

Post-pollination processes and non-random mating among compatible mates

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ABSTRACT

Questions: What factors determine the degree of non-random mating that occurs among compatible donors following pollination? Do species with longer styles exhibit greater inequalities in seed siring success among pollen donors? Does increased gametophytic competition (i.e. higher ratio of pollen load size to ovule number) lead to greater inequality in seed siring success among pollen donors? Are particular life-history traits (i.e. animal- vs. wind-pollinated species or wild vs. cultivated species) associated with greater inequality in seed siring among pollen donors?

Data incorporated: I summarize the results of 51 studies that assessed the paternity of seeds produced following experimental pollinations in which pollen grains from two or more compatible donors competed for ovule fertilization.

Method of analysis: Data from multiple studies were combined to determine the effects of style length, ratio of pollen load size to ovule number, and life-history traits on the degree of non-random mating among compatible mates.

Conclusions: Style length had the strongest association with non-random mating. Surprisingly, species with shorter styles exhibited a significantly greater inequality in seed siring success among pollen donors. The degree of non-random mating due to post-pollination processes was not affected by the intensity of gametophytic competition or by life-history traits.

Keywords: gametophytic competition, pollen siring success, post-pollination performance, ratio of pollen load size to ovule number, style length.

INTRODUCTION

Post-pollination processes can lead to non-random mating among compatible pollen donors (Willson and Burley, 1983; Marshall and Folsom, 1991). When equal proportions of pollen grains from two or more donors are placed on a stigma, each pollen donor rarely sires the same number of seeds (Bemis, 1959; Cruzan, 1990b; Young and Stanton, 1990; Marshall and Folsom, 1991; Marshall, 1998; Mitchell and Marshall, 1998). Pollen tube growth rate is thought to be important for determining

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post-pollination siring success. Pollen grains with faster tube growth rates sire disproportionately more seeds in a variety of species (Snow and Spira, 1991, 1996; Lau and Stephenson, 1993; Delph *et al.*, 1997; Aizen and Raffaele, 1998; Jóhannsson and Stephenson, 1998; Pasonen *et al.*, 1999; Skogsmyr and Lankinen, 1999; Lankinen and Skogsmyr, 2002). The consequences of non-random mating are considerable, given the documented effects of paternal identity on progeny fitness (Antonovics and Schmitt, 1986; Schmitt and Antonovics, 1986; Bertin, 1988; Marshall and Whittaker, 1989; Bertin and Peters, 1992).

It is unclear whether non-random mating or multiple paternity maximizes the fitness of progeny produced by maternal plants. Non-random mating may be advantageous if pollen grains with the fastest tube growth rates sire disproportionately more seeds. Pollen grains with faster growing tubes have sired more vigorous progeny (i.e. heavier seed and seedling masses) in some studies (Mulcahy, 1971, 1974; Mulcahy and Mulcahy, 1975; Ottaviano *et al.*, 1980; McKenna and Mulcahy, 1983; Richardson and Stephenson, 1992; Jóhannsson and Stephenson, 1998), but not in others (Smith *et al.*, 1990; Snow, 1990, 1991; Mitchell, 1997a). When present, correlations between pollen and progeny vigour may be explained by the overlapping gene expression between these two life-history stages (Tanksley *et al.*, 1981; Mulcahy and Mulcahy, 1987; Walsh and Charlesworth, 1992; Hormaza and Herrero, 1994). However, multiple paternity may also be advantageous, as seed and fruit mass have been shown to increase as the number of fathers per fruit increases (Marshall and Ellstrand, 1986, 1988; Marshall, 1990, 1991). Moreover, by increasing the genetic diversity of progeny, multiple paternity may be beneficial when progeny must germinate and survive in heterogeneous environments. Thus, from the perspective of the maternal plant, a higher degree of non-random mating is not necessarily better.

Although non-random mating in plants has been well documented (Willson and Burley, 1983; Marshall and Folsom, 1991), the factors that explain the observed variation in non-random mating have not been elucidated. The three factors that may affect the degree of non-random mating that occurs following pollination are style length, gametophytic competition (i.e. the ratio of pollen load size to ovule number), and life-history traits.

Style length

The probability that the fastest pollen tubes will reach the ovules first is predicted to increase as style length increases (Mulcahy and Mulcahy, 1975; Mulcahy, 1983; Willson and Burley, 1983; Travers and Shea, 2001). Since all pollen grains are unlikely to germinate simultaneously from the same position on the stigma, a longer distance between the stigma and ovules ensures that differences in relative pollen tube growth rates will overcome differences in germination time and stigma position among competing pollen grains (Sari Gorla and Rovida, 1980; McKenna, 1986; Thomson, 1989; Spira *et al.*, 1996; Skogsmyr and Lankinen, 1999). In fact, species with longer styles often produce pollen grains that have faster growing tubes (Williams and Rouse, 1990; Arnold, 1997). Even though the hypothesized relationship between style length and non-random mating has been in the literature over three decades, empirical work that thoroughly examines this relationship is lacking.

Ratio of pollen load size to ovule number

In nature, the number of pollen grains deposited on the stigma varies spatially and temporally (Snow, 1986; Moeller, 2005), depending on a variety of biotic and abiotic factors, including the availability of mates and the activity of effective pollinators. Variation in the intensity of gametophytic competition (i.e. the ratio of the number of pollen grains deposited on the

stigma to the number of ovules) may determine the opportunity for non-random mating. Larger ratios of pollen load size to ovule number generate more intense pollen competition and are therefore likely to lead to greater inequalities in seed siring success among pollen donors (Mitchell, 1997a, 1997b; Delph and Havens, 1998; Shaner and Marshall, 2003, 2007). Thus, non-random mating may be higher in larger populations that are more attractive to pollinators.

Life-history traits

Species may be associated with higher degrees of non-random mating if they have evolved ways to better discriminate among pollen grains. The evolutionary history of a species may therefore influence the degree of non-random mating it exhibits. A species' pollination biology, for example, will impact the quantity and diversity of pollen grains that are deposited on stigmas. While animal-dispersed pollen is normally transferred as clumps of grains from multiple donors (Thomson and Plowright, 1980; Waser and Price, 1982; Marshall and Ellstrand, 1985), wind-dispersed pollen is typically transferred as individual pollen grains (Primack and Silander, 1975; Kress, 1981). Thus, animal-pollinated species may be associated with higher degrees of non-random mating, given their evolutionary history of receiving a greater quantity and diversity of pollen grains. Similarly, wild species are expected to exhibit higher degrees of non-random mating than cultivated species because the stigmas of inbred crops are likely to receive a collection of pollen grains that is more uniform (both in genetic composition and environmental origin) than the collection of pollen grains received by (non-selfing) wild species. The potential effects of pollination biology or cultivation history on the degree of non-random mating have not yet been considered.

In this paper, I summarize the results of studies that have quantified non-random mating following experimental pollinations in which pollen grains from two or more compatible donors competed for ovule fertilization. I examine whether style length, the ratio of pollen load size to ovule number, and life-history traits affect the degree of non-random mating between pollen donors that are equivalently unrelated to the maternal plant. In particular, I ask the following questions: (1) Do species or individuals with longer styles exhibit a higher degree of non-random mating? (2) Does non-random mating increase as the ratio of pollen load size to ovule number increases? (3) Are particular life-history traits (i.e. animal- vs. wind-pollinated species or wild vs. cultivated species) associated with greater inequalities in seed siring success among pollen donors?

MATERIALS AND METHODS

I surveyed the literature for studies that determined seed paternity following experimental pollinations in which pollen grains from two or more compatible (i.e. non-self) donors competed for ovule fertilization. Using the information provided in relevant publications, I compiled a data set to identify factors that explain the degree of non-random mating due to post-pollination processes.

When equal numbers of pollen grains from two donors are placed on a stigma, mating can range from random (i.e. each pollen donor sires the same number of seeds) to non-random (i.e. a single pollen donor sires every seed). To represent the degree of non-random mating numerically, I used the following equation:

$$1 - \frac{\text{proportion of seeds sired by donor 1}}{\text{proportion of seeds sired by donor 2}}$$

which has been used by others (Coyne and Orr, 1989). The numerator always contained the value from the donor that sired the smaller proportion of seeds. When pollen grains from three or more donors competed for ovule fertilization, which was the case for 12% of the total number of data points, the equation above was modified. For example, when three pollen donors competed for ovule fertilization, I used the following equation:

$$1 - \frac{\text{average proportion of seeds sired by donors 2 and 3}}{\text{proportion of seeds sired by donor 1}}$$

Three individual values were calculated, with each resulting from a different donor in the denominator. The final value of non-random mating is the average of the three individually calculated values. In all cases, the degree of non-random mating ranged from zero (each pollen donor sired the same number of seeds) to one (all seeds sired by a single donor).

