

Pollen grains: why so many?

R. W. Cruden

Department of Biological Sciences, University of Iowa, Iowa City, USA

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Abstract. My objective is the examination of selective forces that affect pollen number. Relationships among other floral traits of animal-pollinated plants, including pollen size, stigma area and depth, and the pollen-bearing area of the pollinator may affect pollen number and also provide a model to examine how change in one trait may elicit change in other traits. The model provides a conceptual framework for appreciating intra- and inter-specific differences in these traits. An equivalent model is presented for wind-pollinated plants. For these plants the distance between putative mates may be the most important factor affecting pollen number. I briefly consider how many pollen grains must reach a stigma to assure fruit set. I use pollen-ovule ratios (P/Os) to examine how breeding system, sexual system, pollen vector, and dispersal unit influence pollen grain number. I also compare the P/Os of plants with primary and secondary pollen presentation and those that provide only pollen as a reward with those that provide nectar as part or all of the reward. There is a substantial decrease in P/O from xenogamy to facultative xenogamy to autogamy. Relative to homoecious species the P/Os of species with most other sexual systems are higher. This suggests that there is a cost associated with changes in sexual system. The P/Os of wind-pollinated plants are substantially higher than those of animal-pollinated plants, and the available data suggest there is little difference in the pollination efficiency of the various animal vectors. The P/Os of plants whose pollen is dispersed in tetrads, polyads, or pollinia are substantially lower than those of species whose

pollen is dispersed as monads. There was no difference in the P/Os of plants with primary and secondary pollen presentation. The P/Os of plants that provide only pollen as a reward were higher than those that provide nectar as a reward. All of these conclusions merit additional testing as they are based on samples that are relatively small and/or systematically biased.

Key words: Animal-pollination, breeding systems, duration stigma receptivity, pollen grain number, pollen grain size, pollen packaging units, pollen-ovule ratios, secondary pollen presentation, sexual systems, stigma area and depth, wind-pollination.

In a series of papers my colleagues and I proposed that pollen-ovule ratios (P/Os) reflected pollination efficiency (= total source efficiency of Inouye et al. 1994), i.e. the likelihood of a pollen grain reaching a stigma. That conclusion was based on the differences in P/Os among species with different breeding systems (Cruden 1977, Cruden and Lyon 1989) and differences between species whose pollen is dispersed as monads vis-à-vis those whose pollen is dispersed in polyads or pollinia (Cruden 1977, Cruden 1997, also see Cruden and Jensen 1979). Subsequently, we showed that stigma area relative to the pollen bearing area of the pollinator was negatively correlated with P/O (Cruden and Miller-Ward 1981). In essence, we provided functional explanations for the variation we observed in floral traits and

how interactions among those traits influenced their evolution (also see Cruden 1997).

Alternative hypotheses were proposed to explain a number of the relationships we had observed. For example, the negative relationship between pollen grain number and size was explained as a trade-off between number and size (e.g. Charnov 1982). Local mate competition was invoked to explain the lower P/Os of autogamous and facultatively xenogamous species relative to xenogamous species (Charnov 1982). Both local mate competition (e.g. Queller 1984) and the reduction of sibling rivalry (Kress 1981, Uma Shaanker 1988) were proposed as explanations for the quite low P/Os of plants whose pollen is dispersed in polyads and pollinia. Because substantive data sets are inconsistent with the predictions of most of these hypotheses (Cruden 1997), and little additional data, either pro or con, has become available, I deal only briefly with the relative merits of the model developed below and alternative hypotheses that address particular relationships or traits.

To understand pollen grain number one has to understand the ecological milieu in which pollen grain number evolves. Thus, my initial objective is the examination of floral

traits that contribute to male function and how they might interact evolutionarily. In addition to pollen grain number, these include pollen grain size, stigma depth and area, and the pollen-bearing area of the pollinator. I discuss relationships among these traits in animal-pollinated flowers and then discuss an equivalent set of relationships in wind-pollinated flowers. I consider how many pollen grains per ovule are necessary for fruit and seed set. I examine other traits and interactions that may affect the evolution of pollen number, hence pollen-ovule ratios (P/Os), including breeding system, sexual system, pollen vector, and packaging of pollen grains. I also consider ecological factors that affect pollen grain number and quality.

Animal-pollination: relationships among floral traits

A number of floral traits involved in animal-pollination may interact evolutionarily (Fig. 1). These relationships provide a model for examining how evolutionary change in one trait might effect change in another (see below, Cruden 1997). The model is based on several assumptions. First, seed number, hence ovule number,

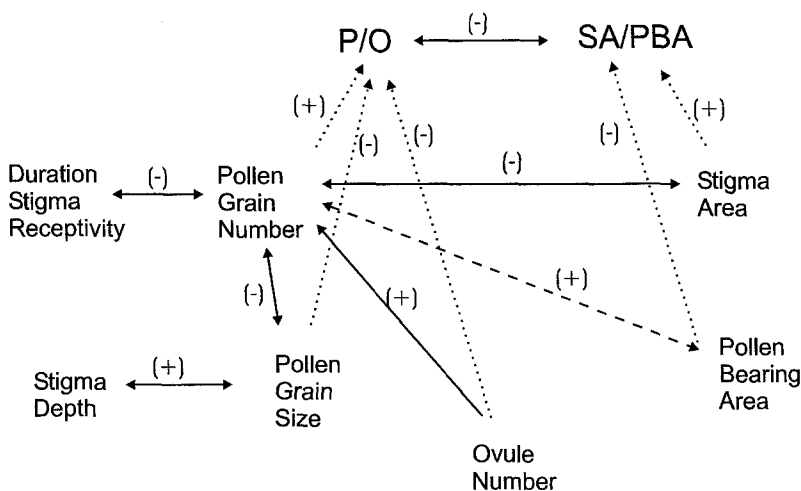


Fig. 1. Relationships among floral traits in animal-pollinated plants. The solid lines indicate relationships that were demonstrated empirically (see text). The dashed line indicates a proposed relationship. The dotted lines indicate that the pollen-ovule ratio (P/O) or stigma area (SA)/pollen bearing area of the pollinator (PBA) might be influenced by change in a given trait

responds to selective pressures that affect offspring survivorship. Thus, in a species that occurs in a variety of habitats seed number and size, hence ovule number, might differ substantially among populations. There is no evidence that ovule number responds to evolutionary change in other floral traits. Second, in most species floral traits respond to selection independently of one another (see Cruden 1997). Third, pollinator numbers and/or their dependability may vary among habitats and pollen number and/or other traits reflect those differences (e.g. Cruden 1976, Ramsey 1993). Fourth, selective pressures that affect ovule number are rarely correlated with those that affect pollinator numbers and/or their dependability.

Differences between populations in ovule and pollen number, hence P/Os, in *Blandfordia grandiflora* R. Br. and *Epacris microphylla* R. Br. in eastern Australia are consistent with the assumptions. Tableland plants of *B. grandiflora* produced more ovules (169.2 vs. 123.5) and nearly twice as many (96.4 vs. 48.7) but smaller seeds (2.13 vs. 3.14 mg) than coastal plants. Tableland plants produced substantially fewer pollen grains per flower (930,000 vs. 1,410,000) and had lower P/Os (5600 vs. 11,500) (Ramsey 1993, also see Ramsey et al. 1994). Stigma pollen loads were equivalent in the Tableland and coastal populations (288 vs. 272) (Ramsey 1993), thus, the Tableland plants were more efficiently pollinated. Because the differences in reproductive traits were retained in a transplant garden they were ecotypically adapted, i.e. the various traits, including pollen grain and ovule number, were adapted to local or regional environmental conditions. Ovule and pollen number also differed between populations of *Epacris microphylla* (Cruden and Lyon pers. obser.). The flowers of a population in the Blue Mountains produced larger and fewer ovules compared to those of a tableland population (35 vs. 120) and fewer pollen grains per flower (1000 vs. 1600). The fewer and larger ovules suggest fewer and larger seeds. The P/O of the Blue Mountains population was twice that of the tableland population

(140:1 vs. 70:1), which suggests differences in pollinator efficiency.

