

COMPETITION-DEPENDENT ABSCISSION OF SELF-POLLINATED FLOWERS OF *PHORMIUM TENAX* (AGAVACEAE): A SECOND ACTION OF SELF-INCOMPATIBILITY AT THE WHOLE FLOWER LEVEL?

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Abstract.—The relative success of fruit from paired self- and cross-pollinations was examined in *Phormium tenax* when the contrasted pollinations were separated by different distances on the same and different inflorescences. We determined whether the retention of selfed fruits differed from that of crossed fruits and whether it depended on the level of competition with crossed fruit, the number of seeds per fruit, and/or the presence of earlier developing fruit. We found that the success of selfed fruits is determined by the degree of competition with crossed fruits and may be an expression of self-incompatibility. Competition-dependence of the abscission of selfed flowers has not been documented previously. It is parallel to cryptic self-incompatibility in which individual self-pollen grains are not as successful as cross-pollen when competing on the same pistil. The competition-dependent abscission of self-pollinations considered here, however, operates at the level of whole flowers. The phenomenon of competition-dependent abscission of selfed flowers in *P. tenax* also has implications for the measurement and interpretation of self-incompatibility in other species. Self-incompatibility is a quantitative phenomenon. The facultative success of selfing shows that the effective strength of self-incompatibility can be highly susceptible to the conditions of competition under which it is measured. The competition-dependent abscission of selfed flowers allows a high level of outcrossing to be achieved while it assures seed set when pollinations are scarce. Several other causes of intermediate selfing frequencies can also be explained by this “best-of-both-worlds” hypothesis.

Key words.—Agavaceae, competition, cross-pollination, flower abscission, *Phormium tenax*, pseudocompatibility, self-incompatibility.

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Flowering plants have a variety of mechanisms that encourage cross-fertilization. One of the most common is self-incompatibility, “the inability of a fertile hermaphrodite seed plant to produce zygotes after self-pollination” (Lundqvist, 1964). The incompatibility barrier to the growth of self-pollen is often incomplete, to varying degrees. A reduced success of self-pollinations has been described in various contexts. A greater “fertilizing power of pollen from another variety or individual” was described as prepotency by Darwin (1876 p. 391 on). For most of this century, the limited successes of partially incompatible pollinations have been known as pseudofertility or pseudocompatibility. The weakest form of self-incompatibility, cryptic self-incompatibility occurs when there is equal success of

self- and cross-pollinations performed on different flowers but self-pollen is less successful in competition with cross-pollen on the same stigmas (Bateman, 1956; Bowman, 1987; Weller and Ornduff, 1989).

Many plants, particularly self-incompatible species, regularly produce more flowers than fruit (Goodwin, 1978; Lloyd et al., 1980; Sutherland, 1986). In recent years, it has been suggested that plants may utilize the reduction in fruit numbers to preferentially abort fruits and seeds of parentages that produce inferior progeny, thereby improving the average quality of seed genotypes (Janzen, 1977; Willson and Burley, 1983; Lee, 1984). The near ubiquity of hybrid vigor (Knight, 1799; Darwin, 1876; Charlesworth and Charlesworth, 1987) suggests that in many species the largest dis-

crepancies among the progenies of different male parents are likely to be those from selfed and outcrossed fruit. Although the preferential abortion of selfed progeny (as they will be called henceforth, for simplicity) was first suggested over a century ago by Darwin (1876 pp. 398–400), it has received relatively little experimental investigation in flowering plants (Brink and Cooper, 1947; Stephenson and Winsor, 1986; Craig and Stewart, 1988; Krebs and Hancock, 1990). The extent to which the differential abortion of selfed progeny contributes to a reduction in the frequency of plants derived from self-fertilization is poorly known. The differential abortion may occur at the level of single seeds or that of whole fruit. A discriminatory abortion of selfed flowers could be caused by reduced numbers or genotype qualities (inbreeding depression) of their seeds, or by a delay in the time of fertilization if a weak incompatibility mechanism is operating (Willson and Burley, 1983; Stephenson and Bertin, 1983; Stephenson et al., 1988; Krebs and Hancock, 1990). Another possibility, introduced below, is that the preferential abortion of selfed flowers is the result of reduced hormonal signals from more slowly growing incompatible pollen tubes. In this case, preferential abortion would be a direct result of self-incompatibility acting at the level of whole flowers.

In experimental pollinations of the New Zealand flax, *Phormium tenax* J.R. et G. Forst., Craig and Stewart (1988) found in their first trial (1982–1983) that only outcrossed fruit developed. In a second trial (1984–1985), a few selfed fruit developed. Craig and Stewart proposed that the self-incompatibility barrier in *P. tenax* is not strict and that there is a preferential retention of outcrossed seeds when resources are limiting.

