Pollen Limitation of Plant Reproduction:
Pattern and Process

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■ **Abstract** Quantifying the extent to which seed production is limited by the availability of pollen has been an area of intensive empirical study over the past few decades. Whereas theory predicts that pollen augmentation should not increase seed production, numerous empirical studies report significant and strong pollen limitation. Here, we use a variety of approaches to examine the correlates of pollen limitation in an effort to understand its occurrence and importance in plant evolutionary ecology. In particular, we examine the role of recent ecological perturbations in influencing pollen limitation and discuss the relation between pollen limitation and plant traits. We find that the magnitude of pollen limitation observed in natural populations depends on both historical constraints and contemporary ecological factors.

INTRODUCTION

Pollen limitation occurs when plants produce fewer fruits and/or seeds than they would with adequate pollen receipt. Inadequate pollination can in turn affect plant abundance and population viability and cause selection on plant mating system and floral traits (e.g., Ashman et al. 2004; Johnston 1991a,b; Lennartsson 2002; Lloyd & Schoen 1992). Thus pollen limitation has attracted considerable attention from both ecologists and evolutionary biologists (Ashman et al. 2004, Burd 1994, Larson & Barrett 2000). Given that floral phenotype can affect pollen receipt (e.g., aerodynamic morphology for abiotic pollination and attraction and rewards for biotic pollination), selection for floral traits may be particularly strong in pollen-limited populations, and thus pollen limitation may play an important role in the evolution of secondary sexual traits (Ashman & Morgan 2004). Furthermore, there is concern that pollinators are declining in many habitats, which could lead to widespread pollen limitation and a global pollination crisis (e.g., Buchmann & Nabhan 1996), affecting not only the sustainability of plant populations but also that of the organisms that either directly or indirectly rely on them. Even ecosystem services provided to humans by plants and pollinators, such as pollination of crops, may be at risk (Buchmann & Nabhan 1996, Kremen et al. 2002, Kremen & Ricketts 2000, Ricketts et al. 2004).

To test for pollen limitation in natural populations, researchers often conduct pollen supplementation experiments in which they compare the reproductive success of control plants with that of plants given supplemental pollen. If plants (or inflorescences or flowers) produce more fruits or seeds when supplemented, then it is usually concluded that reproduction is limited by pollen receipt (e.g., Ashman et al. 2004, Bierzychudek 1981).

Sexual selection theory assumes that female reproductive success is limited by resources rather than by access to mates (receipt of pollen) (Bateman 1948, Janzen 1977, Willson & Burley 1983, Wilson et al. 1994). In addition, one set of predictions, based on optimality theory, suggests that plants should evolve a level of attraction in which the benefits of attraction balance the costs of seed maturation (Haig & Westoby 1988). Both frameworks suggest that pollen addition should not increase fruit or seed set in populations at evolutionary equilibrium because resources should be unavailable for maturation of the additional fertilized ovules. However, empirical tests indicate the contrary: Pollen insufficiency often limits seed production, sometimes severely (reviewed in Ashman et al. 2004, Burd 1994, Larson & Barrett 2000).

There are several possible explanations for the apparent prevalence and strength of pollen limitation. First, recent ecological perturbations may disrupt coevolved interactions between plants and pollinators leading to pollen limitation. Second, pollen limitation may represent an evolutionary equilibrium in a stochastic environment. Finally, plant traits that promote outcrossing may evolve even when pollen limitation increases as a correlated response to selection on these traits.

We begin our consideration of these possible explanations with a brief introduction to the theoretical frameworks proposed to explain the causes and consequences of pollen limitation. Second, we discuss the evidence that ecological perturbations may contribute to pollen limitation. Third, we provide an overview of the extent and distribution of pollen limitation within and among plant species using quantitative meta-analysis (Gurevitch et al. 2001) on the most extensive data set on pollen limitation available. And finally, we use comparative approaches that account for phylogeny to explore relationships between plant traits and the magnitude of pollen limitation.

THEORETICAL BACKGROUND

An optimal plant in a constant environment should allocate resources perfectly between plant attraction and seed provisioning to ensure that enough pollen arrives to fertilize ovules that will mature to seed (Haig & Westoby 1988). As a result, pollen supplementation experiments should not, at least on average, enhance seed production. This is because plants exhibiting the optimal strategy do not have extra resources available for maturation of ovules fertilized by supplemental pollen. However, plants in recently degraded habitats may be pollen limited because they have not had enough time to evolve to their new optimal level of allocation. In a section below, we examine evidence for increased pollen limitation following ecological perturbations.

Even if plants are at an evolved equilibrium, pollen limitation might be expected if there is intraplant variation in pollen receipt. In a theoretical treatment, Burd (1995) considered whether plants should package more ovules within each flower than resources would allow the plant to mature into seeds should they all be fertilized. Such overproduction of ovules allows a plant to capitalize on particularly plentiful pollination of some flowers. Because most plants package ovules in multiple flowers or inflorescences, there is an economy of scale within packages, where per-ovule costs decrease as ovule number increases (Thomson 1989). The model assumes that individual plants can direct resources toward fertilized ovules and can, therefore, take advantage of occasional abundant pollen receipt. Higher flower-to-flower variance in pollen receipt (which increases the frequency of occasional, abundant pollination), greater non-ovule flower costs (e.g., pedicel, corolla), and cheaper ovules all favor excessive ovule production. We expect to see greater pollen limitation in plants that have high ovule numbers per flower and high interflower variation in pollen receipt.

The presence of pollen limitation reduces seed production and, therefore, may have a variety of demographic consequences. Reductions in seed production may have effects on the overall population size, particularly in short-lived species without a seed bank, in species that respond to disturbances by re-establishing from seeds (Ashman et al. 2004, Bond 1994). As landscapes become increasingly

fragmented, the persistence of plant populations may depend on the abilities of their pollinators to move between patches (Amarasekare 2004). Pollen limitation may also play a role in the coexistence among plant species within a community (Feldman et al. 2004, Ishii & Higashi 2001). It is well know that trade-offs among plants in performance traits can facilitate coexistence; therefore, plants that trade-off in their ability to compete for resources and attract pollinators might be better able to coexist. However, to date, the role of pollen limitation on plant community composition has received little theoretical and empirical attention.