Pollen grain number and ovule number. In general, and other things equal, pollen grain number has to be positively related to ovule number. This relationship was observed across families (Cruden and Miller-Ward 1981) and within families (Kirk 1993, López et al. 1999, Plitman and Levin 1990, Small 1988).

Variation in pollen grain and/or ovule number may occur within individuals and/or within or among populations. For any given individual pollen grain and/or ovule number may be more or less constant, e.g. in *Linaria* (Arnold 1982a, also see Devlin 1989), or change during the growing season (see below). In homoecious species variation in pollen grain number may reflect differences in pollen grains per anther and/or anther number, e.g. Bosch (1992), and, in species with other sexual systems, the percentage of male flowers per plant and/or male plants, e.g. in *Lignocarpa* (Webb 1984). Likewise, ovule number may vary as a function of the number of ovules per carpel or ovary, carpels per flower, female flowers per plant and/or female plants.

In homoecious species, i.e. those with only hermaphroditic flowers (see Cruden and Lloyd 1995), both pollen and ovule number may vary within a plant during the flowering season. This need not involve a change in the P/O. In *Clarkia unquiculata* Lindl. both pollen grain and ovule number decreased during the flowering season and the P/O did not change (Vasek et al. 1987). In *Raphanus sativus* L. (Young and Stanton 1990a) and *Chamaecrista fasciculata* Michx. (Frazee and Marquis 1994) both pollen grain number and ovule number decreased across the flowering season. Likewise, in other species ovule number decreased through the flowering season (e.g. Arnold 1982b; Olesen and Warncke 1992; Ornduff 1986; Pellmyr 1985, 1987; Vogler et al. 1999). In contrast, in *Diervilla lonicera* Mill. ovule number increased during the flowering season and coincided with increased pollinator activity (Thomson 1985). In these cases pollen production was not determined.

Some of the seasonal variation in pollen grain and ovule number may reflect dichogamy. In populations of protandrous plants or those with protandrous flowers the pollen from the first flowers to open will not reach a stigma and the plants suffer a loss in reproductive success through male function. Brunet and Charlesworth (1995) suggested that this might result in plants investing less in male function in first opening flowers and relatively more in female function. Thus, one might expect to see an increase in male function and a decrease in female function during the flowering season. Protogyny should produce the opposite pattern. There is mixed support for the hypothesis (Brunet and Charlesworth 1995). The data from *Clarkia* (see above) is inconsistent with the model and that from *Aralia hispida* (see below) is consistent with the model. The hypothesis merits testing because only the first flowers to open on the first plants to flower suffer a reproductive loss, and it is not intuitively clear that this loss, which may have no genetic basis, is sufficient to select for lower pollen production in first opening flowers.

Within plant variation may be independent of season. In *Muntingia* the number of anthers increased from flower to flower within a fascicle and the last opening flowers rarely set fruit (Bawa and Webb 1983). In essence, the first flower of a fascicle was primarily female in function and the last opening primarily male in function.

Pollen grain number and ovule number may vary among plants within a population (e.g. Devlin 1989). Two patterns of variation occurred among individuals of the species that my colleagues and I studied (see Cruden 1977, Cruden and Miller-Ward 1981, Cruden and Lyon 1989). In most species there was no relationship between pollen grain number and ovule number and in a few species there was a positive relationship between them (also see Mione and Anderson 1992). The positive relationship is consistent with the observation that large flowers may contain more pollen grains and ovules than small flowers (e.g. Small 1988, López et al. 1999, also see Dudash

1991). In both *Raphanus sativus* and *Polemonium viscosum* Nutt. pollen grain number, but not ovule number, was positively associated with flower size (Stanton and Preston 1988, Galen and Stanton 1989, also see Mione and Anderson 1992). In no species was there a significant negative relationship between pollen grain number and ovule number.

Pollen grain number and/or ovule number may vary among populations of a species. Such variation may be relatively small and no one has demonstrated a selective basis for it (e.g. Affre et al. 1995, Cruden 1977, Díaz Lifante 1996, Ramsey et al. 1994, Vuille 1988). Such variation may simply reflect sampling error, or have an environmental basis (see below). In some species there was substantial variation among populations that reflected differences in breeding system (e.g. Affre et al. 1995, Dahl 1989, Thomas and Murray 1981, also see below). Finally, there were substantial differences in P/Os among populations with the same breeding system that may reflect pollination efficiency or another selective force. For example, in two populations of *Corokia cotoneaster* Raoul quite different P/Os (19,762:1 and 13,634:1) were associated with pollinator guilds composed primarily of flies and bees, respectively (Webb 1994). Fruit sets of 16% and 24% in the two populations were consistent with the bees being more efficient pollinators.

Variation in pollen grain number also occurs in species with other sexual systems. In andromonoecious species pollen grain number may vary as a function of the number of pollen grains per anther and/or the percentage of male flowers a plant produces. In *Aralia hispida* Vent. the number of hermaphroditic flowers decreased with umbel order and that of male flowers increased (Thomson and Barrett 1981), and the number of pollen grains per flower and pollen grain size increased with umbel order (Thomson et al. 1989). As a consequence the P/O increased substantially with umbel order. Likewise, in *Cimicifuga americana* Michx. the percentage of male flowers increased during the flowering season (Pellmyr 1986). Parallels with

the variation in pollen grain number per flower and seasonal change among homoecious plants is found in andromonoecious *Leptospermum scoparium* J. R. et G. Forst. In this species the percentage of male flowers varied among plants and within plants they tended to open first (Primack 1980a, b), and pollen grain number presumably decreased during the flowering season. Finally, in *Caesalpinia pulcherrima*, an andromonoecious legume, the percentage of male flowers varied among populations and was negatively correlated with the number of pollinator visits (Cruden 1976, Cruden and Hermann-Parker 1979).

Pollen grain number and size. A negative relationship between pollen grain number and size is well documented (e.g. Cruden 1997, Small 1988, Vohnhof and Harder 1995, also see Cruden and Miller-Ward 1981, Dulberger and Ornduff 1980, Mione and Anderson 1992, but see Knudsen and Olesen 1993, López et al. 1999) and has been discussed by numerous authors. Many attributed the relationship to a simple trade-off between number and size, (e.g. Charnov 1982, Vohnhof and Harder 1995) and much of the data is consistent with such an interpretation. However, a number of selective pressures may influence pollen grain size and/or number, including stigma depth and stigma area (see below). The small openings in the anthers of vibratory flowers may select for small pollen grains, e.g. in *Solanum* and various *Cassia*. Larger pollen grains might clog the openings. In other species with porate anthers the anthers dehisce in response to bees tripping a trigger hair, e.g. in various Ericaceae. Here also small pollen grains may be adaptive. Likewise, in *Ficus* selection might favor small to tiny pollen grains. First, small grains are less likely to be removed from the body when a wasp enters a syconium. Second, small pollen grains would probably be favored in those figs whose wasps store pollen in pockets in the exoskeleton because the wasps have to carry sufficient numbers of pollen grains to pollinate all the flowers in a syconium.

