

THE INHERITANCE OF SELF-INCOMPATIBILITY IN HYBRIDS OF *LYCOPERSICON ESCULENTUM* MILL. \times *L. CHILENSE* DUN.^{1,2}

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BOTH self-fertile and self-incompatible species are found in the genus *Lycopersicon* (LAMM 1950). The self-incompatibility in *L. peruvianum* was shown to be of the Nicotiana or multiple-allelic gametophytic type by MCGUIRE and RICK (1954). Less extensive evidence suggested similar genetic control in *L. hirsutum*, *L. glandulosum*, and *L. chilense* (*L. peruvianum* f. *dentatum*). In addition, the inheritance of self-incompatibility in F_1 hybrids of *L. esculentum* \times *L. peruvianum* was investigated. All the plants of both generations were self-incompatible. The F_1 hybrids from a given cross were of two intraincompatible, intercompatible types determined by the incompatibility (*S*) allele inherited from *L. peruvianum*. The pollination relationships of the F_2 indicated a recombination of *S* alleles, as expected, and also a sporophytically determined restriction of crosses of the F_2 to unrelated pistillate *L. peruvianum* plants. This barrier was interpreted as the action of one or two genes from *L. esculentum*.

LEWIS and CROWE (1958) have summarized the results of many attempted hybridizations of self-fertile with self-incompatible species. Usually such crosses are successful only when the self-fertile species is used as female. This phenomenon was termed unilateral hybridization by HARRISON and DARBY (1955). The exceptional self-fertile species which can successfully fertilize self-incompatible types are suggested by LEWIS and CROWE (1958) to be intermediates in the evolution of self-fertility from self-incompatibility.

In only one case has the inheritance of self-incompatibility been studied in such crosses beyond the F_2 generation. In hybrids of *Petunia axillaris* \times *P. violacea*, MATHER (1943) found a dominance of self-incompatibility but a weakening of the reaction in the backcross hybrids. He attributed this to the dilution through backcrossing to the self-fertile parent of the polygenes affecting self-incompatibility.

In the present study the genetic differences between *Lycopersicon esculentum* and *L. chilense* with respect to self-incompatibility and related morphological characteristics were investigated in F_1 , F_2 , and backcross generations.

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MATERIALS AND METHODS

All materials were supplied from the collections of Dr. C. M. RICK, University of California, Davis, California.

L. chilense was represented by six collections made in southwestern Peru between 1938 and 1957. All were self-incompatible. A single plant derived from a collection made in Tacna, Peru, in 1942 by GOODSPEED was used as the parent of hybrids with *L. esculentum* and as one source of inbreds (Figure 1). Other collections were used to verify the type of self-incompatibility and to test the crossability and level of fertility of the hybrids. All collections showed the typical features of *L. chilense* (RICK and LAMM 1955): erect habit, brittle stems, pinnately divided leaf with many segments, very long peduncles, large and showy yellow flowers, exserted styles, and green berries.

As a standard recurrent parent representing the self-fertile species, *L. esculentum*, the variety Tiny Tim was used (Figure 1). This variety originated as a selection from the cross Window Box \times Red Currant (*L. pimpinellifolium*). Its small size, abundant fruit and adaptability to growth in small pots in the greenhouse make it an excellent experimental material. In contrast to *L. chilense*, this tomato has determinate plant growth, stubby, inconspicuous flowers with included styles, and red fruit.

