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SELF-STERILITY AND CRYPTIC SELF-FERTILITY IN CAMPSIS RADICANS (BIGNONIACEAE)

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Campsis radicans is almost completely self-sterile following pollinations of pure self-pollen, but when self- and cross-pollen are present in similar amounts, ca. one in six viable seeds is sired by self-pollen. The amount of selfing depends in part on the identity of the cross-pollen donor in the pollen mixture. Selfed seeds are smaller on average than outcrossed seeds. Seed sizes in fruits from mixed (self + cross) pollinations are more variable than those from cross-pollinations, with a larger number of small, often inviable seeds. Most of these small seeds are presumed to be products of selfing. Selfed seeds do not occur in particular positions along the length of the fruit. After 6–7 wk seedling growth, outcrossed seedlings were taller and heavier than selfed seedlings. Selection for the avoidance of selfing is likely to have been important in the evolution of protandry in *Campsis* and perhaps in the large "overproduction" of flowers, which permits selective fruit abortion. We discuss the possible roles of late-acting self-incompatibility and inbreeding depression in preventing fruit production following pure self-pollinations. We propose the term "pistillate sorting" to refer to events taking place in or on a pistil that cause the parentage of viable seeds to be other than a random sample from the pollen deposited on the stigma.

Introduction

Campsis radicans (L.) Seem. (Bignoniaceae) exhibits cryptic self-fertility (BERTIN and SULLIVAN 1988). That is, application of self-pollen alone (pure self-pollination) rarely leads to fruit production, but pollinations with mixtures of self- and cross-pollen usually yield a substantial percentage of viable selfed seed. Similar phenomena have been described in various cultivated species wherein the combination of normally incompatible pollen (self-pollen, or pollen from the same variety) with killed compatible (mentor) pollen sometimes results in the production of viable selfed (or intravarietal) seed (DAYTON 1974; GILISSEN and LINSKENS 1975; HOWLETT et al. 1975; PANDEY 1977; VISSER 1981, 1983). Such studies are usually intended to shed light on the nature of the self-incompatibility (SI) reaction or to overcome self-sterility barriers in plant-breeding programs. Other studies have demonstrated that the hybridization of species can be enhanced by combining compatible pollen with pollen from a second species (STETTLER 1968; KNOX et al. 1972). However, because such studies involve cultivated species, whose reproductive characteristics are often artificially selected, and killed (often irradiated) mentor pollen, the applicability of such studies to natural populations is uncertain.

This study addresses some basic aspects of cryptic self-fertility in *Campsis radicans*, using mixtures of live self- and cross-pollen. We wish to determine the extent and fitness consequences of

cryptic self-fertility in a natural population. If the production of viable selfed seed is great, and if such progeny have low fitness, selection for avoidance of selfing should be great. Our knowledge of fitness consequences of selfing in self-incompatible populations, however, is scant (BARRETT 1988). We also wish to examine the mechanism of self-sterility in *Campsis radicans*, especially the possibility that selfed seeds are poor competitors for maternal resources and/or that zygote fertilization and abortion within a fruit may be position-dependent, reflecting male parentage as in *Raphanus sativus* (MARSHALL and ELLSTRAND 1988).

We address the following specific questions: (1) What is the extent of cryptic self-fertility, and is it affected by identity of the cross-pollen donors? (2) Is variance in seed weight greater in fruits receiving a mixture of self- and cross-pollen than pure cross-pollen? (3) Do selfed and crossed seeds differ in weight within a fruit? (4) Is seed position within a fruit related to weight or paternity? (5) Do selfed and outcrossed seeds differ in rate of germination? (6) Do growth rates of seedlings from selfed and crossed seeds differ?

Material and methods

Campsis radicans is a perennial liana with large, tubular orange flowers visited by hummingbirds and bees (BERTIN 1982; BERTIN and SULLIVAN 1988). Fieldwork took place at Trelease Prairie, 8 km northeast of Urbana, Illinois. The plants grew along a fence separating a cultivated field from a managed prairie.

