c] When self pollination treatments were not performed, I indicate if authors report a species as self-compatible (SC), self-incompatible (SI), or dioecious (D).

Appendix I
Continued

[d] Test of difference between Natural and Outcross treatments.
ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$
( ), Parentheses indicate my χ^2 test of independence (see Compilation of Data).
◆, ◇, Statistical test not performed by author(s), but pollen limitation is assumed to occur (◆) or not to occur (◇) based on the magnitude of difference between natural pollination and hand outcrossing.

[e] Value estimated from Figure 1 of the corresponding reference.

[f] Value estimated from Figure 2 of the corresponding reference.

[g] Value estimated from Figure 3 of the corresponding reference.

[h] Value estimated from Figure 4 of the corresponding reference.

[i] Value estimated from Figure 5 of the corresponding reference.

[j] Means for hand outcrossing treatment calculated from Table 4 of the corresponding reference.

[k] Value is a median, not mean.

[m] Values not reported, but "[s]eed number per flower showed a slight, but significant increase when pollen was added ($G = 14.18$; $df = 4$; $P < 0.025$)" (Stanton 1987, p. 193).

[n] Control mean calculated from all flowers in MF, MB, and HL sites for 1978 + 1979.

[p] In mature fruits only.

[q] *Experiment performed on 5 weeks. Only one week's results shown, but no differences were significant on any week.*

[r] Experiment performed on 5 weeks. All differences were significant except for week 4.

[s] Experiment performed on 5 weeks. Only the week 4 difference was significant.

[t] Approximate value given in text of article.

[u] Difference is referred to in text of article as significant, but statistical test and significance level not given.

[x] *number of seeds/carpel (multiple carpels per flower)*

[y] percent of locules in which seed formed

[z] percentage difference in mean s/fr for hand outcrossing relative to mean s/fr for natural pollination