THE INHERITANCE OF UNILATERAL INCOMPATIBILITY IN *LYCOPERSICON HIRSUTUM*

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AMONG the mechanisms restricting the flow of genes between discrete populations of plants, unilateral incompatibility (UI) is unique in that one of the reciprocal crossing combinations succeeds whereas the other fails. The term unilateral incompatibility is generally restricted to a phenomenon thought to be closely related to self-incompatibility (SI), for it occurs in matings of self-fertile to self-incompatible species and is controlled by the same physiological mechanism, inhibition of pollen-tube growth (LEWIS and CROWE 1958). The term does not include unilateral crossing failures associated with different ploidy levels, nuclear-cytoplasmic interactions, conditions of sexuality, or mechanical impediments. Although UI most frequently occurs between species, it is also found within species (MARTIN 1961a) and the term unilateral interspecific incompatibility describes the same behavior.

Unilateral incompatibility was first described in the cross of self-fertile *Nicotiana langsdorffii* to self-incompatible *N. alata* (ANDERSON and DE WINTON 1931). These species usually hybridized reciprocally but in one case the cross succeeded only when *N. langsdorffii* was used as female. Failure of the reciprocal cross was associated with the presence of a particular *S* (incompatibility) allele. MATHER (1943) found UI between self-fertile *Petunia axillaris* $\times$ self-incompatible *P. violacea*. The self- and cross-compatibilities of the F_1 and backcross hybrids depended chiefly on the particular *S* alleles present. Any *S* allele from *P. violacea* in the style inhibited growth of any pollen-tube containing *S_a*, the self-fertility allele from *P. axillaris*. However, segregating polygenes affected the strength of the incompatible reactions. STOUT (1952) redefined MATHER's species, and found UI between his self-incompatible *Petunia integrifolia* and self-incompatible *P. axillaris*. Both species were also unilaterally incompatible with males of self-fertile *P. parodii*. Hybrids of the first two species were self-incompatible. About half of the 97 plants were bilaterally compatible with both parents, but 46 could only be classified as of mixed or ill-defined compatibility. Some of these were unilaterally or bilaterally incompatible with the parents. PUSHKARNATH (1953) found UI between several species of series *Commerisiana* (*Solanum*) and *S. aracc-papa*. In the cross of self-incompatible *S. subtile* $\times$ self-incompatible *S. aracc-papa*, all F_1 hybrids were self-incompatible, reciprocally incompatible among themselves and with the male parent, and unilaterally incompatible with the female parent. He hypothesized a factor *R* from the male parent, inhibiting tube growth of pollen containing any *S* allele. GARDÉ (1959) found similar UI in species crosses of *Solanum* and also postulated an *S* and *R* series of alleles. DIONNE (1961) found three mechanisms responsible for failure of *Solanum* species crosses: pollen-tube inhibition, failure of the ovule to develop after fertilization, and embryo abortion.

SI and UI were found in the F_1 hybrids of self-fertile *Lycopersicon esculentum* $\times$ self-incompatible *L. peruvianum* by MCGUIRE and RICK (1954). Of the F_2 hybrids, all were self-incompatible, 28 were unilaterally incompatible with females of *L. peruvianum*, and three were

reciprocally compatible with the latter. In the cross of *L. esculentum* $\times$ *L. chilense*, MARTIN (1961b) found a very similar response except that limited self-fertility occurred in the F_2 , which was attributed to segregation of polygenes. In six backcrosses of self-incompatibility from the latter to the former species, SI and UI were always associated.

