

Individual variation, gametophytic competition and style length: does size affect paternity?

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ABSTRACT

Post-pollination competition among pollen grains for the fertilization of ovules can potentially filter out inferior male gametophytes from the reproductive process. It has been assumed that, in relatively long styles, competition among genetically diverse pollen grains will be more intense than in relatively short styles. However, very few empirical studies have examined the influence of style length on differences among pollen donors in siring success. We developed a model of pollen tube growth based on measures of *in vivo* pollen performance and style length of an annual herb (*Clarkia unguiculata*) to examine the relationship between style length and the percentage of seeds sired by two competing donors with differing pollen performance parameters. We found that there is no increase in the siring success of a superior donor as style length increases under a range of conditions. Moreover, there was a positive relationship between style length and style filtering ability only in styles shorter than those found in wild populations of *C. unguiculata*, suggesting that variation in style length has little influence on filtering ability in natural populations of this species. We conclude that both male and female reproductive success can be influenced by style length, but under a restricted set of conditions.

Keywords: flower morphology, gametophytic competition, sexual selection, style length.

INTRODUCTION

Competition among pollen grains for fertilization of ovules is thought to be an important determinant of both male reproductive success and offspring quality in flowering plants (Mulcahy, 1979; Willson and Burley, 1983; Stephenson and Bertin, 1983). When surplus pollen is deposited on receptive stigmas, such that there is competition among pollen grains to reach the ovary and to fertilize the available ovules, some pollen grains will fail to sire seeds. The results of some studies suggest that this competition for fertilization may act as an important filter, improving the genetic quality and vigour of offspring by preventing pollen grains with slow pollen tubes from siring seed (Mulcahy and Mulcahy, 1975; Winsor *et al.*, 1987; Schlichting *et al.*, 1990; Bjorkman, 1995).

It has been suggested that the ability of a style to filter out slow-growing tubes from the

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fertilization process (or filtering ability) is positively related to the length of that style (Correns, 1928; Mulcahy and Mulcahy, 1975; Sari Gorla and Rovida, 1980; Ottaviano *et al.*, 1982; McKenna, 1986). Few studies have investigated this issue and their results are equivocal. For example, Jones (1928) observed that, in crosses of pollen recipients with mixtures of pollen from two donor types of *Oenothera lucida*, one of the two donors sired a majority of the ovules in long-styled flowers but only half of the ovules in short-styled flowers. In two later studies exploiting the variation in style length in *Zea mays*, there was greater variation in siring success among competing pollen donors following pollinations in long relative to short styles (Sari Gorla and Rovida, 1980; Ottaviano *et al.*, 1982). However, in a study of *Lobelia cardinalis*, Johnston (1993) found no evidence for differential siring success by different pollen donors used in competitive pollinations and no evidence for the evolution of long styles as a result of gametophytic competition.

Other experiments have demonstrated increases in offspring vigour following pollen competition in longer versus shorter styles (Mulcahy and Mulcahy, 1975; Ottaviano *et al.*, 1982; McKenna, 1986; Purrington, 1993; but see Smith *et al.*, 1990). The assumption in these studies is that increased filtering out of slow-growing pollen increases offspring vigour. The results of these studies suggest that style length may play an important role in the evolution of flowering plants. To determine the importance of gametophytic competition for the evolution of style length and the influence of style length on male reproductive success, it is necessary to analyse the relationship between filtering ability and style length.

We developed a model based on *in vivo* measures of pollen tube growth and pollen germination of an annual plant (*Clarkia unguiculata*), to examine the effects of style length on style filtering ability and male reproductive success. We also examined the influence of the means and variances of pollen tube growth rate and the time required for pollen germination (collectively, pollen performance) on the relationship between style length and style filtering ability.

The model was developed to address four questions: (1) What is the expected relationship between filtering ability in *C. unguiculata* and style length? (2) How does the relationship between filtering ability and style length change with changes in the mean and variation in tube growth rate? (3) How does the relationship between siring success and style length change with changes in the mean and variation in germination time? (4) How do possible trade-offs between germination rate and tube growth rate alter the relationship between filtering ability and style length? Using the model to answer these questions will help to direct future empirical work.

METHODS

Clarkia unguiculata is a predominantly outcrossing annual that is endemic to California (Lewis and Lewis, 1955). Individuals in field populations are likely to experience pollen competition. A survey of pollen tube counts in naturally pollinated flowers from a field population of *C. unguiculata* indicated that the number of tubes per style was 112 ± 6.5 (mean $\pm$ standard deviation). The range of tube counts was from 0 to 334, but over half of the styles had between 50 and 150 pollen tubes (S.E. Travers, unpublished data). In the field, *C. unguiculata* styles range from 9 to 18 mm in length (S.E. Travers, unpublished data) and fruits produce an average of 50 seeds.

Pollen competition model

We developed a pollen competition model to investigate the siring success of two competing pollen donors in styles of varying length. In this stochastic model, we assume that germination times, g , and growth rates, r , for each donor are normally distributed. Each donor contributes a number of pollen grains, which are assumed to arrive simultaneously on the stigma (see Discussion for relaxation of this assumption). These pollen grains germinate and grow down the style. For a given style length, L , we can thus estimate the time to fertilization (from pollination) of each individual pollen grain, t_i , by:

$$t_i = g_i + \frac{L}{r_i}$$

The model estimates a value for t_i for each pollen grain for each donor by generating normal random variates (with the appropriate mean and standard deviation) for g_i and r_i . We used the Box-Muller method (Press *et al.*, 1989) to generate normal random variates. We assume that the ovaries have 50 ovules (this approximates the average number of seeds produced by *C. unguiculata* in the field; S.E. Travers, unpublished data) and that the 50 pollen tubes that first reach the ovaries lead to successful fertilization of the ovaries. All later pollen tubes are unsuccessful. Thus, paternity is assigned to the 50 pollen grains with the shortest time to fertilization. The paternity success of a donor is defined as the percentage of those 50 ovules fertilized by that donor.