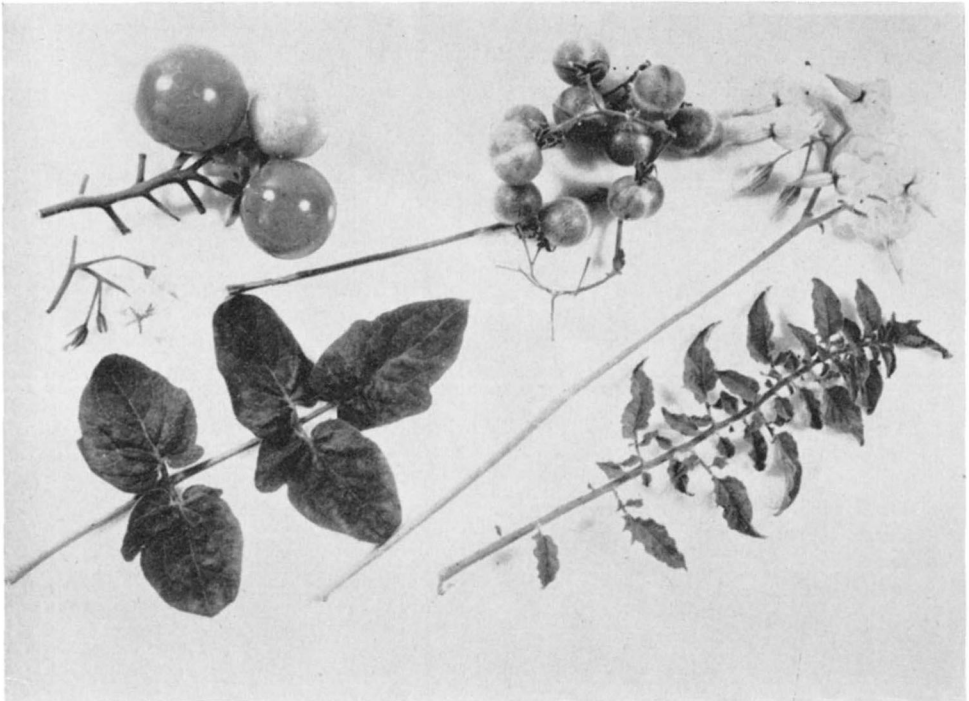


FIGURE 1.—Leaf, flower cluster, and fruit of *L. chilense* (right) and *L. esculentum* var. Tiny Tim (left).

Two *L. esculentum* stocks carrying marker genes, and the Pearson variety, a large-fruited commercial type tomato, were also used as recurrent parents for some backcrossing experiments.

The F_1 hybrids were obtained by embryo culture by DR. C. M. RICK. Pearson was the female parent. Two hybrids were used representing the two possible intraincompatible, intercompatible types (McGUIRE and RICK 1954) determined by the two *S* genes of a single *L. chilense* parent. The plant identified herein as 4-2 carried S_1 , and that identified as 4-8 carried S_2 . The F_1 hybrids were self-incompatible. Their crossing relationships as determined by RICK (unpublished) and verified here are given in Figure 2.

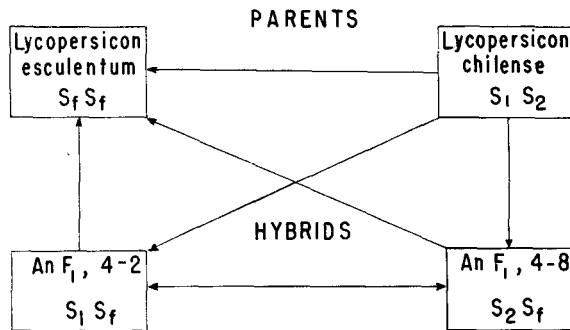


FIGURE 2.—Crossing relationships of *L. chilense* and *L. esculentum*. Arrows point from pollen to pistillate parent for the successful crosses.

All backcrosses were made using the self-fertile parent as female and the self-incompatible as male. The experimental materials were all grown in fumigated soil, in pots in an insect-free greenhouse maintained at 75°F during the day and 65°F during the night. The *L. chilense* parent plant and the F_1 hybrids were maintained clonally whereas the remainder of the materials were grown from fermentation-cleaned seed.

Buds were pollinated after careful emasculation to avoid contamination of pollen. Pollinated flowers were tagged or marked appropriately. Self-incompatible plants were pollinated at anthesis without emasculation. Pollen was often stored until use at 32°F under dry conditions.