Pollen grain size and stigma depth. The positive relationship between pollen grain size

and stigma depth, i.e. the distance from the surface of the stigma to the transmission tissue in the style, reflects the distance a pollen tube has to grow to reach resources in the style. This relationship is based on two sets of observations. First, in a number of taxa there was a positive relationship between pollen grain size and stigma depth (Cruden and Lyon 1985, Williams and Rouse 1990, also see Small 1988) and in several of them there was no relationship with style length (Cruden and Lyon 1985). Second, there is now a considerable body of literature on the types of resources in the style or transmission tissue, which do not occur in the stigma, that are utilized by growing pollen tubes. For example, in Kiwifruit (González et al. 1996) and some Apiaceae and Brassicaceae (Cruden and Lyon 1985) starch is stored in the style and as the pollen tubes grow through the transmission tissue the starch grains disappear. The underlying assumption is that larger pollen grains contain more nutrients than smaller ones, at least those that store starch, and this allows their pollen tubes to grow through deep stigmas that can not be traversed by pollen tubes from small pollen grains.

Pollen number and duration of stigma receptivity. The likelihood of a stigma receiving sufficient numbers of pollen grains is increased by the length of time it is receptive. Differences in the period of receptivity may reflect ecological and/or physiological factors or genetic differences among populations. In many species unpollinated stigmas remained receptive longer than pollinated stigmas (e.g. Devlin and Stephenson 1984, Richardson and Stephenson 1989). In *Nemophila menziesii* H. and A. this allowed efficient fly pollination in habitats where the bees that usually pollinated the flowers were absent (Cruden 1972).

Inter- and intra-specific differences in duration of stigma receptivity are associated with different traits that affect the likelihood of pollination (see Dafni and Firmage this volume and discussion of *Potamogeton* below under wind-pollination). In *Blandfordia grandis* the stigmas of Tableland plants remained

receptive longer than those of coastal plants and this was associated with lower P/Os and more efficient pollination (Ramsey 1993). In gynodioecious *Sidalcea oregana* flowers of female plants received fewer visits and stigma pollen loads increased slowly relative to flowers on hermaphroditic plants, but the female flowers stayed open longer and eventually their stigma pollen loads were equivalent to those of hermaphroditic flowers (Ashman and Stanton 1991). Also, if pollen grains remain on the vector for a substantial period of time, as those of *Caesalpinia pulcherrima* do (Cruden and Hermann-Parker 1979), the likelihood of a pollen grain reaching a stigma increases.

Pollen grain number and stigma area.

Because stigmas with a large area contact more of the pollen-bearing area (PBA) compared to stigmas with a small area fewer pollen grains should be required for equivalent pollination success. In both *Symphionema* and *Isopogon* (Proteaceae) pollen grain number and stigma area were negatively related (Cruden 1997). This relationship is not easily accommodated in models that examine male and female function as essentially separate, sometimes antagonistic, properties.

Pollen grain number and pollen-bearing area. Pollen number should be positively related to the pollen-bearing area of the pollinator (PBA) (Cruden 1997). If the PBA decreases the pollen grains are closer together thus increasing the likelihood of a pollen grain contacting a stigma and pollen number should decrease. Conversely if the PBA is large the pollen grains are farther apart and it takes more pollen grains to achieve a density that is equivalent to species with smaller PBAs.

Pollen grain number and size, stigma area and P/O. The interactions described above (see Fig. 1) provide a means for predicting the direction of change in a trait in response to change in a second trait. For example, a decrease in pollen grain number should be associated with an increase in pollen grain size, an increase in stigma area, and/or a decrease in the pollen-bearing area. The complimentary

differences between the morphs of distylous species nicely illustrate some of the predictions. Legitimate pollinations involve the larger numbers of smaller pollen grains in long-styled plants and the smaller SAs of the short-styled plants and smaller numbers of larger pollen grains in short-styled plants with the larger SAs of long-styled plants. In contrast to most distylous species *Amsinckia grandiflora* and some populations of *Hedyotis caerulea* the floral morphs produced equivalent numbers of pollen grains but long-styled plants produced smaller pollen grains (Ornduff 1976, 1980). Thus, it is reasonable to assume that pollen grain number in long styled plants had decreased. The decrease in pollen number was associated with an increase in stigma area in the short styled plants. Data from *Cryptantha* (Casper 1983) provide a similar picture (Cruden 1997).

Comparisons within and between families are consistent with the relationships observed in distylous species. In Fabaceae most species in *Medicago* had larger SAs, lower P/Os, and produced fewer and larger pollen grains than species in *Trigonella* (Small 1988). Likewise, large pollen grains, low P/Os (<1000:1), and large SAs are characteristic of species in Cactaceae, Cucurbitaceae, Onagraceae, and Nyctaginaceae (Cruden pers. obser., Nassar et al. 1997, Nepi and Pacini 1993, Osborn et al. 1988). In contrast, species in *Amsinckia* (Ornduff 1976), *Cryptantha* (Casper 1983), *Cassia* (Dulberger 1981), and *Isopogon* (Cruden 1997) had small SAs, tiny pollen grains and high P/Os (>25,000:1).

Stigma area/pollen-bearing area and P/O. Stigma area relative to the pollen-bearing area directly influences the likelihood of a pollen grain reaching a stigma, hence pollen grain number and P/O. At one extreme are species with quite low P/Os and SAs that are large relative to the PBAs. For example, in *Isotria verticillata* (Willd.) Raf. the PBA was a small area on the backs of bees and the P/O was 3.9 (Mehrhoff 1983). Based on the illustrations provided, the SA was approximately the same size or somewhat smaller than the PBA. Likewise, in *Cabomba caroliniana* Gray the

SA was approximately the size of the PBA (see photos in Schneider and Jeter 1982) and the P/O was 62 (Osborn et al. 1991). In *Stylidium* (Stylidiaceae) pollen was placed with great precision on a relatively small area on the pollinator (1–2 mm² in Western Australian species) (Armbruster et al. 1994), and the stigmas were large relative to the PBA. The P/Os of two eastern Australian species were ca. 55:1 and 102:1 (Cruden pers. obser.). In contrast, the stigmas of *Cassia* spp. (Dulberger 1981) and *Isopogon anethifolius* (Salisb.) Knight (Cruden pers. obser.) were situated within a tiny cavity at the tip of the style, which was small relative to the PBA, and the P/Os were high.

Finally, the relationships discussed above (see Fig. 1) provide a mechanism for understanding intra- and inter-specific differences in the various traits, e.g. in distylous species. Such differences may reflect different responses to a common selective pressure. For example, an increase in ovule number might elicit an increase in pollen number, or, secondarily, an increase in pollen size and/or an increase in stigma area. When the differences are large and easily detected the adaptive significance can be deduced (e.g. Ramsey 1993). If the response involves small changes in several

traits, the differences among populations in any one trait may be subtle and the evolutionary significance difficult, if not impossible, to discern.