HARRISON and DARBY (1955) suggested that mutation could separate SI and UI functions. They showed that self-fertile *Antirrhinum majus*, which they consider has only recently acquired self-fertility, crosses unilaterally with "primitive" self-fertile species. It has thus retained certain characteristics of self-incompatible species from which it arose. LEWIS and CROWE (1958) showed pollen-tube inhibition to be a general feature of self-incompatible $\times$ self-fertile species, whereas reciprocal crosses ordinarily are free of such inhibition. Exceptional self-fertile species which do not fit in this pattern, such as *A. majus*, were considered to be intermediates in the evolution of self-incompatibility to self-fertility. Pollen-tube growth reactions, even in crosses involving different families, followed the general model, suggesting a uniform physiological mechanism. However, the model as stated cannot explain UI between self-incompatible species (STOUT 1952; PUSHKARNATH 1953; PANDEY 1962) or the step-wise or complex UI of *L. hirsutum* (MARTIN 1961a). A hypothesis of complementary balances of growth-control reactions can explain these discrepancies, however (MARTIN 1963). This hypothesis states that incompatibility occurs whenever growth inhibition in the style is not sufficiently complemented by growth stimulation in the pollen. Balances of growth stimuli could be controlled by polygenic systems.

The understanding of unilateral incompatibility and its relation to self-incompatibility requires two approaches: studies of the physiology of pollen-tube inhibition, and studies of the genetic control of UI. The present article is the first of two studies of the genetic control of UI in the tomato.

MATERIALS AND METHODS

Lycopersicon hirsutum Humb. and Bonpl. was used for these studies because of its wide range of degrees of self-fertility, SI, and UI among lines (MARTIN 1963) and because of a relatively low level of embryo abortion; hybrid sterility, and other barriers within the species. This species occurs in two botanical forms, *hirsutum* and *glabratum*. The former is usually self-incompatible whereas the latter is usually self-fertile. Two self-fertile and one self-incompatible line were chosen for the present study. These lines cross unilaterally with each other. The line referred to herein as Baños is a self-fertile f. *glabratum* from the Rio Pastasa, near Baños, Ecuador. The line was inbred two to four generations before use here, but showed no inbreeding depression. The second line, Surco, came from the Rio Rimac, near Surco, Perú. Twenty-five plants grown in 1960 from the original seed from this accession were entirely self-fertile with 20 to 50 seeds per fruit. However, the morphology as well as geographic source clearly indicate that this accession is f. *hirsutum*. This line has proved very difficult to maintain as its seeds germinate poorly and its progeny are weak and abscise flowers and fruit prematurely. These are typical signs of inbreeding depression. Plants of first and second inbred generations were used for this study. The third line, Cajamarca, is a self-incompatible f. *hirsutum* from north of Cajamarca, Perú. All lines were collected and supplied to us by C. M. RICK.

All plants were grown in an insect-free greenhouse. For production of hybrids, flowers were emasculated during the bud stage and were pollinated within 24 hours. For measurements of incompatibility, flowers were not emasculated before pollination, but comparable unpollinated controls were maintained. Normally five flowers per plant were pollinated as a test of SI or UI, but the tests were often repeated. Fruits were collected when mature, and seeds were spread on papers to dry and to be counted.

Evaluations of compatibility were made in terms of seeds per fruit. Other indices could have been used, such as fruits per pollination or seeds per pollination. However, these measures of compatibility are too readily affected by other factors such as fruit load, position of flower in the cluster, and physiological state of the plant.

The available parent, F_1 , F_2 , and backcross generations of each of the three possible crosses were tested for UI against pollen of the female parent, and for SI. The male and female fertilities of representative hybrids of all families were tested in compatible crosses with the original parents. Pollinated styles were often inspected for pollen-tube growth. At least two progenies of each type were grown, and in some cases duplicate progenies were grown during different seasons.

RESULTS

Unpollinated flowers rarely set fruit, whether plants were self-fertile or self-incompatible. Such rare fruits contained very few seeds. The male and female fertility of hybrids could always be checked by backcrosses to the parents in compatible directions. Although not all plants were checked for fertility, representative plants of each family were evaluated. In all cases the hybrids were fertile as males and females, although mean fertility was often reduced to not less than 50 percent (20 seeds per fruit). Exceptional cases of poor crossability were recorded in crosses using the somewhat infertile male Surco. Seeds were well formed and full-sized. Germination in petri-dishes was excellent.