In contrast to the results of individual studies (Marshall and Ellstrand, 1986; Marshall, 1991; Shaner and Marshall, 2007), the number of pollen donors competing for ovule fertilization did not affect the degree of non-random mating in this data set ($F = 0.48$, error d.f. = 26, $P > 0.4$). In my analyses, I therefore combined data from all mixed-donor pollinations, regardless of the number of pollen donors.

Exclusions from the data set

This meta-analysis focuses on non-random mating that is due to factors that occur after pollen grains are deposited on the stigma. Therefore, I excluded values that could have been affected by processes that occurred before pollen grains reached the stigma. The effects of factors that occur before and during pollination on non-random mating are discussed elsewhere. For example, individuals that produce more flowers or larger inflorescences are expected to fertilize disproportionately more ovules (Willson and Rathcke, 1974; Willson and Price, 1977; Wolfe, 1987). During pollination, the size, shape, fragrance, and nectar of flowers (Waddington, 1983; Waser, 1983; Galen, 1985), as well as the morphology and behaviour of pollinators (Schmitt, 1980; Waser and Price, 1983), can influence the efficiency with which pollen grains are removed from one flower and deposited on the receptive stigmas of another flower.

This meta-analysis also focuses on the degree of non-random mating that occurs among compatible donors. Therefore, I excluded values of non-random mating that resulted following the deposition of self pollen or pollen that was known to share an incompatibility allele with the seed parent. Non-random mating resulting from the operation of the self-incompatibility system has been addressed in studies that examined paternity following the deposition of self and outcross pollen on stigmas of species that have weak or strong self-incompatibility. In these cases, non-random mating is typically high because the performance of self pollen is hindered, enabling outcross pollen to sire disproportionately more seeds (Montalvo, 1992; Jones, 1994; Baker and Shore, 1995; Travers and Mazer, 2001).

Non-random mating was only calculated following pollinations in which equal amounts of pollen from two or more donors were deposited on the stigma simultaneously or sequentially (separated by a few seconds). I did not include values of non-random mating that were calculated following pollinations in which pollen grains from one donor outnumbered the pollen grains from the other donor (Barnes and Cleveland, 1963; Marshall and Ellstrand, 1986; Bertin, 1990) or pollen grains from one donor were deposited on the stigma minutes or hours earlier than pollen grains from the other donor (Epperson and Clegg, 1987; Snow *et al.*, 2000; Jolivet and Bernasconi, 2007). Thus, high values of non-random mating in this data set are not due to an extreme

competition advantage because one pollen donor either had more pollen grains or was deposited on the stigma minutes or hours earlier.

Analyses

All analyses were performed using JMP, version 4.0 (SAS Institute Inc., Cary, NC, USA).

The effect of style length on the degree of non-random mating due to post-pollination processes was analysed by a regression using the average value of non-random mating for each species. I was not able to include species whose style lengths have not been published. When non-random mating had been estimated for individuals with different style lengths within species, I calculated that species' average value of non-random mating for the style length that had the greatest sample size. The effect of style length was not analysed when controlling for phylogenetic relationships because values of style length and non-random mating were distributed evenly across the tree, according to analyses in Phylocom (Webb *et al.*, 2007). It was possible to examine the effect of intra-specific variation in style length on non-random mating within *Eichhornia paniculata* and *Hibiscus moscheutos*. One-way analyses of variance (ANOVAs) were performed to determine if style length affected the degree of non-random mating within these two species. For each species, data were compiled across two or three studies.

To analyse the effect of gametophytic competition on non-random mating, the average value of non-random mating was calculated for each ratio of pollen load size to ovule number across all species. A regression was performed using these data points to determine the relationship between the degree of non-random mating and the ratio of pollen load size to ovule number. Non-random mating has been calculated for multiple pollen load sizes within *Campsis radicans*, *Cucurbita pepo*, *Cucurbita texana*, *Raphanus sativus*, and *Clarkia unguiculata*. For each of these species, I examined the effect of the ratio of pollen load size to ovule number on the degree of non-random mating by performing one-way ANOVAs (for two pollen load sizes) or regressions (for more than two pollen load sizes). In some cases within-species data came from a single study, but in other cases the data were compiled from multiple studies. Unfortunately, I was unable to include data from a portion of one study that examined the effect of pollen load size on non-random mating (Shaner and Marshall, 2007) because I could not deduce the proportion of seeds sired by each pollen donor.

Additionally, I examined the degree of non-random mating in animal- versus wind-pollinated species and in wild versus cultivated species. These life-history traits were analysed with one-way ANOVAs using species' averages. Power analyses were used to determine the difference between treatment means required for statistical significance. The effects of these life-history traits on non-random mating were not analysed when controlling for phylogenetic relationships because values of non-random mating and each life-history trait were distributed evenly across the tree, according to analyses in Phylocom (Webb *et al.*, 2007).

Limited replication across the different factors prevented the use of multivariate analyses. Univariate analyses, however, are appropriate for this data set due to the lack of statistically significant relationships among the factors analysed.

RESULTS

Summary of data set

This meta-analysis consists of 51 studies, which were collected from 19 different sources (two books and 17 journals). Collectively, the 51 studies examine 23 different species from 17 different families (Table 1). The most commonly studied family is Brassicaceae (17 studies), followed by Poaceae and Cucurbitaceae (6 studies each).

Table 1. The degree of non-random mating due to post-pollination processes was estimated for the species listed

Family	Species	No. of studies	References
Betulaceae	<i>Betula pendula</i>	1	Pasonen <i>et al.</i> (1999)
Bignoniaceae	<i>Campsis radicans</i>	1	Bertin (1990) (S = 31, R = 18)
Brassicaceae	<i>Lesquerella</i>	2	Mitchell and Marshall (1995) (R = 24)
	<i>fendleri</i>		Mitchell and Marshall (1998)
Brassicaceae	<i>Raphanus</i>	3	Snow and Mazer (1988) (S = 24)
	<i>raphanistrum</i>		Young and Stanton (1990) (S = 5)
			Strauss <i>et al.</i> (2001) (S = 1)
Brassicaceae	<i>Raphanus sativus</i>	12	Marshall and Ellstrand (1986) (S = 4)
			Marshall and Ellstrand (1988) (S = 15)
			Marshall and Ellstrand (1989) (S = 3)
			Marshall (1991) (S = 57, R = 57)
			Marshall and Fuller (1994) (S = 7, R = 7)
			Marshall <i>et al.</i> (1996) (S = 16)
			Marshall (1998) (S = 26, R = 26)
			Marshall <i>et al.</i> (2000) (S = 12, R = 12)
			Marshall and Diggle (2001) (S = 6, R = 6)
			Marshall and Oliveiras (2001) (S = 13, R = 13)
			Shaner and Marshall (2003) (S = 18, R = 18)
			Shaner and Marshall (2007) (S = 8)
Caryophyllaceae	<i>Silene alba</i>	1	Taylor <i>et al.</i> (1999)
Caryophyllaceae	<i>Silene vulgaris</i>	1	Delph <i>et al.</i> (1998) (S = 1)
Convolvulaceae	<i>Ipomoea</i>	1	Epperson and Clegg (1987) (S = 1, R = 1)
	<i>purpurea</i>		
Cucurbitaceae	<i>Cucurbita pepo</i>	4	Quesada <i>et al.</i> (1991) (S = 33, R = 33)
			Lau and Stephenson (1993) (S = 4, R = 4)
			Lau and Stephenson (1994) (S = 4, R = 4)
			Jóhannsson and Stephenson (1998) (S = 4)
Cucurbitaceae	<i>Cucurbita texana</i>	2	Quesada <i>et al.</i> (1995) (S = 2, R = 2)
			Jóhannsson <i>et al.</i> (1998) (S = 2, R = 2)
Fabaceae	<i>Medicago sativa</i>	1	Barnes and Cleveland (1963)
Liliaceae	<i>Allium cepa</i>	1	Currah (1981) (S = 21)
Liliaceae	<i>Erythronium</i>	2	Rigney <i>et al.</i> (1993) (S = 56)
	<i>grandiflorum</i>		Thomson <i>et al.</i> (1994) (S = 26)
Malvaceae	<i>Hibiscus</i>	3	Snow and Spira (1991) (S = 2, R = 2)
	<i>moscheutos</i>		Snow and Spira (1996) (S = 51, R = 54)
			Snow <i>et al.</i> (2000) (S = 4, R = 4)
Onagraceae	<i>Clarkia gracilis</i>	1	Jones (1996)

Onagraceae	<i>Clarkia unguiculata</i>	1	Travers and Holtsford (2000) (S = 77, R = 77)
Pinaceae	<i>Pseudotsuga menziesii</i>	2	Apsit <i>et al.</i> (1989) Nakamura and Wheeler (1992)
Poaceae	<i>Zea mays</i>	6	Pfahler (1965, 1967a, 1967b, 1974) Ottaviano <i>et al.</i> (1975) Sari Gorla <i>et al.</i> (1975)
Polemoniaceae	<i>Phlox drummondii</i>	1	Levin (1975)
Pontederiaceae	<i>Eichhornia paniculata</i>	2	Cruzan and Barrett (1993) (S = 4) Manicacci and Barrett (1995) (S = 2)
Proteaceae	<i>Persoonia mollis</i>	1	Krauss (2000)
Solanaceae	<i>Lycopersicon esculentum</i>	1	Poulton <i>et al.</i> (2001)
Violaceae	<i>Viola tricolor</i>	1	Skogsmyr and Lankinen (1999) (S = 47, R = 47)

Note: The numbers in parentheses following references indicate the number of data points from that source that were used to calculate (1) the average degree of non-random mating of a species with a published style length (S) or (2) the average degree of non-random mating for a particular ratio of pollen load size to ovule number (R).