In this study, we defined donor 2 as the baseline donor in all runs. We then asked what is the percentage of seeds sired by a competitor, donor 1, with pollen having specified differences from the baseline donor in germination time and/or tube growth rate. In this way, we can determine which components of pollen performance influence fitness at a variety of style lengths. For all runs, we varied style length from 0.1 to 30 mm in 0.1 mm increments, spanning the range of sizes observed in the field. We varied the pollen performance of donor 1 systematically to assess the effect of mean and variation in germination time and pollen tube growth rate within an individual on siring success, and how this changes with style length. Mean values of g and r for donor 1 were increased or decreased by one or three standard deviations, either independently or in combination. These changes correspond to increases of approximately 6.5% and 19.5% of the means respectively. In the figures, we refer to these conditions as +1 SD and +3 SD respectively. The standard deviations of g and r for donor 1 were increased or decreased by 10%, again either alone or in combination with changes in mean parameters.

Pollen performance is known to be affected by temperature (Herrero and Johnson, 1980; Zamir *et al.*, 1981; Stephenson *et al.*, 1992; Travers, 1999a,b). However, our model assumes that temperature is either unvarying or has an equal effect on all pollen grains. These assumptions are valid in the absence of gene $\times$ environment interactions in a field setting.

Additionally, we examined the effect that pollen load and performance trade-offs have on siring success. We simulated the condition where we increased the number of pollen grains of donor 1, or of both donors together, to double that of default conditions. We simulated pollen performance trade-offs by simultaneously changing the germination rate and the tube growth rate for donor 1 in opposite directions.

Parameter estimation

Estimates of pollen germination time (the time between pollen deposition and tube emergence from the grain) and pollen tube growth rate were obtained from *Clarkia unguiculata* plants grown in a greenhouse. We determined the distribution of pollen germination times (g) in hours by hand-pollinating two flowers on each of five different plants and recording the proportion of pollen grains that had germinated during nine sequential time intervals lasting an average of 25 min. The time required for a pollen grain to germinate was normally distributed with a mean of 1.42 h (standard error = 0.092, $n = 10$).

We also measured the distance grown by pollen tubes in the styles of 17 hand-pollinated plants in a 4 h period. One flower was pollinated on each of the 17 plants with pollen from one of the other 16 plants. Methods for staining pollen tubes for microscopy were the same as those in Travers (1999a). Pollen tube lengths were estimated by counting the number of tubes at 0.8 mm intervals with an ocular micrometer and assuming that pollen tubes ending within an interval stopped halfway through the interval. We calculated the mean and standard error for tube growth rate for each of the 17 flowers and used the average of these values to set default parameters. The mean distance grown in 4 h, D , averaged 7.38 mm (standard error = 0.412).

These two observational studies provided estimates of the mean and variance of the germination time, g , and of the distance travelled in 4 h, D . For a single pollen grain, i , with germination time, g_i , and distance grown in 4 h, D_i , we can thus estimate the rate of pollen tube growth (following germination), r_i , as:

$$r_i = \frac{D_i}{4 - g_i}$$

assuming $g_i < 4$. However, we use moment expansion approximations of the expectation variance of the ratio of two random variables (Mood *et al.*, 1974) to estimate the mean and variance of the pollen tube growth rate, r .

$$E\left(\frac{X}{Y}\right) = \frac{E(X)}{E(Y)} - \frac{1}{E(Y)^2} \text{cov}(X, Y) + \frac{E(X)}{E(Y)^3} \text{var}(Y)$$

$$\text{var}\left(\frac{X}{Y}\right) = \left(\frac{E(X)}{E(Y)}\right)^2 \left(\frac{\text{var}(X)}{E(X)^2} + \frac{\text{var}(Y)}{E(Y)^2} - \frac{2\text{cov}(X, Y)}{E(X)E(Y)}\right)$$

We assume that there is no covariance between germination time and distance grown in 4 h (see Discussion for more details). Then substituting $X = D$ and $Y = 4 - g$, and using the fact that $E(4 - g) = 4 - E(g)$ and $\text{var}(4 - g) = \text{var}(g)$, we obtain:

$$E(r) = \frac{E(D)}{4 - E(g)} + \frac{E(D)}{(4 - E(g))^3} \text{var}(g)$$

and

$$\text{var}(r) = \left(\frac{E(D)}{4 - E(g)}\right)^2 \left(\frac{\text{var}(D)}{E(D)^2} + \frac{\text{var}(g)}{(4 - E(g))^2}\right)$$

This gives a value of pollen tube growth rate, r , of $2.86 \text{ mm} \cdot \text{h}^{-1}$ (standard error = 0.189). All parameters are summarized in Table 1 for convenience. We have defined donor 2 as the baseline donor in all runs. The pollen performance parameters for donor 2 are given in Table 1.

RESULTS

In the case where donor 1 and donor 2 were identical, as expected each donor sired 50% of the seeds produced at all style lengths when averaged over 1000 iterations of the model (Fig. 1). Nevertheless, there was considerable variation in siring success within a particular realization of the model, and siring success varied from about 40% to around 60%. Increasing or decreasing the variation in the mean germination time or the mean growth rate of donor 1 pollen did not diminish this variation in siring success.