Persistent pollen limitation has evolutionary consequences; most notably, pollen limitation may favor the evolution of self-compatibility and/or increased selfing when selfing offers reproductive assurance. Pollen discounting and inbreeding depression are expected to counteract any selection pressures to increase the selfing rate; however, pollen discounting may be reduced when plants are pollen limited, which would promote the evolution of increased selfing (Porcher & Lande 2005). Evolution of self-compatibility and/or increased selfing has been suggested for plants in recently established habitats (as in Baker's law; Pannell & Barrett 1998), for plants occurring at low densities (Morgan et al. 2005), and for plants in variable pollination environments (Morgan & Wilson 2005). Furthermore, pollen limitation has been proposed as a mechanism by which androdioecy can evolve from dioecy; hermaphrodites suffer less pollen limitation than female plants (Liston et al. 1990, Maurice & Fleming 1995, Wolf & Takebayashi 2004). Also, it has been suggested that plants evolve to have only partial expression of self-incompatibility as an adaptation to avoid pollen limitation (Vallejo-Marín & Uyenoyama 2004). In all, plants that are hermaphroditic and self-compatible are expected to have lower levels of pollen limitation than those that are obligate outcrossers. In the evolutionary consequences of pollen limitation section below, we examine the evidence for this from pollen supplementation experiments.

Likewise, wind pollination should reduce the reliance of plants on pollinators and as such may evolve when plants are pollen limited; this possibility has been discussed in detail for dioecious species. Dioecious species are often sexually dimorphic (females typically inconspicuous relative to males), and during years of low pollinator abundance, this makes female reproductive success particularly prone to pollen limitation (Vamosi & Otto 2002). While the order of origin of dioecy and of wind pollination is a matter of debate, it may be that dioecious species that persist evolve mechanisms, such as wind pollination, that reduce reliance on pollinators. A related argument notes that separation of genders in dioecious species increases variance in reproductive success (i.e., pollen limitation) (Wilson & Harder 2003) and leads to selection for variance-reducing mechanisms such as high pollen or seed dispersal.

Pollen limitation may cause stronger selection on attractive traits that enhance reliability of pollinator visits (Ashman & Diefenderfer 2001; Johnston 1991a,b; Wilson et al. 1994). Similarly, pollen limitation may select for changes in floral shape; zygomorphic flowers attract more specialized pollinators than actinomorphic flowers, and these pollinators may provide more reliable pollination (Neal

et al. 1998). Thus we expect that plants that make larger and more specialized flowers may have lower levels of pollen limitation than those that make smaller actinomorphic flowers.

ECOLOGICAL PERTURBATIONS AND POLLEN LIMITATION

Changes in the abiotic or biotic features of the habitat and changes in the range of plants and/or pollinators can disrupt plant-pollinator interactions (Bond 1994, Kearns et al. 1998, Wilcock & Neiland 2002). Because plants in recently perturbed environments will not have made evolutionary adjustments, these plants may show unusually high levels of pollen limitation.

Types of Ecological Perturbations

Here, we briefly discuss several types of ecological perturbations, the mechanisms by which they alter the magnitude of pollen limitation, and the evidence of their occurrence from pollen supplementation experiments (Table 1).

PRESENCE OF CO-FLOWERING PLANT SPECIES   Changes in abiotic or biotic conditions may change the identity or abundance of co-flowering plant species, and the presence of co-flowering species can reduce or increase pollination success of a focal species (Table 1). Facilitation may be more likely when plant species offering little reward are surrounded by rewarding plant species (Johnson et al. 2003, Laverty 1992), whereas competition for pollinators may be more likely between equally rewarding species.

DECREASES IN PLANT POPULATION SIZE/DENSITY   Many ecological perturbations such as habitat fragmentation (Cunningham 2000), human harvesting (Hackney & McGraw 2001), and increases in herbivore abundance (Vàzquez & Simberloff 2004) reduce plant abundance. Decreases in plant density are generally assumed to decrease pollination success and increase the magnitude of pollen limitation of both animal- and wind-pollinated plant species (Table 1). In addition, reductions in plant density may affect offspring quality. If pollinators visit more flowers on the same plant when density is low, this will increase the level of inbreeding for self-compatible plants (e.g., Karron et al. 1995). Alternatively, increases in the interplant distance traveled by pollinators may increase the outcrossing rate if plants that are further away are also less related (Lu 2000, Schaal 1978).

POLLINATOR LOSS   Ecological perturbations that displace pollinators may result in pollen limitation in plants that utilize those pollinators. However, there are few studies demonstrating that the loss of a pollinator results in increased pollen limitation (Table 1). It may be that such cases occur but have not been documented

TABLE 1 For each type of ecological perturbation, we provide the predicted consequences for pollen limitation (PL), an explanation of the mechanism, and supporting studies

Ecological perturbation	Predicted consequence for pollen limitation	Explanation	Empirical support
Presence of other plant species	$PL_{coflowering\ species} > PL_{single\ flowering\ species}$	Co-flowering results in pollinator competition, increased heterospecific pollen delivery, and/or stigma clogging by heterospecific pollen[a]	Campbell 1985, Gross 1996, Gross & Werner 1983
	$PL_{coflowering\ species} < PL_{single\ flowering\ species}$	Co-flowering results in increased pollinator attraction[b]	Moeller 2004
Plant population size/density	$PL_{in\ small\ populations} > PL_{in\ large\ populations}$	Small populations have reduced pollinator visitation, pollen deposition[c], ratio of conspecific to heterospecific pollen delivered[d] and more intraplant pollinator visits[e]	Ågren 1996, Davis et al. 2004, Forsyth 2003, Knight 2003, Kunin 1997, Moeller 2004, Sih & Balthus 1987, Waites & Ågren 2004, Ward & Johnson 2005
Pollinator loss	$PL_{with\ fewer\ pollinators} > PL_{with\ more\ pollinators}$	Pollinator visitation rate increases with pollinator abundance and diversity[f]	Liu & Koptur 2003
Resource additions	$PL_{in\ resource\ rich\ habitat} > PL_{in\ resource\ poor\ habitat}$	Seed production depends solely on pollen receipt when resources are unlimited	Galen et al. 1985
Habitat size and isolation	$PL_{in\ fragmented\ habitat} > PL_{in\ continuous\ landscape}$	Habitat fragmentation reduces the abundance of plants and/or pollinators, alters pollinator composition[g]	Cunningham 2000, Groom 2001, Johnson et al. 2004, Moody-Weis & Heywood 2001, Steffan-Dewenter & Tscharntke 1999, Wolf & Harrison 2001

(Continued)

TABLE 1   (*Continued*)

Ecological perturbation	Predicted consequence for pollen limitation	Explanation	Empirical support
Plant enemies (herbivores, pathogens)	$PL_{\text{with high enemy abundance}} > PL_{\text{with low enemy abundance}}$	Enemies decrease pollinator attraction and pollinator visitation[h]	None
	$PL_{\text{with high enemy abundance}} < PL_{\text{with low enemy abundance}}$	Enemies decrease plant resource status; plants become more limited by resources than pollen	Parker 1987
Plant mutualists (mycorrhizal fungi)	$PL_{\text{with high mutualist abundance}} < PL_{\text{with low mutualist abundance}}$	The presence of soil mutualists facilitates plant resource acquisition, pollinator visitation and seed set[i]	None
Pollinator predators	$PL_{\text{with pollinator predators}} > PL_{\text{without predators}}$	Predators reduce pollinator abundance and visitation rate[j]	Knight et al. 2005
Non-native plant species	$PL_{\text{non-native plants}} > PL_{\text{native plants}}$	Non-native plants lack effective pollinators[k]	None
	$PL_{\text{non-native plants}} < PL_{\text{native plants}}$	Non-native plants have a higher frequency of autogamy[l]	None
Non-native pollinators	$PL_{\text{with non-native pollinator}} > PL_{\text{without non-native pollinator}}$	Non-native pollinators compete with native pollinators, and are less efficient pollinators of crops and wild plants[m]	None

[a]Campbell & Motten 1985; Caruso 1999, 2001; Galen & Gregory 1989; Waser 1983.