The degree of non-random mating due to post-pollination processes varied considerably among species (Fig. 1). In some cases, mating was extremely non-random, as nearly every seed was sired by a single donor (i.e. Barnes and Cleveland, 1963). In other cases, however, mating was random, such that pollen grains from each donor sired a similar number of seeds (i.e. Levin, 1975; Poulton *et al.*, 2001). When an average value of non-random mating was calculated for each species, the values ranged from 0.09 (nearly completely random) to 0.89 (nearly completely non-random), with a mean and standard error of 0.41 ± 0.04 (Fig. 1).

Style length

Style length significantly affected the degree of non-random mating, but not in the expected direction. Inequality in siring success among pollen donors was highest in species with shorter styles and lowest in species with longer styles ($r^2 = 0.3494$, $n = 13$, $P < 0.05$) (Fig. 2). Within species, however, style length did not have the same effect on the degree of non-random mating (Fig. 3). Naturally occurring variation in style length did have a marginally significant effect on the degree of non-random mating in *Hibiscus moscheutos*; specifically, non-random mating was slightly higher in individuals with longer styles ($F = 3.67$, error d.f. = 58, $P < 0.1$) (Fig. 3b). Thus, the direction of the effect of style length on the degree of non-random mating within *H. moscheutos* was opposite from its effect when analysed across species.

Ratio of pollen load size to ovule number

The ratio of pollen load size to ovule number did not affect the degree of non-random mating due to post-pollination processes ($F = 0.02$, error d.f. = 65, $P > 0.1$) (Fig. 4). When examined within individual species, the intensity of gametophytic competition only affected the degree of non-random mating in one of the five species. Non-random mating increased as the ratio of pollen load size to ovule number increased in *Cucurbita pepo* ($r^2 = 0.184$, $F = 8.80$, error d.f. = 39, $P < 0.01$) (Fig. 5a), but was not affected by the intensity of

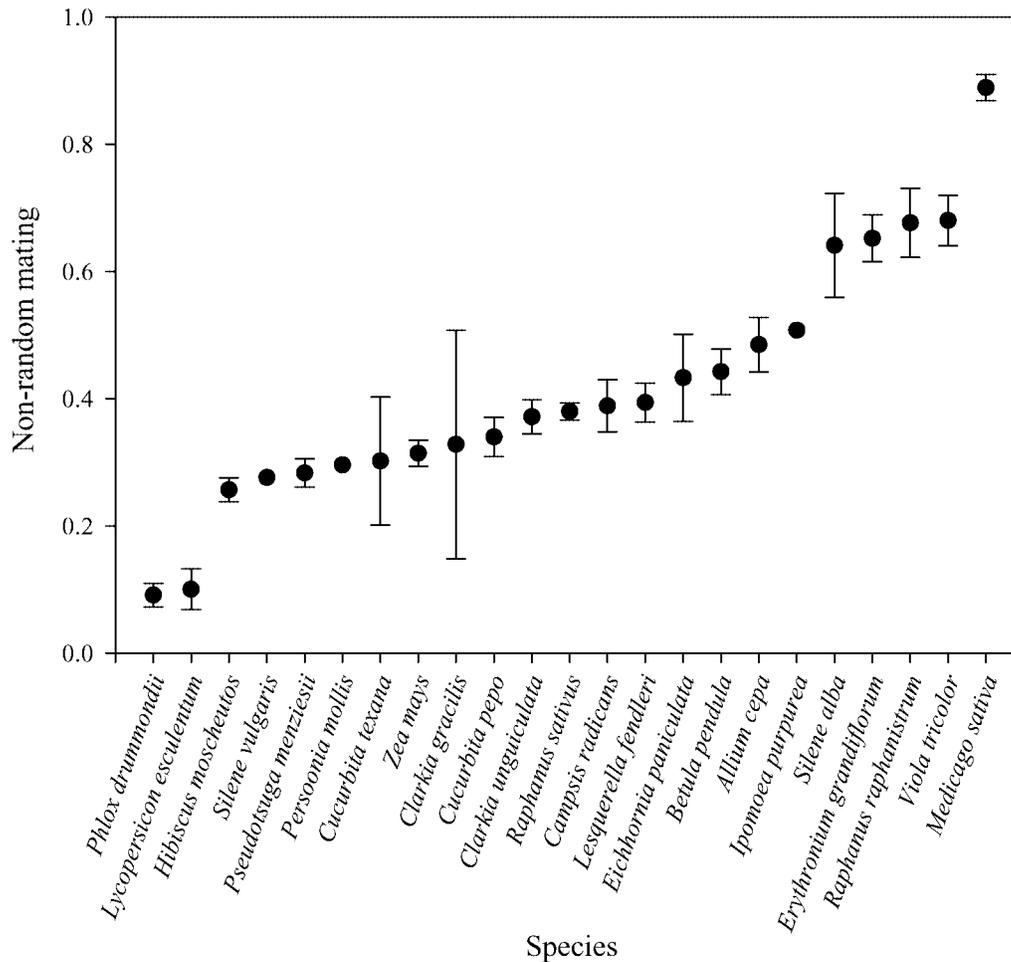


Fig. 1. Mean values of non-random mating due to post-pollination processes for each species included in this data set. Standard errors are given. Values of non-random mating ranged from 0.09 in *P. drummondii* (each donor sired a similar number of seeds) to 0.89 in *M. sativa* (a single donor sired nearly every seed).

gametophytic competition in *Raphanus sativus*, *Cucurbita texana*, *Campsis radicans* or *Clarkia unguiculata* (Fig. 5b,c,d,e).

Life-history traits

Species that are expected to have a stronger evolutionary history of gametophytic competition did not exhibit a higher degree of non-random mating following experimental pollinations (Fig. 6). Values of non-random mating were not significantly higher in animal-compared with wind-pollinated species (error d.f. = 21, error MS = 0.0376, $t = 0.42$, power = 0.2498) or in wild compared with cultivated species (error d.f. = 21, error MS = 0.0378, $t = 0.31$, power = 0.1833). Additional life-history traits (i.e. annual vs.

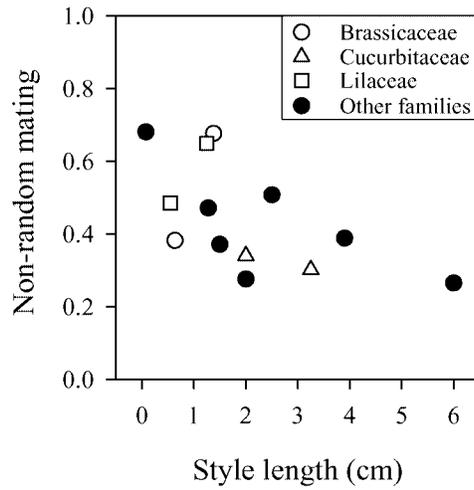


Fig. 2. Effect of style length on the degree of non-random mating due to post-pollination processes. Each data point represents the degree of non-random mating for a particular species with a specific style length. Inequality in siring success among pollen donors was highest in species with shorter styles and lowest in species with longer styles ($r^2 = 0.3494$, $n = 13$, $P < 0.05$). Data points from species within the same family share similar open shapes.

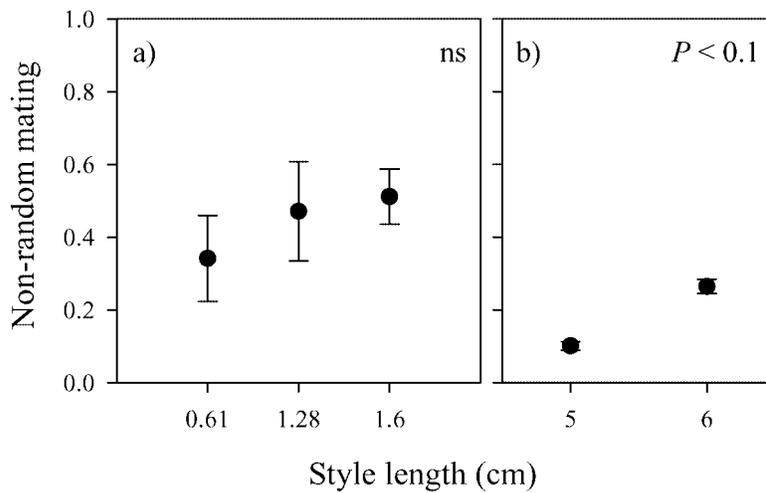


Fig. 3. Effect of naturally occurring variation in style length on the degree of non-random mating due to post-pollination processes within (a) *Eichhornia paniculata* and (b) *Hibiscus moscheutos*. Standard errors are given. Statistical significance was determined by a one-way ANOVA for each species.