In early July 1986, two plants, referred to as 10A and 12, each with at least eight accessible inflorescences, were arbitrarily chosen as pollen recipients. Two cross-pollen donors were selected for

each plant: 3A and 46 for plant 10A, and 1 and 3A for plant 12. Except for the combination 10A:46, all other crosses had been previously performed and shown to be highly interfertile. Furthermore, each cross-pollen donor was known to be homozygous for a slow allele at the 6-phosphogluconate dehydrogenase locus, while both recipients were homozygous for a fast allele at the same locus. Pollen mixtures were prepared by emptying the pollen from one anther containing self-pollen and one anther containing cross-pollen into a small petri dish. The pollens were thoroughly mixed and applied to receptive stigmas with toothpicks. The two mixtures for each recipient plant were used on alternate days from July 2 to 12, with all receptive flowers pollinated on a given day. Tags marked each pollinated flower. Fruits were taped on August 8 to prevent dehiscence and collected in November.

We chose randomly eight sound fruits, or fewer when material was insufficient, from each pollination treatment on each recipient. We counted seeds and drew a random sample of at least 120 seeds from each fruit. We weighed each seed to the nearest 0.1 mg and divided the seeds into four quartiles by weight to determine whether seed parentage differed among weight classes. The seeds were germinated in flats of vermiculite in a glasshouse. We checked the seeds at least once a week and removed any that had germinated, storing them in a freezer at −100 C. Then we used electrophoresis to determine the male parentage of each seedling (BERTIN and SULLIVAN 1988).

Effects of seed position on weight and male parentage were evaluated in four to five fruits from each of three donor/recipient combinations. Each fruit was marked into four segments of equal length. We extracted seeds separately from each length quartile and weighed 30 from each quartile in each fruit. These were germinated and assigned male parentage as above.

To compare the variability in seed weight following cross-pollinations with that following mixed (self + cross) pollinations, we used fruits from 1983, 1984, and 1986. Fruits from 1983 and 1984 were from plants 12 and 10A, respectively, and had been sired by pollen from donors 1 and 3A, respectively. The 1986 fruits were from plant 12 (sired by a mixture of pollen from donors 1 and 12) and plant 10A (sired by a mixture of pollen from donors 3A and 10A). Fifty randomly selected seeds from eight fruits on each plant were weighed to the nearest 0.1 mg.

To evaluate performance of progeny derived from selfing and outcrossing, we selected two fruits from plant 12 (with cross-pollen donors 1 and 3A, respectively), and two fruits from plant 10A (with donors 3A and 46). Each fruit resulted from pollination with a 50:50 mixture of self- and cross-pollen in 1986. We weighed at least 60 randomly

selected seeds from each fruit to the nearest 0.1 mg. Four-inch (10-cm) pots were filled with 270 ml Metromix 350 under 130 ml of vermiculite. Seeds were planted in the vermiculite in separate pots and placed in a growth chamber with a 14 h 30 C/10 h 20 C day/night cycle, watered as needed and fertilized every 2 wk. Dates of germination were recorded. We harvested the seedlings from plant 12 35 d after germination and those from plant 10A 42 d after germination. The different growth periods were for scheduling reasons. We measured shoot length and number of nodes bearing leaves at least 10 mm in length, removed a small amount of root tissue for electrophoretic determination of male parentage (selfed or outcrossed), and dried and weighed the above-ground tissue. We also rinsed, dried, and weighed the tap roots.

For all statistical tests involving proportions, the data were transformed by arcsin square root prior to analysis. All reported means were back-transformed.

Results

The mean percentage of selfed seeds among the viable seeds tested in the four treatments was 8%–32%. For individual fruits, the range was 0%–44% (table 1). For plant 12, significantly more selfed seeds were detected when the cross-pollen donor was 1 than when it was 3A ($t = 3.77$, $P = .002$). No significant difference was detected between the two cross-pollen donors to plant 10A ($t = 1.75$, $P = .12$).