[b]Moeller 2005, Rathcke 1983.

[c]Fausto et al. 2001, Feinsinger et al. 1991, Regal 1982, Whitehead 1983.

[d]Caruso 2002, Kunin 1993.

[e]Franceschinelli & Bawa 2000, Iwaizumi & Sakai 2004, Klinkhamer & de Jong 1990, Mustajärvi et al. 2001.

[f]Buchmann & Nabhan 1996, Kearns et al. 1998, Thomson 2001.

[g]Jennersten 1988, Linhart & Feinsinger 1980.

[h]Mothershead & Marquis 2000; Steets & Ashman 2004; Strauss et al. 1996; Irwin, Brody & Waser 2001.

[i]Wolfe et al. 2005.

[j]Dukas 2001, Dukas & Morse 2003, Muñoz & Arroyo 2004, Suttle 2003.

[k]Parker 1997.

[l]Rambuda & Johnson 2004.

[m]O'Toole 1993, Paini 2004, Paton 1993, Sugden & Pyke 1991.

or that the majority of plants are buffered against the loss of any single pollinator species (Morris 2003) because of generalized pollination systems (Waser et al. 1996), the presence of other functionally redundant pollination species (Balvanera et al. 2005, Fenster et al. 2004), and/or autogamous pollination.

RESOURCE AVAILABILITY   Several perturbations may rapidly increase or decrease the resources available to plants (i.e., agricultural runoff, competition with non-native plant species). Based on theoretical predictions (Haig & Westoby 1988), increases in resource availability should cause plant reproductive output to become more limited by pollen receipt than by resources. Although several studies have factorially manipulated pollen and resources (i.e., water, nutrients, light), only one study reported a significant interaction between pollination and resource treatments in the expected direction (Table 1). This may reflect the abilities of plants to plastically respond to resource additions in their attraction traits or could suggest that factors in addition to resource availability and pollen receipt are influencing seed production (Campbell & Halama 1993).

HABITAT FRAGMENTATION   Habitat fragmentation simultaneously affects a variety of abiotic and biotic factors, which directly or indirectly change the abundance and composition of plants and pollinators, and may lead to increased pollen limitation (Table 1). The effect of fragmentation on the magnitude of pollen limitation will depend on the extent of habitat loss and isolation. Pollinators with limited movement may be lost from fragmented habitats unless corridors are present (Townsend & Levey 2005). Furthermore, self-incompatible plants with specialized pollinators may be particularly prone to pollen limitation following habitat fragmentation (Bond 1994), although there are not enough studies of pollination within fragmented landscapes to make generalizations at this time (Aizen et al. 2002).

OTHER INTERACTING SPECIES   Changes in the abundance of plant enemies (e.g., herbivores, pathogens, nectar robbers), plant mutualists (e.g., mycorrhizal fungi), and pollinator enemies (predators) may all affect interactions between plants and pollinators and thus the magnitude of pollen limitation (Table 1). Whereas many studies have factorially manipulated plant enemies and pollen receipt (Bertness & Shumway 1992, Garcia & Ehrlen 2002, Holland 2002, Juenger & Bergelson 1997, Krupnick & Weis 1999, Lehtila & Syrjanen 1995, Mizui & Kikuzawa 1991, Mothershead & Marquis 2000), only Parker (1987) found a significant interaction; enemies decreased the magnitude of pollen limitation. Other interacting species in the community have received much less attention and should be the target of future empirical work.

INTRODUCED PLANTS   To date it is unclear what role pollen limitation has in the establishment and spread of non-native plants (Richardson et al. 2000). Plant ecologists have argued that introduced plants may be more or less likely to suffer pollen limitation (Table 1). Studies comparing the breeding system and magnitude

of pollen limitation of native and non-native plant species would be particularly informative, especially if phylogeny could be accounted for (i.e., by comparing related species). Once established, non-native plants may have consequences for the pollination of native species (Brown et al. 2002, Grabas & Laverty 1999, Moragues & Traveset 2005).

INTRODUCED POLLINATORS   Pollinators, and in particular honeybees (*Apis mellifera*), have been introduced widely outside of their native range (Hanley & Goulson 2003). The presence of non-native pollinators is expected to increase the magnitude of pollen limitation in native plants (Table 1). However, no study to date has demonstrated this.

Population-Level Effects

Although we have shown that a variety of ecological perturbations can alter the magnitude of pollen limitation among plant species, plant species will not be equally responsive. We expect that plant species that are pollinated by specialists, those that are non-rewarding, and those that are self-incompatible or dioecious should be particularly vulnerable to ecological perturbations leading to increased levels of pollen limitation (Bond 1994). In addition, even if pollen limitation does occur, this will not necessarily have large effects on the abundance and viability of plant populations (Ashman et al. 2004). Plants that are long-lived or capable of asexual reproduction are less vulnerable to pollination-driven extinction (Bond 1994, Johnson et al. 2004). Few studies have examined whether plant traits related to pollination biology can help to explain large-scale patterns of rarity in plants; those that have, however, provide intriguing results (Neiland & Wilcock 1998, Vamosi & Vamosi 2005a, Wilcock & Neiland 1998). For example, non-rewarding orchid species are rarer than their rewarding counterparts (Neiland & Wilcock 1998), and dioecious families were more often listed as threatened or endangered than their hermaphrodite sister taxa (Vamosi & Vamosi 2005a).

PATTERNS OF POLLEN LIMITATION

Here, we describe the pattern of pollen limitation documented from pollen supplementation experiments conducted over the past 25 years. In particular, we ask the following questions:

1. Which components of seed production (e.g., fruit set, seeds per plant) are most commonly studied, and do these components show similar patterns?
2. What is the prevalence and magnitude of pollen limitation?
3. How much of the variation in the magnitude of pollen limitation occurs across plant taxa, across populations within a species, and across individuals within a population?