Here we examine the comparative success of fruit from paired self- and cross-pollinations in *P. tenax* when the contrasted pollinations are at different distances from each other on the same and different inflorescences. We sought to determine whether selfed fruit are differentially aborted and whether this depends on the level of resource competition with crossed fruit (measured as the morphological distance be-

tween selfed and crossed fruit), the number of seeds per fruit, and/or the presence of earlier-developing fruit.

MATERIALS AND METHODS

Phormium tenax is a large, bird-pollinated agave-like plant. Its reproductive biology was described by Craig and Stewart (1988). *Phormium tenax* propagates vegetatively by ramets attached by underground rhizomes. Each ramet is semelparous and produces a large (up to 3 m high) paniculate inflorescence (Fig. 1). These inflorescences consist of a main branch that supports 8 to 15 alternating or subopposite secondary peduncles. Peduncles in turn produce up to seven tertiary branches, to which are attached one to four clusters, each containing one to five flowers. Thus the proximity of flowers and fruits increases as they share the same unit in successive levels of a hierarchy: inflorescence, secondary branch, tertiary branch, and terminal cluster. The total number of flowers produced by an inflorescence is typically between 250 and 700. Flowers are hermaphroditic, dichogamous (protandrous), and herkogamous (during the female phase the style curves forward, and the stamens remain behind it). The opening of flowers is staggered in the whole inflorescence and among flowers on the same peduncle. Usually, flowers of the peduncles located in the middle and bottom of an inflorescence open first, and the flowers of the uppermost peduncles open last. The development of the tertiary branches and their terminal clusters is cymose; terminal flowers in the tertiaries and clusters open first.

All field experiments were performed on 11 genetic individuals (genets) from a population growing at the Field Station of the University of Canterbury at Cass, New Zealand, during the 1988–1989 flowering season (Nov.–Jan.). The chosen plants had a minimum of three flowering ramets. In every plant (genet, identified morphologically as all ramets within a tight cohesive clump), all treatments were performed on three inflorescences (on three ramets) that were in approximately the same stage of flowering development. During the experiment, all inflorescences were kept enclosed in individual net bags. After pollination, plastic tubes that extended beyond the corollas were at-

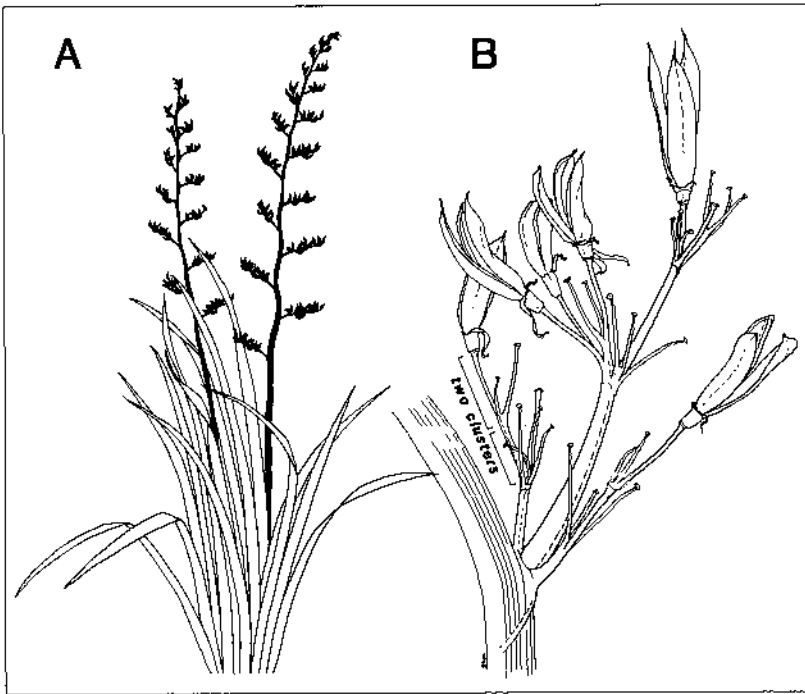


FIG. 1. A. An individual of *Phormium tenax* with two inflorescences. Every inflorescence produces up to 15 secondary peduncles. B. A secondary peduncle with four tertiary branches. A tertiary branch consists of several clusters (two or three in the examples shown), each with a few florets.

tached to the flowers to prevent the stigmas from losing pollen or being damaged by movement of the bags.