Self-incompatibility was scored by the evaluation of a group of tests, supplemented, when necessary, by experienced judgment. The first five or more flowers of young plants were self-pollinated at anthesis and tagged, whereupon the plants were set aside for observation. Self-fertile plants normally set fruit quickly and pea-sized fruit developed in seven to ten days. When two or more fruit developed on a plant, the plant was considered to be self-fertile. Decisive scoring of self-incompatibility was more difficult, for unfruitfulness was often due to poor fertility (see results). Such plants were therefore further pollinated. Those that set fruit with *L. chilense* and with the F_1 hybrid carrying the other *S* gene, but failed to set fruit when pollinated by *L. esculentum* were considered self-incom-

patible. When a question of self-fertility still existed, pollinated styles were examined for pollen tube growth and the incompatibility reaction. Only about two percent of all plants tested were unclassifiable, and these were weak or sick.

Pollen tubes were observed in fixed styles under ultraviolet light using the method of MARTIN (1959). Pollen tubes fluoresced bright yellow and stoppage of pollen tube growth was clearly evident after incompatible pollination. Pollen tube growth was measured using a calibrated objective with a binocular dissecting microscope by measuring from the surface of the stigma to that point where an estimated 90 percent of the tubes were inhibited.

Inbreds of *L. chilense*, desired for further study of self-incompatibility in the parent plant, were obtained by treatment of individual flowers after self-pollination with one percent alpha naphthalene acetamide in pure lanolin smeared on the anther column, corolla or calyx (EMSWELLER and STUART 1948). The treatment resulted in regular fruit set, and seed set at the mean rate of 0.16 seed per pollination. In comparison, thousands of self-pollinations without hormone treatment failed to set. Compatible crosses yield 50 or more seeds per pollination.

Certain characteristics of the mature flower were measured to see if any of the differences between *L. esculentum* and *L. chilense* were associated with self-incompatibility and were therefore carried along during the backcrossing process. In the parent materials including Pearson, the F₁, F₂, and a sample of the backcross hybrids, measurements were made of the length of style, length and width of corolla segments, length and width of anther column and length of peduncle. Counts were made of the number of flowers per cluster.

Marker genes were scored in all families in which they segregated.

The number of classes of offspring with respect to incompatibility occurring in a single F₁ family of *L. chilense* plants was determined by a screening technique (McGUIRE and RICK 1954). A given plant was chosen as pollen parent and all other plants were pollinated by it. A standard pollination consisted of two clusters of three flowers each. The plants which failed to set fruit were concluded to belong to the same group as the pollen parent. The fruitful plants consisted of several groups which were further screened out by the choice of other pollen parents and further rounds of pollinations. Intragroup cross-fertility was tested by pollinating five plants of each group in all possible combinations.

RESULTS

Inheritance in L. chilense and hybrids with L. esculentum: The evidence collected from a number of sources leaves no doubt that the self-incompatibility in *L. chilense* is of the Nicotiana or multiple-allelic gametophytic type. In each of two reciprocal F₁ families of *L. chilense*, four intraincompatible, intercompatible groups were found. The actual numbers were 11, 12, 7, and 5 in one family and 9, 12, 8, and 11 in the corresponding classes of the other family. The segregation of the 75 plants tested was in a 1:1:1:1 ratio ($\chi^2 = 3.456$). One anomalous plant not fitting into one of the four groups above appeared to result from a stray pollination. The four groups of one family corresponded to the four groups of

the other. No reciprocal differences in compatibility were found. In the inbred generations, plants were found of the constitutions S_1S_1 , S_1S_2 , and S_2S_2 , but too few inbreds were obtained to test for ratio. The compatibility relations of these plants were in accordance with the Nicotiana scheme.