Wind-pollination: relationships among floral traits

A different set of relationships exists among floral traits of wind-pollinated plants (Fig. 2). The primary relationship is that between pollen number and the distance between putative mates. Because pollen grains are lost from the vector due to gravity and become more dispersed as they are moved away from their origin, pollen grain number, hence P/Os should be positively related to the distance between putative mates. It follows that seed set will decrease with distance from a pollen source (e.g. Allison 1990, Berry and Calvo 1989, Honig et al. 1992) and be positively correlated with pollen number (Allison 1990). As in animal-pollinated plants there may be a negative relationship between pollen grain number and both SA, e.g. in *Taxus* (Weis and Hermanutz 1993), and the duration of stigma receptivity. Also, the higher the point of release the longer pollen grains remain in the air, thus pollen grain number should reflect the height of release. In monoecious plants male

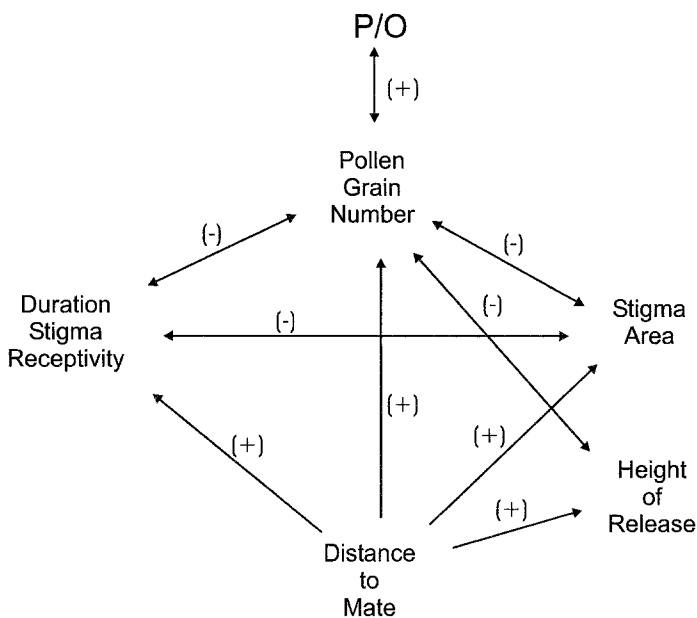


Fig. 2. How various relationships among floral traits and distance between putative mates might affect pollen grain number and the pollen-ovule ratio in wind-pollinated plants. It is likely that all of the traits interact evolutionarily

flowers should be borne higher on the plant or inflorescence, e.g. in *Zea* and *Myriophyllum*. In protogynous homoecious and monoecious species the inflorescence or petiole of individual flowers might elongate following the female phase. It follows that there are at least four evolutionary responses that might result from insufficient pollen grains reaching the stigmas of a population, i.e. an increase in pollen number, stigma area, duration of stigma receptivity, and/or height of pollen release (Fig. 2).

The interaction between inflorescences and/or flowers and the wind creates an aerodynamic environment in which pollen grains can contact and adhere to a stigma (Niklas 1985). There are considerable differences in inflorescence architecture, e.g. among Cyperaceae, Poaceae, and Potamogetonaceae, as well as considerable differences among stigmas, e.g. exerted and feathery in Poaceae and Cyperaceae and sessile in Potamogetonaceae. There are no data as to whether pollination efficiency, hence pollen number, varies as a function of inflorescence architecture and/or floral morphology.

Several relationships that are important in animal-pollinated plants probably have minimal selective impact in wind-pollinated plants. There is probably no relationship between pollen grain number and size and minimal differences in stigma depth because of the constraints on pollen grain size. Although ovule number must dictate the minimal number of pollen grains produced, the distance between

putative mates appears to be the most important factor in determining pollen grain number.

Preliminary data from temporally dioecious *Potamogeton* (Table 1) are consistent with the model. Most of the species can be placed into one of three categories based on flower number per inflorescence, how long the stigmas were receptive, and the distance between male and female phase inflorescences. The differences among the three groups were striking. The inflorescences of species with 2–8 flowers per inflorescence were the closest together, had relatively small SAs, stigmas that were receptive 1–2 days, and the lowest P/Os. Those with 10–20 flowers per inflorescence were intermediate in all respects. The inflorescences of species with 20–30 flowers were the farthest apart, had the largest SAs, stigmas that were receptive for 4–7 days, and the highest P/Os. Further, the height of pollen release increased from group to group (Cruden pers. obser.).

The exception to the above pattern is *Potamogeton zosteriformis* Fern. (Table 1) and it demonstrates that natural selection may produce quite different combinations of pollen number, stigma area, and duration of stigma receptivity. The inflorescences of this species were the farthest apart of all the species I studied and the stigmas the largest. However, the stigmas were receptive for only 2–4 days. Compared to other species with intermediate sized inflorescences, i.e. *P. gramineus* L. and *P. richardsonii* (Benn.) Rydb., the large SA and

Table 1. Traits of species in *Potamogeton* that may affect pollen-ovule ratios. Flower number per inflorescence, stigma area (mm²), duration of the female phase (in days), the distance between putative mates, and the P/O are given

	Flower Number	Stigma Area	Female Phase	Distance between	P/O
<i>P. foliosus</i>	4–8	small	1–2	short	9000:1
<i>P. pusillus</i>	2–6	small	1–2	short	9406:1
<i>P. filiformis</i>		0.38		short	2446:1
<i>P. richardsonii</i>	12–16	intermediate	2–4	intermediate	25000:1 ^a
<i>P. gramineus</i>	14–20	0.76	2–4	intermediate	
<i>P. zosteriformis</i>	14–20	3.11	2–4	long	32000–39000:1 ^a
<i>P. nodosus</i>	24–32	1.12	4–7	long	26500:1 ^a
<i>P. natans</i>	24–30	1.50	4–5	long	36000:1 ^a

^a Pollen-ovule ratio from Philbrick and Anderson (1987)

high P/O of *P. zosteriformis* may reflect the greater distances between putative mates. Further, relative to species with equivalent P/Os, i.e. *P. natans* L. and *P. nodosus* Poir., the larger stigma of *P. zosteriformis* may compensate for the shorter duration of stigma receptivity.

Pollen number and fecundity: how many does it take?

The numbers of pollen grains reaching the stigmas has to be sufficient to account for the fertilization of the available egg cells (not ovules!), produce a pollen population effect (see below), provide some minimal level of sexual selection, and swamp the effect of incompatible or low quality pollen. A limited amount of data suggests that some minimal amount of pollen must be available to pollen vectors or reproductive success decreases. Horovitz and Beiles (1980) reported that seed set declined in gynodioecious *Hirschfeldia incana* (L.) Lagreze-Fossat when the number of female plants in garden populations exceeded that in wild populations. In monoecious *Calyptrogyne ghiesbreghtiana* Linden ex. H. Wendl. fruit set was higher when male phase plants outnumbered female phase plants (Cunningham 1995). In this species the number of male phase plants usually exceeded that of female phase plants because the male phase lasts 4–5 nights and the female phase usually lasts two nights. However, in gynodioecious *Saxifraga granulata* L. flowers on female plants set fewer seeds, which is consistent with pollen limitation, but the survivorship of seedlings to reproductive adults was greater from those seeds (Stevens 1988). In this instance pollen limitation was not detrimental even though fecundity was reduced.

Stigma pollen loads must be sufficiently high to produce a pollen population effect, i.e. a sufficient number of pollen grains per ovule to trigger germination and/or produce viable pollen tubes (e.g. Schemske and Fenster 1983, also see Cruzan 1986). This number may be smaller in species with large pollen grains and larger in species with small pollen grains. Further, in

some species stigma pollen loads have to be sufficiently large to account for some minimal number of developing seeds. For example, in *Ruellia bourgaei* Hemsl. and *Bartsia alpina* L. a minimum of 10 seeds have to develop to assure fruit development. Fruits with fewer developing seeds aborted (Cruden pers. obser., Molau 1991, also see Hannan and Prucher 1996, Schemske and Fenster 1983, Stephenson 1981).

Because larger and/or mixed parent stigma pollen loads frequently result in higher quality offspring (e.g. Niesenbaum 1999), it seems reasonable that plants will produce sufficient pollen grains to produce some minimal level of sexual selection. Thus, pollen grain number should be large enough to account for stigma pollen loads that exceed the number of ovules in the ovary and sufficient pollen carry-over to produce multipaternal stigma pollen loads (e.g. Campbell 1998). However, pollen production can not be so high that the pollen produced by one plant swamps the stigmas of the next plant visited by a pollinator. This would reduce or eliminate pollen carry-over and limit considerably the number of potential mates. In essence, both minimal and excessive pollen production may have a detrimental effect on fitness.