Patterns of Fruit Set

The three selected inflorescences on each plant were randomly assigned to receive only crossed or selfed pollinations, or a mixture of the two types on different flowers. In the selfed inflorescences, following anthesis the flowers were emasculated and later, when the stigmas were visibly receptive (Craig and Stewart, 1988), a generous load of pollen from flowers of the same inflorescence was deposited on the stigmas. In the crossed inflorescences, comparable pollen loads from other plants were deposited. In the mixed inflorescences the flowers were also emasculated; of every pair of flowers in female phase, one was randomly chosen to receive pollen from another plant and the other one was pollinated with pollen from flowers of the same inflorescence. Every time a flower was hand pollinated, its pedicel and corolla were marked with permanent paint. Pedi-

cells remain attached to the tertiary branches until the inflorescence collapses, even when the flowers or fruits have already fallen. Similarly, corollas remain attached to the fruits throughout development. The marks on the pedicels allowed us to distinguish, at the end of the experiment, the treatments that had been applied to the retained and aborted fruits. Most fallen flowers and fruits were collected in the net bags. Hence by looking at the marks on the corollas of the fallen flowers, we could monitor how soon after pollination fruits were aborted. We allowed 20 days for fruits to develop, and at the end of this time, the percentages of retained fruit were recorded for each inflorescence.

Cross Versus Self-Pollination.—For inflorescences that received mixed pollinations, the percentage of retention of crossed-pollinated fruits was compared to that of self-pollinated fruits. In addition, 61 fruits resulting from the last pollination performed in six of these inflorescences were collected. *P. tenax* produces capsules with

three different kinds of seeds. One kind is large, contains a developed embryo, and is assumed to be viable. The other two types are minute and nonviable (Craig and Stewart, 1988). For the fruit samples the number of viable seeds, the average seed weight, and the percentage of viable seeds per crossed fruit were compared with those of selfed fruits.

Flower Thinning.—Six of the 11 plants were randomly selected for thinning. In each inflorescence, for every pair of flowers that were pollinated, six nonpollinated flowers were cut off. Thus, only approximately 25% of the original number of flowers growing in the inflorescence were allowed to remain. In the other five plants, we pollinated all flowers that we could. The levels of pollination in the inflorescences of these five plants varied from 55 to 80% of all the flowers ($\bar{x} = 67\%$). At the end of the experiment, we examined the differences in the percentages of retention on the thinned and unthinned plants and the interaction between parentage (crossed, selfed, and mixed) and thinning.

Position of Flowers in the Inflorescence.—Every inflorescence was divided into four parts with as nearly as possible equal numbers of peduncles. The first group included the peduncles of the lowest quarter of the inflorescence, the second the peduncles of the second lowest quarter, etc. We compared the percentages of retention among the quarters, the effect of parentage (crossed, selfed, mixed), and its interaction with position.

Timing of Pollination.—We visited the inflorescences to conduct pollinations every two or three days, depending on the number of flowers opening in the inflorescences. To recognize their date of pollination, we marked the pedicels with different colors for every date of pollination. The percentages of retention among sequential pollinations (first, second, etc., for each inflorescence) were examined. The effect of parentage and its interaction with timing were also taken into account in the analyses.

Closeness of Competition.—Fruits that start developing near to one or several earlier fruits may experience stronger competition for maternal resources than fruits that develop in the absence of previous fruits.

This competition could also be affected by the distance that separates earlier from recent fruits. To examine the effects of presence of earlier fruits and distance on fruit abscission, fruit set after selfing and crossing was compared with and without prior fruits at various distances (levels of inflorescence organization). Fruit set was compared when flowers belonged to a) the same whole inflorescence, b) the same secondary peduncle, c) the same tertiary, and d) the same cluster. For each one of these hierarchical levels, each pollinated flower was categorized as to whether it was retained or aborted, selfed or crossed, and whether there was or was not an earlier developing fruit. While the data were classified at each of these hierarchical levels, the percent retention for each of the four categories (selfed or crossed and prior or no prior fruit) was calculated for the whole inflorescence to avoid pseudoreplication. The analyses were performed on mixed inflorescences and on the separate selfed and crossed inflorescences as well. In several inflorescences, the number of pollinated flowers for some of the four categories was not large enough to perform some of the analyses; consequently those analyses included fewer than 11 plants.

The results of cross- and self-pollination in separate and mixed inflorescences, the results of seed set in mixed inflorescences, and the results of the comparisons of pollination order were summed up in a Self-compatibility Index (percentage retention after selfing divided by percentage retention after crossing). The Self-compatibility Index corrects for erratic failures of pollination from causes other than incompatibility (Lloyd, 1968). If there were any incompatible cross-pollinations, the index would overestimate the level of compatibility.

Because some of the above treatments may not be independent, a more complex analysis was performed in which fruit set was examined taking into account the effects of parentage, thinning, and position. An overall analysis with the effects of all treatments was not possible because of lack of degrees of freedom.