Coefficients of variation for seed weight were significantly greater in fruits from pollinations with mixtures of self- and cross-pollen than in those from pollinations with pure cross-pollen (table 2). This greater variation usually reflects a more bimodal distribution of weights of self + cross seeds than the cross seeds, with greater emphasis on the peak

TABLE 1

PROPORTIONS OF VIABLE SEED RESULTING
FROM SELFING IN CAMPSIS FRUITS

	RECIPIENT 10A		RECIPIENT 12	
	Donors 10A/3A	Donors 10A/46	Donors 12/1	Donors 12/3A
	.097(72)	.113(71)	.290(69)	.231(65)
	.125(66)	.120(50)	.435(69)	.091(77)
	.196(51)	.118(17)	.208(72)	.067(75)
	.108(37)	.000(64)	.298(84)	.157(70)
	.143(35)	.091(55)	.225(89)	.139(79)
	.106(66)	.079(63)	.210(171)	.133(75)
	.136(59)	.042(71)	.235(85)	.053(75)
	.140(57)	.169(71)	.229(83)	.217(69)
Mean ...	.143	.083	.320	.142

NOTE.—Each entry is for a different fruit. Numbers of seeds tested are given in parentheses. These data overlap in part those presented in table 6 of BERTIN and SULLIVAN (1988).

TABLE 2

Variation in seed weight in fruits resulting from pollination with mixtures of self- and cross-pollen, and pure cross-pollen

Recipient Plant	POLLEN TREATMENT			
	Self + Cross	Cross	t	P
10A	48.2 ± 1.22	40.7 ± 2.94	2.34	.04
12	43.9 ± 1.78	20.3 ± 0.66	12.45	.00

Note.—Each entry is the mean coefficient of variation for seed weight in eight fruits ± SE. The same cross-donor was used for each recipient plant.

at small seed sizes (fig. 1). Virtually all of these small seeds were inviable, as shown by their inability to germinate (see below).

To compare the weights of viable seeds resulting from self- and cross-fertilization, we compared the percentage of selfed seed with the percentage of outcrossed seeds in the different weight quartiles. Only germinable seeds were considered because the seeds had to germinate before paternity could be assigned by electrophoresis. For most fruits, no germination of seeds in the smallest quartile occurred, and germination of seeds in the second quartile was sometimes also low. Therefore, data for the smallest three quartiles were combined and compared using paired t-tests with data in the largest quartile (table 3). In all treatments the proportion of selfed seeds in the smallest three quartiles was substantially (by a factor of 3–8×) and significantly higher than in the largest quartile.
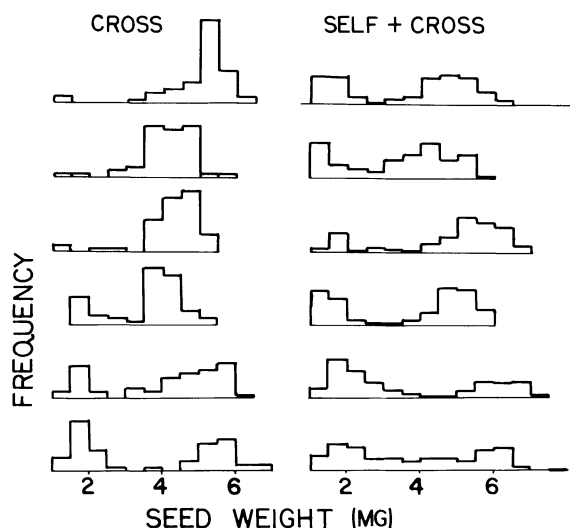

FIG. 1.—Distributions of seed weights in fruits resulting from pollination with loads of pure cross-pollen and mixtures of self- and cross-pollen. The upper six graphs are from plant 12, the lower six from plant 10A. Note the increased fraction of very small seeds in the self + cross fruits in the upper five pairs of graphs.

The position of a seed within a fruit was related to its weight but not to its paternity. Position in fruit (quartile) had a significant effect on average seed weight, as determined by an unreplicated two-way ANOVA for each donor/recipient combination (table 4). Seed weight was low in the most proximal quartile (1) and to a lesser extent in the most distal quartile (4) compared to the middle quartiles. However, no difference was detected in the frequency of selfed seeds among quartiles, as determined by two-way analyses of variance for each donor/recipient combination (table 5).

Date of germination did not differ greatly between seeds resulting from selfing and those from outcrossing. For each fruit the mean time from sowing until emergence was calculated separately for selfed and outcrossed seeds that were germinated to examine incidence of selfing in the four weight quartiles. These means were then compared using a paired comparisons test for each of the four donor/recipient combinations. Date of germination for selfed seeds was slower in three of four cases, but significantly slower in only one (table 6).