Table 1. Baseline pollen performance parameters measured from a greenhouse population of *Clarkia unguiculata* (Onagraceae)^a

Variable	Symbol	Mean value	Standard error	Observed/estimated
Germination time	g	1.42 h	0.092	observed
Distance grown in 4 h	D	7.38 mm	0.412	observed
Rate of pollen tube growth	r	$2.86 \text{ mm} \cdot \text{h}^{-1}$	0.189	estimated

^aIn the model, donor 2 pollen had these parameters (unless otherwise stated in the text) and changes in donor 1 pollen performance were made in relation to these parameters.

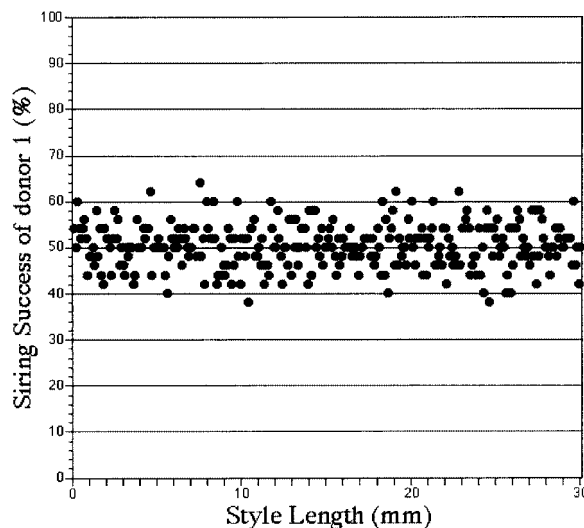


Fig. 1. The outcome of competition in the absence of pollen performance differences. When donors are identical, they sire on average 50% of the seeds produced. Nevertheless, there is considerable variation between individual realizations of this random process; in any particular instance, one of the donors may sire more seeds by chance.

Increasing mean germination time, g , for donor 1 pollen resulted in a reduction in siring success of donor 1 relative to donor 2 (Fig. 2). The decrease in success was greater for larger increases in germination time, and the reduction in siring success was greater in short relative to long styles. Decreasing germination time increased donor 1 siring success relative to the baseline donor.

Increasing mean pollen tube growth rate, r , for donor 1 resulted in an increase in siring success relative to the baseline donor (Fig. 3). The overall increase was greater for larger increases in r . Siring success increased with increasing style length if donor 1 had faster tubes than donor 2. However, over the range of style lengths observed in the field (9–18 mm) and beyond, the effect levelled off. Decreasing r resulted in a decrease in siring success. Again the effect was greater with a larger change in the mean growth rate, and varied with style length only over shorter style lengths.

Doubling the number of pollen grains of donor 1 deposited on the stigma from 50 to 100 substantially increased the siring success of that donor with respect to donor 2 (which still only had 50 grains deposited). Additional increases to 150 and 200 pollen grains further increased the siring success, but at a slower rate. Increasing pollen deposition from 50 to 200 grains increased paternity from 50% to 80%. There was no change in any of these results with increasing style length (Fig. 4a). Increasing the overall number of pollen grains competing, without changing the ratio of pollen from donor 1 to donor 2, increased the advantage of donor 1 beyond that observed for lower pollen loads (Fig. 4b,c). In these cases, the shape of the relationship between siring success of donor 1 and style length remained unchanged with the exception of large pollen loads (200:200) and large growth

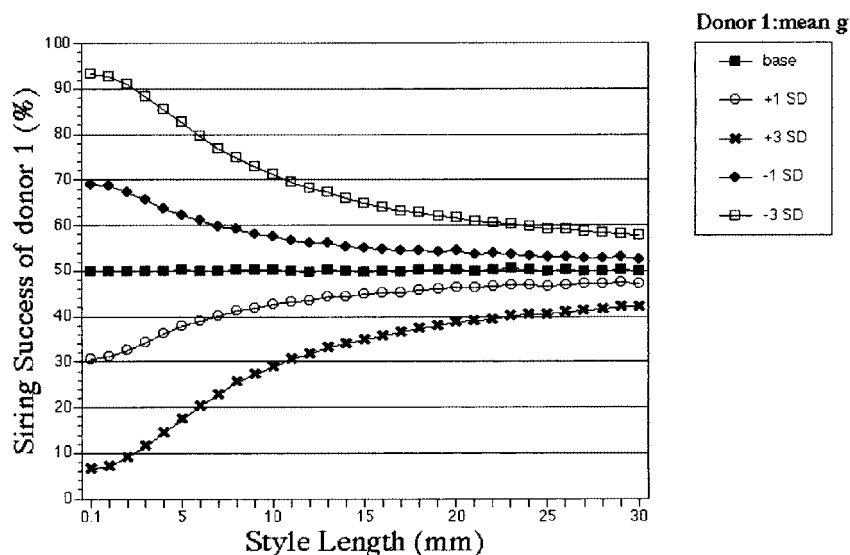


Fig. 2. Effect of changes in mean germination time on paternity of competing donors. Mean siring success (% seeds sired) of donor 1 against female style length for the baseline scenario (both donors are equal) and for cases where mean germination times for donor 1 are higher and lower than for the average donor (donor 2) by either 1 or 3 standard deviations.

