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POLLEN-POLLEN AND POLLEN-STYLE INTERACTIONS DURING POLLEN TUBE GROWTH IN ERYTHRONIUM GRANDIFLORUM (LILIACEAE)[1]

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ABSTRACT

Using pairs of pollen donors, I analyzed the growth of pollen tubes growing in different channels of the same style in *Erythronium grandiflorum.* After 24 hr the length of pollen tubes of randomly selected pollen donors was affected by the presence of other donors. The mean pollen tube lengths of donors did not differ when taken across all of the donor pairings, but in individual pairs, pollen from one donor was often significantly longer than pollen from the other donor when tested across several recipients. Pollen tube lengths were also consistently longer for pollen paired with pollen from the same donor than when paired with pollen from other donors, apparently because of mutual stimulation between the pollen populations from the same plant. In a second experiment, the amount of pollen tube attrition after five days of growth of pollen from a donor growing near (within 3 m) the recipient depended upon the source of other pollen growing in the same style. Local pollen experienced more attrition paired with self pollen than when paired with outcross pollen. Pollen from different outcross distances also modified the attrition of local pollen, but local pollen usually outcompeted pollen from greater distances. Since the growth of local pollen was modified depending upon the source of other pollen growing in the same style, it is probable that recipient styles are selectively inhibiting pollen tubes to produce the patterns of pollen tube interaction observed. The results from these two experiments indicate that the amount of attrition for pollen can be dependent on the composition of the pollen pool. Both direct pollen tube interactions and mediation by the stylar tissue appear to affect the growth rate and attrition of pollen in *Erythronium.*

AN IMPLICIT ASSUMPTION in many studies of plant reproductive biology is that patterns found for single-donor pollinations reflect patterns expected under natural pollination conditions. One way in which the normal reproductive process of plants differs from most experimental manipulations is the composition of the stigmatic pollen pool. Animal pollinators deposit pollen from several donors (Thomson and Plowright, 1980; Marshall and Ellstrand, 1985; Thomson and Thomson, 1989). The fertilization success of one donor's pollen may be modified depending on what other pollen is present on the stigma. This could happen because of interactions between pollen types; pollen tubes may germinate and/or grow at different rates, resulting in one donor obtaining the majority of fertilizations, or they may produce substances that inhibit (or facilitate) each other's growth. Stylar control of pollen tube growth when a mixture of pollen from different donors is present could be expressed in two ways: 1) the acceptability for a donor could be exaggerated over the acceptability exhibited after single donor pollinations, or conversely 2) the fertilization success of the individual donors in a pollen mixture could be equalized compared to their performance after single-donor pollinations, so that they all obtain similar numbers of fertilizations. Reported modifications of the fertilization ability of self pollen due to the presence of outcross pollen (e.g., pollen mentor effects [Visser, 1983], or cryptic self-incompatibility [Bateman, 1956; review in Barrett, 1988]) are typically attributed to mediation by the style. In the case of the mentor effect, the style is apparently fooled by compatibility substances produced by the mentor pollen and allows normally incompatible pollen to fertilize ovules. In cryptic self-incompatibility, normally self-compatible pollen does not fertilize as many ovules when outcross pollen is present, presumably because it is not allowed to grow as fast as the nonself

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tubes. Little information exists about the potential for interactions (either direct or mediated by the style) between outcross pollen from different sources.

In this paper I use two-donor pollinations to explore the possible types of pollen interactions that affect the amount of pollen tube attrition (inability to grow to the ovary) of a donor's pollen. I make two measurements of in vivo pollen performance: 1) pollen tube growth rate after 24 hr, and 2) the proportion of pollen tubes not reaching the ovary after all growth has ceased (pollen tube attrition). Previous work indicates that pollen tubes in *E. grandiflorum* begin reaching the ovary after 24 hr, and that there is no additional growth after 72 hr (Cruzan, 1989). I measure the pollen tube growth of pairs of donors growing in the same style, and analyze the data obtained to infer the possible roles of direct pollen tube interactions and mediation by the stylar tissue.