Compatibilities of the parents. Baños and Surco were both self-compatible during all seasons, whereas Cajamarca was always self-incompatible (Table 1). The cross-compatibility reactions were as expected; all three pairs of accessions were unilaterally incompatible. These compatibilities did not change during fall, winter, and spring tests. The plants did not bloom during the summer due to a short-day requirement. There was no sign of pseudocompatibility in either self- or unilaterally-incompatible crosses. Fruit- and seed-setting was most reliable during cool or winter months.

Compatibilities of the F_1 's, Baños $\times$ Cajamarca: This parental combination was unilaterally incompatible when Baños was used as pollen parent. The self-incompatibility of Cajamarca was expected to be dominant in the hybrids. Two F_1 families were grown in two plantings each, but because of the small number of plants in each, the data presented herein represent totals of all four. Segregation in the F_1 occurred. Classification of hybrids for SI and UI with Baños is summarized in Table 2. The two kinds of incompatibility were usually associated (adjusted contingency chi-square = 8.64, $P = .01$). However, neither self- nor

TABLE 1
*Self- and cross-compatibilities of three accessions of Lycopersicon
hirsutum in terms of seeds per fruit*

Female parents	Male parents			
	Baños	Surco	Cajamarca	Sib Cross
Baños	40.3 (75)*	34.0 (110)	31.5 (72)	29.7 (21)
Surco	0.0 (273)	18.9 (138)	33.9 (54)	26.7 (52)
Cajamarca	0.0 (166)	0.0 (162)	0.0 (180)	31.4 (63)

* Lower figure in parentheses represents number of pollinations on which the average is based.

TABLE 2

Compatibility classification and seed-setting of the F_1 hybrids of Baños $\times$ Cajamarca

F_1 sets seed with:	Number of plants	Mean seeds per fruit	
		Self	Baños
Both self and Baños	6	20.8	16.6
Self only	9	13.2	...
Baños only	2	...	11.7
Neither self nor Baños	40	...	...
Total	57		

cross-compatibility was very strong (Figure 1, A). Seed set was seldom over 20 per fruit or 50 percent of that of either parent. As each plant carried an S allele, the slightly fertile plants could be said to be pseudocompatible.

Compatibilities of the backcross progenies, Baños $\times$ Cajamarca: Only F_1 plants which were clearly incompatible or clearly compatible after both self and Baños

FIGURE 1.—Distributions of plants with respect to seeds per fruit after self-pollination (solid histograms) and after pollination by Baños (lined histograms). (A) F_1 hybrids, Baños $\times$ Cajamarca; (B) BC hybrids, (Baños $\times$ Cajamarca) $\times$ Cajamarca; (C) BC hybrids, Baños $\times$ (Baños $\times$ Cajamarca); (D) F_2 hybrids, Baños $\times$ Cajamarca, produced by sib-pollination; (E) F_2 hybrids Baños $\times$ Cajamarca, produced by pseudocompatible self-pollination; (F) F_1 hybrids, Baños $\times$ Surco, fall planting; (G) F_1 hybrids, Baños $\times$ Surco, winter planting; (H) BC hybrids, Baños $\times$ (Baños $\times$ Surco); (I) BC hybrids, (Baños $\times$ Surco) $\times$ Surco.

pollinations were selected for backcrossing. Only backcrosses to female Baños and male Cajamarca were made. These crosses, made in the same direction as the successful parental crosses, were expected to be free of incompatibility which might have led to pollen selection. The segregation of the BC hybrids depended chiefly on the recurrent parent rather than the compatibilities of the F_1 hybrids. BC hybrids from crosses with Cajamarca tended to be both self-incompatible and unilaterally-incompatible with Baños, but a few plants were partially fruitful (Figure 1B). The relatively low number of seeds per fruit suggests that the term pseudocompatible is more appropriate to the behavior of these plants than is the word fertile. On the other hand, backcross hybrids from crosses to Baños tended to be much more self-fertile and cross-fertile with Baños than did the F_1 (Figure 1C). The classification for incompatibility after self pollination was 16 SI to 61 SF ($P = 0.5$ for 1:3), whereas the segregation after Baños pollination was 13:55 ($P = 0.3$ for 1:3). The distributions of seeds per fruit were bimodal, the modes corresponding to the compatibility classes. The 1:3 ratios found could have been due to the segregation in the BC hybrids of two dominant genes for both self- and unilateral incompatibility. The two kinds of incompatibility were usually associated. Of the 68 BC hybrids fully tested, 10 were incompatible in both cases, 46 were compatible in both cases, and 12 were of mixed compatibility. Some of the plants of mixed compatibility were of the pseudocompatible (few seeds) type, but others were not.