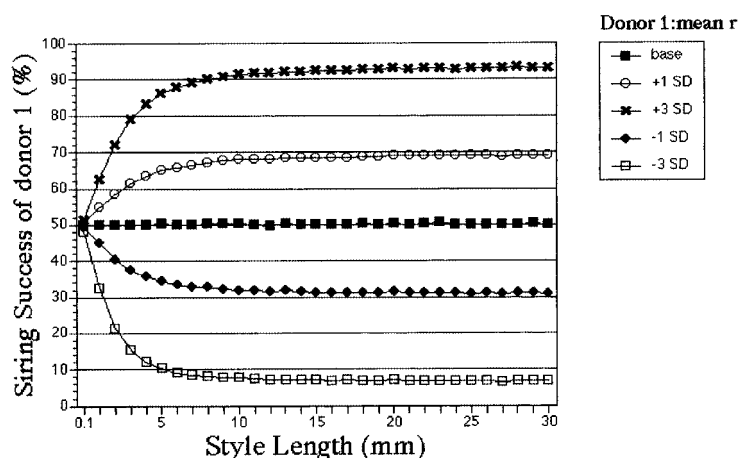


Fig. 3. The siring success of relatively fast and slow pollen donors. Mean siring success (% seeds sired) of donor 1 against female style length for the baseline scenario (both donors are equal) and for cases where mean pollen tube growth rates for donor 1 are higher and lower than for the average donor (donor 2) by either 1 or 3 standard deviations.

rate advantages for donor 1 (+3). Under these conditions, the siring success of donor 1 asymptotes at 100% (Fig. 4c).

Increasing or decreasing the variation in the mean germination time or the mean growth rate of donor 1 altered the siring success of donor 1 if the mean values for the two donors also differed. Increasing the variation of r or g reduced the impact of changing the mean in all cases (Fig. 5a,b show the effect of doubling the standard deviation). If the mean of g was relatively large for donor 1, then higher variation in germination time made the loss in paternity less extreme (Fig. 5a). Decreasing the mean germination time relative to the baseline resulted in less of an improvement in siring success when the variation was high (Fig. 5a). These results were mirrored by the results for changing r . If the mean of r was low, decreasing the siring success of donor 1, then higher variation in tube growth rate reduced the effect (Fig. 5b). If mean r was high, so that siring success was high, increasing the variation removed some of the advantage (Fig. 5b). The effect of altering the variation in g was most noticeable at short style lengths and declined for longer styles, being minimal for style lengths observed in the field. Conversely, altering the variation in r had little effect at short style lengths, but led to sustained changes in siring success for longer styles.

We assessed how the relationship between pollen performance parameters (germination rate and pollen tube growth rate) affected siring success of donor 1 (Fig. 6a). Increasing r increased siring success, but predominantly in longer styles, while increasing g decreased siring success overall, but with most effect for short styles. Combining the two effects resulted in an extreme variation in paternity over style lengths, with the germination time dominating siring success at short style lengths and the tube growth rate at longer style lengths. When donor 1 had shorter germination time and slower growth rates than donor 2, germination effects again dominated for short styles and growth rates in long styles (Fig. 6b).