MATERIALS AND METHODS—*Erythronium grandiflorum* Pursh is a common herbaceous perennial in the Rocky Mountains in the western United States and often covers extensive portions of the subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL) at Gothic, Colorado. Plants overwinter as corms, and flowering plants produce two leaves and from one to several flowers soon after snowmelt. Flowers are large, with petals 2 to 3 cm in length, and bear six large anthers in two whorls. Styles vary from 10 to 17 mm in length. The stigma is three-lobed, with the cleft in each lobe continuous with one of the three channels of the style's lumen, which is Y-shaped. Pollen placed on one lobe will grow down the corresponding channel of the style; however, the channels are open to each other throughout the length of the style, and pollen tubes growing in different channels will intermingle in the last few mm at the base of the style. Plants are self-compatible, but often produce fewer seeds after selfing than after crossing (Thomson and Cruzan, in preparation; Cruzan, 1989). Although there are often over 100 pollen tubes present in the stigma, only 20 to 80% of these typically reach the ovary because of pollen tube attrition in the style (the fraction of pollen tubes present in the stigma not reaching the ovary; Cruzan, 1989). Because of stylar attrition of pollen tubes, only a portion of the 30 to 90 ovules present are typically fertilized (unpublished data), and variation in stylar attrition contributes to variation in seed set to a greater extent than ovarian processes (Cruzan, 1989). Most of pollen dispersal is within 5 m; however, pollinators occasionally make longer flights (30 to 100 m) between plants (Thomson and Thomson, 1989).

I analyzed the interactions between pollen loads from different donors growing in the same stylar environment by growing pollen in different channels of the same style. I placed pollen from one donor on one lobe of a recipient stigma and pollinated a second lobe of the same stigma with pollen from a second donor. In order to have a point of reference to identify the two pollinated lobes, I excised the third stigma lobe at the time of pollination. I removed styles and fixed them in 70% ethanol after 24 hr of growth or after pollen tube growth had ceased (see below). I measured pollen tube growth by slitting styles longitudinally and laying them open on a slide. After staining pollen tubes with acidified aniline blue and acetocarmine (Cruzan, 1989), I observed them with a stereoscopic microscope at 50×. Using a fine insect pin to manipulate the pollen tubes, I obtained highly repeatable counts (Cruzan, 1989). Pollen tubes occasionally crossed between the stylar channels, but I was usually able to separate each pollen population into its own channel. I discarded a few of the styles because they had excessive mixing of pollen tubes from the two populations.

Pollen tube growth rate—I grew pollen from pairs of donors in the styles of cut flowers in the lab in order to assess the effect of donor-donor interactions on in vivo pollen tube growth rate. I collected approximately 60 flower buds with their scapes from within 30 m of each other in a single population on 24 June 1985, and placed them into vases filled with water. Buds treated in this way appear to undergo normal anthesis and their pollen tube growth is similar to intact plants (personal observation). From these flower buds I chose four plants to act as pollen donors and used the rest as recipients. I pollinated each of two lobes of the recipient flowers with pollen from one of the four donors in a cross design that included all possible combinations of donors, including donors paired with themselves. I replicated each combination of donors three times using a different recipient flower each time. Twenty-four hr after pollination I fixed styles in 70% ethanol. I analyzed tube length by making serial counts along the length of the style at 1.5 mm intervals. By assuming that pollen tubes ended midway between census points (i.e., tubes not reaching the subsequent census point were assigned a length equal to the midpoint between census points), I was able to calculate a mean pollen tube length for each pollen population (see Cruzan, 1985). Since each style contained two donors, I alternately assigned each donor as being either the focal donor (the one whose pollen tube length was being analyzed) or as the nonfocal donor (the donor potentially affecting the growth of the focal donor) so that both pollen populations in each style were used in both roles. I entered the mean length of each focal donor pollen population as the dependent variable in a two factorial analysis of variance, treating the identity of the focal and nonfocal donors as random factors, and the number of pollen tubes for both the focal and nonfocal donor as covariates, using the GLM procedure of SAS (SAS Institute, 1985). In a separate analysis, I used a modification of the path model used by Mitchell-Olds (1987) to determine the effect of the number of pollen tubes present in the stigma for each donor on the mean pollen tube length of the focal donor using the REG procedure of SAS (SAS Institute, 1985).