The available data suggest that a minimum 4–6 pollen grains per ovule are necessary for maximum seed set (e.g. Murcia 1990; Schuster et al. 1993; Snow 1982, 1986). The data represent animal-pollinated species with low P/Os, e.g. *Mirabilis jalapa* L. (Cruden 1977), and high P/Os, e.g. *Cassia* (Dulberger 1981), wind-pollinated species, e.g. dioecious *Staberoha banksii* Pillans (Honig et al. 1992), and self-pollinating plants, e.g. the cleistogamous flowers of *Viola nephrophylla* Greene (Cruden 1977). Stigmatic pollen loads of this magnitude should be sufficient to produce a pollen population effect, greatly reduce the likelihood of a low quality pollen tube reaching an ovule, and insure some sexual selection.

Pollen-ovule ratios and pollination efficiency

In the following sections I use P/Os to examine hypotheses concerning traits and/or relation-

ships that may affect pollen number. First, I briefly review the relationship between P/Os and breeding system. Next, I consider P/Os in the context of sexual systems and pollen vectors. I also examine the P/Os of plants whose pollen is dispersed in tetrads, polyads, and pollinia because earlier work suggested they were lower than those of species whose pollen is dispersed as monads (Cruden 1977, 1997). Finally, I examine two additional hypotheses: first, the P/Os of species with secondary pollen presentation are lower than those of species with primary pollen presentation (see Yeo 1993), and second, species that offer only pollen as a reward produce more pollen per ovule than those that provide nectar as a reward (e.g. Vogel 1978; Pellmyr 1985, 1986).

My conclusions should be viewed as hypotheses that require testing. With the exception of the breeding system data, the sample sizes are small and may include species from just one or a small number of families. For example, all of the gynodioecious species are in Apiaceae and all the gynomonoeious species are in Asteraceae. Although comparisons across families are relatively compelling, comparisons within genera and families may be equally instructive. The data were analyzed with a Mann-Whitney *U*-test or Wilcoxon two-sample test (Sokal and Rohlf 1969).

Pollen ovule ratios and breeding systems

There is a strong correlation between P/O and breeding system (Fig. 3). P/Os decreased from xenogamous to facultatively xenogamous to autogamous species ($X > FX$: $t = 9.825$; $n = 310,86$; $p \ll 0.001$ and $FX > A$: $t = 6.218$; $n = 86,77$; $p \ll 0.001$). The relationship holds within species (Affre et al. 1995, Dahl 1989, and Hannen and Prucher 1996), genera (Feliner 1991, Lawrence 1985, Mione and Anderson 1992, Sharma et al. 1992, Spira 1980, Vuille 1987), and families (Feliner 1991, Lawrence 1985, Plitmann and Levin 1990, Preston 1986, Schlising et al. 1980, Short 1981, Vasek et al. 1987, Webb 1984). However, there is tremendous variation in P/Os among species

with equivalent breeding systems (Fig. 3). The P/Os of most xenogamous, animal-pollinated species are between 1200:1 and 8,000:1. But in some families, e.g. Onagraceae, the P/Os of most xenogamous species are less than 500:1 and those of species with other breeding systems are correspondingly lower (Cruden pers. obser., Vasek and Weng 1988). In other families, e.g. Boraginaceae, the P/Os of xenogamous species are extremely high (30,000:1–200,000:1) and the P/Os of species with other breeding systems are frequently higher than average (see Cruden 1977, Cruden and Lyon 1989).

The differences in P/Os between xenogamous, animal-pollinated plants and related species with other breeding systems also characterize wind-pollinated species and their facultatively xenogamous and autogamous relatives (Cruden 1977, Hammer 1978, Sharma et al. 1992). In addition to having higher P/Os, the stigmas of xenogamous *Plantago* were receptive 4–5 days prior to the dehiscence of the anthers whereas the autogamous species were homogamous (Sharma et al. 1992). The little available data indicate that facultatively xenogamous and autogamous species derived from wind-pollinated species have higher P/O's than species with equivalent breeding systems derived from animal-pollinated, xenogamous species (e.g. Cruden 1977, Sharma et al. 1992).

For many species the P/O is sufficient to correctly identify the breeding system but for xenogamous species with relatively low P/Os the P/O may confuse rather than clarify. Many xenogamous species with low P/Os have large pollen grains and/or large stigma areas (see above). Thus, both the P/O and pollen grain size and/or other traits should be used to determine a plant's breeding system in lieu of determining it experimentally (see Cruden and Lyon 1989).

Pollen-ovule ratios and sexual systems

The available data suggest that homoecious species have lower P/Os than those with other sexual systems (Fig. 4) and that the P/Os of

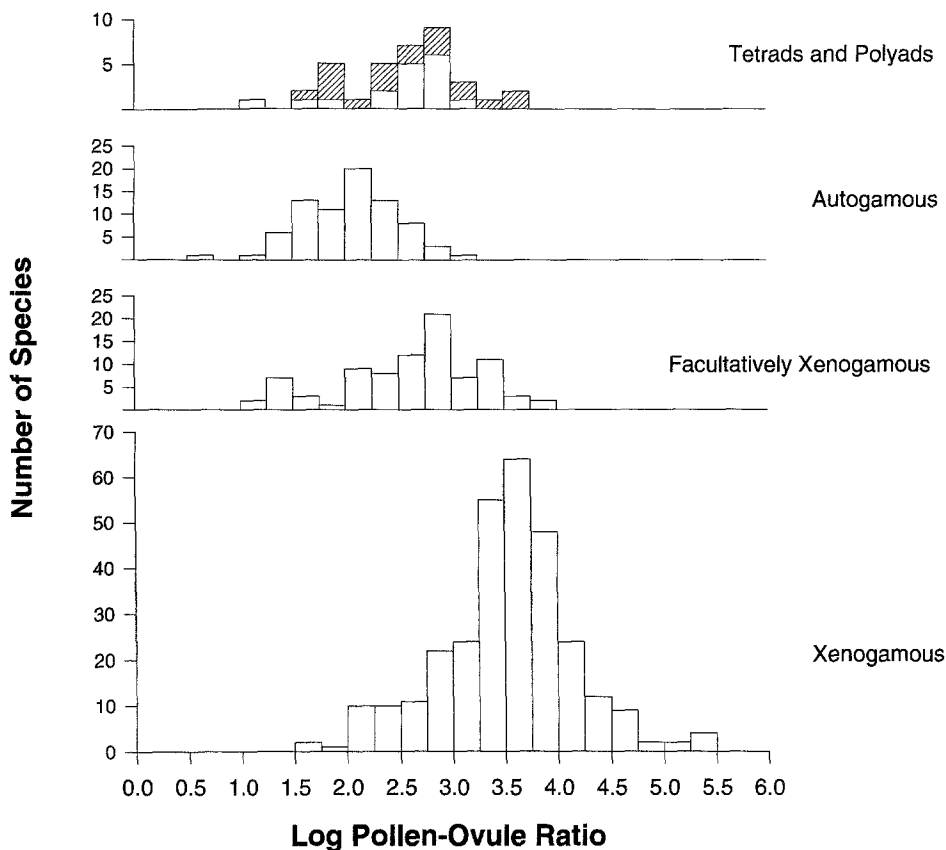


Fig. 3. Distribution of pollen-ovule ratios of animal-pollinated, homoecious species and those of species with other breeding systems. The differences between breeding systems are significantly different (see text). Tetrads are indicated by open bars and polyads by hatched bars. The P/Os of species with tetrads and polyads were equivalent (see text)

wind-pollinated species are higher than those of animal-pollinated species with the same sexual system (Fig. 4).