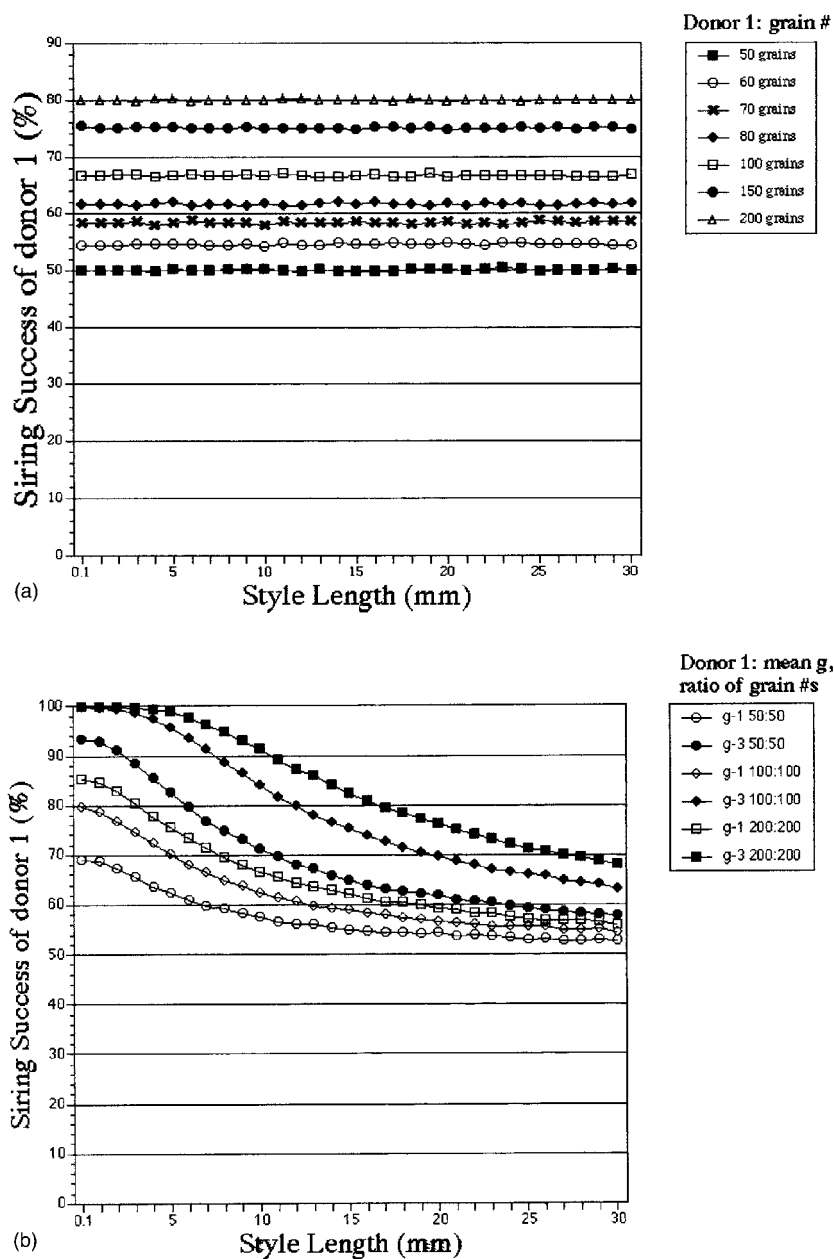
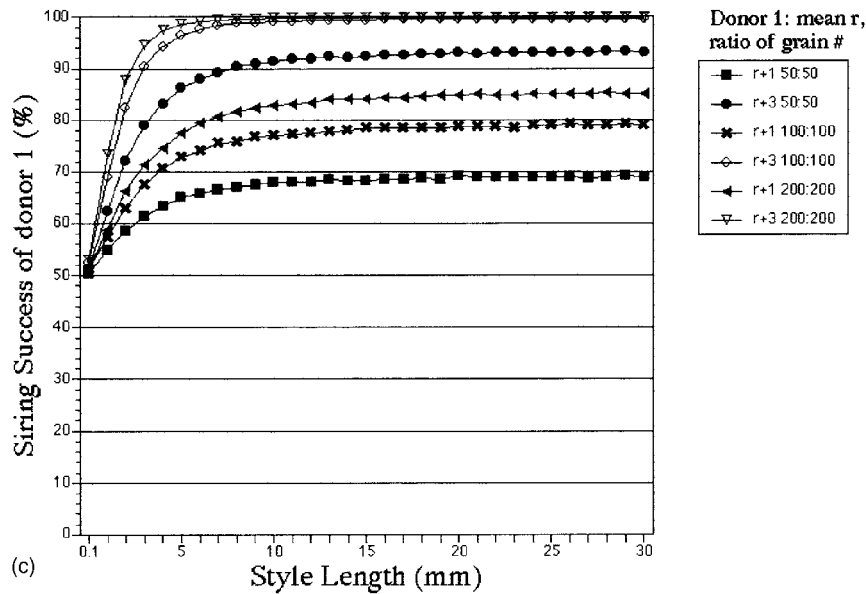


Fig. 4. Mean siring success (% seeds sired) of donor 1 against female style length for the baseline scenario (both donors are equal) and for cases where (a) donor 1 only has a higher number of pollen grains deposited on the stigma, (b) where the mean germination time for donor 1 is lower than for donor 2 by 1 or 3 standard deviations and both donors have the same number of pollen grains deposited on the style, and (c) where the mean growth rate of donor 1 is higher than that of donor 2 by 1 or 3 standard deviations and both donors have the same number of pollen grains deposited on the style.



DISCUSSION

The relationship between style length and siring success

The results of this model suggest that, in contrast to earlier predictions, the relationship between style length and the siring success of a pollen donor with superior pollen performance is rarely a positive linear relationship. The results from the default runs (Fig. 3) indicate that, across a range of relatively short styles (< 9 mm), the percentage of seeds sired by a donor with superior pollen tube growth rate should increase with increasing style length in *Clarkia unguiculata*, but only up to a point. The relationship between a superior donor's siring success and style length reached an asymptote in all runs when there was a difference in mean growth rate between the two competing donors.

Moreover, improvements in pollen germination rate of one donor relative to another completely reversed the expected pattern between siring success and style length. If donor 1 had a faster pollen germination rate (i.e. shorter g), then the siring success of donor 1, while greater than that of donor 2 overall, actually decreased with increasing style length (Fig. 2). This decreasing pattern in siring success is probably due to a decrease in the importance of fast pollen germination for siring success as the style length increases.

Discussions of the influence of style length on filtering ability of pollen tubes have generally assumed that there is a linear relationship between the two variables (e.g. Mulcahy and Mulcahy, 1975). A model by Mulcahy (1983) found that filtering ability, as indicated by average tube growth rate of successful pollen tubes, increased as style length increased. Our results agree qualitatively with this work, but we explicitly investigated the form of the relationship and showed that the increase in filtering ability is non-linear and, in fact, saturates at longer style lengths.