Pollen tube attrition and outcrossing distance—In a second experiment I measured the amount of pollen tube attrition in intact plants for combinations of donors from different outcrossing distances in a population at the upper end of the East River Valley near the RMBL. In these crosses, one lobe always received local (within 3 m) outcross pollen, as a standard; the second lobe received pollen from varying distances, henceforth "treatment pollen." I chose six groups of ten two-flowered plants as recipients and local donors with members of a group within 3 m of each other and with at least 10 m between groups of recipients. From each group of these plants, I chose two individuals as pollen donors for the group (local donors) and collected undehisced anthers from those plants. To obtain treatment pollen, I collected undehisced anthers from six groups of five plants, two sites for each distance class in opposite compass directions from the recipients, for distances classes of 30, 100, and 300 m, and stored them in air-tight vials. I collected all of the pollen on the same day to help control for possible pollen age effects. I allowed the pollen to dehisce prior to pollinating recipients and thoroughly mixed the pollen in vials containing more than one donor. For each of the recipient flowers, I applied pollen from one of the local donors to one stigma lobe, and either self pollen, pollen from a local donor (within 3 m), or a pollen mixture from a 30, 100, or 300 m site to a second stigma lobe. I replicated each treatment on both flowers of two recipient plants within each group, using a different distance class site for each of the two plants. Five days after I had made pollinations I fixed the styles in ethanol. This is sufficient time for the growth of pollen tubes in the style to have ceased (Cruzan, 1989). I made pollen tube counts for both populations in the stigma and within 3 mm of the base of the style, above the region where pollen tubes became entangled.

I analyzed data as both raw counts of tubes in the stigma and at the base of the style, and as the portion of pollen tubes present in the stigma that did not reach the base of the style (pollen tube attrition; see Cruzan, 1989) for both pollen populations in each style. Since the pairs of pollen populations growing in the same style were not independent of each other (see below), I analyzed the performance of local standard pollen separately from the treatment pollen (i.e., pollen from self, local, 30, 100, or 300 m). I entered the pollen source (distance class) of the treatment pollen, recipient flower position, and local pollen donor identity as fixed factors, the site as nested within the distance class, and the number of pollen tubes present in the stigma for both local and treatment pollen as covariates in analyses of covariance using the GLM procedure of SAS (SAS Institute, 1985).

RESULTS—*Pollen tube growth rate*—The growth of pollen tubes in the styles of cut flowers of *E. grandiflorum* is not independent of pollen from other sources growing in the same style. After 24 hr the mean length of pollen tubes was 4.09 mm (N = 88, s = 0.84), and the longest tubes had grown approximately three-quarters the length of the style. Although focal donors did not differ in their average pollen tube length, there was a significant interaction effect (Table 1), indicating that the growth rate of a donor's pollen was partly dependent on the other donor present. Part of the interaction was due to the difference between the pollen tube length of donors when paired with themselves compared to being paired with other donors (Table 1). The average pollen tube length for donors paired with themselves (4.37 mm, $s = 0.82$, $N = 24$ styles) was significantly greater than the average pollen tube length when paired with other donors (3.98 mm, $s = 0.84$, $N = 64$ styles; $F_{1/81} = 4.96, P < 0.03$); however, when the effect of self-pairings is removed, the interaction between donors is still significant ($F_{5/50} = 2.06$, $P < 0.04$). The strength of the effect of a second donor on the mean length of a pollen population is partly dependent on the number of pollen tubes present; however, this effect is much stronger for self pairings than it is for nonself pairings (Table 2). The lack of a significant effect for second donors indicates that individual donors did not have consistent

TABLE 1. *An analysis of the effect of interactions between pairs of pollen donors on the number of pollen tubes present and mean tube length after 24 hr in* Erythronium grandiflorum. *All possible combinations of four donors were used in paired pollinations of two donors at a time on separate lobes of the same style. F values for the effect of donor identity (focal donor) and the identity of the other donor present (nonfocal donor) entered as fixed factors, and the number of pollen tubes present in the stigma for each donor entered as covariates are given. The effect of a donor being paired with itself vs. being paired with another donor is also given*

		F values for focal donor	
Source	df	No. of tubes	Mean length of tubes
Focal donor identity	3	3.90*	0.74
Nonfocal donor	3	0.54	0.03
Donor × donor interaction	9	1.20	2.53*
Self vs. nonself	1	–	5.16*
No. of tubes (focal donor)	1	–	0.00
No. of tubes (nonfocal donor)	1	0.03	5.34*

* $P < 0.05$.

effects on the other donors used (i.e., the average growth of all focal donors was not consistently inhibited or facilitated by the presence of a particular nonfocal donor).