We used analysis of covariance to evaluate the effect of pollination treatment (selfing vs. outcrossing) on six measures of offspring performance in the seedling growth experiment: germination date, stem height, number of leaf pairs, root weight, shoot weight, and total weight. In each experiment, seed weight was the covariate. Outcrossed seeds germinated slightly but not significantly more quickly than selfed seeds from each fruit. The number of leaves did not differ between treatments. All other measures of performance were greater for outcrossed than selfed progeny, significantly so in 12 of 16 tests (table 7). Measures of height and weight of selfed seedlings were considerably greater than for outcrossed seedlings: 32%–102% greater for stem height, 19%–87% for shoot weight, 50%–107% for root weight, and 28%–90% for total weight.

Discussion

SELF-FERTILITY AND THE CROSS-POLLEN DONOR

The extent of cryptic self-fertility reported here is similar to that reported earlier, based on a smaller sample of fruits (BERTIN and SULLIVAN 1988). Overall, about one of six germinating seeds in a fruit pollinated with a mixture of self- and cross-pollen was the product of selfing. In the most extreme case, nearly half of the germinating seeds resulted from selfing (table 1). Clearly, one should not take self-sterility following single-donor pollinations as evidence that selfing does not occur in nature (VISSER 1983; BERTIN and SULLIVAN 1988).

The identity of the cross-pollen donor in the self/cross-pollen mixture can influence the percentage of selfed seeds within a fruit. The proportion of

TABLE 3

PROPORTION OF SEED SIRED BY SELF-POLLEN FOLLOWING POLLINATIONS
WITH A MIXTURE OF SELF- AND CROSS-POLLEN

	RECIPIENT 10A				RECIPIENT 12		
Donors 3A + 10A		Donors 46 + 10A		Donors 1 + 12		Donors 3A + 12	
Small	Large	Small	Large	Small	Large	Small	Large
.167(42)	.000(30)	.167(42)	.034(29)	.462(39)	.067(30)	.314(35)	.133(30)
.100(40)	.115(26)	.143(28)	.091(22)	.512(41)	.321(28)	.125(48)	.034(29)
.400(25)	.000(26)	.000(25)	.000(39)	.333(42)	.033(30)	.111(45)	.000(30)
.118(17)	.100(20)	.148(27)	.036(28)	.315(54)	.267(30)	.238(42)	.036(28)
.154(13)	.136(22)	.121(33)	.033(30)	.295(61)	.071(28)	.224(49)	.000(30)
.154(39)	.037(27)	.073(41)	.000(30)	.293(116)	.036(55)	.200(45)	.033(30)
.258(31)	.000(28)	.286(42)	.000(29)	.309(55)	.100(30)	.075(53)	.000(22)
.207(29)	.071(28)	...	...	.296(54)	.103(29)	.307(29)	.100(30)
$\bar{X}$ .188	.035	.113	.015	.350	.110	.192	.024
t	2.82		3.24		6.05		8.86
P	.03		.02		.00		.00

NOTE.—Small seeds are the smallest 75% of the sample; large seeds are the largest 25%. T and P values are for paired comparisons within each donor × recipient combination. Germination of seed from the last fruit in 10A × 46 + 10A was insufficient for analysis.

selfed seeds in fruits of recipient 12 was more than twice as great when the cross-pollen donor was plant 1 than when it was 3A. Such a difference could have several causes. The numbers of pollen grains per anther or their viability could differ among donors, so that ratios of viable self- and cross-pollen grains differed in mixtures involving different donors. Also possible are differences among donors in the growth rate of pollen tubes, ability of tube nuclei to effect fertilization, or ability of progeny to compete for maternal resources. Maternal tissue could also respond differently to pollen of different donors. One consequence of these differences among pollen donors is that the degree of self-pollination in nature may be influenced by the identity of plants that contribute cross-pollen. Differences in the degree of selfing as a function of cross-pollen donor in a self/cross-pollen mixture also occur in chicory (Cichorium intybus, EENINK 1982).