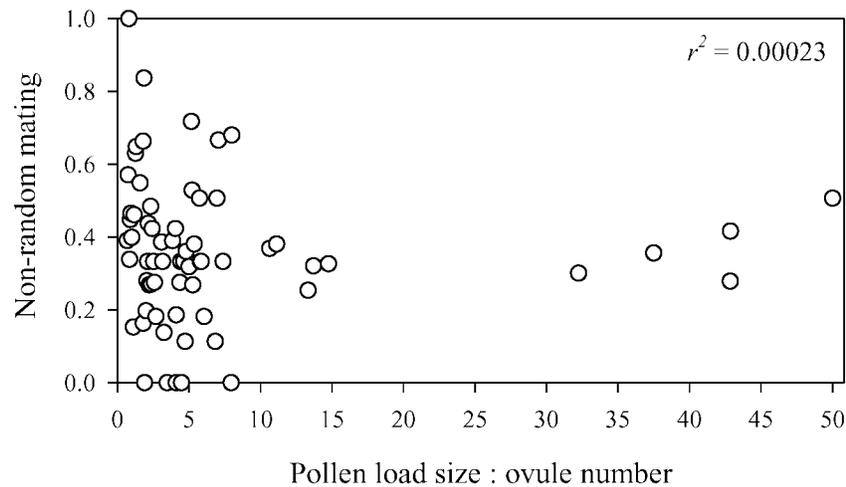


Fig. 4. Effect of the ratio of pollen load size to ovule number on the degree of non-random mating due to post-pollination processes. Data points include every pollen load size used for each species. The ratio of pollen load size to ovule number did not affect the degree of non-random mating ($F = 0.01$, error d.f. = 64, $P > 0.1$).

perennial, self-compatible vs. self-incompatible, native vs. introduced) did not affect the degree of non-random mating (data not shown).

DISCUSSION

Style length

The proportion of seeds sired by the donor with the fastest growing pollen tubes – and thus the degree of non-random mating – did not increase as the style length increased. This finding refutes the hypothesis that species with longer styles exhibit higher degrees of non-random mating. In fact, mating was significantly more (less) random in species that had longer (shorter) styles. Thus, characters other than pollen tube growth rate are likely to influence post-pollination siring success.

In addition to pollen tube growth rate, pollen germination may generate non-random mating among pollen grains from different donors. Differences in the rates of pollen germination are more likely to generate non-random mating in species with shorter styles, as short styles limit the ability of grains that germinate later to outcompete grains that germinated quickly (Sari Gorla and Roviada, 1980; McKenna, 1986; Thomson, 1989; Spira *et al.*, 1996; Skogsmyr and Lankinen, 1999). A mathematical model, which calculates the siring success of two donors with different rates of pollen germination and/or pollen tube growth within styles ranging from 0.1 to 30 mm in length, predicts that quicker pollen germination increases siring success when styles are short and faster tube growth increases siring success when styles are long (Travers and Shea, 2001). In other words, the degree of non-random mating may be determined by pollen germination in species with short styles and by pollen tube growth rates in species with long styles. Thus, the higher values of non-random mating in species with shorter

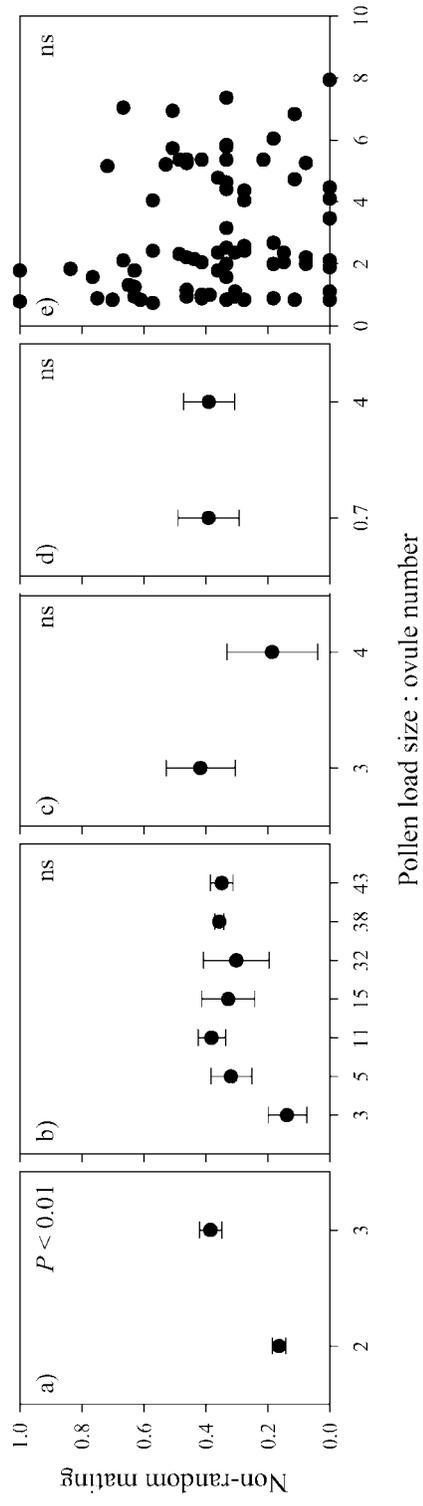


Fig. 5. Effect of pollen load size on the degree of non-random mating within (a) *Cucurbita pepo*, (b) *Raphanus sativus*, (c) *Cucurbita texana*, (d) *Campsis radicans*, and (e) *Clarkia unguiculata*. Standard errors are given. Statistical significance was determined by one-way ANOVAs (for two pollen load sizes) or regressions (for more than two pollen load sizes).

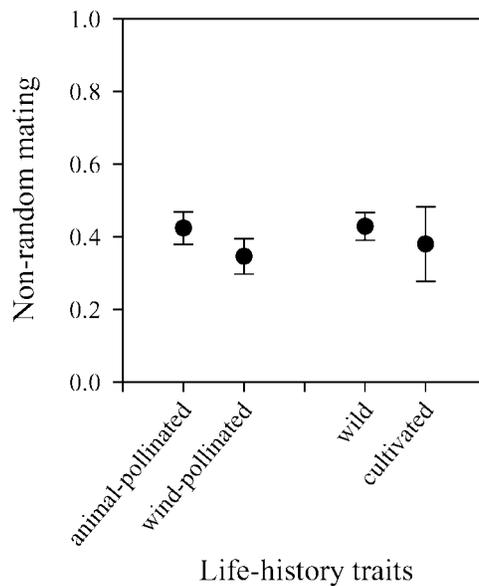


Fig. 6. The mean degree of non-random mating for animal- versus wind-pollinated species and for wild versus cultivated species. Standard errors are given. Neither life-history trait significantly affected the degree of non-random mating, as determined by one-way ANOVAs.

styles could have resulted if variation in pollen germination rates among donors exceeded the variation in pollen tube growth rates among donors.

The greater degree of random mating in species with long rather than short styles may also be due to the greater amount of maternal tissue that pollen grains must navigate to reach the ovules. Although obvious, this is an important distinction because the style can control pollen tube growth (Steer and Steer, 1989; Walsh and Charlesworth, 1992; Holdaway-Clarke and Hepler, 2003). By forcing pollen grains to travel a greater distance to the ovules, longer styles may give maternal plants a better opportunity to determine the fertilization success of pollen grains (Willson and Burley, 1983). Since mating was more random in species with longer styles, stylar tissue may act to equalize the fertilization success of pollen grains from different donors so that each donor obtains a similar number of fertilizations (Cruzan, 1990a). Longer styles may therefore enable maternal plants to maximize the genetic diversity of their progeny.

Although the degree of non-random mating may influence the evolution of style length (Lankinen and Skogsmyr, 2001), it is not the sole influence. The length of an individual's style is also important because it dictates herkogamy, or the degree to which the stigma and anthers are spatially separated. Since shorter distances between stigmas and anthers are associated with higher frequencies of self-fertilization (Runions and Geber, 2000; Takebayashi and Delph, 2000; Elle and Hare, 2002), style length may evolve to optimize the frequency of self-fertilization. Moreover, in animal-pollinated species, style length may evolve in such a way that maximizes the effectiveness by which pollinators transfer pollen (Vaknin *et al.*, 2001). Both self-fertilization and pollination effectiveness have important fitness consequences and are therefore likely to

largely determine the evolution of style length. Nevertheless, the length of an individual's style will continue to impact the likelihood of non-random mating, and therefore the degree to which siblings are related to each other.