Dioecy. In animal-pollinated plants the P/Os of dioecious species (median = 10,655:1, quartiles = 4050:1, 67,500:1) were higher than those of homoecious species (median = 3450:1, quartiles = 1550:1, 7338:1) ($t = 3.308$, $n = 19,310$, $p < 0.001$) (see Webb 1984; Mione and Anderson 1992). Likewise, the P/Os of the two wind-pollinated dioecious species (Lisci et al. 1995, Ramirez and Seres 1994) were higher than those of most wind-pollinated homoecious species (Fig. 4; $t = 4.531$, $n = 2,22$, $p < 0.001$). Also, the P/Os of the two wind-pollinated, dioecious species were higher than those of animal-pollinated dioecious species ($U = 35$, $n = 2,19$, $p < 0.025$).

Gynodioecy. The only P/Os for gynodioecious species are in animal-pollinated Apiaceae and they are higher than those of related homoecious species (Webb 1984). The increase in P/Os in most species was a result of greater pollen production per flower and/or increased numbers of male flowers. In a number of gynodioecious species seed production in hermaphroditic plants was lower than in female plants (e.g. Ågren and Willson 1991, Maki 1993), which may reflect the resources needed to support increased pollen production (but see Ågren and Willson 1991).

Monoecy. Across families the difference between the P/Os of animal-pollinated homoecious (see above) and monoecious (median = 10,194:1, quartiles = 1479:1, 18,310:1) taxa was not statistically significant ($t = 1.735$,

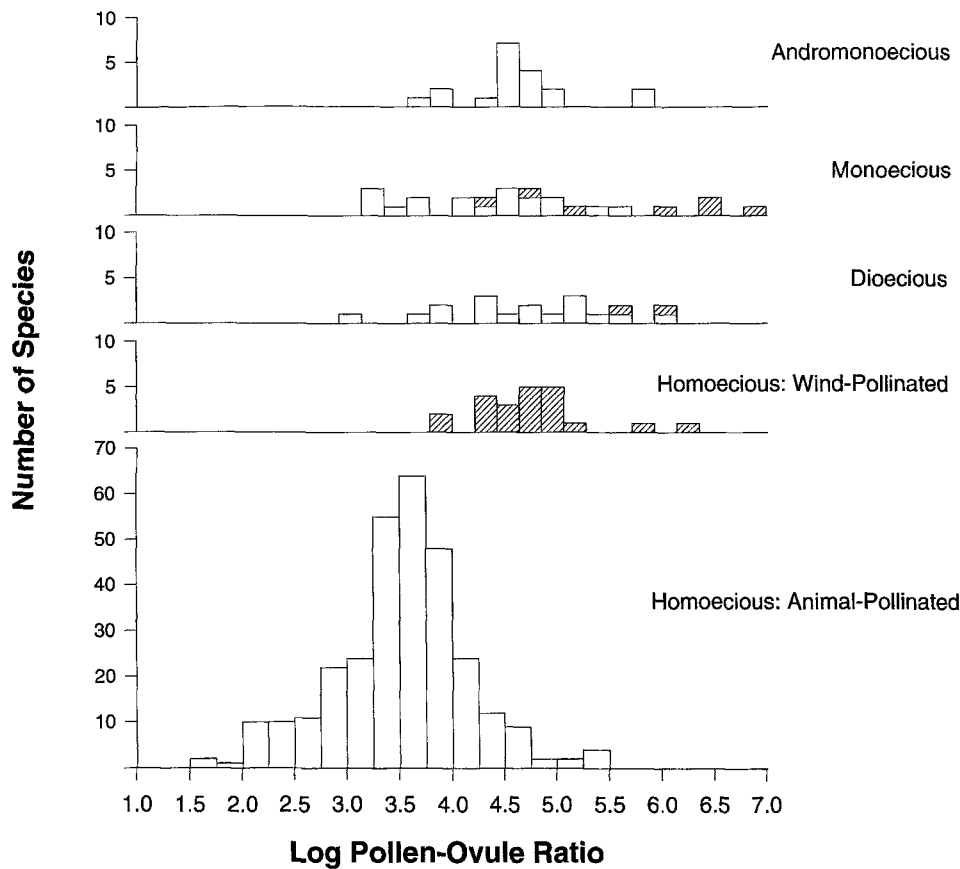


Fig. 4. Distributions of pollen-ovule ratios of animal-pollinated (open bars) and wind-pollinated (hatched bars) species with different sexual systems. The P/Os of wind-pollinated homoecious species are higher than those of animal-pollinated species. Likewise, the wind-pollinated dioecious and monoecious species have higher P/Os than animal-pollinated species with the same sexual system. Animal-pollinated dioecious and andromonoecious have higher P/Os than animal-pollinated homoecious species. The P/Os of animal-pollinated homoecious and monoecious species are equivalent

$n = 19,310$, $p > 0.05$). In contrast, the P/Os of the monoecious, wind-pollinated species were significantly higher than those of homoecious wind-pollinated species ($t = 2.347$; $n = 7,22$; $p < 0.02$). This is probably attributable, at least in part, to the distance between individuals as 7 of the 8 monoecious species were trees, which are generally further apart than herbaceous plants. Also, the two homoecious wind-pollinated species with the highest P/Os were woody plants. Finally, the P/Os of wind-pollinated species were higher than those of animal-pollinated species ($U = 110$, $n = 18,7$, $p < 0.005$). Also, in *Espeletia* (Asteraceae) the wind-pollinated species produced substantially more

pollen per disk floret and many more disk florets per head relative to the animal-pollinated species (Berry and Calvo 1989).

Andromonoecy. Across families the P/Os of andromonoecious, animal-pollinated species (median = 14,983:1, quartiles = 9936:1, 26,020:1) were higher than those of homoecious species (median = 3450:1, quartiles = 1550:1, 7338:1) ($t = 4.111$, $n = 20,310$, $p < 0.001$). Approximately half of the andromonoecious species were in Apiaceae and the same pattern was observed (Lindsey 1982, Schlesmann 1982, Webb 1984). Likewise, in Rhamnaceae the P/Os of andromonoecious taxa were higher than those of homoecious

taxa (Cruden 1977; Medan 1993, 1994; Medan and D'Ambrogio 1998; Oliveira and Sazima 1990).

Gynomonoecy. In gynomonoecious species the pollen produced by the hermaphroditic flowers was thought to be sufficient to account for the pollination of small numbers of female flowers (Horovitz and Beiles 1980, also see Lloyd 1979). However, in *Senecio*, the P/Os of 17 gynomonoecious taxa were, on average, 25% higher than those of 7 homoecious, xenogamous taxa (Lawrence 1985) ($U = 92$; $df = 17,7$; $P < 0.025$). The only other gynomonoecious species whose P/O was known also was in Asteraceae. In these gynomonoecious taxa the hermaphroditic disk flowers greatly exceeded the number of pistillate ray flowers, a situation in which one might expect little or no increase in pollen production.

The selective reasons for high P/Os in animal-pollinated, dioecious species is not clear and more data are needed from both animal- and wind-pollinated monoecious species to know whether their P/Os are higher or equivalent to those of homoecious species. The higher P/Os of gynomonoecious and gynodioecious species (Lawrence 1985, Webb 1984) may reflect selection to maintain the pollen pool available to vectors above some critical level. As the frequency of female flowers or plants increases, pollen grain number has to increase, or another trait has to change to maintain minimal stigma pollen loads, or fecundity and/or offspring quality will decrease (see above).

Finally, the data discussed above suggest that there may be a cost associated with the evolution of alternative sexual systems and that may help to explain their rarity.