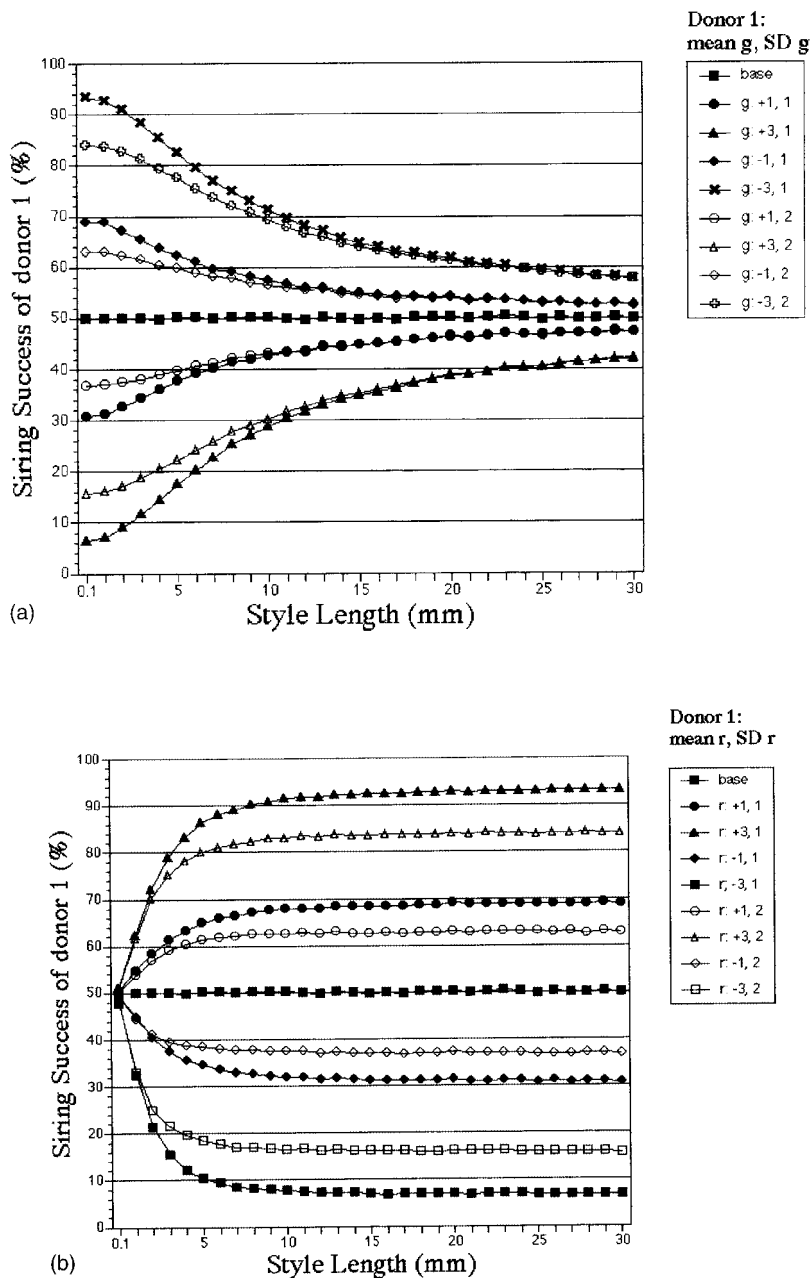


Fig. 5. Mean siring success (% seeds sired) of donor 1 against female style length for cases where (a) mean germination times for donor 1 are higher and lower than those of donor 2 by either 1 or 3 standard deviations and the variation of germination times for donor 1 is the same or doubled (compare with Fig. 2), and (b) mean pollen tube growth rates for donor 1 are higher and lower than those of donor 2 by either 1 or 3 standard deviations and the variation of pollen tube growth rates for donor 1 is the same or doubled (compare with Fig. 3.).

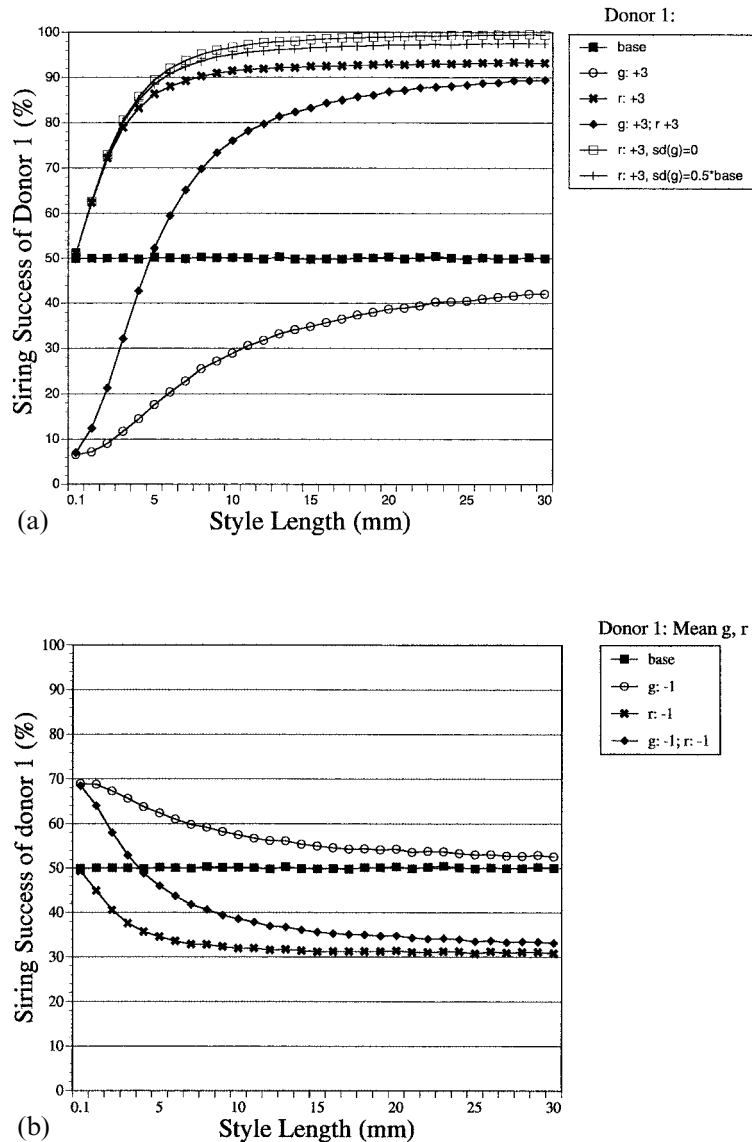


Fig. 6. Trade-offs in pollen performance parameters. Mean siring success (% seeds sired) of donor 1 against female style length for cases where (a) pollen from donor 1 has a longer mean germination time but a faster mean pollen tube growth rate than the average donor, and (b) pollen from donor 1 has a shorter mean germination time but a slower mean pollen tube growth rate than the average donor.