Ratio of pollen load size to ovule number

Non-random mating did not increase as the ratio of pollen load size to ovule number increased. The lack of a significant correlation between gametophytic competition and non-random mating in this analysis was not due to an insufficient range of pollen competition intensities (Mitchell, 1997a), as ratios ranged from less than two pollen grains per ovule [which is not enough for complete seed set in some species (Snow, 1986; Richardson and Stephenson, 1991)] to 50 grains per ovule. Instead, the intensity of gametophytic competition was likely limited by the number of pollen donors that competed for ovule fertilization. Only 12% of the values of non-random mating in this analysis resulted from pollinations in which pollen grains from more than two donors competed for ovule fertilization. Pollen loads that consist of both a large number of grains and a collection of grains from a large number of donors would maximize the intensity of gametophytic competition, and therefore the opportunity for non-random mating (Shaner and Marshall, 2007).

Although larger ratios of pollen load size to ovule number did not lead to greater inequalities in seed siring success among pollen donors when data were pooled across multiple studies, a significant correlation between pollen load size and non-random mating could exist within individual plants. For example, in a careful examination of the effects of pollen load size on the total number of seeds set by *Lesquerella fendleri*, Mitchell (1997b) found a significant relationship between these two variables when data were analysed within maternal plants, but not when data were pooled across maternal plants. Although not yet tested experimentally, the effect of increasing pollen load sizes on the degree of non-random mating may also vary across maternal plants. In other words, maternal plants may differ both in the maximum level of non-random mating they can attain and in the size of the pollen load required to achieve their maximum level of non-random mating. Variation in these traits could indicate differences in reproductive strategies and could explain why pollen siring success is not always consistent across maternal plants.

Life-history traits

The degree of non-random mating was not significantly different for animal- versus wind-pollinated species or for wild versus cultivated species. Thus, an evolutionary history of intense pollen competition, as is expected in animal-pollinated species and wild species, was not associated with maternal plants that exhibited greater discrimination among pollen from different donors. Increased non-random mating via greater maternal discrimination, however, may be masked by the co-evolution between pollen grains and pistils. For example, selection for increased maternal discrimination in the presence of intense pollen competition is likely to be counteracted by selection for increased pollen performance. Thus, although the degree of non-random mating between species that experience different evolutionary histories of pollen competition was similar, pollen grains may be more aggressive and pistils may be more selective in species that experience more intense pollen competition. However, it is also possible that selection for increased pollen siring success and increased maternal discrimination does not result in the evolution of these traits (Snow and Mazer, 1988).

Other factors

Additional factors, not considered in this paper, also have the potential to influence non-random mating among compatible donors. For example, interactions between pollen grains from different donors can determine pollen siring success (Cruzan, 1990a). Single-donor pollinations only sometimes predict the performance of pollen donors in mixed-loads, presumably because pollen performance is altered by the presence of grains from other donors. Interference competition among pollen grains occurs when pollen from one donor decreases the performance of pollen from a different donor (Marshall and Folsom, 1992; Murphy and Aarssen, 1995; Marshall *et al.*, 1996). Variation in non-random mating can result when pollen grains from different donors differ either in their ability to decrease the performance of pollen from other donors or in their susceptibility to allelopathic chemicals produced by pollen from other donors.

Differential performance of paternal donors can continue after fertilization has occurred, as the final number of seeds set is often considerably fewer than the number of ovules fertilized (Willson and Burley, 1983). Competition among developing seeds sired by different donors is expected, as zygotes benefit from not having to share maternal resources with siblings from different sires (Kress, 1981; Uma Shaanker *et al.*, 1988). Both paternal effects [i.e. the ability of developing zygotes sired by different donors to compete for maternal resources (Arathi *et al.*, 1999)] and maternal effects [i.e. selective seed provisioning and selective seed abortion (Marshall and Ellstrand, 1988; Havens and Delph, 1996; Burd, 2004)] likely determine the final number of seeds sired by each donor.

The environment can affect pre- and post-zygotic processes that determine siring success following pollination (Ruane and Donohue, 2007). The relative abilities of pollen donors to sire seeds can depend on the amount of water or herbivory the maternal plant has received (Marshall and Ellstrand, 1988; Marshall and Fuller, 1994). Thus, the growth environment of the plant to which pollen grains are dispersed may ultimately determine pollen siring success. The environment in which pollen grains develop can also influence pollen performance; for example, when pollen grains produced by plants grown in low- and high-nutrient conditions compete for ovule fertilization, disproportionately more seeds are typically sired by the grains derived from high-nutrient plants (Young and Stanton, 1990; Lau and Stephenson, 1993; Delph *et al.*, 1997; Jóhannsson and Stephenson, 1998). Thus, non-random mating may be more prevalent in heterogeneous environments, where stigmas commonly receive pollen grains derived from donors grown in a variety of environmental conditions.

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REFERENCES

- Aizen, M.A. and Raffaele, E. 1998. Flowering-shoot defoliation affects pollen grain size and post-pollination pollen performance in *Alstroemeria aurea*. *Ecology*, **79**: 2133–2142.
- Antonovics, J. and Schmitt, J. 1986. Paternal and maternal effects on propagule size in *Anthoxanthum odoratum*. *Oecologia*, **69**: 277–282.

- Arathi, H.S., Ganeshaiah, K.N., Shaanker, R.U. and Hegde S.G. 1999. Seed abortion in *Pongamia pinnata* (Fabaceae). *Am. J. Bot.*, **86**: 659–662.
- Arnold, M.L. 1997. *Natural Hybridization and Evolution*. Oxford: Oxford University Press.
- Baker, A.M. and Shore, J.S. 1995. Pollen competition in *Turnera ulmifolia* (Turneraceae). *Am. J. Bot.*, **82**: 717–725.
- Barnes, D.K. and Cleveland, R.W. 1963. Genetic evidence for nonrandom fertilization in alfalfa as influenced by differential pollen tube growth. *Crop Sci.*, **3**: 295–297.
- Bemis, W.P. 1959. Selective fertilization in lima beans. *Genetics*, **44**: 555–562.
- Bertin, R.I. 1988. Paternity in plants. In *Plant Reproductive Ecology* (J. Lovett-Doust and L. Lovett-Doust, eds.), pp. 30–59. New York: Oxford University Press.
- Bertin, R.I. 1990. Effects of pollination intensity in *Campsis radicans*. *Am. J. Bot.*, **77**: 178–187.
- Bertin, R.I. and Peters, P.J. 1992. Paternal effects on offspring quality in *Campsis radicans*. *Am. J. Bot.*, **140**: 166–178.
- Burd, M. 2004. Offspring quality in relation to excess flowers in *Pultenaea gunnii* (Fabaceae). *Evolution*, **58**: 2371–2376.
- Coyne, J.A. and Orr, H.A. 1989. Patterns of speciation in *Drosophila*. *Evolution*, **43**: 362–381.
- Cruzan, M.B. 1990a. Pollen–pollen and pollen–style interactions during pollen tube growth in *Erythronium grandiflorum* (Liliaceae). *Am. J. Bot.*, **77**: 116–122.
- Cruzan, M.B. 1990b. Variation in pollen size, fertilization ability, and post-fertilization siring ability in *Erythronium grandiflorum*. *Evolution*, **44**: 843–856.
- Delph, L.F. and Havens, K. 1998. Pollen competition in flowering plants. In *Sperm Competition and Sexual Selection* (T.R. Birkhead and A.P. Moller, eds.), pp. 55–90. San Diego, CA: Academic Press.
- Delph, L.F., Jóhannsson, M.H. and Stephenson, A.G. 1997. How environmental factors affect pollen performance: ecological and evolutionary perspectives. *Ecology*, **78**: 1632–1639.
- Elle, E. and Hare, J.D. 2002. Environmentally induced variation in floral traits affects the mating system in *Datura wrightii*. *Funct. Ecol.*, **16**: 79–88.
- Epperson, B.K. and Clegg, M.T. 1987. First-pollination primacy and pollen selection in the morning glory, *Ipomoea purpurea*. *Heredity*, **58**: 5–14.
- Galen, C. 1985. Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. *Ecology*, **66**: 792–797.
- Havens, K. and Delph, L.F. 1996. Differential seed maturation uncouples fertilization and siring success in *Oenothera organensis* (Onagraceae). *Heredity*, **76**: 623–632.
- Holdaway-Clarke, T.L. and Hepler, P.K. 2003. Control of pollen tube growth: role of ion gradients and fluxes. *New Phytol.*, **159**: 539–563.
- Hormaza, J.I. and Herrero, M. 1994. Gametophytic competition and selection. In *Genetic Control of Self-incompatibility and Reproductive Development in Flowering Plants* (E.G. Williams, A.E. Knox and R.B. Clarke, eds.), pp. 372–400. Dordrecht: Kluwer Academic.
- Jóhannsson, M.H. and Stephenson, A.G. 1998. Effects of temperature during microsporogenesis on pollen performance in *Cucurbita pepo* L. (Cucurbitaceae). *Int. J. Plant Sci.*, **159**: 616–626.
- Jolivet, C. and Bernasconi, G. 2007. Within/between population crosses reveal genetic basis for siring success in *Silene latifolia* (Caryophyllaceae). *J. Evol. Biol.*, **20**: 1361–1374.
- Jones, K.N. 1994. Nonrandom mating in *Clarkia gracilis* (Onagraceae): a case of cryptic self-incompatibility. *Am. J. Bot.*, **81**: 195–198.
- Kress, W.J. 1981. Sibling competition and evolution of pollen unit, ovule number, and pollen vector in angiosperms. *Syst. Bot.*, **6**: 101–112.
- Lankinen, Å. and Skogsmyr, I. 2001. Evolution of pistil length as a choice mechanism for pollen quality. *Oikos*, **92**: 81–90.
- Lankinen, Å. and Skogsmyr, I. 2002. Pollen competitive ability: the effect of proportion in two-donor crosses. *Evol. Ecol. Res.*, **4**: 687–700.