Compatibilities of the F_2 's, Baños $\times$ Cajamarca: Two types of F_2 progenies were obtained, those from sib-pollinations of incompatible plants, and those from self-pollinations of pseudocompatibles. The two kinds of progenies did not segregate similarly for SI and UI with Baños, or for seeds per fruit (Table 3 and Figure 1D, E). Although in both cases the curves were bimodal (the modes representing incompatibility and partial compatibility) a greater proportion of the progeny of incompatible plants were incompatible than of the progeny of pseudocompatible plants. The actual ratios fit several F_2 models satisfactorily (Table 3). In sib crosses with no pseudocompatibility, selection against S_f , the fertility allele of the S series, would insure that each F_2 plant contained an S allele. Recombination for a recessive fertility modifier would result in a 3:1 ratio of incompatibility to fertility. Pseudocompatibility could permit free recombination of all genes and result in a 9:7 ratio. Again, selection against S_f would result in a 3:1 ratio.

Compatibilities of the F_1 hybrids, Baños $\times$ Surco: This parental combination was unilaterally incompatible when Baños was used as male. In contrast to the first family, both parents were self-fertile but of different botanical forms. Two F_1 families were grown which represented two entirely different matings of the parental lines. Each family was grown at two different seasons, early fall and winter. Emphasis is placed herein on the second of the two families, but segregations and influence of season were similar in both cases. The F_1 's were unexpectedly found to segregate for both SI and UI (Table 4). The most frequent types of plants in all four screenings were those showing either both SI and UI, or both self- and reciprocal fertility. A smaller percentage of plants was self-fertile but unilaterally incompatible with Baños.

TABLE 3

Chi-squares for possible gene models of F_2 segregations of the cross Baños $\times$ Cajamarca

Source of F_2	Type of pollination	Number of plants		Chi-square value for	
		Incompatible	Compatible	3:1	9:7
Sib cross of F_1 's	Self	30	13	0.63	3.18
	Baños	32	10	0.03	6.82*
Self pollination of F_1 's	Self	18	18	12.00*	0.57
	Baños	24	13	2.03	1.12
Totals	Self	48	31	8.55*	0.66
	Baños	56	23	0.73	6.92*

Models

- 3:1 Two dominant genes necessary for incompatibility and selection against the S_f allele. This model applicable to sib crosses.
- 9:7 Two dominant genes necessary for incompatibility, and free recombination. This model applicable to pseudocompatible self pollinations.
- 1:0 Two dominant genes necessary for incompatibility but selection against both alleles for fertility. No chi-square calculation possible.

* Significant ($P = .05$) deviation from model.

TABLE 4

Classification for self- and unilateral-incompatibility in F_1 hybrids of Baños $\times$ Surco, in terms of numbers of plants

Family	Season	F_1 sets fruit with				Totals
		Self and Baños	Self only	Baños only	Neither self nor Baños	
1961	Fall	11	11	1	14	37
1961	Winter	16	3	1	7	27
1962	Fall	4	4	1	14	23
1962	Winter	10	7	0	1	18
Totals		41	25	3	36	105

The distribution of plants with respect to seeds per fruit is graphed in Figure 1F and G, for fall and winter plantings of a single family (1962). The histograms demonstrate that winter plantings were more self-fertile and more cross-fertile with male Baños than were fall plantings.

The similarity of the histograms for seeds per fruit after self- and cross-pollination suggests that the two types of incompatibility are related. A series of self- and backcrosses made in the 1962 winter planting bore out this contention (Table 5). Correlation coefficients were calculated for all possible crossing combination of parents and hybrids, and are summarized in Table 6.