All analyses were performed using the SAS statistical package (SAS Institute Inc., 1988). Analyses of variance that involved comparison of percentages were done on the arc-

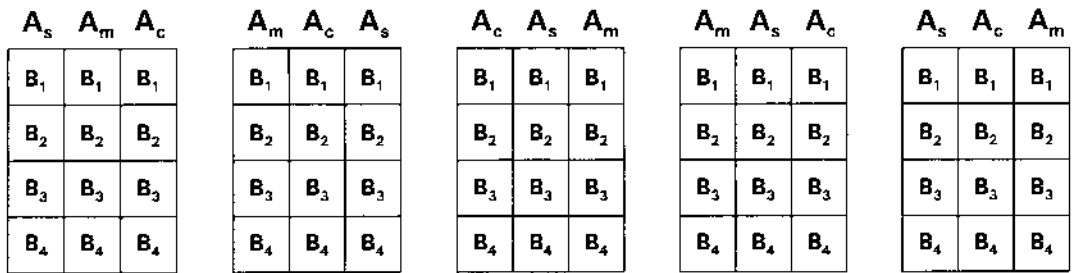


FIG. 2. Assignment of parentage to inflorescences (whole plots) grouped by genets, and position to quarters within inflorescence (subplots). The symbols A_c, A_s, and A_m denote selfed, crossed, or mixed parentage. B₁, B₂, B₃, and B₄ denote quarters within inflorescences.

sin transformed percentages to satisfy the assumptions of normality of ANOVA. Because the proportions may be based on different numbers of pollinated flowers and this also affects the variance of sample proportions, the analyses were performed with weighted least squares, using the number of pollinated flowers as the weight for each percentage (Neter and Wasserman, 1974).

Many of our analyses involved a combination of split-plot and repeated measures designs. In general, split-plot designs have a treatment structure with at least two factors (e.g., parentage and position), each factor has its own level of blocking (e.g., quarters within the inflorescences, inflorescences within a plant), and more than one size of experimental unit. The larger experimental units are called whole plots (e.g., inflorescences), and the smaller experimental units are called subplots (e.g., quarters within inflorescence). Each experimental unit has its own design structure, and because there is more than one size of experimental unit, there is more than one error term used in the analysis (Milliken and Johnson, 1984; Fig. 2). The experimental design of both whole plots and subplots consist of a one-way treatment structure in a randomized complete block design, though in some of our analyses the whole plots are arranged in a completely randomized design. Repeated measures designs differ from split-plot designs in that the levels of one or more factors cannot be randomly assigned (e.g., position of quarters within inflorescence cannot be randomized).

Repeated measures designs were analyzed as split-plot designs. This is valid because most of our analyses were nonsignif-

icant and, if the *F*-ratio is nonsignificant with a split-plot design, it will also be nonsignificant with repeated measures [repeated measures is a more conservative test than split-plot designs; (Greenhouse and Geisser, 1959, in Milliken and Johnson, 1984 pp. 359–360)]. When analyses with split-plot designs were significant, we also followed Greenhouse and Geisser's suggestion of using Box's Conservative Correction, which radically decreases the degrees of freedom associated with the *F*-tests. All of our repeated measures designs were either nonsignificant with a split-plot analysis, or significant using Box's Conservative Correction to the split-plot analysis.

RESULTS

Patterns of Fruit Set

Abortion of fruits usually occurred soon after pollination. About 75% of the fruits abscised one or two days after pollination. The rest fell up to 10 days later. The overall percentages of retention did not differ significantly for either crossed, selfed or mixed inflorescences (one way ANOVA, randomized complete block design, Table 1).

Cross- versus Self-Pollination.—Among inflorescences that received only cross- or self-pollinations, the frequencies of fruit set were not significantly different (Table 1). In contrast, on the inflorescences that received mixed pollinations, the percentage of crossed-pollinated fruits that were retained was significantly higher than the percentage of self-pollinated fruits retained on both unthinned and thinned inflorescences (paired *t*-tests, unthinned inflorescences, *df* = 4, *P* < 0.001; thinned inflorescences *df* = 5, *P*

TABLE 1. Average per cent fruit set and the numbers and sizes of seeds after self- and cross-pollinations (untransformed means).

| | Selfed | Crossed | Mixed | Self-com- patibility index | |
|---|--------|---------|-------|----------------------------------|--------------|
| A. Percent fruit set | | | | | |
| Total | 41.2 | 43.5 | 40.1 | — | $P = 0.76$ |
| Separate inflorescences | 41.2 | 43.5 | | 0.95 | $P = 0.50$ |
| Mixed inflorescences | 30.3 | 49.0 | | 0.62 | $P < 0.0001$ |
| B. Number of seeds per fruit (mixed inflorescences) | 88.8 | 75.4 | | 1.18 | $P = 0.59$ |
| C. Percent viable seeds (mixed inflorescences) | 69.9 | 59.5 | | 1.17 | $P = 0.51$ |
| D. Average weight viable seeds (mg) (mixed inflorescences) | 3.82 | 4.02 | | 0.95 | $P = 0.73$ |