- Lau, T.-C. and Stephenson, A.G. 1993. Effects of soil nitrogen on pollen production, pollen grain size, and pollen performance in *Cucurbita pepo* (Cucurbitaceae). *Am. J. Bot.*, **80**: 763–768.
- Levin, D.A. 1975. Gametophytic selection in *Phlox*. In *Gamete Competition in Plants and Animals* (D.L. Mulcahy, ed.), pp. 207–217. Amsterdam: North-Holland.
- Marshall, D.L. 1990. Non-random mating in a wild radish, *Raphanus sativus*. *Plant Spec. Biol.*, **5**: 143–156.
- Marshall, D.L. 1991. Nonrandom mating in wild radish: variation in pollen donor success and effects of multiple paternity among one- to six-donor pollinations. *Am. J. Bot.*, **78**: 1404–1418.
- Marshall, D.L. 1998. Pollen donor performance can be consistent across maternal plants in wild radish (*Raphanus sativus*, Brassicaceae): a necessary condition for the action of sexual selection. *Am. J. Bot.*, **85**: 1389–1397.
- Marshall, D.L. and Ellstrand, N.C. 1985. Proximal causes of multiple paternity in wild radish, *Raphanus sativus*. *Am. Nat.*, **126**: 596–605.
- Marshall, D.L. and Ellstrand, N.C. 1986. Sexual selection in *Raphanus sativus*: experimental data on nonrandom fertilization, maternal choice, and consequences of multiple paternity. *Am. Nat.*, **127**: 446–461.
- Marshall, D.L. and Ellstrand, N.C. 1988. Effective mate choice in wild radish: evidence for selective seed abortion and its mechanism. *Am. Nat.*, **131**: 739–756.
- Marshall, D.L. and Folsom, M.L. 1991. Mate choice in plants: an anatomical to population perspective. *Annu. Rev. Ecol. Syst.*, **22**: 37–63.
- Marshall, D.L. and Folsom, M.L. 1992. The potential for interference competition among the pollen grains of wild radish. In *Angiosperm Pollen and Ovules* (E. Ottaviano, D.L. Mulcahy, M. Sari Gorla and G.B. Mulcahy, eds.), pp. 435–550. New York: Springer.
- Marshall, D.L. and Fuller, O.S. 1994. Does nonrandom mating among wild radish plants occur in the field as well as in the greenhouse? *Am. J. Bot.*, **81**: 439–445.
- Marshall, D.L. and Whittaker, K.L. 1989. Effects of pollen donor identity on offspring quality in wild radish, *Raphanus sativus*. *Am. J. Bot.*, **76**: 1081–1088.
- Marshall, D.L., Folsom, M.W., Hatfield, C. and Bennett, T. 1996. Does interference competition among pollen grains occur in wild radish? *Evolution*, **50**: 1842–1848.
- McKenna, M.A. 1986. Heterostyly and microgametophytic selection: the effect of pollen tube competition on sporophyte vigor in two distylous species. In *Biotechnology and Ecology of Pollen* (D.L. Mulcahy, G.B. Mulcahy and E. Ottaviano, eds.), pp. 443–448. New York: Springer-Verlag.
- McKenna, M.A. and Mulcahy, D.L. 1983. Ecological aspects of gametophytic competition in *Dianthus chinensis*. In *Pollen: Biology and Implications for Plant Breeding* (D.L. Mulcahy and E. Ottaviano, eds.), pp. 419–424. New York: Elsevier Biomedical.
- Mitchell, R.J. 1997a. Effects of pollen quantity on progeny vigor: evidence from the desert mustard *Lesquerella fendleri*. *Evolution*, **51**: 1679–1684.
- Mitchell, R.J. 1997b. Effects of pollination intensity on *Lesquerella fendleri* seed set: variation among plants. *Oecologia*, **109**: 382–388.
- Mitchell, R.J. and Marshall, D.L. 1998. Nonrandom mating and sexual selection in a desert mustard: an experimental approach. *Am. J. Bot.*, **85**: 48–55.
- Moeller, D.A. 2005. Pollinator community structure and sources of spatial variation in plant–pollinator interactions in *Clarkia xantiana* ssp. *xantiana*. *Oecologia*, **142**: 28–37.
- Montalvo, A.M. 1992. Relative success of self and outcross pollen comparing mixed- and single-donor pollinations in *Aquilegia caerulea*. *Evolution*, **46**: 1181–1198.
- Mulcahy, D.L. 1971. A correlation between gametophytic and sporophytic characteristics in *Zea mays* L. *Science*, **171**: 1155–1156.
- Mulcahy, D.L. 1974. Correlation between speed of pollen tube growth and seedling height in *Zea mays* L. *Nature*, **249**: 491–493.
- Mulcahy, D.L. 1983. Models of pollen tube competition in *Geranium maculatum*. In *Pollination Biology* (L. Real, ed.), pp. 152–160. Orlando, FL: Academic Press.

- Mulcahy, D.L. and Mulcahy, G.B. 1975. The influence of gametophytic competition on sporophyte quality in *Dianthus chinensis*. *Theor. Appl. Genet.*, **46**: 277–280.
- Mulcahy, D.L. and Mulcahy, G.B. 1987. The effects of pollen competition. *Am. Sci.*, **75**: 44–50.
- Murphy, S.D. and Aarssen, L.W. 1995. Allelopathic pollen extract from *Phleum pratense* L. (Poaceae) reduces germination, *in vitro*, of pollen of sympatric species. *Int. J. Plant Sci.*, **156**: 425–434.
- Ottaviano, E., Sari Gorla, M. and Mulcahy, D.L. 1980. Pollen tube growth rates in *Zea mays*: implications for genetic improvement of crops. *Science*, **210**: 437–438.
- Pasonen, H.L., Pulkkinen, P., Käpylä, M. and Blom, A. 1999. Pollen tube growth rate and seed siring success among *Betula pendula* clones. *New Phytol.*, **143**: 243–251.
- Poulton, J.L., Koide, R.T. and Stephenson, A.G. 2001. Effects of mycorrhizal infection and soil phosphorus availability on *in vitro* and *in vivo* pollen performance in *Lycopersicon esculentum* (Solanaceae). *Am. J. Bot.*, **88**: 1786–1793.
- Primack, R.B. and Silander, J.A. 1975. Measuring the relative importance of different pollinators to plants. *Nature*, **255**: 143–144.
- Richardson, T.E. and Stephenson, A.G. 1991. Effects of parentage, prior fruit set and pollen load on fruit and seed production in *Campanula americana*. *Oecologia*, **87**: 80–85.
- Richardson, T.E. and Stephenson, A.G. 1992. Effects of parentage and size of the pollen load on progeny performance in *Campanula americana*. *Evolution*, **46**: 1731–1739.
- Ruane, L.G. and Donohue, K. 2007. Environmental effects on pollen–pistil compatibility between *Phlox cuspidata* and *P. drummondii* (Polemoniaceae): implications for hybridization dynamics. *Am. J. Bot.*, **94**: 219–227.
- Runions, C.J. and Geber, M.A. 2000. Evolution of the self-pollinating flower in *Clarkia xantiana* (Onagraceae). I. Size and development of floral organs. *Am. J. Bot.*, **87**: 1439–1451.
- Sari Gorla, M. and Rovida, E. 1980. Competitive ability of maize pollen: intergametophytic effects. *Theor. Appl. Genet.*, **57**: 37–41.
- Schmitt, J. 1980. Pollinator foraging behavior and gene dispersal in *Senecio* (Compositae). *Evolution*, **34**: 934–943.
- Schmitt, J. and Antonovics, J. 1986. Experimental studies of the evolutionary significance of sexual reproduction. III. Maternal and paternal effects during seedling establishment. *Evolution*, **40**: 817–829.
- Shaner, M.G.M. and Marshall, D.L. 2003. Under how wide a set of conditions will nonrandom mating occur in *Raphanus sativus* (Brassicaceae)? *Am. J. Bot.*, **90**: 1604–1611.
- Shaner, M.G.M. and Marshall, D.L. 2007. How robust is nonrandom mating in wild radish: do small pollen loads coupled with more competing pollen donors lead to random mating? *Am. J. Bot.*, **94**: 266–273.
- Skogsmyr, I. and Lankinen, Å. 1999. Selection on pollen competitive ability in relation to stochastic factors influencing pollen deposition. *Evol. Ecol. Res.*, **1**: 971–985.
- Smith, S.E., Conta, D.M. and Behcert, U. 1990. Pollen load, seed position, and agronomic performance in alfalfa. *Crop Sci.*, **30**: 561–565.
- Snow, A.A. 1986. Pollination dynamics in *Epilobium canum* (Onagraceae): consequences for gametophytic selection. *Am. J. Bot.*, **73**: 139–151.
- Snow, A.A. 1990. Effects of pollen-load size and number of donors on sporophyte fitness in wild radish (*Raphanus raphanistrum*). *Am. Nat.*, **136**: 742–758.
- Snow, A.A. 1991. Effects of pollen-load size on sporophyte competitive ability in two *Epilobium* species. *Am. Midl. Nat.*, **125**: 348–355.
- Snow, A.A. and Mazer, S.J. 1988. Gametophytic selection in *Raphanus raphanistrum*: a test for heritable variation in pollen competitive ability. *Evolution*, **42**: 1065–1075.
- Snow, A.A. and Spira, T.P. 1991. Differential pollen-tube growth rates and nonrandom fertilization in *Hibiscus moscheutos* (Malvaceae). *Am. J. Bot.*, **78**: 1419–1426.