To describe patterns in pollen limitation within and across plant species, we created a data set from published and unpublished pollen supplementation experiments. We searched ISI's *Web of Science* and *Biological Abstracts* for the publication years 1981–2003 using the key words pollen limit*, supplement* poll*, and hand poll*. We also solicited unpublished data, which were generously provided by Chris Ivey, Susan Kephart, Renate Wesselingh, Lorne Wolfe, and Helen Young. We only included studies that reported the sample size, mean, and some measure of variance among plants in pollen-supplemented and control treatments, and studies that measured one of the following five response variables: percent fruit set (percent of flowers setting fruit), percent seed set (percent of ovules setting seed), number of seeds per fruit, number of seeds per flower, and number of seeds per plant. When variance was not presented and data were binary (i.e., fruit set), we calculated variance from the mean and sample size of each treatment. Data published in graphical form were estimated using digitizing software (Grab It, version 1, 1998). We also recorded other information regarding plant traits, pollinator environment, habitat, and methodology; these are discussed in detail in the analyses below.

To describe general patterns of pollen limitation, we included data only from plants that were not manipulated in other ways (e.g., nutrient addition). When a study involved multiple populations, we considered each population to be a separate data record. Likewise, when a study considered multiple years, each year was considered a separate data record (as long as the treatments were not applied to the same plants each year). However, when studies included within-year variation (e.g., studies that applied treatments to some plants early in the season and others later in the season) and/or within-population variation (e.g., plants with different style morphs within a population), we averaged across these to produce a single value of pollen limitation for each response variable. For the few studies that applied pollination treatments in more than one year on the same plants, only the first year of the study was included. In all, we had 655 records from 263 studies, which were conducted on 306 plant species in 80 plant families.

To examine the magnitude of pollen limitation for each response variable, we calculated effect size from pollen supplementation experiments as the log response ratio (ln *R*),

$$\ln R = \ln(\bar{X}^E / \bar{X}^C),$$

where $\bar{X}$ is the mean of the response variable, and *E* and *C* denote the experimental (supplemented) and control treatments (Gurevitch et al. 2001, Hedges et al. 1999). A value of 0 reflects no difference in reproductive success between plants in the supplemented and control treatments, a positive value indicates higher reproductive success in the supplemented treatment, and a negative value indicates higher reproductive success in the control treatment. Because studies varied in sample size and therefore sampling variance, we weighted individual studies by their variances before calculating the average effect size (Gurevitch et al. 2001).

Pollen supplementation experiments may indicate higher magnitudes of pollen limitation when only a fraction of the plant's flowers receive the experimental treatment relative to whole-plant treatment (Zimmerman & Pyke 1988). Many plant species can reallocate resources among flowers within inflorescences, and many polycarpic species can reallocate unused resources to reproduction in future years (Calvo 1993, Campbell & Halama 1993, Dudash & Fenster 1997, Ehrlen & Eriksson 1995, Primack & Hall 1990, Primack & Stacy 1998, Stephenson 1981, Zimmerman & Pyke 1988). As a result, fruit set for the flowers hand-pollinated may exceed the controls even though a whole plant would be unable to respond with higher fruit set. Although these reallocation problems were pointed out in detail by Zimmerman & Pyke (1988), most pollen supplementation experiments are still conducted on only a portion of a plant's flowers, likely because of the difficulty in pollinating all flowers on long-lived plants. Because the level at which the treatments are applied influences the overall magnitude of pollen limitation (T.M. Knight, J.A. Steets, T.-L. Ashman, unpublished data), we distinguished between studies conducted on all or a portion of the flowers on a plant in our analyses.

Which Components of Seed Production Are Most Commonly Studied and Do These Components Show Similar Patterns?

Studies differed in the number and type of response variables (e.g., fruit set, seeds per plant) measured. Of the 655 records described above, 482 report measures of pollen limitation for percent fruit set, 170 for percent seed set, 182 for number of seeds per fruit, 94 for number of seeds per flower, and 87 for number of seeds per plant. Because percent fruit set was the most commonly measured response variable, we primarily use percent fruit set effect size for the analyses in this review. However, seeds per plant is the most appropriate response variable for most questions related to the study of pollen limitation, as it measures the effect on maternal fitness of an individual plant (Ashman et al. 2004, Dudash & Fenster 1997). To determine how well the magnitude of pollen limitation reported for fruit set (the most commonly measured response variable) correlated with the magnitude of pollen limitation reported for seeds per plant (the best response variable), we correlated these effect sizes for the 63 data records in which both response variables were reported. Most of these 63 data records were for herbaceous species, in which pollination treatments at the whole plant level were possible. We find a strong correlation between these effect sizes (Pearson's $r = 0.567$, $P < 0.001$) (Figure 1), suggesting that pollen limitation in percent fruit set is a good indicator of pollen limitation in the number of seeds produced by the entire plant. However, we note that there are two outlier points in which strong pollen limitation was present for percent fruit set but not in total seed production. This could result from plants in the supplement treatment making fewer flowers than plants in the control treatment.

What Is the Prevalence and Magnitude of Pollen Limitation?

Sixty-three percent of the 482 data records on percent fruit set showed significant pollen limitation (for each data record, significant pollen limitation was determined
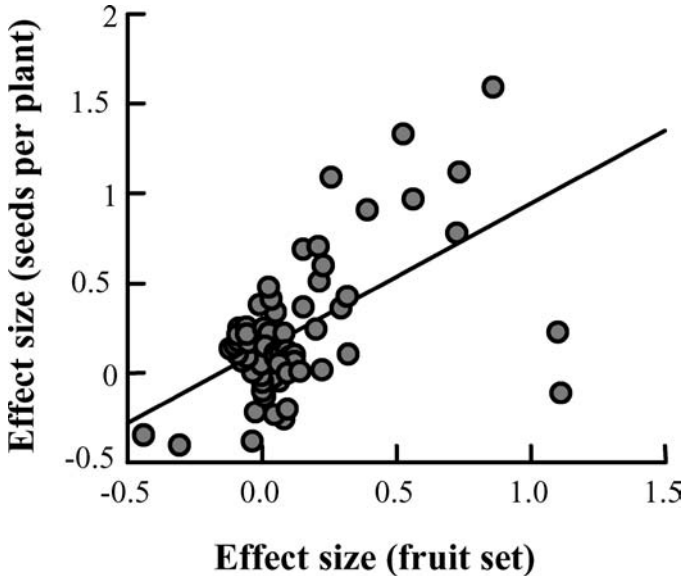
Figure 1   Relationship between two measures of pollen limitation effect size, percent fruit set and number of seeds per plant, for data records in which both were measured.

by a 1-tailed t-test). These results are similar to the prevalence calculated in slightly different ways in previous reviews of pollen limitation. For example, Burd (1994) reported that 62% of plant species showed pollen limitation in some populations or years (see also Ashman et al. 2004, Larson & Barrett 2000, Young & Young 1992).