Our results are surprising for two reasons. They clearly indicate that filtering ability of a style is not expected to depend on its length across a range of longer style lengths. In *Clarkia*, we expect no change in filtering ability across the range of style lengths found in natural populations. The implication is that it cannot be assumed for all angiosperm

species that longer styles benefit pollen recipients by more effectively filtering out slower and potentially lower quality pollen. Moreover, our results could not have been predicted from a simple understanding of any single measure of pollen performance. Variation among and within individuals in their pollen performance variables may have profound effects on the form of the relationship between style length and filtering ability.

Sexual selection and pollen recipient traits

Style length has the potential to influence both male reproductive success, by influencing the strength of selection on pollen performance, and female reproductive success, by influencing the ability of pistils to filter out inferior potential sires (Lankinen and Skogsmyr, 2001). It has been suggested that gametophytic competition is an effective filter preventing ovule fertilization by genetically inferior pollen donors because the pollen performance of a donor is correlated with the vigour of offspring sired by that donor (Miller and Schonhorst, 1968; Tanksley *et al.*, 1981; Pedersen *et al.*, 1987; Winsor *et al.*, 1987; Evans *et al.*, 1988; Hormaza and Herrero, 1992; Stephenson *et al.*, 1992; Ottaviano and Sari Gorla, 1993; Quesada *et al.*, 1993; Touraev *et al.*, 1995; Johannsson and Stephenson, 1997). The ubiquity of such a correlation is controversial. There is even some evidence to support an alternative mechanism for increased vigour due simply to environmental effects (Havens and Delph, 1996; Delph *et al.*, 1998). However, if pollen performance and offspring vigour are correlated, then female reproductive success measured as the vigour of seeds and seedlings produced should improve with improvement in her ability to prevent slow-growing pollen tubes from fertilizing her ovules.

In the absence of any other evolutionary forces, we might expect selection due to variation in filtering ability to be directional selection for longer styles. The increase in donor 1 siring success with increasing style length when donor 1 has a relatively fast tube growth rate is equivalent to an increase in filtering ability and should result in selection for longer styles. However, this selection would only favour longer styles up to the point at which the filtering ability asymptotes, including an asymptote level of 100%.

The evolution of style length in outcrossing plants has almost certainly been influenced by multiple selective pressures. The traditional view is that style length has evolved in response to selection for optimal stigma positioning where the stigma will receive the maximum amount of either outcross or self-pollen from pollinators (Darwin, 1877; Grant and Grant, 1965; Stebbins, 1970). Empirical studies support the assertion that selection favours style lengths that place the stigma in a position relative to the corolla and anthers that minimize pollen limitation (Galen and Stanton, 1989; Wolfe and Barrett, 1989; Murcia, 1990; Young and Stanton, 1990; Monteiro *et al.*, 1991; Campbell *et al.*, 1994; Arroyo and Dafni, 1995; Conner *et al.*, 1995; but see Conner and Sterling, 1995) and/or decrease the amount of self-pollen received relative to outcross pollen (Webb and Lloyd, 1986; Holtsford and Ellstrand, 1992; Motton and Antonovics, 1992; Barrett *et al.*, 2000). In contrast, selection on style length due to filtering ability should be directional selection for longer styles, at least for species with variation among donors in pollen tube growth rate. Based on the siring success patterns created by this model, we suggest that style length may evolve in response to simultaneous and potentially conflicting selective forces due to stigma positioning and variation in offspring quality as a result of gametophytic competition. The style length most favoured by selection should simultaneously maximize the probability that the stigma will receive a surplus of pollen and minimize the proportion of ovules that are

fertilized by slow-growing pollen tubes. Rather than plants simply evolving the longest style possible, different species should evolve style lengths that represent an optimum that will be influenced by species-specific pollen performance parameters. These parameters include variation in pollen tube growth rate among donors, among-donor variation in germination rate, the relationship between pollen performance and offspring quality, the frequency of limiting, intermediate and large pollen loads and the morphology of pollinators visiting the plants. Variation among and within species in these factors influencing selective pressures on style length could potentially explain both intra- and inter-specific variation in style length.

The range of style lengths of field populations of *C. unguiculata* are consistent with the pattern expected if selection for filtering ability has increased style length up to the length at which the siring success of faster growing donors asymptotes. Style lengths range from 9 to 18 mm with a mean of 14 mm based on data collected on a single population of *C. unguiculata* in Santa Barbara county, California. In runs with between-donor differences in tube growth rate values (Fig. 3), filtering ability did not increase with increasing style lengths above 10 mm. The range of style lengths in field populations may thus reflect selection for maximum filtering ability and optimal pollen deposition.

Some angiosperm taxa demonstrate the equivalent of extreme variation in style length as a result of elongate stigmas. In these species, such as members of the family *Caryophyllaceae*, the style is receptive to pollen deposition and germination along the majority of its length. In our model, this situation is equivalent to style length, L , also having a mean and variance. We predict that, in taxa with elongate stigmas, the filtering ability of a style will not be as closely related to style length as it is in species with stigmas only at the style tip. Regardless of pollen performance, any pollen grain deposited at the base of an elongate stigma will have an increased chance of fertilizing an ovule relative to any pollen grain deposited at the tip of the elongate stigma. Because the location of deposition of any particular pollen grain is assumed to be randomly determined, there should be a reduced benefit in terms of siring success for those donors that on average produce pollen that germinates quicker or grows more quickly. Thus, we predict that, in taxa with elongate stigmas, the importance of style length in determining both male and female reproductive success will be diminished.