The number of pollen tubes present in the stigma varied significantly for individual donors, but was not affected by the presence of pollen from other donors (Table 1).

Pollen tube attrition and outcrossing distance—In mixtures of pollen from two sources placed on the same stigma, the level of pollen tube attrition was dependent on the source of the pollen and upon the presence of pollen from other sources growing in the same style. Local pollen performed better than pollen from the different treatment classes in all cases (Table 3, Fig. 1A, B). There was more pollen tube attrition for self pollinations than for outcross pollinations (Table 3, Fig. 1A), and consequently fewer self pollen tubes reached the base of styles than local outcross pollen tubes (Fig. 1B).

The growth of the local pollen appeared to depend on the distance class of the pollen it was paired with (Table 4). Local pollen paired with self pollen had fewer pollen tubes at the base of styles than did local pollen paired with either the local, 30, or 100 m pollen (Fig. 1B). The number of pollen tubes of the local pollen reaching the base of the style increased with the distance class of the treatment pollen up to 100 m, but decreased at the 300 m distance (Fig. 1B), and this pattern was consistent for both sites at these distance classes (Table 4).

TABLE 2. *The effect of the number of pollen tubes present in the stigma on the length of pollen tubes in* Erythronium grandiflorum. *Standardized partial regression coefficients are given for the number of pollen tubes present in stigmas for both the target and the second donor. Three separate analyses were done: 1) the whole data set (all data), 2) for pairings in which pollen from a donor was paired on the stigma with pollen from the same donor (self pairings), and 3) for pairings involving donors that were not the same (nonself pairings)*

No. of pollen tubes	All data	Self	Nonself
Focal donor	0.058	0.058	0.081
Nonfocal donor	0.244*	0.454*	0.181
Sample size	88	24	64

* $P < 0.05$.

The degree of pollen tube attrition for local pollen showed the same general pattern as the number of pollen tubes reaching the base of the style, but differences between the treatments were not as strong (Table 4, Fig. 1A).

DISCUSSION—The growth rate and amount of pollen tube attrition for pollen from different sources in *Erythronium grandiflorum* depended upon the composition of the pollen pool. Either direct pollen-pollen interactions, or interactions mediated by the style (pollen-style interactions) could be responsible for the patterns found. Changes in the performance of pollen during pollen tube growth due to the presence of pollen from other donors could be detected in several ways: 1) individual donors or classes of pollen may perform consistently better or worse than other donors, 2) the performance of an individual donor or class of pollen may depend on which donor it is paired with, but the ranking of the pair of donors is consistent across recipients, and 3) the ranking for a pair of individual donors or classes of pollen may change for each recipient. For the first two cases the outcome of the competitions could be due to either direct donor-donor interactions or to mediation on the part of the recipient style. In the last case the determination of the competitive outcome can almost certainly be assigned to the recipient, although the exact mechanism (i.e., active inhibition or facilitation vs. differences in the stylar environment) remains obscure without further analysis. Evidence for the first two classes of pollen interactions was seen in this set of experiments.

Reports of pollen interactions during growth in the style typically involve large effects on the fertilization ability of pollen. Pollen mentor effects (Nettancourt, 1977) have been reported between normally self-incompatible pollen and compatible pollen growing in the same style for several species (Visser, 1983; Bertin and

TABLE 3. *The effect of pollen source on pollen tube growth and attrition in* Erythronium grandiflorum. *Pollen from either self (the same plant), a local donor, or pollen from 30, 100, or 300 m away (treatment pollen) was paired with pollen from a local donor in each treatment. The effect of pollen source (distance class), the site for a distance class (site within distance class), local donor identity, flower position, the number of pollen tubes of the local donor in the stigma, and the number of pollen tubes of the treatment donor in the stigma are given as F values from an analysis of covariance using the GLM procedure of SAS (SAS Institute, 1985)*

Source	df	Pollen tube no.		Stylar attrition
		Stigma	Style base	
Pollen source	4	4.17**	4.98**	5.34***
Site (distance)	3	0.42	3.32*	0.84
Local donor	11	3.00**	1.25	0.92
Flower position	1	1.12	1.02	1.47
Source × position	4	0.56	0.52	0.11
Tubes in stigma (local donor)	1	5.82*	0.01	0.33
Tubes in stigma (treatment donor)	1	—	74.07***	0.02