THE MENTOR EFFECT

Despite the demonstration that mentor pollen can overcome barriers to interspecific or intraspecific incompatibility (DAYTON 1974; HOWLETT et al. 1975; STETTLER and GURIES 1976; PANDEY 1977; VISSER 1981; EENINK 1982), the mechanism or mechanisms involved are unclear. One suggestion is that the compatible mentor pollen provides some sort of recognition material that allows the incompatible pollen to penetrate the incompatibility barrier (KNOX et al. 1972; HOWLETT et al. 1975). Another possibility is that the mentor pollen provides a nonspecific promotor, perhaps hormonal, of pollen tube growth (PANDEY 1977; LANE 1984). The latter explanation is unlikely in Campsis because growth of self-pollen tubes is as fast as growth of cross-pollen tubes (BERTIN and SULLIVAN 1988). PANDEY (1977) observed the curious result that adding irradiated incompatible pollen to untreated incompatible pollen initiated some seed production and concluded that the radiation treatment, commonly employed in mentor pollen studies, released some growth-promoting substance. This explanation would not apply to the Campsis results because no pollen was irradiated. A further mode of action of mentor pollen may be to stimulate fruit

TABLE 4

WEIGHTS (mg) OF SEEDS AT DIFFERENT POSITIONS IN FRUITS

Recipient/donors	N	Q1	Q2	Q3	Q4	F
12/12-3A	4	3.0	3.5	3.7	3.4	5.43*
10A/10A-46	5	2.9	3.7	3.6	3.6	5.76*
10A/10A-3A	5	3.1	4.2	4.0	3.5	44.11*

NOTE.—Quartile (Q) 1 is most proximal, quartile 4 is most distal. The reported values are means of means, obtained by taking the mean weights of 30 seeds per quartile per fruit and averaging these over the N fruits. F-values test the significance of position (quartile) effects.
    * $P < .05$.

TABLE 5

PROPORTIONS OF SEED SIRED BY SELF-POLLEN AT DIFFERENT POSITIONS IN FRUITS

Recipient/donors	Q1	Q2	Q3	Q4	F
12/12-3A	.112 (69)	.091 (72)	.051 (76)	.153 (72)	1.02
10A/10A-46	.038 (63)	.068 (70)	.149 (66)	.180 (82)	1.21
10A/10A-3A	.119 (75)	.119 (86)	.013 (82)	.117 (75)	1.57

NOTE.—Quartile (Q) 1 is most proximal, quartile 4 is most distal. The reported values are means of 4–5 fruits. Total numbers of seeds examined are in parentheses. No difference among positions is significant, as determined by a two-way ANOVA for each donor/recipient combination.

production, independent of any effect on pollen tube growth or zygote formation. Fruit production has been observed in *Populus* and *Malus* even when few or no viable seeds occur in the fruit (STETTLER and GURIES 1976; VISSER 1981). When potent, as opposed to irradiated, pollen is added, the presence of additional zygotes that are products of cross-fertilization is likely to further enhance fruit production (VISSER and MARCUCCI 1984). Of the above hypotheses, the provision of recognition material and stimulation of fruit production because of the additional cross-fertilized zygotes are the only two applicable to our results, but we cannot distinguish their relative importance.

CONSEQUENCES OF SELF-FERTILIZATION

Zygotes and seeds resulting from selfing are at a clear disadvantage compared with those produced by outcrossing. Direct evidence for the inferior ability of selfed zygotes to compete for maternal resources is provided by the lower average weights of germinating selfed seeds compared to outcrossed seeds. Circumstantial evidence also suggests that zygotes resulting from self-fertilization abort at higher rates than those resulting from cross-fertilization. This is reflected in the greater variability in weight among seeds in fruits sired by mixed self- + cross-pollen than among those in fruits sired by pure cross-pollen. This increased variability results largely from the increased incidence of small seeds (fig. 1). Seeds less than 2–3 mg

rarely germinate, show little cotyledon development, and presumably abort following embryo death and/or inadequate maternal provisioning. Similarly, in *Pyrus* spp., VISSER and MARCUCCI (1984) observed fewer viable seeds as the proportion of self-pollen in mixtures of self- and cross-pollen increased. If we assume that the additional small seeds in *Campsis* fruits are products of selfing and consider also that the numbers of inviable seeds smaller