The influence of pollen performance parameters on the relationship between style length and filtering ability

Variation in siring success with style length is a property of differences in the mean and variation in both of the pollen performance measures. Changes in mean values for tube growth rate and germination time resulted in changes in the y-intercept and the asymptote of the line for donor 1 siring success versus style length. Donors with faster growing tubes will enjoy a higher siring success, as indicated by the increased magnitude of the asymptote. Similarly, donors with faster germinating pollen will enjoy higher siring success, as indicated by the relatively high y-intercept. Both of these improvements in siring success will signal stronger selection on pollen performance parameters in natural populations.

Variation in the mean germination time is equivalent to variation in the time of arrival of pollen at the stigma. The arrival of pollen over a period of time has the effect of increasing the mean time at which pollen tube growth begins. Different pollen arrival times could also influence between-donor means in germination time if pollen from different donors arrives

at different times. It is difficult to know how often surplus pollen arrives simultaneously compared with over a longer period of time, but in other species surpluses of pollen were deposited only after a series of visits by pollinators (Mulcahy, 1983; Snow, 1986; Spira *et al.*, 1992). The extent to which variation in germination time influences siring success in a particular species should also depend on patterns of stigma receptivity in that species. Longer periods of stigma receptivity are predicted to increase the intensity of competition among grains (Galen *et al.*, 1986) by allowing more grains to germinate within the window of opportunity. The actual number that germinate will depend on variation in the time required to germinate.

The default conditions of the model assume that there is no relationship between pollen germination rate and pollen tube growth rate. However, a correlation between germination time and pollen tube growth rate have been demonstrated in *Viola diversifolia*. Dajoz *et al.* (1993) found that pollen grain aperture number influenced both the speed of germination and pollen tube growth rate; faster germinating pollen grains produced slower growing pollen tubes. Our simulation of this pollen performance trade-off indicated that donor 1 will sire a majority of the seeds per fruit in relatively short (< 5 mm) but not long styles if donor 1 has fast germination and slow tube growth (Fig. 6b). The opposite is true for donors with slow germination and fast tube growth (Fig. 6a). The implication is that, in those species with a negative correlation between germination rate and tube growth rate, most seeds per fruit (in extreme cases 100%) will be sired by different donors in different flowers with short versus long styles. In a population of plants demonstrating a wide variety of style lengths, this type of correlation could account for the maintenance of genetic variation in pollen tube growth rate and germination time.

The results also suggest that selection influencing style length will be stronger in those instances where there is a negative relationship between germination rate and tube growth rate. The slope of siring success as a function of style length is much greater when donor 1 has a relatively fast tube growth rate and a relatively slow germination rate (Fig. 6a) than it is when the two are unrelated (Fig. 3). This suggests that, below the style length at which the line asymptotes, even a small increase in style length will result in a relatively large increase in female reproductive success if faster tubes produce offspring that are more vigorous. Style lengths below the optimum length which now corresponds with the range seen in the field will have greatly reduced filtering abilities when germination rate and tube growth rate are correlated in this way. The degree of correlation is thus an important target of future empirical work.

The siring success of donor 1 was dependent on variation in pollen performance parameters as well as the magnitude of the means for the parameters. Increasing the variation in either r or g decreased the relative advantage or disadvantage associated with any change in mean for those parameters. As indicated by Fig. 5, the magnitude of asymptotes changed for those siring success–style length relationships that had asymptotes. The decrease in asymptote magnitude associated with the increase in tube growth rate variation should represent a decrease in the intensity of selection for faster tube growth rate, all else being equal. Similarly, donors with relatively slow germinating pollen will not experience as severe a disadvantage in siring success when the variation in germination time is higher relative to if it is lower. The style length at which selection for longer styles is expected to relax also appears to be influenced by variation in tube growth rate. Increased variation in tube growth rate decreased the style length at which the relationship between siring success and style length asymptotes (Fig. 5b). Shorter styles might be expected to evolve in species with a

positive relationship between mean tube growth rate and within-donor variation in tube growth rate.

Our model is a simple one and focuses on only two pollen performance parameters (germination time and tube growth rate). We also examined the effects of differences in numbers of competing pollen grains. There are other variables that will undoubtedly play a role in gametophytic competition; although our model does not address them explicitly, it can provide insight into their possible effects by analogy. For example, differences in arrival time of pollen grains will generate outcomes similar to those resulting from differences in germination times of co-arriving grains. Differences in pollen tube attrition, an important component of pollen performance (Cruzan and Barrett, 1996), could also influence the outcome of gametophytic competition. Loss of competing pollen grains at a given style length can be understood by assuming that fewer arrived in the first place, which we addressed here by varying the relative numbers of pollen grains from each sire. However, there are aspects we cannot address with the present model. Gene $\times$ environment effects, whereby some donors may show superior pollen performance under some environmental conditions and inferior pollen performance under other conditions, could also influence paternities (Delph *et al.*, 1997). Future modelling approaches would benefit from including such effects. Our work emphasizes the need for more experimental work measuring variation in pollen performance parameters and the changes in siring success among competing pollen donors across a range of style lengths.

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