The distribution of effect sizes for percent fruit set across all our data records suggests a high magnitude of pollen limitation in angiosperms. The weighted average effect size of 0.52 was significantly positive (i.e., 95% confidence intervals do not overlap with zero) and the distribution was leptokurtic distribution. The weighted average effect size corresponds to 75% higher fruit set in the supplemented compared with that in the control treatment (Figure 2).

How Much of the Variation in the Magnitude of Pollen Limitation Occurs Across Plant Taxa, Within Plant Species, and Within Populations?

Although we did not find differences in effect size for percent fruit set among Classes or Orders of plants in our full data set, the effect size differed significantly among plant families (variance component = 22% of the total variance within Class), among genera within families (variance component = 15%), and among
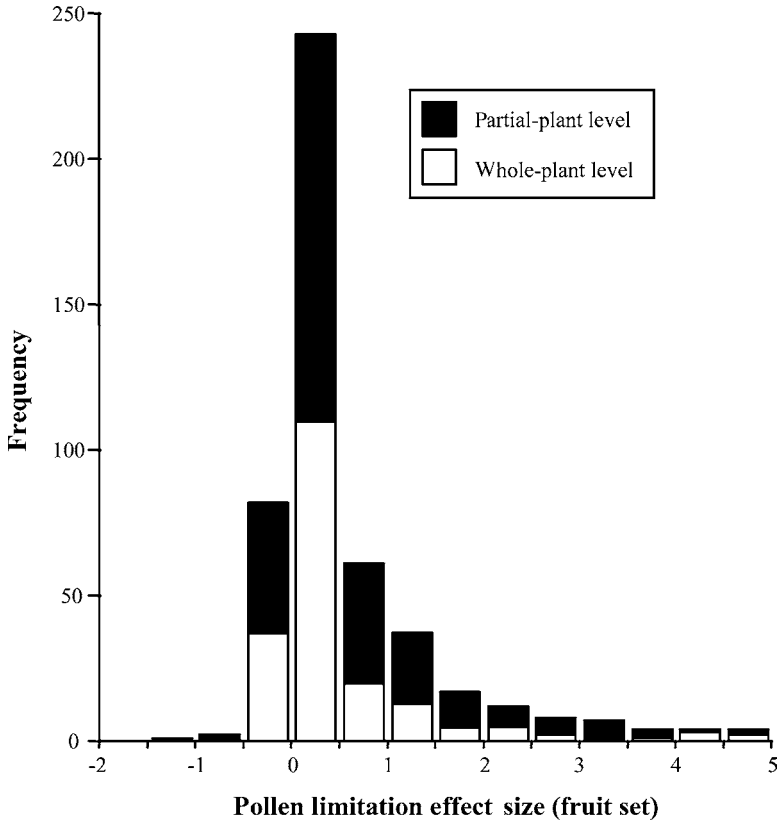
Figure 2   Histogram showing pollen limitation effect size for percent fruit set ($N = 482$ data records). See text for calculation. Shading indicates the level of treatment (whole-plant versus partial-plant) used in the pollen supplementation experiment.

species within genera (33%)[1]. Variation among families still existed when we restricted the analysis to the studies conducted at the partial-plant level (variance component $= 37\%$), suggesting that differences in pollen limitation among taxa are not solely due to methodological differences in how these taxa are studied. For studies at the whole-plant level, which give the least biased estimates of pollen limitation, significant taxonomic variation was retained only for variation among species in fruit set ($P < 0.05$). These findings suggest that related taxa may share

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[1]For these analyses we treated Class (Monocots vs. Eudicots) as a fixed factor and all other levels (Order, Family, Genus, Species) as random factors fully nested within the higher levels. Because our sampling at various taxonomic levels was unbalanced, we used the Mixed procedure in SAS software (version 8.2; SAS 2001) to find restricted maximum likelihood estimates of the variance components (Littell et al. 1996).

traits that affect the degree of pollen limitation and justify further analyses using phylogenetically corrected methods (see below).

Significant variation among populations of a species may signify that ecological features of the habitat, which vary in space and time, drive patterns of pollen limitation. In addition, high variation in pollen limitation may occur among individuals within a population as a result of microsite differences or phenotypic differences between individual plants. In our data set, three species were studied in more than 10 localities or years, and several studies examined within season and within individual variation in pollen limitation. In general, variation within these species, seasons, and across individuals within a population was small relative to the variation observed across taxa. Specifically, the range of pollen limitation observed for three well-studied species was 0 to 0.30 for *Trillium grandiflorum* (Kalisz et al. 1999, Knight 2003); −0.31 to 0.31 for *Silene dioica* (Carlsson-Graner et al. 1998); and −0.03 to 1.11 for *Narcissus assoanus* (Baker et al. 2000).

Pollen limitation may vary among individuals within a population owing to variation in plant traits. A trait that has received much attention is flowering time, and several studies have suggested that pollination success can select for changes in flowering time (e.g., Campbell 1985, Gross & Werner 1983, Ramsey 1995, Santrandreu & Lloret 1999, Widén 1991). For example, Santrandreu & Lloret (1999) found that *Erica multiflora* individuals flowering at the peak of the population bloom were less pollen limited than those flowering early or late, possibly because peak flowers are more likely to receive pollinator visits and outcross pollen. Others have suggested that temporal variation in pollen limitation may be caused by interspecific competition for pollinators (e.g., Campbell 1985, Gross & Werner 1983, Ramsey 1995) and temporal shifts in the sex ratio of the population (Jennersten et al. 1988, Le Corff et al. 1998).

MACROEVOLUTIONARY PATTERNS OF POLLEN LIMITATION

A number of traits may cause, or coevolve with, increased pollen limitation, and these can be divided into two main categories: (*a*) traits associated with sexual reproduction, including flower size, floral longevity, breeding system, floral shape, pollination syndrome, and ovule number per flower; and (*b*) life-history traits, including the number of reproductive episodes and the capability for asexual reproduction. Associations or correlations among species between a trait and pollen limitation can be from two distinct phenomena: (*a*) A direct causal relationship owing to the effects of the trait phenotype on pollinator behavior (e.g., flower size and pollen limitation; large-flowered species may attract more pollinators and are therefore less pollen limited) and (*b*) a coevolutionary adaptation (e.g., it may be adaptive for species with chronically unpredictable pollinator service to produce excess ovules per flower, which frequently make its flowers appear

pollen limited). In the latter case, there is the joint evolution of two (or more) traits because the particular combination of traits represents the outcome of natural selection.