TABLE 6

GERMINATION RATE (mean days from sowing) OF SEEDS RESULTING FROM SELF- AND CROSS-FERTILIZATION

Recipient/ donors	N	Self	Cross	t	P
10A/10A-3A ..	8	48.6	47.6	.85	.43
10A/10A-46 ..	7	46.7	41.2	2.02	.09
12/12-1	8	24.2	25.3	1.17	.28
12/12-3A	8	36.6	33.7	3.06	.02

NOTE.—Each reported value is a mean of means from N fruits in each treatment. The t and P values are from paired comparisons tests on means for individual fruits.

TABLE 7

ADJUSTED MEANS FOR ANALYSES OF COVARIANCE COMPARING SELFED AND OUTCROSS PROGENY FROM FOUR FRUITS

	ADJUSTED MEANS		
CHARACTER AND FRUIT	Selfed	Outcrossed	F
Days to germination:			
12-1-4	16.9	15.4	.32
12-1-9	20.9	15.7	3.01
10A-1-3	18.5	17.6	.73
10A-9-7	19.1	18.4	.33
Stem height (mm):			
12-1-4	185	373	9.61*
12-1-9	255	457	6.56*
10A-1-3	207	274	2.35
10A-9-7	202	338	4.56*
Number of nodes:			
12-1-4	10.3	10.3	.00
12-1-9	10.7	10.2	.44
10A-1-3	7.8	8.0	.24
10A-9-7	8.0	8.6	1.59
Shoot weight (g):			
12-1-4	.84	1.57	16.99*
12-1-9	1.04	1.40	3.58
10A-1-3	.62	.74	3.54
10A-9-7	.59	.85	5.09*
Root weight (g):			
12-1-4	.14	.29	16.67*
12-1-9	.22	.29	5.73*
10A-1-3	.13	.21	13.53*
10A-9-7	.12	.18	7.18*
Total weight (g):			
12-1-4	.98	1.86	18.24*
12-1-9	1.26	1.69	4.02
10A-1-3	.75	.96	8.10*
10A-9-7	.71	1.04	6.05*

NOTE.—Numbers of selfed and outcrossed seeds = 4,36 for 12-1-4, 6,27 for 12-1-9, 11,32 for 10A-1-3, and 7,43 for 10A-9-7.

* Denotes F values significant at P = .05.

than 1.0 mg may have been similarly increased, and that some number of nongerminating larger seeds result from selfing, the incidence of self-fertilization was probably higher than the 8%–32% calculated from germinating seeds.

We found no evidence indicating that the slower growth and presumably greater abortion of selfed seeds resulted from fertilization of seeds at different positions in the fruit by self- and cross-pollen. Seeds at different positions in the fruit differ in average weight but not in paternity. Therefore, the weight differences may reflect the smaller amount of room at either end of the pod where the fruit is constricted, or different relationships with nutrient sources, but not the spatial position of fertilizations. Consequently, the position-dependent mechanism of selective abortion described for *Raphanus sativus* (MARSHALL and ELLSTRAND 1988) does not operate in *C. radicans*. Instead, it seems that fertilization within the fruit is approximately random with respect to position, and the differential growth and abortion of selfed seeds reflects their genetic makeup. This interpretation is consistent with the similar growth rates of self- and cross-pollen tubes in vivo (BERTIN and SULLIVAN 1988). If self- and cross-pollen tubes arrive in the ovary at about the same time, it seems unlikely that they would sort themselves among ovules by position.

The inferior vigor of selfed progeny is also evident in the performance of seedlings. While the long life span makes it impractical to estimate actual seedling fitness in *Campsis*, the 19%–107% differences in seedling height and weight after only 35–42 d of growth in a noncompetitive environment suggest that selfed progeny would be at a profound disadvantage under natural conditions.