Further evidence for the multiple-allelic hypothesis was obtained from the hybrids of *L. esculentum* \times *L. chilense*. Only two incompatibility classes, determined by the two *S* alleles present, were found in the F_1 by RICK (unpublished). The segregations found in F_2 families were skewed in the direction of the *L. chilense* type (i.e., in one family there were 32 S_1S_2 to 18 S_2S_1). Two factors were probably responsible for this deviation. First, no recombination for the self-fertility allele of the *S* series might have occurred due to an inhibition of pollen tubes carrying S_f by all self-incompatible plants. Second, a high degree of pollen and seed sterility could have offered opportunity for selection.

Apparently because of selection against pollen containing the self-fertility allele, all F_2 plants contained at least one *S* gene for self-incompatibility. However, a weak self-fertility in some plants was manifest in a segregation for degree of pollen tube inhibition, in full pollen tube growth in some cases, and in very limited fruit and seed set. These results contrast with those of MCGUIRE and RICK (1954) in F_2 hybrids of *L. esculentum* \times *L. peruvianum* where no such attenuated self-incompatibility was found.

Five small families were grown which, with respect to *S* alleles, comprised F_2 generations. These were obtained by crossing self-incompatible plants of the third backcross generation (see later) to an F_1 plant carrying the other *S* allele. The plants were expected to be of two genotypes, S_1S_2 and S_2S_1 . All of the families were similar in that each contained both self-fertile and self-incompatible progeny. Among a total of 87 plants, 39 were classified self-fertile and 48 were self-incompatible. The results agree with those of the true F_2 except that the self-incompatibility was weaker, perhaps due to the loss through backcrossing of some polygenes. The styles of the incompatible plants revealed that segregation for degree of pollen tube inhibition was extreme. The self-fertile plants probably represent one tail of the segregation. The genotypes of these plants with respect to *S* alleles was not determined.

Crosses of the F_1 , F_2 , and backcross hybrids to unrelated, pistillate *L. chilense* plants were seldom successful. Observations of the style showed poor germination of the pollen, but uninhibited pollen tube growth. Successful crosses were characterized by various degrees of embryo abortion. Taken together, the observations point to a multigenic influence of *L. esculentum*.

Backcross transfer of self-incompatibility. The S_1 allele was transferred to *L. esculentum* (Tiny Tim) through six backcrosses and the S_2 was transferred through three. Furthermore, S_1 was transferred from incompatible plants of the second backcross generation to two *L. esculentum* gene marker stocks for two additional generations. Each backcross generation was scored for self-incompatibility and for other segregating characteristics. Several plants of each generation then were selected for further backcrosses.

In Table 1 the segregations for self-incompatibility in the six backcross genera-

TABLE 1

Segregation for self-incompatibility from L. chilense in six backcross generations to L. esculentum variety Tiny Tim

| Backcross generation | Number of plants | | | Actual ratio | Chi-square for ratio of | |
|----------------------|------------------|-----|-------|--------------|-------------------------|----------|
| | SF | SI | Total | | 3:1 | 7:1 |
| 1 | 69 | 12 | 81 | 5.75:1 | 4.48* | 0.39 |
| 2 | 79 | 18 | 97 | 4.39:1 | 2.15 | 3.25 |
| 3 | 209 | 42 | 251 | 4.98:1 | 9.15** | 4.11 |
| 4 | 355 | 93 | 448 | 3.81:1 | 4.30* | 27.94*** |
| 5 | 61 | 21 | 82 | 2.90:1 | 0.16 | 12.88** |
| 6 | 66 | 24 | 90 | 2.75:1 | 0.13 | 19.27** |
| Total | 839 | 210 | 1049 | 4.00:1 | 13.87** | 54.22*** |

* Significant at .05 level of probability.
 ** Significant at .01 level of probability.
 *** Significant at .001 level of probability.

tions of one *S* allele are given together with chi-square analyses. The numerical figures in some cases represent the sums of data from several smaller, similarly segregating families. The segregation for self-fertility *versus* self-incompatibility approached a 3:1 ratio although significant departures from such a ratio were found in three of the six backcross generations. The data do not show a better fit to any other simple ratio. The low heterogeneity chi-square for the 3:1 ratio ($\chi^2_h = 6.50$) indicates homogeneity of the six generations. When the actual ratios are compared, a trend toward a 3:1 ratio is apparent as self-incompatibility was progressively brought into the Tiny Tim genotype. It is evident, therefore, that in addition to an *S* allele, an independent dominant gene from *L. chilense* is necessary for the expression of self-incompatibility in Tiny Tim.