We conducted two types of analyses to detect associations between plant traits and pollen limitation. First, we performed traditional statistical analyses (in this case, meta-analysis), often referred to as TIPS analyses, in which each species represents an independent data point (Burd 1994, Sutherland 1986). When more than one data record was present for a species, we calculated a weighted average effect size for each species (see above and Verdu & Traveset 2004). Randomization tests were performed to determine whether qualitative variables such as self-compatibility predict levels of pollen limitation among species; linear regression was used to determine whether quantitative variables such as ovule number or flower size predict the magnitude of pollen limitation. TIPS analyses are vulnerable to two primary criticisms. First, closely related and phenotypically similar species may not represent statistically independent data (Felsenstein 1985). Second, unmeasured variables that are associated with taxonomic membership may confound the statistical relationships among the measured variables. Nevertheless, TIPS analyses of taxonomically highly diverse data sets can provide ecologists with tests of whether observed relationships among traits support predictions based on clear causal mechanisms.

Second, we used a more conservative approach—the analysis of phylogenetically independent contrasts (or PICs) that takes into account the evolutionary relationships among species—to detect the direction or magnitude of joint evolutionary change in focal traits (Felsenstein 1985, 1988; Garland et al. 1992; Harvey & Mace 1982; Harvey & Partridge 1989; Pagel & Harvey 1988). PICs statistically analyze contrasts, i.e., differences in trait values between each pair of sister taxa or clades that represent independent evolution of the trait from a common starting point (common ancestor). Wilcoxon signed-rank tests (Vamosi & Vamosi 2005b) and regression tests (Webb et al. 2002) were used to determine whether a unidirectional change in an independent trait is associated with a positive (or negative) directional change in a dependent trait more frequently than one would expect by chance for discrete and continuous traits, respectively.

Larson & Barrett (2000) conducted both TIPS and PICs analyses on 224 species of biotically pollinated plants to examine the association between plant traits and pollen limitation. Their TIPS analyses indicated that pollen limitation was significantly associated with numerous plant traits, whereas their PICs analyses of the same data detected limited significant results; pollen limitation was found to be lower in clades that are self-compatible and herbaceous. The TIPS analyses may have detected more significant associations than the PICs analyses because the focal traits exhibit strong phylogenetic signals and because pollen limitation was measured on a nonrandom sample of angiosperm taxa. Since this analysis was performed, however, not only has a more extensive data set been compiled, but there have been many refinements and adjustments in the phylogenetic reconstruction

of angiosperms, in the use of meta-analytical approaches in phylogenetic analyses (Verdu & Traveset 2004) and the recognition of the impact of methodology on pollen limitation estimates (T.M. Knight, J.A. Steets, T.-L. Ashman, unpublished data), making a re-analysis warranted.

We used the online software utility, Phylomatic (Webb & Donoghue 2005), to provide a phylogenetic tree with taxonomic resolution to at least the family level. All branch lengths in the phylogeny were set to unity. When more than one data record was present for a species, we calculated a weighted average effect size for each species (see above and Verdu & Traveset 2004). We recorded the plant traits reported by authors of the studies in our data set (or through personal communication with those authors), or obtained from other published sources. We considered studies conducted on only portions of the plant (partial-plant level) and measuring percent fruit set as the greatest number of data were available for this level of treatment and response variable. We used the software program MetaWin (Rosenberg et al. 2000) for TIPS analyses and Phylocom (Webb et al. 2004) for PICs analyses.

Is There a Phylogenetic Signal for Pollen Limitation or Plant Traits of Interest?

We detected a phylogenetic signal (sensu Blomberg et al. 2003) for pollen limitation among species ($N = 166$, mean contrast $= 0.494$, $P = 0.002$) and among the plant traits we examined (Table 2A). This suggests that an examination of the relationship between pollen limitation and each plant trait is warranted.

Is There an Association Between Pollen Limitation and Plant Traits?

Below, for each trait evaluated, we discuss its predicted association with pollen limitation and present results from TIPS and PICs analyses. A potential shortcoming of these analyses is that sample size limitations precluded conducting multivariate analyses, i.e., our bivariate analyses did not control for potentially confounding third variables.

Traits Associated with Sexual Reproduction

FLOWER SIZE Species with large flowers may attract more pollinators than small-flowered species (Momose 2004, Valido et al. 2002) and are therefore less pollen limited. However, flower size is likely confounded with mating system, as species that are capable of autogamous selfing often have smaller flowers than those that are primarily outcrossing (Armbruster et al. 2002, Jain 1976). We conducted analyses with and without the inclusion of autogamous species, predicting that a negative relationship between flower size and pollen limitation would be more likely when

TABLE 2 Results from TIPs and PICs analyses examining the relationship between plant traits and pollen limitation

Trait	Test for phylogenetic signal in plant traits[A]			TIPS[B]		PICs[C]		
	Sample size (number of species)[a]	Mean contrast[b]	P-value[c]	Sample size (number of species)[d]	P-value	Mean contrast or slope	Positive/ total contrasts	P-value
Flower size	115	16.41	0.03	105	0.04	0.27	43/76	0.24
Floral longevity	96	2.62	0.09	74	0.39	−0.31	20/49	0.40
Breeding system: self-compatible versus self-incompatible	182	0.29	<0.01	155	<0.01	0.30	11/19	0.08
Breeding system: perfect versus imperfect	206	0.17	<0.01	166	0.43	−0.03	9/12	0.47
Floral shape: zygomorphic versus actinomorphic	207	0.14	<0.01	166	0.46	−0.20	5/14	0.15
Pollination syndrome: abiotic versus biotic	189	0.03	<0.01	150	0.30	0.10	2/3	0.38
Number of pollinating species: one, few, many	141	0.38	<0.10	111	0.01	−0.32	29/69	0.048
Ovule number per flower	183	144.3	<0.01	148	<0.01	0.29	51/84	0.04

(Continued)

TABLE 2 (*Continued*)

Trait	Test for phylogenetic signal in plant traits[A]			TIPS[B]			PICs[C]		
	Sample size (number of species)[a]	Mean contrast[b]	P-value[c]	Sample size (number of species)[d]	Mean contrast or slope	P-value	Positive/ total contrasts	P-value
Number of reproductive episodes: monocarpic versus polycarpic	194	0.10	<0.01	156	0.11	*0.09*	3/5	0.41
Growth form: woody versus herbaceous	207	0.32	<0.01	166	0.27	0.10	44/91	*0.07*
Capacity for asexual reproduction: clonal versus not clonal	160	0.24	<0.01	130	−0.03	*0.08*	5/16	0.22

For each plant trait, the results of a test for phylogenetic signal, [A] and the relationship between the trait and pollen limitation from TIPS[B], and PICs[C] analyses. TIPS and PICs analyses were restricted to those studies treating portions of the flowers on a plant and measuring percent fruit set. For TIPS, randomization tests were used to test for significant associations between pollen limitation and discrete plant traits, and linear regression was used to detect significant associations between pollen limitation and continuous plant traits. For PICs, the ratio of positive contrasts to total contrasts is shown. In the case of discrete traits, the *P*-value is derived from Wilcoxon-signed-rank tests to detect whether the mean contrast differs significantly from zero. In the case of continuous traits, the *P*-value is derived from a regression analysis to detect whether the slope differs from zero. All continuous traits were log-transformed before analysis. For both TIPS and PICs, the *P*-values are shown (bold: $P < 0.05$; italics $0.05 < P < 0.10$).