- Snow, A.A. and Spira, T.P. 1996. Pollen-tube competition and male fitness in *Hibiscus moscheutos*. *Evolution*, **50**: 1866–1870.
- Snow, A.A., Spira, T.P. and Liu, H. 2000. Effects of sequential pollination on the success of ‘fast’ and ‘slow’ pollen donors in *Hibiscus moscheutos* (Malvaceae). *Am. J. Bot.*, **87**: 1656–1659.
- Spira, T.P., Snow, A.A. and Puterbaugh, M.N. 1996. The timing and effectiveness of sequential pollinations in *Hibiscus moscheutos*. *Oecologia*, **105**: 230–235.
- Steer, M.W. and Steer, J.M. 1989. Pollen tube tip growth. *New Phytol.*, **111**: 323–358.
- Takebayashi, N. and Delph, L.F. 2000. An association between a floral trait and inbreeding depression. *Evolution*, **54**: 840–846.
- Tanksley, S.D., Zamir, D. and Rick, C.M. 1981. Evidence for extensive overlap of sporophytic and gametophytic gene expression in *Lycopersicon esculentum*. *Science*, **213**: 453–455.
- Thomson, J.D. 1989. Germination schedules of pollen grains: implications for pollen selection. *Evolution*, **43**: 220–223.
- Thomson, J.D. and Plowright, R.C. 1980. Pollen carryover, nectar rewards and pollinator behavior with special reference to *Diervilla lonicera*. *Oecologia*, **46**: 68–74.
- Travers, S.E. and Mazer, S.J. 2001. Trade-offs between male and female reproduction associated with allozyme variation in phosphoglucosomerase in an annual plant (*Clarkia unguiculata*: Onagraceae). *Evolution*, **55**: 2421–2428.
- Travers, S.E. and Shea, K. 2001. Individual variation, gametophytic competition and style length: does size affect paternity? *Evol. Ecol. Res.*, **3**: 729–745.
- Uma Shaanker, R., Ganeshaiah, K.N. and Bawa, K.S. 1988. Parent–offspring conflict, sibling rivalry, and brood size patterns in plants. *Annu. Rev. Ecol. Syst.*, **19**: 177–205.
- Vaknin, Y., Gan-mor, S., Bechar, A., Ronen, B. and Eisikowitch, D. 2001. Are flowers morphologically adapted to take advantage of electrostatic forces in pollination? *New Phytol.*, **152**: 301–306.
- Waddington, K.D. 1983. Foraging behavior of pollinators. In *Pollination Biology* (L. Real, ed.), pp. 213–241. Orlando, FL: Academic Press.
- Walsh, N.E. and Charlesworth, D. 1992. Evolutionary interpretations of differences in pollen tube growth rates. *Q. Rev. Biol.*, **67**: 19–37.
- Waser, N.M. 1983. The adaptive nature of floral traits: ideas and evidence. In *Pollination Biology* (L. Real, ed.), pp. 242–286. Orlando, FL: Academic Press.
- Waser, N.M. and Price, M.V. 1982. A comparison of pollen and fluorescent dye carry-over by natural pollinators of *Ipomopsis aggregata* (Polemoniaceae). *Ecology*, **63**: 1168–1172.
- Waser, N.M. and Price, M.V. 1983. Optimal and actual outcross in plants, and the nature of Plant–pollinator interaction. In *Handbook of Experimental Pollination Ecology* (C.E. Jones and R.J. Little, eds.), pp. 341–359. New York: Van Nostrand Reinhold.
- Webb, C.O., Ackerly, D.D. and Kembel, S.W. 2007. *Phylocom: software for the analysis of community phylogenetic structure and character evolution*, Version 3.41. (<http://www.phylodiversity.net/phylocom/>).
- Williams, E.G. and Rouse, J.L. 1990. Relationships of pollen size, pistil length, and pollen tube growth rates in *Rhododendron* and their influence on hybridization. *Sex. Plant Reprod.*, **3**: 7–17.
- Willson, M.F. and Burley, N. 1983. *Mate Choice in Plants*. Princeton, NJ: Princeton University Press.
- Willson, M.F. and Price, P.W. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution*, **31**: 495–511.
- Willson, M.F. and Rathcke, B.J. 1974. Adaptive design of the floral display in *Asclepias syriaca* L. *Am. Midl. Nat.*, **92**: 47–57.
- Wolfe, L.M. 1987. Inflorescence size and pollinaria removal in *Asclepias curassavica* and *Epidendrum radicans*. *Biotropica*, **19**: 86–89.
- Young, H.J. and Stanton, M.L. 1990. Influence of environmental quality on pollen competitive ability in wild radish. *Science*, **248**: 1631–1633.

STUDIES INCLUDED IN DATA SET

Note: The number in parentheses at the end of each reference indicates the number of data points acquired from that study.