In Table 2 the data for the backcross generations to *L. esculentum* marker stocks are summarized. Data were obtained for two generations of two stocks but only one generation of the third. The most surprising feature is the difference between the two generations in segregation ratio. The abrupt shifts in ratio between backcrosses to Tiny Tim and the first backcross to *L. esculentum* and between the first and second backcross to *L. esculentum* are most easily explained on the assumption that the gene marker stocks and Tiny Tim lack certain genes

TABLE 2

Segregation for self-incompatibility in two backcross generations to L. esculentum gene marker stocks

| Marker stock | Actual BC generation | Number of plants | | | Actual ratio | Adjusted chi-square for ratio of | | | |
|-------------------|----------------------|------------------|----|-------|--------------|----------------------------------|----------|--------|------|
| | | SF | SI | Total | | 1:1 | 3:1 | 7:1 | 15:1 |
| <i>a, d, c, l</i> | 3 | 22 | 15 | 37 | 1.47:1 | 0.97 | 4.77 | ... | ... |
| <i>a, d, c, l</i> | 4 | 58 | 6 | 64 | 9.67:1 | ... | 39.06*** | 0.32 | 0.70 |
| <i>Wo, d</i> | 3 | 25 | 9 | 34 | 2.78:1 | 6.62 | 0.00 | ... | ... |
| <i>Wo, d</i> | 4 | 134 | 5 | 139 | 26.80:1 | ... | 36.68*** | 9.67** | 1.25 |
| <i>rv, al, H</i> | 3 | 16 | 10 | 26 | 1.60:1 | 0.96 | 1.85 | ... | ... |

necessary for the expression of self-incompatibility, but not the same genes. The segregation in the two generations was due to random assortment of these genes in the pollen since in both generations the same homozygous pistillate lines were used.

The above hypothesis assumes that four dominant genes are necessary for self-incompatibility in the recurrent parent materials. This is the least number of genes that could account for a 15 to 1 ratio. The necessary genotypes to explain these results are given in Table 3. If the hypothesis proves correct, a search for more such genes would be useful.

Inspections of the styles of the self-incompatible plants of the backcross generations revealed a segregation for strength of the reaction as shown by variable mean pollen tube lengths. Furthermore, a progressive weakening of the self-incompatibility was found to occur as backcrossing progressed. In contrast to mean pollen tube length of about 15 percent of the style in *L. chilense*, it reached about 50 percent in the fifth backcross.

The weakening of self-incompatibility in the later backcrosses to Tiny Tim was also manifest by the occurrence of plants which were intermediate with respect to self-incompatibility and self-fertility. Such plants set a few fruit containing a few seeds after self-pollination but set vigorously when cross-pollinated appropriately. These plants were classified as self-fertile, and probably account for the ratios of less than 3:1 in the fifth and sixth backcrosses (Table 1).

Four plants which were weakly self-fertile were backcrossed to Tiny Tim and the progeny were screened for self-incompatibility. Among 141 plants none were found to be strongly self-incompatible but 12 were of the intermediate type. One or more such plants were found in each of the four families. Weak self-fertility thus appears to be a valid intermediate, heritable condition but one readily confused with self-fertility.

Crosses among backcross hybrids carrying different *S* alleles usually failed due to poor pollen germination. However, pollen viability in crosses to *L. esculentum* was high. In the few successful crosses among hybrids, extreme embryo abortion was evident. As discussed later, this barrier may be due to an interaction of the *S* gene and *L. esculentum* genotype.