< 0.001 ; Table 1). The comparison of the percentages of viable (large) seeds in selfed and crossed fruits showed no significant differences between them (paired t -test). There were no significant differences either in the number of seeds per fruit or average seed weight between the seeds produced by crossed and selfed fruits (paired t -test of the square root transformed number; paired t -test of the logarithm transformed weights).

Flower Thinning. — The percentages of retention of fruit were slightly, but not significantly higher on the thinned inflorescences than on the unthinned inflorescences ($N = 11$, $P = 0.10$; Table 2). The interaction of parentage with thinning was not significant either. Because the plants were not blocked for thinning, the analyses were performed using a two-way ANOVA, split-plot design with the whole plots in a completely randomized design structure.

Position of Flowers in the Inflorescence. — In the unthinned inflorescences, there were significant differences in the percentages of retention on different quarters of the inflorescence. The peduncles at the top of the inflorescence retained a higher proportion of fruits than the ones in lower positions (two-way ANOVA, split-plot design with Box's Conservative Correction position effect, $P < 0.01$, Table 2). In the thinned inflorescences also, the peduncles of the top quarter had a higher percentage of retention but it was not significantly different from the percentages of retention on the other quarters (two-way ANOVA, split-plot design, Table 2). There were no significant effects of parentage, parentage by position interaction, thinning by position interaction, or parentage, thinning, and position interaction (three-way ANOVA split-split-plot design).

TABLE 2. Patterns of fruit set (% retention) resulting from thinning, position, and timing differences (untransformed mean percentages).

| A. Effects of Thinning | | | | | |
|------------------------------|------------------------|------|----------------------|---------|------------|
| Type of inflorescence | Unthinned pollinations | | Thinned pollinations | | |
| Crossed only | 41.9 | | 44.9 | | |
| Selfed only | 39.4 | | 42.7 | | |
| Mixed | 28.3 | | 49.2 | | |
| Total | 36.7 | | 45.8 | | $P = 0.10$ |
| B. Position on Inflorescence | | | | | |
| Quarter of infl. | 1 (bottom) | 2 | 3 | 4 (top) | |
| Unthinned infls. | 29.7 | 32.7 | 38.2 | 61.7 | $P < 0.01$ |
| Thinned infls. | 43.3 | 44.4 | 42.4 | 60.2 | $P = 0.61$ |
| C. Timing of Pollination | | | | | |
| Order of pollination | 1 | 2 | 3 | | |
| Unthinned infls. | 30.6 | 33.3 | 39.1 | | $P = 0.76$ |
| Thinned infls. | 47.7 | 45.7 | — | | $P = 0.74$ |

TABLE 3. Variation in the percentages of fruit set from self- and cross-pollinations (untransformed means) and the relative selfing success (Self-compatibility Index) associated with the inflorescence level and the presence or absence of previous fruit at that level.

| Level examined for previous fruit | No prior fruit | With prior fruit | Significance | | |
|---|---------------------------|------------------|--------------|----------|---------------|
| | | | Parentage | Priority | Par. × prior. |
| A. Mixed Inflorescences | | | | | |
| Inflorescence | 41/56 × 0.73 ¹ | 30/44 = 0.68 | NS | NS | NS |
| Secondary branch | 33/50 = 0.64 | 29/43 = 0.67 | *** | *** | NS |
| Tertiary branch | 33/46 = 0.71 | 19/49 = 0.39 | *** | ** | NS |
| Terminal cluster | 41/54 = 0.76 | 5/64 = 0.08 | *** | *** | *** |
| B. Separate Selfed and Crossed Inflorescences | | | | | |
| Inflorescence | 42/33 = 1.27 | 40/45 = 0.89 | | | |
| Secondary branch | 42/43 = 0.98 | 44/37 = 1.27 | | | |
| Tertiary branch | 38/41 = 0.92 | 39/39 = 0.99 | | All NS | |
| Terminal cluster | 43/45 = 0.96 | 42/38 = 1.08 | | | |

¹ Each fraction represents the percentage of fruit set after self-pollination divided by the percentage of fruit set after cross-pollination, which equals the Self-compatibility Index.

** = $P < 0.05$; *** = $P < 0.005$.

Timing of Pollination.—The percentages of retention did not differ significantly among sequential pollinations in either thinned or unthinned inflorescences (two-way ANOVA, split-plot designs, Table 2). Also in these ANOVAs, neither the parentage effect (differences among crossed, selfed and mixed inflorescences) nor the interaction of parentage with timing of pollination was significant.