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Sullivan, 1988). In these cases self seed is obtained from a normally self-incompatible species by mixing self pollen with compatible pollen. The converse case has also been reported as cryptic self-incompatibility (Bateman, 1956; Weller and Ornduff, 1977; Bowman, 1987; Thomson and Cruzan, unpublished data). In this type of pollen interaction no self seed is obtained from a normally self-compatible plant when self and outcross pollen are mixed. Interference between self pollen tubes and subsequently applied outcross pollen is also known (Crowe, 1971; Shore and Barrett, 1984), but these observations appear to be due to physical blocking in the style or the ovary rather than chemical interactions. Instances of pollen allelopathy, where pollen from one species effectively kills pollen from another species, have also been reported (Sukada and Jayachandra, 1980; Thomson, Andrews, and Plowright, 1981). Reports of an alteration of the fertilization success of pollen due to an interaction between two sources of compatible pollen are rare. In one study (Kearney, 1932), pollen from a strain of cotton applied to individuals of the same strain had a consistent advantage over pollen from a different strain. The magnitude of the advantage depended upon the degree of mixing of the two pollen types. The number of seeds fertilized by pollen of the two strains was apparently not simply a function of the growth rate ability of each type of pollen, but involved more complicated interactions between the pollen populations. Although Kearney interpreted his results as being due to direct pollen interactions, he did not completely rule out the possibility of mediation by the style. The types of interactions between different classes of compatible pollen found in *E. grandiflorum* are also not simply a function of differential pollen tube growth rates, and the roles of direct pollen interactions and stylar mediation are unclear.

Pollen tube interactions that are not mediated by a recipient (i.e., direct pollen stimulation or inhibition due to the presence of other pollen) have not been reported in the literature. For the mentor pollen interactions described above, the determination of the fertilization success of self pollen can be attributed to the presence of outcross pollen, and to interactions with the recipient style. For mentor effects it has been determined that the success of self pollen in pollen mixtures is due to compatibility substances diffusing out of the compatible pollen. The proximate cause of the mentor effect is the presence of compatible pollen; however, the ultimate success of pollen is determined by the recipient. Direct pollen interactions have been sought during *in vitro* pollen tube growth (Schemske and Fenster, 1983), but were not found. Cryptic self-incompatibility is probably due to stylar depression of self pollen tube growth rates, whereby outcross pollen outcompetes self pollen (Bateman, 1956). Both direct pollen interactions and interactions mediated by the recipient style may be occurring in *Erythronium.* Although one would expect that maternal parents should influence the paternity of their zygotes, there should also be strong selection for pollen characters which confer a competitive advantage during pollen tube growth in the style (Willson and Burley, 1983).

Direct interactions between pollen from different donors might be responsible for the observed greater pollen tube growth rate of pollen paired with pollen from the same donor over the same pollen paired with pollen from another donor. Pollen from a single donor may often make up the majority of the pollen delivered to a stigma, due to pollen carryover schedules

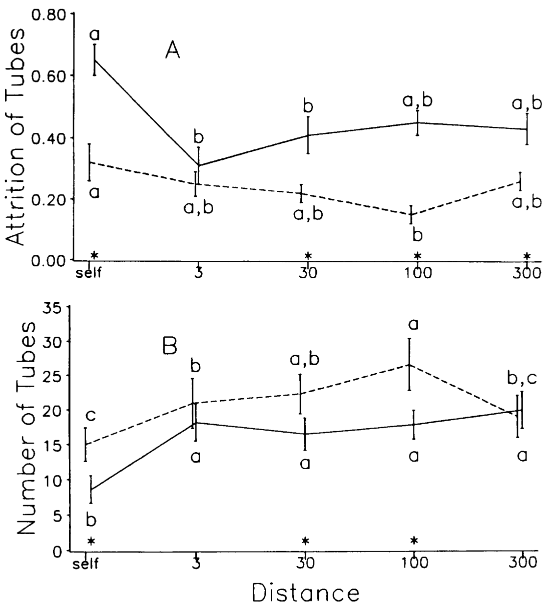

Fig. 1. The effect of outcrossing distance on pollen tube attrition (**A**), and on the number of pollen tubes reaching the base of the style (**B**) for mixtures of pollen local to the recipient and pollen from different distance classes in *Erythronium grandiflorum.* For each mixture, the attrition of local pollen (dashed lines) and pollen from different distance classes (treatment pollen: solid lines) were measured separately in the same style. Means within the same type of line having the same small case letter are not significantly different from each other. A significant ($P < 0.05$) difference in the performance of the local pollen and outcross pollen for a particular distance class (between lines) is indicated by the asterisks.