Pollen vectors

Wind-pollination. Wind-pollinated, xenogamous plants produce large numbers of pollen grains (see Ackermann this volume, Pohl 1937, Proctor and Yeo 1972), and because most flowers have just a single ovule their P/Os should be high relative to those of animal-pollinated

plants. The P/Os of the few wind-pollinated, homoecious plants whose P/Os have been determined (Fig. 4; from Campbell 1982, Dajoz and Sandmeier 1997, Hammer 1978, Osborn et al. 1991, Pohl 1937, Sharma et al. 1992, Tomlinson et al. 1979) were higher than those of homoecious, animal-pollinated plants (wind: median = 22,150:1, quartiles = 9,238:1 and 36,000:1; animal: median = 3,450:1; quartiles = 1,550:1 and 7,338:1) ($t = 5.406$; $n = 22,310$; $p \ll 0.001$). Finally, even though half of the wind-pollinated species for which there were data are in *Potamogeton* ($n = 11$) (Cruden pers. obser.; Philbrick and Anderson 1987), and there were little or no data from such families as Poaceae, Cyperaceae, and Restionaceae, it seems reasonable to conclude that homoecious wind-pollinated plants have higher P/Os than those of animal-pollinated plants.

The comparisons among wind-pollinated species with different sexual systems were based on quite small sample sizes. However, there is reason to believe that the observed relationships are correct. In dioecious and many monoecious species the distance between putative mates is probably greater than in homoecious species. In dioecious species if the sexes are equitably dispersed half of a plant's neighbors will be of the same sex. Second, if the dispersion of plants has an ecological bias, e.g. female plants in moister sites and male plants in drier sites (e.g. Freeman et al. 1976), there may be a substantial distance between male and female plants. Based on distances between putative mates monoecious species should not produce more pollen than related homoecious species, because nearest neighbors will not be farther apart. However, many monoecious species are temporally dioecious and the dispersion of male and female phase plants will be equivalent to those of dioecious species. Hence, their P/Os should be higher than those of related homoecious species.

Animal-pollination. Based on the available data it appears that various insect groups and birds are equally efficient as pollinators. Most of the homoecious species whose P/Os and

pollinators were known were bee-pollinated, and there were few data from species pollinated by insects in other orders. Based on that data the P/Os of bee- and bird-pollinated species were equivalent ($t = 0.862$, $n = 103,19$, $p > 0.4$) as were those of bee- and fly-pollinated species ($t = 0.832$, $n = 103,8$, $p > 0.4$). The P/Os of 6 bat-pollinated species were low relative to bee-pollinated species ($t = 2.391$, $n = 103,6$, $p < 0.02$) but five of the six were in Cactaceae (Nassar et al. 1997) and their P/Os did not differ from three bee-pollinated cacti ($U = 8$, $n = 5,3$, $p > 0.1$). Cacti have low P/Os regardless of pollen vector. There were too few P/Os from species with other vectors to justify an analysis. Species in Polemoniaceae (Plitman and Levin 1990) were not included in the analyses because information on their pollinators was not available.

That different animal vectors may be equally efficient in transferring pollen is consistent with the observation that a variety of vectors were pollinators of plants whose pollen is dispersed in tetrads, polyads and pollinia (Hesse et al. this volume; Johnson and Edwards this volume). Tetrads were dispersed by bees, birds, flies and beetles (Cruden and Lyon pers. obser., Lloyd and Wells 1992, Norman et al. 1992, Oliveira et al. 1990) and polyads were effectively transferred by bats, bees, birds, hawkmoths, and settling moths (Bernhardt et al. 1984; Cruden 1977, 1997; Hernández 1989; Hopkins 1984; Koptur 1984). Massulae of various orchids were dispersed by bees, flies, and lepidoptera (Johnson and Edwards this volume, Neiland and Wilcock 1995). Likewise, pollinia of orchids and milkweeds were transferred by a variety of animals.

The relative effectiveness of different vectors merits additional study. However, the examination of related taxa may not prove any more revealing than comparisons of unrelated taxa. Bees were more efficient pollinators of *Corokia cotoneaster* than flies (see above), but among xenogamous Onagraceae fly-pollinated species ($n = 5$) had lower P/Os than those pollinated by bees ($n = 17$), hummingbirds

($n = 5$), hawkmoths ($n = 8$) and settling moths ($n = 5$) (Cruden pers. obser.). In Polemoniaceae flowers pollinated by butterflies had higher P/Os than flowers pollinated by bees, hummingbirds, and flies (Plitmann and Levin 1990). Finally, based on a limited survey of a diverse group of tropical monocots Ramirez and Seres (1994) observed that the P/Os of beetle and/or fly flowers were higher than those of flowers pollinated by bees, bats, and birds.

Tetrads, polyads, and pollina

In general, the P/Os of species whose pollen grains are dispersed in tetrads and polyads (see Cruden 1977, 1997; Oliveira and Sazima 1990; Jacquemart 1997; Kenrick and Knox 1982; Knudsen and Olesen 1993; Koptur 1984; Lloyd and Wells 1992; Norman and Clayton 1986) were lower than those of species whose pollen was dispersed as monads (Fig. 3; $t = 7.577$, $n = 37,310$, $p \ll 0.001$). There was no difference between the P/Os of species whose pollen was dispersed in tetrads vs. polyads ($t = 0.122$; $n = 20,17$; $p > 0.9$). The general pattern was mirrored in several families. For example, in Epacridaceae the P/Os of *Dracophyllum secundum* R. Br. (372:1), *Epacris purpurascens* R. Br. (87:1), *E. reclinata* Cunn. ex Benth. (139:1), and *Rupicola apiculata* (Cunn.) Telford (219:1) were lower than those of *Brachyloma daphnoides* (Smith) Benth. (456:1), *Leucopogon parviflorus* (Andrews) Lindley (648:1), and *Styphelia triflora* Andrews (1072:1), whose pollen grains were dispersed as monads (Cruden and Lyon person. obser., also see Knudsen and Olesen 1993).

A similar pattern is found in species whose pollen is dispersed in polyads. In *Xyris*, the P/O of *X. juncea* R. Br. (15:1) was lower than those of *X. operculata* Labill. (125:1) and *X. gracilis* R. Br. (142:1), whose pollen was dispersed as monads (Cruden 1997). In Pyrolaceae the P/O of *Chimaphila umbellata* (L.) W. Barton was less than half that of *Orthila secunda* (L.) House, whose pollen was dispersed in monads (Knudsen and Olesen 1993).

The pollen of very few families is dispersed in pollinia. The P/Os of 10 Asclepiadaceae range from 3.8:1–18.4:1 (Ali and Ali 1989, Cruden 1977, Wyatt and Broyles 1992). In most of these species each pollinium contained one to two pollen grains for each ovule in a carpel or ovary. The P/Os of the few orchids that have been determined were uniformly low ($n = 8$; range 3.9:1–24:1) (Mehrhoff 1983, Neiland and Wilcock 1995). The pollen of these orchids was dispersed in massulae, rather than pollinia.

Several factors may contribute to the lower P/Os of plants whose pollen is dispersed in tetrads or larger units. First, there is an immediate pollen population effect. Second, just a single tetrad or polyad may be sufficient to produce a fruit (e.g. Cruden 1977, Snow 1986), and, in some, sufficient pollen grains to account for the fertilization of all the eggs (e.g. Hernández 1989, Knox and Kenrick 1983, Koptur 1984). Third, the cost of pollen production may be less because the plants produce fewer pollen grains and those may be smaller than in related species that produce monads, e.g. in *Xyris* (Cruden pers. obser.).