In mixed inflorescences, the percentage of retention of crossed fruits was higher than the percentage of retention of selfed fruits, both with and without previous fruit set and at all hierarchical levels (whole inflorescences, secondary peduncles, tertiaries and clusters; Table 3). With the exception of the comparisons at the level of whole inflorescences, these differences between selfed and crossed fruits were significant. The higher success after crossing as compared to selfing was more pronounced in the tertiaries and terminal clusters when prior fruits were present—that is when the competition between fruits was more intense. For tertiaries, the difference between the percentages of success after selfing and crossing was 30% (49 minus 19%) with fruits present but only 14% with no previous fruits (Table 3). At the level of clusters, the reduction of fruit set of selfs compared to crosses was 60% with prior fruits present but only 14% without prior fruit (the interaction of parentage × priority was significant, $P < 0.001$). A two-way ANOVA, randomized block de-

sign, was performed for every hierarchical level. The experimental unit for both treatments, parentage and priority, was inflorescence. The error term consists of the priority·parentage·block interaction + the priority·block + parentage·block interaction. This experimental design (two-way ANOVA in randomized blocks) is described in Neter and Wasserman, 1974 p. 731).

For the separate crossed and selfed inflorescences, there was no significant difference in percent retention between selfed and crossed flowers, nor between flowers with prior fruits versus those without, nor was there any interaction between these factors at any hierarchical level (two-way ANOVA's split-plot designs, Table 3; the experimental unit for parentage was plant, and for priority was inflorescence).

The Self-compatibility Index was always equal to or above 0.9 when there was one source of pollen per inflorescence (the index for full self-compatibility is one; Table 3). On average, self-pollinations succeeded 0.95 times as frequently as cross-pollinations (Table 1). For mixed inflorescences, however, the index decreased to 0.62 (Table 1). The Self-compatibility Indices were higher when there was one source of pollen on an inflorescence, with or without prior fruits and at every hierarchical level (Table 3, comparison of mixed and separate inflorescences). The Self-compatibility Index was particularly low for clusters with prior fruits

in mixed inflorescences. While the relative selfing success for this hierarchical level was very close to 1.0 in separate inflorescences, it was very low (8%) in mixed inflorescences (Table 3).

The relative Self/Cross indices for number of seeds per fruit, percentage of large seeds, and average seed weight did not differ significantly from 1.0 (Table 1). That is, the seeds of selfed and crossed fruits were equal in number and size.

DISCUSSION

Quantitative Measures of Self-Compatibility

Botanists often make a qualitative distinction between self-incompatibility and self-compatibility, treating them as though they were discrete classes. Self-incompatibility is frequently incomplete, however (Darwin, 1876; Stout, 1920; East, 1934), even to the extent in the case of cryptic self-incompatibility of being undetectable when self- and cross-pollen are placed on different flowers. A quantitative scale of reactions, such as the Self-compatibility Index we have used is required to measure grades of incomplete self-compatibility. The Self-compatibility Indices reported here are based on fruit numbers, and in principle could include post-zygotic effects of inbreeding depression on the number of selfed fruits.

Previously Craig and Stewart (1988) and Craig (1989) reported the results of self-pollinations of *P. tenax* over three flowering seasons near Auckland (ca. 800 km northeast of our Cass population). In the first year, only outcrossed fruit developed, giving a Self-compatibility Index of zero. In the second year, 1 of 44 selfed flowers and 10 of 22 crossed flowers produced fruit, giving a Self-compatibility Index of $0.0227/0.455 = 0.05$. The difference in the success of selfs and crosses that year is significant ($\chi^2 = 19.90$, $df = 1$, $P < 0.01$, our calculation). In the third season, $6/75 = 0.08$ of self-pollinated flowers produced fruit, but no crosses were reported (Craig, 1989). The best estimate of self-compatibility in the Auckland population is obtained by taking the average over the three seasons of the success rates on selfing and dividing that by the success rate on crossing for the second

season (the only figure given). The overall Self-compatibility Index is $0.0342/0.455 = 0.08$, at the lower extreme of the range of figures we obtained (0.08–1.27, Table 3).