Of ten coefficients, only three are of moderate size, and these are not significant. The data suggest, however, that plants that are strong in the paternal trait, UI with male Baños, tend to be self-incompatible and cross-fertile with Surco. The

TABLE 5

Seeds per fruit after self- and backcross-pollinations of hybrids of Baños × Surco

Number of hybrid	Self-pollination	Male parents		Female parents	
		Baños	Surco	Baños	Surco
1	24.1	0.0	14.6	32.4	0.0
2	4.3	29.5	12.2	17.3	4.9
3	8.0	0.0	9.4	27.0	1.0
4	19.0	24.6	15.3	26.0	2.0
5	21.5	0.0	19.0	19.8	3.2
6	23.8	24.0	10.8	29.5	0.0
8	12.0	0.0	4.5	40.2	12.0
9	9.0	0.0	16.1	16.7	25.3
10	14.8	10.4	14.3	27.0	5.1
11	24.6	12.0	15.3	19.9	0.0
12	13.2	17.3	7.2	16.9	12.9
13	29.2	16.8	12.2	42.0	0.0
14	16.6	19.0	13.4	21.5	10.6
15	33.7	33.4	14.4	23.8	0.0
17	0.0	0.0	14.8	30.4	17.2
18	12.5	0.0	9.0	29.6	5.1
19	23.5	22.8	5.1	33.5	0.0
20	13.5	0.0	7.7	14.7	12.3

TABLE 6

Correlations among crossing behavior of Baños, Surco, and their hybrids

Type of crossing behavior compared		Correlation	Probability
Hybrid × Baños	Hybrid × Surco	.00	—
Hybrid × Baños	Baños × Hybrid	+.01	—
Hybrid × Baños	Surco × Hybrid	— .42	.05–.10
Hybrid × Baños	Self-pollination	+.43	.05–.10
Hybrid × Surco	Baños × Hybrid	— .03	—
Hybrid × Surco	Surco × Hybrid	.00	—
Hybrid × Surco	Self-pollination	+.02	—
Baños × Hybrid	Surco × Hybrid	— .37	.10
Baños × Hybrid	Self-pollination	+.02	—
Surco × Hybrid	Self-pollination	— .07	—

self-fertility of the hybrids as a group was considerably stronger than the cross-fertility with Baños (16.85 versus 11.63 seeds per fruit for the second winter generation).

Two selected plants representing each of the four compatibility groups were retested weekly over a period of 4 months for SI and UI with male Baños. Each eventually set fruit and a few seeds by both types of pollination. However, the plants retained their relative positions with respect to strength of incompatibility.

A series of observations of styles after incompatible pollinations demonstrated that both the SI and UI were associated with good pollen germination but inhibited pollen-tube growth.

To summarize, the F_1 hybrids segregated both for SI and UI. Neither phenomenon was as strong in the hybrids as in the parents. Both types of compatibility were strongly affected by season of bloom. In contrast to the data from the F_1 hybrids of Baños $\times$ Cajamarca, these data strongly suggest polygenic effects.

Compatibilities of the backcross hybrids, Baños $\times$ Surco: The lack of discrete classes among the F_1 hybrids complicated the choice of plants for backcrossing and the subsequent analysis of BC progeny. The four classes of hybrids, defined by their self-compatibility and cross-compatibility with Baños, could have been backcrossed in ten different ways with the parents. Actually, some of the backcrosses to female Surco were poorly compatible, further restricting possible BC combinations. Ten progenies representing six BC combinations were grown in fall and winter seasons. The segregation for compatibility is summarized in Table 7 and for seed set in Figure 1H and I.