(Thomson and Plowright, 1980; Thomson and Thomson, 1989). Mutual stimulation of the growth of like pollen could lead to a greater proportion of the fertilizations than would otherwise have been obtained. Density-dependent responses, in which pollen tube growth rates increased with increasing numbers of pollen tubes, have been reported (Cruzan, 1985), but it is not clear whether this effect is dependent on the composition of the pollen pool. For *E. grandiflorum,* mutual stimulation apparently occurred between populations of pollen from the same donor, but not between pollen from different donors (Table 2). Even though the pollen populations were spatially separated, substances secreted from growing pollen tubes could potentially diffuse between the channels of the style. The observed increase in the growth of pollen paired with pollen from the same donor may also have been mediated by the style. Although multiply sired fruits are common for some species (Marshall and Ellstrand, 1986), there may be reduced competition among the ovules within fruits sired by a single donor (Kress, 1981), which may be advantageous for the recipient. In a previous experiment with *E. grandiflorum,* there was no effect on postfertilization processes of the number of donors contributing to the stigmatic pollen load (Cruzan, 1989), so plants do not appear to suffer greater ovule abortion when more than one donor sires the seeds in a fruit. The increase in the growth rate of pollen paired with pollen from the same donor appears likely to be due to mutual stimulation among pollen tubes rather than to mediation by the style.

In most of the combinations of pollen local to the recipient and pollen from different distance classes, local pollen was competitively superior. This advantage could be due to either mediation on the part of the style, or to local pollen being better adapted to local stylar environments; however, the latter could not explain the changes in the attrition of local pollen that depended on the class of treatment pollen present. It is possible that a multilocus compatibility system, which involves stylar in-

TABLE 4. *The effect of the presence of pollen from different sources on the growth of pollen from a local donor growing in the same style of* Erythronium grandiflorum. *Pollen from a local donor was paired with either self pollen, local pollen, or pollen from 30, 100, or 300 m away (treatment pollen). The effect of pollen source (distance class), the site for a distance class (site within distance class), local donor identity, flower position, the number of pollen tubes of the local donor in the stigma, and the number of pollen tubes of the treatment donor in the stigma are given as F values from an analysis of covariance using the GLM procedure of SAS (SAS Institute, 1985)*

Source	df	Pollen tube no.		Stylar attrition
		Stigma	Style base	
Pollen source	4	2.25	3.25*	1.90
Site (distance)	3	0.24	0.43	0.11
Local donor	11	3.61***	1.08	0.60
Flower position	1	1.09	0.01	0.21
Source × position	4	0.42	0.23	0.02
Tubes in stigma (local donor)	1	—	269.52***	0.48
Tubes in stigma (treatment donor)	1	5.82*	0.10	0.10

* $P < 0.05$; *** $P < 0.001$.

hibition of pollen tubes, is functioning in *Erythronium.* A compatibility system that favored pollen local to the recipient might be advantageous to preserve adaptive gene complexes or to insure that the offspring are adapted to the local microsite (Waser et al., 1987). Although the genetic basis of pollen tube attrition in *Erythronium* is not known, it seems clear that stylar inhibition of pollen tubes determines a large portion of the variation in pollen tube attrition. With the possible exception of mutual stimulation of like pollen, selective inhibition by the style is probably responsible for the interactions observed between pollen populations in *Erythronium grandiflorum.*

The patterns of pollen tube performance observed in *Erythronium* indicate that compatibility substances may have been produced by the style after pollination and that their concentration or composition depended on the source of the pollen present. Styles may have been induced to produce substances which selectively inhibited pollen tubes. Classical models of incompatibility assume that inhibition substances are produced in styles during flower maturation, and remain at constant levels throughout anthesis (Nettancourt, 1977; Clarke and Gleeson, 1981). Increased metabolic activity and postpollination production of stylar substances are known (reviews in Nettancourt, 1977, and Ascher, 1984), but it is not known whether, as I postulate for *Erythronium,* the compounds produced after pollination play a role in the compatibility response. Our understanding of pollen-style interactions is far from complete. It may be necessary to allow for inducible compatibility responses in future models of incompatibility.

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