Modifying Lundqvist's (1964) definition of self-incompatibility (see the introduction) to take partial incompatibility into account, we define self-incompatibility as the partial or complete inability of a functionally bisexual seed plant to produce zygotes after self-pollination. The experiments of Craig and Stewart (1988) and Craig (1989) showed the Auckland population of *P. tenax* to be self-incompatible with only infrequent pseudocompatibility. Our data from self- and cross-pollinations conducted on separate inflorescences, in which the two pollination types do not compete with each other at all, show an insignificant reduction in the success of selfed flowers compared with crossed flowers. Based on those experiments alone, our Cass population would be judged to be self-compatible. In the mixed inflorescences, however, the selfed flowers have a significantly reduced ability to set fruit. On the latter results, the population is considered to be self-incompatible with a high frequency of pseudocompatibility. The strength of self-incompatibility increases as the pairs of selfed and crossed flowers come together more closely on an inflorescence. The facultative success of selfing shows that the effective strength of self-incompatibility can be highly susceptible to the conditions of competition under which it is measured, as well as to the better-studied physical conditions. In many species, the success of self-pollinated fruits in pollinations done without heed to the level of competition among developing fruit may give an overestimate of the likelihood of producing self-fertilized seeds under natural conditions.

Thinning and Closeness of Competition

In many angiosperm species, the frequency of fruit that are retained depends on the position a flower occupies, the number of competing fruit, or the sequence of their initiation (Stephenson, 1981). In natural populations of *P. tenax*, there is a strong nonrandom distribution of fruit on an inflorescence; fruit tend to be evenly distributed over an inflorescence, with usually only

1–3 per tertiary branch and 0–1 (occasionally 2) per ultimate cluster (pers. obs.). The pattern of natural fruit set, as well as the less frequent retention of experimentally selfed flowers in close proximity to crossed flowers and the effects of previous fruit, suggest that there is competition among potential fruit for limited resources. The effects of competition on the retention of selfed flowers is most apparent in the same tertiary branch and particularly in the same ultimate cluster. Our results indicate that the degree of competition among flowers for retention depends on the proximity of the flowers to each other. We observed, however, that the frequency of retained flowers was unaffected by the prior thinning of potential fruit or by the sequence of pollination. These results may have arisen because the pairs of flowers to be crossed and selfed, although chosen to be as close as possible, were often available only on different tertiary or even secondary branches. This could have reduced the effective level of competition among the paired flowers and caused the lack of effects of the number of pollinated flowers and the sequence of pollination. Two previously described patterns show partial parallels with the abscission of selfed flowers in *P. tenax*. In *Campsis radicans* the number of prior pollinations in an inflorescence influences the relative likelihood that cross-pollinations from different pollen donors yield fruit (Bertin, 1985). Here too, the relative success of different pollinations seems to depend on the level of competition for resources. In *Espeletia schultzii*, the proportion of filled achenes is lower in crosses between individuals that are close together in natural populations than in crosses between individuals that are farther apart, but the difference is apparent only later in the season when fruit set is generally lower and resources are more limited. The conditional seed set may be caused by self-incompatibility (Sobrevila, 1988).

We describe the Cass population of *P. tenax* as having “competition-dependent abscission of selfed flowers.” Competition-dependence of the abscission of selfed flowers has not been documented previously, to our knowledge, although it has been suggested by Darwin (1876), Stephenson and Winsor (1986), and Craig and Stewart

(1988). It is parallel to cryptic self-incompatibility, in which *individual self-pollen grains* are as successful as cross-pollen when put on separate flowers but not when competing on the same pistil (Bateman, 1956). The competition-dependent abscission of self-pollinations in *P. tenax*, however, operates at the level of *whole flowers*. Consequently, it is more amenable to experimentation because it does not require the identification of progeny by genetic markers.

There are several possible physiological causes of the increased abscission of selfed flowers in the proximity of crossed flowers. It might be a post-fertilization phenomenon based solely on the relative genetic *qualities of seeds* from outcrossed and selfed flowers (Willson and Burley, 1983), or on a *reduced number of seeds* in selfed fruit (Stephenson and Winsor, 1986). A third possibility is that an incomplete incompatibility barrier could cause a *delay in the initiation* of selfed fruit. In a number of species, it is known that later-initiated fruit are more likely to be aborted (Stephenson et al., 1988). Finally, the maternal parent might react to *hormonal signals from the growing pollen tubes* themselves and preferentially retain fruit from pistils with many actively growing tubes. In self-incompatible species, such pistils are more likely to have been cross-pollinated. The latter mechanism, unlike the other three differential fruit abortion factors, operates before fertilization as a direct effect of the incompatibility reaction, at the level of whole pistils rather than single pollen tubes. The four potential sources of discrimination against selfed fruit are not mutually exclusive and they could operate together.