Certain features were common to all the backcross progenies. First, all had plants that were self-incompatible. All had plants that were unilaterally incompatible with male Baños. The two types of compatibility were highly correlated (for all BC data, $r = .65$, $P = .05$). Furthermore, all segregations were more or less bimodal. One mode always represented fully incompatible combinations, whereas the other mode represented partial fertility. There was no obvious relationship between compatibility of the F_1 hybrids used and of their backcross progenies. However, progenies of backcrosses to Baños were slightly more self- and cross-fertile than progenies with Surco. Influence of season on fertility was not as evident among BC as F_1 progenies but the data were not extensive enough to make such discriminations. One- and two-gene models could not be fitted to the data.

A representative group of plants that were either SI or UI was studied in detail. Extensive pollinations demonstrated that the incompatibilities were not absolute in a single plant. Treatment of the flower with 0.1 percent alpha-naphthalene acetamide in lanolin after pollination resulted in regular fruit set, as it does in the case of many tomatoes. Fruits set by this process usually contained one or more seeds.

TABLE 7

Segregation for compatibility in various first backcrosses of hybrids of Baños $\times$ Surco

Compatibility of hybrid				Number of progeny that set seed with			
With self	With Baños	Recurrent parent	Season of growth	Self and Baños	Self only	Baños only	Neither
Yes	Yes	Baños	Winter	11	7	0	2
Yes	Yes	Baños	Winter	4	3	1	0
Yes	No	Baños	Fall	13	6	0	2
Yes	No	Baños	Fall	11	3	5	2
Yes	No	Surco	Fall	0	2	0	6
Yes	No	Surco	Fall	5	4	1	0
No	Yes	Baños	Winter	11	7	0	2
No	No	Baños	Fall	3	1	1	0
No	No	Baños	Winter	12	3	0	5
No	No	Surco	Fall	4	3	3	0

Compatibilities of the F₂ hybrids, Baños × Surco: Twenty plants each of five F₂ families obtained by self-pollination of F₁ hybrids of various levels of compatibility were all self-fertile and cross-fertile with male Baños. Although detailed seed setting data were not collected, it was obvious that some plants set fruit more readily than others, and that seeds per fruit varied considerably.

The cross of Surco × Cajamarca: Although several progenies of this cross were grown, the high pollen abortion of the test parent, Surco, prevented a realistic analysis for UI. The data suggested strong SI and UI with Surco, and a small percentage of pseudocompatible plants.

DISCUSSION

The two crossing studies reported herein provide an opportunity to compare the inheritance of unilateral incompatibility in two related but unique combinations. The fairly close relationship of the botanical forms of *L. hirsutum*, the ease of crossability in at least one direction, and the absence of aborted seeds, such as characterize the intraspecific hybrids of *L. peruvianum* (RICK 1963), permit an analysis little affected by species isolating barriers. However, conditions of the environment, particularly temperature, may cause some variations in pollen-style interactions and may thus lead to pseudocompatibility and distortion of segregation ratios. The continuous distribution of fertility measurements (seeds per fruit) in all of the families reported herein and the changes in distribution associated with season suggest that a quantitative process might have been so influenced.

The cross of self-fertile Baños to self-incompatible Cajamarca resembles several other crosses reported in the literature. MATHER's cross (1943) of *Petunia axillaris* × *P. violacea* was also characterized by pseudocompatibility and segregation of minor genes in the F₂ generation. STOUT's *Petunia* crosses differed somewhat from each other, but again unilateral barriers tended to break down, segregations for compatibility were more or less continuous and discrete ratios were not found. MCGUIRE and RICK's (1954) cross of *Lycopersicon esculentum* × *L. peruvianum* produced self- and unilaterally-incompatible F₁ and F₂ progenies. Even in this case, however, a few F₂ plants were reciprocally compatible with one of the parental species. MARTIN's (1961) cross of *L. esculentum* × *L. chilense* was similar, but limited self-fertility was found in the F₂. The unifying feature of all of these crosses is that apparently both major and minor genes were segregating.