[a]Sample size depended on the availability of trait information for each species.

[b]The average phenotypic difference in the focal trait between sister taxa.

[c]*P*-values are based on the rank of the mean contrast compared with the 999 mean contrasts calculated in the randomized phylogenies. A drank below 50/1000 indicates a probability less than 5% of obtaining an observed mean contrast as low as it is by chance. This is interpreted as evidence of a significant phylogenetic signal.

[d]Sample size identical for TIPS and PICs analyses.

autogamous species are excluded. Flower size can be measured in many ways, so in each species we used the measurement that we thought would best indicate the floral dimension visible to prospective pollinators (generally, flower diameter). The TIPS analysis (Table 2B) revealed that pollen limitation decreased with increasing flower size; however, when we controlled for phylogenetic history or removed autogamous species from the analysis, this relationship was not statistically significant (Table 2B,C).

FLORAL LONGEVITY   The longer flowers are open, the more likely they are to receive pollinator visits and pollen (Ashman & Schoen 1994; Campbell et al. 1994, 1996; Rathcke 2003). Consequently, we expect a negative relationship between floral longevity and the magnitude of pollen limitation. However, we did not find evidence for a relationship between floral longevity and pollen limitation in the TIPS or PICs analyses (Table 2B,C).

BREEDING SYSTEM   Plants facing chronic pollen limitation may evolve self-compatibility for reproductive assurance (Baker 1955, 1967). In our data set, we classified plants as either self-compatible or self-incompatible using the categorizations stated by the authors of the pollen limitation study. In accord with other reviews (Burd 1994, Larson & Barrett 2000), we found that self-incompatible plants were more pollen limited than self-compatible plants in the TIPS and PICs analyses (but only marginally so in the PICs analysis; Table 2C).

Perfect-flowered species have male and female structures in the same flower and thus a single pollinator visit may be adequate to transfer pollen; however, species with imperfect (unisexual) flowers often require a pollinator to move between a male and a female flower for pollen transfer. Moreover, female flowers are often avoided by pollinators (e.g., Ashman 2000), indicating that the potential exists for species with unisexual flowers to be more pollen limited than hermaphroditic ones, especially when sexual-dimorphism between the sexes is high and pollinators are scarce (Ashman & Diefenderfer 2001, Vamosi & Otto 2002). On the other hand, unisexual species are more often pollinated by generalists (Charlesworth 1993), which may make them less prone to pollen limitation than perfect-flowered species (see below). We do not find differences in pollen limitation between perfect-flowered species and species with unisexual flowers or unisexual morphs (Table 2B,C). This result corroborates findings of a meta-analysis by Shykoff et al. (2003), who found no difference in pollen limitation between hermaphrodite and female morphs of gynodioecious species.

FLORAL SHAPE, POLLINATION SYNDROME, AND NUMBER OF POLLINATING SPECIES   Zygomorphic flowers encourage more precise placement of pollen and generally attract more specialized pollinators than actinomorphic flowers (Fenster et al. 2004, Neal et al. 1998, Sargent 2004). Similarly, plants pollinated by biotic pollinators are usually considered to be more specialized than those pollinated by abiotic

vectors (Culley et al. 2002). Such specialization may provide more reliable pollination, resulting in lower levels of pollen limitation. Alternatively, plants relying on specialized pollinators may experience greater variation in their pollination success (e.g., because abundance of a few specialized pollinators may fluctuate more in space or time than that of many generalized species), and hence be more prone to pollen limitation (Eckhart 1992; Fishbein & Venable 1996; Herrera 1988, 1996; Horvitz & Schemske 1990; Waser et al. 1996). We classified the species in our data set on the basis of their floral shape (actinomorphic versus zygomorphic) and pollination syndrome (biotic versus abiotic pollination). When the appropriate information was provided in a study, we classified biotic pollination into three categories on the basis of the number of pollinating taxa: one (specialist plants visited primarily by one pollinating species), few (2–5 species of pollinators), and many (>5 pollinating species). In both TIPS and PICs analyses, pollen limitation decreased with an increase in the number of pollinating taxa (Table 2B,C). We detected no difference between zygomorphic and actinomorphic species or between biotic and abiotic pollinated plants in their degree of pollen limitation (Table 2B, C). However, the low sample size of abiotically pollinated species ($N = 10$) may have limited our ability to detect a difference in pollen limitation between biotically and abiotically pollinated species.

OVULE NUMBER PER FLOWER   Burd (1995) proposed that whole-plant seed output is maximized at an ovule number per flower determined by the resource cost of ovule production and the flower-to-flower variance in pollen receipt and fertilizations. This theory predicts that selection may favor the production of more ovules per flower than the average number of fertilizations per flower obtained in a given environment because individual flowers with many ovules are able to capitalize on occasional but unpredictable receipt of large pollen loads. If selection acts in this way, flowers would often have unused capacity for seed production and frequently appear to be pollen limited. Both TIPS and PICs analyses detected a positive correlation between ovule number and pollen limitation (Table 2B,C).