There is some circumstantial evidence that the differential fruit set in *P. tenax* is caused by events acting before fertilization. First, most aborted flowers fall within one or two days after pollination. Taking into account the fact that flower fall occurs only after an abscission layer has operated, the fate of selfed flowers must usually be decided some time prior to 24–48 hours after pollination. There seems to be little time for the decision to be based on differential embryo growth. In the most closely studied case of seed abortion after selfing, *Medicago*

sativa, seeds collapsed between two and four days after pollination (Brink and Cooper, 1947). Second, the selfed fruits that are matured are not inferior to those from cross-pollinations in seed size or number. It is unlikely that differences in the post-fertilization growth of seeds are sufficiently decisive to cause a massive preferential abortion of whole selfed flowers after one to two days, and yet produce no further sign of differential behavior of selfed and crossed seeds after another 18–19 days of development. The failure of seed development results in defective seeds of varying weights as a result of the expression of recessive lethals in maize and other species, as well as in interspecific hybrids and in natural abortion (Brink and Cooper, 1947; Crumacker, 1967; Wiens et al., 1987).

The increased abscission of selfed flowers in *P. tenax* could be caused by an inhibition of self-pollen tubes, which reduces the amount of growth substances in the pistil and thereby lowers the probability of fruit set. In many self-incompatibility species, or even cryptically self-compatible species, the pollen tubes grow down the style more slowly after self-pollination (Stout, 1920; Arasu, 1968; Weller and Ornduff, 1989). The deposition and growth of pollen without fertilization (e.g., with dead or interspecific pollen) has repeatedly been shown to prevent the abscission of pistils and to initiate fruit growth (Nitsch, 1971; Goodwin, 1978). Both auxins and gibberellins increase in styles after pollination and can promote the parthenocarpic development of fruit (Lund, 1956; Martin et al., 1982). These experiments demonstrate that pollen hormones have an effect on fruit development that could differ between self- and cross-fertilizations. Further work is required to determine with certainty whether the preferential abortion of selfed flowers in *P. tenax* is an expression of self-incompatibility acting before fertilization or is caused by the abortion of selfed seeds after fertilization. *Phormium tenax* has hollow styles and so pollen tube growth rates in the style are unlikely to be different after self- and cross-pollination (Nettancourt, 1977). Direct observations of cleared ovules of selfed and crossed flowers at the time of abscission should establish whether the ovules of abscised flowers are

fertilized, as expected on the seed abortion hypothesis, or not, as predicted on the self-incompatibility hypothesis. The importance of the failure of pollen tube stimulation in reducing the seed set from incompatible pollinations could be assessed by determining the number of fertilized ovules in abscised flowers. Pollination chase experiments, with cross-pollen following self-pollen after a delay, might also establish whether self- and cross-pollinations result in equal complements of fertilized ovules, as only the seed abortion hypothesis predicts.

The Adaptive Significance of Competition-Dependent Selfing

Bowman (1987) has suggested that cryptic self-incompatibility, in which the failure of individual self-pollen tubes is dependent on competition within a pistil, allows maximum outcrossing when pollination conditions permit and yet provides an assurance of full seed set when cross-pollination is inadequate. On this hypothesis, cryptic self-incompatibility gives a means of adjusting the level of selfing to pollination conditions and provides the maximum advantages possible from both selfing and outcrossing.

This "best-of-both-worlds" hypothesis can be extended to the competition-dependent success of selfed flowers in *P. tenax* and to several other phenomena. In a fully self-compatible population, "delayed" selfing in a flower, which occurs only after opportunities for crossing have passed (Lloyd, 1987; Schoen and Brown, submitted), also maximizes both the frequency of outcrossing and the seed set in uncertain pollination conditions. If self-pollen is deposited before cross-pollen or simultaneously, a mixture of self- and cross-pollination provides the dual advantages of more assured seed set and greater outcrossing if there is a weak self-incompatibility barrier that causes the success of self-pollen to depend on the degree of competition among seeds or fruit.

The joint maximization of seed set and outcrossing associated with competition-dependent selfing can also explain the frequent occurrence of species with incomplete self-incompatibility barriers. It has previously been difficult to explain how pseudocompatibility could be selected if the bar-

rier operates with the same strength under different pollinating conditions. When cross-pollination is not adequate for seed set, a uniformly operating partial self-incompatibility system would allow some selfing although that would not be advantageous. On the other hand, when cross-pollination is inadequate for a full seed set, a partial self-incompatibility barrier would restrict selfing, which would again be detrimental. The best-of-both-worlds hypothesis, however, can readily explain pseudocompatibility; if associated with a competitive advantage of outcrossed pollen, pseudocompatibility simultaneously encourages the maximum level of outcrossing and provides a full seed set.

On this interpretation, pseudocompatibility and the other mechanisms of competition-dependent selfing success should not be regarded as providing selection for intermediate frequencies of selfing as such. Instead they represent a means of jointly selecting for the otherwise opposing targets of frequent outcrossing and high seed set.

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