Strong selection should exist for characteristics minimizing self-pollination and self-fertilization. One trait likely to have a strong influence on self-pollination is the marked protandry within flowers. This trait reduces the degree of within-flower self-pollination to virtually zero at some sites, because all pollen is removed before the stigma is exposed (BERTIN 1982). A reduction of geitonogamous pollinations could be achieved if phenology of flowers on an individual plant were synchronized. While some synchrony was observed at the population level (BERTIN 1982), we have not examined this at the level of the individual plant. A self-incompatibility system would also minimize the deleterious effects of inbreeding depression, but it is not clear that such a system exists. Even if it does exist, it is obviously ineffective at preventing self-fertilizations in mixed pollinations. Consequently, a final barrier to the production of offspring by selfing is the much higher rate of abortion of fruits sired by a mixture of self- and cross-pollen than of fruits sired by cross-pollen (BERTIN and SULLIVAN 1988). The high flower to fruit ratios in *C. radicans* (10:1–50:1,

BERTIN 1982) may well be an adaptation to permit such selective fruit abortion relative to paternity, thereby raising the average level of offspring fitness (DARWIN 1877; STEPHENSON 1981).

MECHANISM OF SELF-STERILITY

The ability of self-pollen tubes to grow to full length as rapidly as outcross tubes (BERTIN and SULLIVAN 1988) indicates that no stigmatic or stylar SI exists in *C. radicans*. While some workers would presumably interpret this as evidence that SI is absent, we think that restricting SI to stigmatic and stylar phenomena is arbitrary and follow SEAVEY and BAWA (1986) in recognizing the possibility of late-acting SI.

The self-sterility observed in *C. radicans* must, therefore, result either from late-acting SI or regular and profound inbreeding depression at the zygotic stage. In the latter case, the large number of dead or feeble zygotes in a self-pollinated ovary would presumably create a weak sink for maternal resources, eventually leading to abortion of the ovary. Because of the scarcity of empirical evidence of self-sterility caused by inbreeding depression and the incompatibility of such an explanation with theoretical models of genetic load, SEAVEY and BAWA (1986) consider inbreeding depression to be an unlikely cause of self-sterility. However, we cannot yet rule out this explanation for *Campsis*.

While distinguishing postzygotic SI from inbreeding depression may prove difficult (SEAVEY and BAWA 1986; BARRETT 1988), SEAVEY and BAWA (1986) suggest four possible approaches. Data on two of these were obtained in the present study. First, blockage of embryos at various stages of development suggests inbreeding, while uniform failure suggests SI. The former seems to occur in *Campsis* as evidenced by an apparent arrest of development and inviability of many selfed seeds in the range of 1–3 mg, while others attain greater weights and are viable. However, this spectrum of selfed seed sizes could at least partly result from stimulatory effects of the additional outcrossed seeds present. Second, expression of inbreeding effects could continue into the time of seedling growth, as they do in *Campsis*. An SI system would not affect seedling growth, and an SI interpretation of the above results requires a combination of partial SI with inbreeding depression occurring in those selfed seeds evading the SI barrier.

We cannot make a clear choice between the two explanations of self-sterility in *Campsis*, and in fact it may be impossible to do so, both practically and conceptually. While most selective processes within the pistil have traditionally been explained in terms of SI or some variant (cross-incompatibility, partial SI, post-zygotic SI, pseudo SI, cryptic SI), it is by no means clear that classical or even modified views of SI explain all such pistillate phenomena.

Recent discussions of mate choice (STEPHENSON and BERTIN 1983; WILLSON and BURLEY 1983; MARSHALL and ELLSTRAND 1988), distance-dependent outcrossing success (WASER and PRICE 1983), sibling competition (KRESS 1981), inclusive fitness (WESTOBY and RICE 1982), nonrandom ovule abortion (LEE and BAZZAZ 1986), and inbreeding at the seed zygote stage (SEAVEY and BAWA 1986) all are testimony to the realization of the impossibility or undesirability of attempting to stretch the notion of SI beyond its already elastic limits. We suggest, therefore, the term "pistillate sorting" to refer to those processes taking place in or on a pistil that cause the parentage of viable seeds to be other than a random sample from the pollen population on the stigma. This term does not imply a mechanism for the sorting, nor the relative effects of maternal, paternal, and zygotic influences, which sometimes are impossible to distinguish. Rather, it is an inclusive and nonspecific term to describe certain events in pistils until more detailed work elucidates a specific physiological and genetic basis.

Acknowledgments

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