We explore this result further by asking, is high ovule number favored in highly stochastic pollination environments [as proposed by Burd (1995)]? To address this question, we characterized the stochasticity in pollination and fertilization by the degree of intraplant variation in seeds per fruit under natural pollination. For those species in the data set with appropriate data, we calculated the coefficient of variation in seeds per fruit (CV = standard deviation/mean) obtained under natural pollination. When there were multiple studies or multiple population-years for a species, we used the mean CV among studies to obtain one CV value per species. There were 43 species for which we could obtain both the CV of seeds per fruit and the ovule number per flower. We performed a PICs analysis to examine the association of these two variables. The regression through the origin of contrasts in ovule number per flower versus contrasts in the CV of seeds per fruit had a significant positive slope ($t_{34} = 2.16$, $P = 0.038$) (Figure 3). A sign test indicated that there were 23 positive contrasts in ovule number and 11 negative contrasts
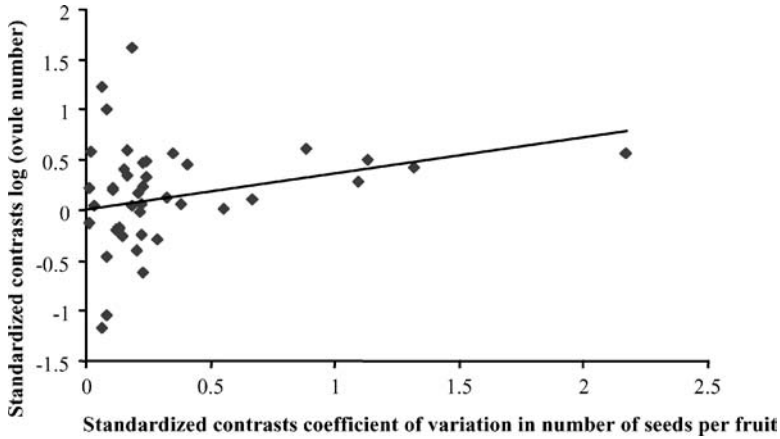
Figure 3 Ovule number per flower in relation to intraplant variation in floral fertilization. Individual points in the diagram represent standardized contrasts obtained from PICs analysis. The horizontal axis shows contrasts in the coefficient of variation (CV) of seed number per fruit (seed number is used as an easily measured surrogate for fertilization level); the vertical axis shows contrasts in ovule number per flower (logarithmically transformed). The least-squares regression line is shown [bivariate regressions of PICs must pass through the origin (Garland et al. 1992)]. The significantly positive slope ($t_{34} = 2.16$, $P = 0.038$) implies that increases in the variance of fertilization success (seed number) are, on average, accompanied by increases in ovule number per flower.

(2-tailed sign test, $P = 0.057$). This result is consistent with the idea that higher numbers of ovules per flower evolved in response to variable pollen receipt among flowers (Burd 1995). That is, high ovule number is a bet-hedging strategy to deal with stochastic pollen receipt.

Life-History Traits

NUMBER OF REPRODUCTIVE EPISODES   Monocarpic and short-lived species are expected to be less pollen limited than polycarpic and long-lived species for two reasons. First, pollination treatments are applied to all reproductive bouts for monocarpic plants. As a result, experimental measures of pollen limitation are not subject to between-year resource reallocation. Second, selection for traits that may reduce pollen limitation (e.g., larger flowers, self-compatibility) has probably been stronger and more effective in short-lived than in long-lived species. If pollinator abundance fluctuates, the lifetime fitness of a short-lived individual would be irrevocably reduced if it experiences pollen limitation for one or several successive years (Vamosi & Otto 2002) whereas a long-lived species could better endure a short pollinator drought (Calvo & Horvitz 1990, Primack & Hall 1990, Zhang

& Wang 1994). Similarly, because woody species live longer than most herba-
ceous species, trees and shrubs are likely to display more pollen limitation than
herbs.

There was a trend for higher pollen limitation among polycarps than monocarps
in the TIPS analysis (Table 2B). However, when we controlled for phylogenetic
relationships, this pattern was not evident, perhaps owing to the reduced number
of contrasts available for analysis (Table 2C). In both TIPS and PICs analyses
there were trends for woody species to be more pollen limited than herbs (Table
2B,C). This result is in accord with Larson & Barrett (2000), who found higher
pollen limitation in woody plants compared with that in herbs. However, their
analyses did not control for the level at which the treatment was applied, and woody
plants are more likely to have treatments applied at the partial-plant level than
herbs.

CAPACITY FOR ASEXUAL REPRODUCTION   Pollen limitation may be more preva-
lent in species capable of asexual reproduction because fitness of these species
depends less on pollination success and sexual reproduction. As a result, we ex-
pect species with the capacity for asexual reproduction to evolve lower levels of
resource allocation to floral traits and pollinator attraction than their exclusively
sexual counterparts (Charpentier 2001, Ronsheim & Bever 2000). However, we did
not find higher pollen limitation among asexually relative to sexually reproducing
species (Table 2B,C).

CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE STUDIES

In this concluding section, we highlight our key results. Overall, our review and
analyses suggest that the magnitude of pollen limitation found in pollen supple-
mentation experiments is high (see also Burd 1994, Larson & Barrett 2000). The
observed effect sizes, however, are quite variable among populations or treatments
that differ in ecological factors and among taxa.

Because of the stochastic nature of pollination and resource availability, plants
may be pollen limited at some times and resource limited at other times, but
not severely limited by either over their lifetimes (e.g., Casper & Niesenbaum
1993). The magnitude of pollen limitation varies among flowers within a plant,
among plants within a season, and among seasons. However, plants that are able to
redistribute resources temporally may not be limited by pollen receipt or resource
availability over longer time intervals. We found that evolutionary increases in
the number of ovules per flower were correlated with increases in the magnitude
of observed pollen limitation among species. Thus our analyses suggest that high
ovule number may be a bet-hedging strategy that allows plants to tolerate intraplant
stochastic pollen receipt.

Plant traits may evolve despite their association with strong pollen limitation. For example, self-incompatibility has evolved multiple times (Charlesworth 1985, Igic et al. 2003, Steinbachs & Holsinger 2002), and yet we find that this trait is associated with higher levels of pollen limitation. Thus it is likely that the benefits that these plants receive from outcrossing outweigh the costs of often being limited by pollen receipt. These benefits could include increased seed set through higher pollen quality, higher seed germination, and seedling survivorship probabilities. We suggest that pollination researchers will gain considerable insight into these benefits by increasing their scope of research beyond measuring seed production and including measurements of offspring quality.

Reduced seed production as a result of pollen limitation does not necessarily result in demographic consequences for the plant population. This is because for many plant populations, particularly long-lived species with multiple reproductive bouts, the sensitivity of the population to increased seed set is low relative to other vital rates such as adult survivorship (Ashman et al. 2004). To understand the role of pollination in the dynamics of species, such as the viability of rare species or the spread of invasive species, we suggest increasing the scope of the study to include other aspects of a plant's life-cycle.

Although these factors suggest that pollen limitation might not be as frequent or as severe as is often thought, or as demographically critical, pollen limitation may still be of great importance for evolutionary or ecological processes. In particular, in our rapidly changing world, variation in the pollination environment will probably alter the population dynamics and future evolutionary potential of many plant species. There is evidence that a variety of ecological perturbations increases the magnitude of pollen limitation. For example, the magnitude of pollen limitation often increases with habitat fragmentation. Currently, however, few studies are available that directly examine the effects of particular ecological conditions on the magnitude of pollen limitation. We hope that in the future, ecologists and conservation biologists will explore the role of pollen limitation in these and other contexts, so that we can begin to make such generalizations.

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