The cross of Baños × Cajamarca differs from the above crosses in that segregation occurred even in the F₁, as manifest by the presence of pseudocompatible plants. Although the differences in self-fertility could have been due to segregation of F₁ pollen, the fruit set by the more uniform pollen from Baños could have been due only to differences among F₁ progeny, probably polygenic in nature. Nevertheless, the close fit of the backcross and F₂ data to simple ratios indicates that polygenes play a minor role in this segregation. The hypothesis of two dominant genes which could account for these ratios also fits the data obtained by MARTIN (1961b) in backcrossing self- and unilateral-incompatibility from *L. chilense* to *L. esculentum*.

The second cross reported herein between Baños and Surco differed from the first chiefly in that the male parent was also self-fertile. Nevertheless, the facts that Surco agreed in morphology with the self-incompatible form of *L. hirsutum* and that strong depression occurred after inbreeding suggest that this introduction would normally outbreed in the wild. Surco corresponds in its general crossing behavior to what LEWIS and CROWE (1958) have called recently derived self-fertility. Results in the F_1 were similar to results of the previous cross in that both SI and UI occurred. Whether *S* alleles or their fertility derivatives were present is difficult to say, but the occurrence of self-incompatible plants among the progeny of self-fertile parents indicates genes for SI were present. These were most likely contributed by the Surco parent. The wide distribution of fertility measurements in the backcross generations shows that many minor genes affecting compatibility were segregating. The similarity of segregation patterns in backcrosses of the two different parents would suggest that no major genes are involved, but the bimodal distribution of data could be interpreted otherwise. Or, bimodality may be the result of a threshold effect. Nevertheless, environmental influences were capable of modifying both major and minor gene effects. Although SI and UI were usually associated, sufficient cases of nonassociation were found to suggest some differences in genetic control. However, the physiological mechanism, pollen tube inhibition, appears to be the same in both cases.

The suggestion of major and minor modifications of incompatibility systems by genes not of the *S* locus is not a new one (MATHER 1943). DENWARD (1963) has found evidence of polygenic modification even of *S* gene specificity in *Trifolium pratense*. Polygenes could act in a variety of ways to affect the strength of an incompatibility reaction. It is conceivable that the stylar and pollen components of the reaction could be separately affected. MARTIN (1963) hypothesized that different polygenic balances effecting pollen and style reactions could lead to fortuitous unilateral incompatibilities between species. As demonstrated herein, hybridization can rapidly break down such barriers. When UI is viewed as a polygenic phenomenon, the apparent exceptions to the LEWIS and CROWE hypothesis of the relationship of UI and SI are reconcilable. Stepwise UI (MARTIN 1961a) and UI between self-incompatible species may then be interpreted as fortuitous consequences of the SI mechanism. Finally, to the LEWIS and CROWE hypothesis must be added the provision that breakdown of polygenic systems either by gene fixation after pseudocompatibility or after hybridization, can lead to self-fertility just as readily as an *S* gene mutation. The hypothesis of polygenic modification of SI and UI reemphasizes that breeding systems are a consequence of the total genotype, and not of an isolated series of alleles.

SUMMARY

The F_1 hybrids of self-fertile Baños (*Lycopersicon hirsutum* f. *glabratum*) and self-incompatible Cajamarca (f. *hirsutum*) were self-incompatible and unilaterally incompatible with Baños although some pseudocompatibility also occurred. Analysis of backcross and F_2 progeny suggested that both self- and unilateral in-

compatibility were controlled by two dominant genes from the Cajamarca parent and that polygenic modifiers were responsible for pseudocompatibility. In a second cross, Baños $\times$ self-fertile Surco (f. *hirsutum*), the hybrids segregated for compatibilities even in the F_1 . Season of growth strongly influenced the segregation. Backcross and F_2 data could not easily be fitted to simple ratios, but bimodal distributions suggested that at least one dominant gene from Surco was operating. The wide range of fertility values suggested segregation of polygenes also. Polygenes which regulate growth interactions between stylar or pollen components may, when in stable combinations, be the cause of fortuitous unilateral incompatibilities, and when segregating, give rise to a continuous array of fertile or pseudocompatible combinations. Unilateral incompatibility is herein regarded as an accidental consequence of systems of self-incompatibility, which can occur therefore between any combination of self-incompatible or self-fertile species.

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