- Apsit, V.J., Nakamura, R.R. and Wheeler, N.C. 1989. Differential male reproductive success in Douglas fir. *Theor. Appl. Genet.*, **77**: 681–684. (55)
- Barnes, D.K. and Cleveland, R.W. 1963. Genetic evidence for nonrandom fertilization in alfalfa as influenced by differential pollen tube growth. *Crop Sci.*, **3**: 295–297. (6)
- Bertin, R.I. 1990. Paternal success following mixed pollinations of *Campsis radicans*. *Am. Midl. Nat.*, **124**: 153–163. (31)
- Cruzan, M.B. and Barrett, S.C.H. 1993. Contribution of cryptic incompatibility to the mating system of *Eichhornia paniculata* (Pontederiaceae). *Evolution*, **47**: 925–934. (12)
- Currah, L. 1981. Pollen competition in onion (*Allium cepa* L.) *Euphytica*, **30**: 687–696. (21)
- Delph, L.F., Weinig, C. and Sullivan, K. 1998. Why fast-growing pollen tubes give rise to vigorous progeny: the test of a new mechanism. *Proc. R. Soc. Lond. B*, **265**: 935–939. (1)
- Epperson, B.K. and Clegg, M.T. 1987. First-pollination primacy and pollen selection in the morning glory, *Ipomoea purpurea*. *Heredity*, **58**: 5–14. (1)
- Jóhannsson, M.H. and Stephenson, A.G. 1998. Effects of temperature during microsporogenesis on pollen performance in *Cucurbita pepo* L. *Int. J. Plant Sci.*, **159**: 616–626. (4)
- Jóhannsson, M.H., Gates, M.J. and Stephenson, A.G. 1998. Inbreeding depression affects pollen performance in *Cucurbita texana*. *J. Evol. Biol.*, **11**: 579–588. (2)
- Jones, K.N. 1996. Pollinator behavior and postpollination reproductive success in alternative floral phenotypes of *Clarkia gracilis* (Onagraceae). *Int. J. Plant Sci.*, **157**: 733–738. (2)
- Krauss, S.L. 2000. The realized effect of postpollination sexual selection in a natural plant population. *Proc. R. Soc. Lond. B*, **267**: 1925–1929. (1)
- Lau, T.-C. and Stephenson, A.G. 1993. Effects of soil nitrogen on pollen production, pollen grain size, and pollen performance in *Cucurbita pepo* (Cucurbitaceae). *Am. J. Bot.*, **80**: 763–768. (4)
- Lau, T.-C. and Stephenson, A.G. 1994. Effects of soil phosphorus on pollen production, pollen size, pollen phosphorus content, and the ability to sire seeds in *Cucurbita pepo* (Cucurbitaceae). *Sex. Plant Reprod.*, **7**: 215–220. (4)
- Levin, D.A. 1975. Gametophytic selection in *Phlox*. In *Gamete Competition in Plants and Animals* (D.L. Mulcahy, ed.), pp. 207–217. Amsterdam: North-Holland. (5)
- Manicacci, D. and Barrett, S.C.H. 1995. Stamen elongation, pollen size, and siring ability in tristylous *Eichhornia paniculata* (Pontederiaceae). *Am. J. Bot.*, **82**: 1381–1389. (4)
- Marshall, D.L. 1991. Nonrandom mating in wild radish: variation in pollen donor success and effects of multiple paternity among one- to six-donor pollinations. *Am. J. Bot.*, **78**: 1404–1418. (57)
- Marshall, D.L. 1998. Pollen donor performance can be consistent across maternal plants in wild radish (*Raphanus sativus*, Brassicaceae): a necessary condition for the action of sexual selection. *Am. J. Bot.*, **85**: 1389–1397. (26)
- Marshall, D.L. and Diggle, P.K. 2001. Mechanisms of differential pollen donor performance in wild radish, *Raphanus sativus* (Brassicaceae). *Am. J. Bot.*, **88**: 242–257. (6)
- Marshall, D.L. and Ellstrand, N.C. 1986. Sexual selection in *Raphanus sativus*: experimental data on nonrandom fertilization, maternal choice, and consequences of multiple paternity. *Am. Nat.*, **127**: 446–461. (4)
- Marshall, D.L. and Ellstrand, N.C. 1988. Effective mate choice in wild radish: evidence for selective seed abortion and its mechanism. *Am. Nat.*, **131**: 739–756. (15)
- Marshall, D.L. and Ellstrand, N.C. 1989. Regulation of mate number in fruits of wild radish. *Am. Nat.*, **133**: 751–765. (3)

- Marshall, D.L. and Fuller, O.S. 1994. Does nonrandom mating among wild radish plants occur in the field as well as in the greenhouse? *Am. J. Bot.*, **81**: 439–445. (7)
- Marshall, D.L. and Oliveras, D.M. 2001. Does differential seed siring success change over time or with pollination history in wild radish, *Raphanus sativus* (Brassicaceae)? *Am. J. Bot.*, **88**: 2232–2242. (13)
- Marshall, D.L., Folsom, M.W., Hatfield, C. and Bennett, T. 1996. Does interference competition among pollen grains occur in wild radish? *Evolution* **50**: 1842–1848. (16)
- Marshall, D.L., Avritt, J.J., Shaner, M. and Saunders, R.L. 2000. Effects of pollen load size and composition on pollen donor performance in wild radish, *Raphanus sativus* (Brassicaceae). *Am. J. Bot.*, **87**: 1619–1627. (12)
- Mitchell, R.J. and Marshall, D.L. 1995. Effects of pollination method on paternal success in *Lesquerella fendleri* (Brassicaceae). *Am. J. Bot.*, **82**: 462–467. (24)
- Mitchell, R.J. and Marshall, D.L. 1998. Nonrandom mating and sexual selection in a desert mustard: an experimental approach. *Am. J. Bot.*, **85**: 48–55. (8)
- Nakamura, R.R. and Wheeler, N.C. 1992. Pollen competition and paternal success in Douglas-fir. *Evolution*, **46**: 846–851. (6)
- Ottaviano, E., Sari Gorla, M. and Mulcahy, D.L. 1975. Genetic and intergametophytic influences on pollen tube growth. In *Gamete Competition in Plants and Animals* (D.L. Mulcahy, ed.), pp. 125–134. Amsterdam: North-Holland. (10)
- Pasonen, H.L., Pulkkinen, P., Kapyta, M. and Blom, A. 1999. Pollen-tube growth rate and seed-siring success among *Betula pendula* clones. *New Phytol.*, **143**: 243–251. (29)
- Pfahler, P.L. 1965. Fertilization ability of maize pollen grains. I. Pollen sources. *Genetics*, **52**: 513–520. (8)
- Pfahler, P.L. 1967a. Fertilization ability of maize pollen grains. II. Pollen genotype, female sporophyte and pollen storage interactions. *Genetics*, **57**: 513–521. (16)
- Pfahler, P.L. 1967b. Fertilization ability of maize pollen grains. III. Gamma irradiation of mature pollen. *Genetics*, **57**: 523–530. (12)
- Pfahler, P.L. 1974. Fertilization ability of maize (*Zea mays* L.) pollen grains. IV. Influence of storage and the alleles at the shrunken, sugary and waxy loci. In *Fertilization in Higher Plants* (H.F. Linskens, ed.), pp. 15–25. Amsterdam: North-Holland. (84)
- Poulton, J.L., Koide, R.T. and Stephenson, A.G. 2001. Effects of mycorrhizal infection and soil phosphorus availability on *in vitro* and *in vivo* pollen performance in *Lycopersicon esculentum* (Solanaceae). *Am. J. Bot.*, **88**: 1786–1793. (3)
- Quesada, M., Schlichting, C.D., Winsor, J.A. and Stephenson, A.G. 1991. Effects of genotype on pollen performance in *Cucurbita pepo*. *Sex. Plant Reprod.*, **4**: 208–214. (33)
- Quesada, M., Bollman, K. and Stephenson, A.G. 1995. Leaf damage decreases pollen production and hinders pollen performance in *Cucurbita texana*. *Ecology*, **76**: 437–443. (2)
- Rigney, L.P., Thomson, J.D., Cruzan, M.B. and Brunet, J. 1993. Differential success of pollen donors in self-compatible lily. *Evolution*, **47**: 915–924. (56)
- Sari Gorla, M., Ottaviano, E. and Faini, D. 1975. Genetic variability of gametophyte growth rate in maize. *Theor. Appl. Genet.*, **46**: 289–294. (40)
- Shaner, M.G.M. and Marshall, D.L. 2003. Under how wide a set of conditions will nonrandom mating occur in *Raphanus sativus* (Brassicaceae)? *Am. J. Bot.*, **90**: 1604–1611. (18)
- Shaner, M.G.M. and Marshall, D.L. 2007. How robust is nonrandom mating in wild radish: do small pollen loads coupled with more competing pollen donors lead to random mating? *Am. J. Bot.*, **94**: 266–273. (8)
- Skogsmyr, I. and Lankinen, A. 1999. Selection on pollen competitive ability in relation to stochastic factors influencing pollen deposition. *Evol. Ecol. Res.*, **1**: 971–985. (47)
- Snow, A.A. and Mazer, S.J. 1988. Gametophytic selection in *Raphanus raphanistrum*: a test for heritable variation in pollen competitive ability. *Evolution*, **42**: 1065–1075. (24)
- Snow, A.A. and Spira, T.P. 1991. Differential pollen-tube growth rates and nonrandom fertilization in *Hibiscus moscheutos* (Malvaceae). *Am. J. Bot.*, **78**: 1419–1426. (2)

- Snow, A.A. and Spira, T.P. 1996. Pollen-tube competition and male fitness in *Hibiscus moscheutos*. *Evolution*, **50**: 1866–1870. (54)
- Snow, A.A., Spira, T.P. and Liu, H. 2000. Effects of sequential pollination on the success of 'fast' and 'slow' pollen donors in *Hibiscus moscheutos* (Malvaceae). *Am. J. Bot.*, **87**: 1656–1659. (4)
- Strauss, S.Y., Conner, J.K. and Lehtila, K.P. 2001. Effects of foliar herbivory by insects on the fitness of *Raphanus raphanistrum*: damage can increase male fitness. *Am. Nat.*, **158**: 496–504. (1)
- Taylor, D.R., Saur, M.J. and Adams, E. 1999. Pollen performance and sex-ratio evolution in a dioecious plant. *Evolution*, **53**: 1028–1036. (2)
- Thomson, J.D., Rigney, L.P., Karoly, K.M. and Thomson, B.A. 1994. Pollen viability, vigor, and competitive ability in *Erythronium grandiflorum* (Liliaceae). *Am. J. Bot.*, **81**: 1257–1266. (26)
- Travers, S.E. and Holtsford, T.P. 2000. Differential siring success of Pgi genotypes in *Clarkia unguiculata* (Onagraceae). *Am. J. Bot.*, **87**: 1091–1098. (77)
- Young, H.J. and Stanton, M.L. 1990. Influence of environmental quality on pollen competitive ability in wild radish. *Science*, **248**: 1631–1633. (5)