Both local mate competition (Queller 1984) and the reduction of sibling rivalry (Kress 1981, Uma Shaanker et al. 1988) were proposed as explanations for the low P/Os of species whose pollen grains are dispersed as polyads or pollinia. Both hypotheses were based on the observation that the number of pollen grains per pollen unit usually equaled or exceeded the number of ovules in an ovary or carpel (e.g. Cruden 1977), thus seeds in a developing fruit had a single father. However, in various taxa the number of ovules in an ovary greatly exceeded the number of pollen grains per pollen unit (Cruden 1997, Knudsen and Olesen 1993, Lloyd and Wells 1992, Neiland and Wilcock 1995), and the developing fruits were certainly multipaternal. In some *Acacia* some stigmas received more than a single polyad (e.g. Knox and Kenrick 1983) and multipaternal fruits were identified by using genetic markers (Muona et al. 1991). In *Calliandra* stigmas frequently received more than a single polyad and the eight pollen grains

in a polyad were less than the number of ovules per ovary in most species (Cruden 1977). Complete seed set in such species (Cruden et al. 1976) was evidence of multipaternity. Finally, multipaternity is possible in those Asclepiadaceae in which pollen tubes from a single pollinium may end up in both carpels (see Kunze 1991, Kunze and Liede 1991) and those orchids whose stigmas regularly receive more than a single pollinium (e.g. Proctor and Harder 1994).

Secondary pollen presentation

In plants with primary pollen presentation pollen grains move directly from the anther to the pollen vector and in those with secondary pollen presentation the pollen grains are placed on another flower part and from there they move to the pollinator. Secondary pollen presentation occurs in ca. 25 families (Yeo 1993). It is a family trait in Asteraceae, Campanulaceae, Lobeliaceae, and Goodeniaceae, and is a common trait in other families, e.g. Fabaceae, Proteaceae, and Rubiaceae. Howell et al. (1993) suggested that plants with secondary pollen presentation enjoyed a selective advantage due to precise placement and receipt of pollen. Such was not the case in many bird-pollinated *Grevillea* (Proteaceae), which place the pollen widely over a bird's breast (Lyon and Cruden pers. obser.) and various Asteraceae, Goodeniaceae, Campanulaceae, and Lobeliaceae (Cruden pers. obser.), or in wind-pollinated *Hippohae rhamnoides* L. (Kerner 1897). Most of the species in these families with low P/Os also had large stigmas. Finally, taxa that are models for the precise placement of pollen do have low P/Os but they also have large stigmas and primary pollen presentation, e.g. *Stylidium* and orchids.

Based on a limited data set Yeo (1993, p. 220–221) suggested that the P/Os of species with secondary pollen presentation might be lower than those of species with primary pollen presentation, thus more efficiently pollinated than those with primary pollen presentation. The suggestion is not supported by the data

available today. There was little difference between the P/Os of homoecious species with primary (median = 3546:1, quartiles = 1173, 8130) and secondary pollen presentation (median = 3220, quartiles = 2037, 5062) ($t = 0.329$; $N = 239$, 71; $p > 0.5$). Yeo's hypothesis merits further testing because a majority of the species with secondary pollen presentation were in Asteraceae ($n = 28$) and Fabaceae ($n = 29$) (see Cruden 1977, Cruden and Miller-Ward 1981, Lawrence 1985, López et al. 1999, Mejias 1994, Short 1981) and four other families (see Cruden 1997, Dahl 1989, Devlin 1989, Inoue et al. 1996, Lamont and Barrett 1988, Ohara and Higashi 1994, Ramirez and Seres 1994, Ramsey and Vaughton 1991).

Nectarless flowers

Various workers suggested that flowers that provide only pollen as a reward to foraging bees will produce larger numbers of pollen grains than species that provide nectar as a reward (e.g. Pellmyr 1985, Vogel 1978, but see Mione and Anderson 1992). The available data support the hypothesis ($t = 2.250$, $n = 66,124$, $p < 0.05$). Over 70% of the nectarless taxa were in *Solanum* ($n = 18$; Mione and Anderson 1992) and Fabaceae ($n = 29$; Cruden 1977, López et al. 1999), and 26 of the nectarless taxa were buzz-pollinated. There was no difference in the P/Os of buzz- and non-buzz pollinated nectarless flowers ($t = 0.314$, $n = 26,40$, $p > 0.5$). With respect to the reward bees receive from nectarless flowers, it is surely the biomass of pollen not the number of pollen grains that is important. The hypothesis merits additional study because there is no data on the biomass of pollen produced by related nectarless and nectariferous flowers.

Pollen number and quality: environmental factors

Any factors that affect the nutritional status of a plant may affect the amount and quality of pollen produced. Both pollen production and

pollen size decreased in response to the loss of leaves to herbivores (Frazee and Marquis 1994, Lehtilä and Strauss 1999, Quesada et al. 1995). Pollen quality as measured by pollen tube growth rates and seeds sired was negatively affected by herbivory (Quesada et al. 1995, Mutikainen and Delph 1996, also see review by Delph et al. 1997). In *Alstroemeria* leaf removal resulted in smaller pollen grains whose pollen tubes grew at a slower rate, aborted more frequently and sired fewer seeds (Aizen and Raffaele 1998).

A number of experiments indicate that low nutrient levels may negatively affect pollen number and/or size as well as pollen tube performance. High nitrogen and phosphorus levels were positively correlated with pollen grain number and size in zucchini (Lau and Stephenson 1993, 1994). In addition, pollen from plants in the high nutrient treatments sired more seeds, which was a consequence of faster pollen tube growth. Likewise, in *Clarkia unguiculata*, both pollen and ovule numbers were positively related to nutrient levels (Vasek et al. 1987) but not the P/O (also see Travers 1999). In wild radish the competitive ability of pollen tubes from plants grown in low nutrient conditions was reduced but not pollen grain number or size (Young and Stanton 1990b).

Further, damage to flowers by herbivores may reduce pollen available to pollinators (Krupnick et al. 1999) and/or reduce pollinator visits to both damaged and undamaged flowers (Strauss 1997, Krupnick and Weis 1999, Krupnick et al. 1999).

Pollen protection

Pollen that is exposed to dew or rain may lose proteins and other compounds that render it inviable, thus adaptations that provide protection to such pollen would have a direct and positive impact on fitness. This aspect of pollen biology was discussed at length by Kerner (1897, Vol. 2: 104–129) but has attracted little attention by modern workers. Adaptations that protect pollen from exposure to dew or rain include anthers that close when exposed to dew or rain,

e.g. in *Mirabilis nyctaganea* (Michx.) MacM. (Cruden 1973), *Lilium philadelphicum* L. (Edwards and Jordan 1992), *Bulbocodium*, *Alchemilla*, and various Lauraceae (Kerner 1897), and flowers that close at night or in response to cloudy and rainy weather, e.g. *Nemophila menziesii* (Cruden 1972), *Sanguinaria canadensis* L. (Lyon 1992), *Hepatica*, *Crocus*, *Eranthus* (Kerner 1897), and *Tulipa* (Cruden pers. obser.). In *Hepatica* and *Eranthus* the sepals increase in length and provide continuing protection to the pollen in anthers whose stamens have elongated (Kerner 1897). Kerner also suggested that such traits as pendulous flowers, flowers that are sheltered beneath leaves or bracts, and anthers that are hidden by other floral structures protect both the anthers and the pollen (see Eisikowitch and Woodell 1974). In wind-pollinated *Hippophae rhamnoides* L. the pollen was deposited on the bottom of the flower from whence it was subsequently dispersed. Prior to dispersal the pollen was protected by the sepals (Kerner 1897). It is unclear whether some of the adaptations Kerner discusses are adaptations in response to rain or dew or whether protection of the pollen is a secondary benefit from an adaptation to some other selective pressure, e.g. pollinators. Kerner's observations provide numerous hypotheses that should be tested (also see Dafni 1996).

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Address of the author: Robert William Cruden, Department of Biological Sciences, University of Iowa, Iowa City, IA 52242, USA.