Since only about one fourth of the progeny of any backcross generation to

TABLE 3

Theoretical genotypes of L. chilense and L. esculentum stocks with respect to genes necessary for self-incompatibility

| Stock | Genotype of stock | Genotype of self-incompatible hybrid |
|--------------------------------------|--------------------|--------------------------------------|
| <i>L. chilense</i> | $S_f S_2 AABBCDD$ | |
| Tiny Tim | $S_f S_f aaBBCCDD$ | $S_n S_f AaBBCCDD$ |
| Marker stock <i>a, d, c, l</i> | $S_f S_f AAbbccdd$ | $S_n S_f AABbCcDd$ |
| Marker stock <i>W_o, d</i> | $S_f S_f aaBBccdd$ | $S_n S_f AaBBCcDd$ |
| Marker stock <i>rv, al, H</i> | $S_f S_f AA-----$ | $S_n S_f AA-----$ |
| All self-incompatible plants | $S_n -A-B-C-D-$ | $S_n -A-B-C-D-$ |

Tiny Tim were found to be self-incompatible, it is highly probable that about one third of the self-fertile progeny carried an *S* allele other than *S_T*. The presence of *S* alleles in a few self-fertile plants of the first backcross generation was demonstrated by successfully pollinating self-incompatible plants of the same generation but carrying the other *S* allele. However, no thorough screening for such unexpressed *S* alleles was made.

Linkage relations: In addition to self-incompatibility, a number of known genes and one newly discovered marker gene segregated in the backcrosses. These were dwarf (*d_i*), self-pruning (*sp*), Hairless (*H*), anthocyaninless (*a_i*), Woolly (*Wo*), lutescent (*l_i*), and potato leaf (*c*). Complete descriptions of the characteristics determined by these genes are given by RICK and BUTLER (1956). A necrotic condition segregating in the backcrosses, apparently derived from *L. chilense* was given the name Necrotic (*Nec*). The condition is first apparent as elevations or hypertrophic pustules along the veins of the leaf. In and around these growths, chlorosis and then necrosis occurs. As the leaf weakens, secondary fungus infections may occur and the leaf abscises prematurely. The intensity of this character increased as backcrossing progressed.

All of the marker genes segregated in the expected 1:1 ratio except as noted below. In one family among five, an excess of dwarf plants was apparent. This character was difficult to score because of its modification by self-pruning and without a doubt by other minor genes. Inaccurate classification could have caused this apparent deviation. In two families from crosses to Woolly-dwarf marker stocks, Necrotic segregated in a 3:1 ratio indicating that two recessive genes controlling this character were present in the stock.

Tests of association of the marker genes, made to detect gene linkages, are summarized in Table 4. The analyses show association of self-incompatibility with dwarf, Woolly, and Necrotic. The first two of these genes are known to lie on the second chromosome of the tomato (RICK and BUTLER 1956). Tests for association of Necrotic with dwarf and Woolly place that gene also in the same

TABLE 4

Tests for association of self incompatibility with eight marker genes

| Gene | Recurrent parent | Backcross generations | Number of plants | | | | Total | Adjusted contingency chi-square |
|------------|------------------|-----------------------|------------------|-----------|------|-----------|-------|---------------------------------|
| | | | SF + | SF marker | SI + | SI marker | | |
| <i>d</i> | Tiny Tim | 2, 3, 4 | 166 | 234 | 51 | 37 | 488 | 7.26** |
| <i>d</i> | Marker stocks | 4 | 164 | 159 | 21 | 0 | 344 | 17.29*** |
| <i>Nec</i> | Tiny Tim | 4, 5 | 186 | 96 | 8 | 63 | 353 | 66.33*** |
| <i>Nec</i> | Marker stocks | 4 | 208 | 57 | 4 | 11 | 280 | 18.01*** |
| <i>Wo</i> | Marker stocks | 4 | 110 | 155 | 15 | 0 | 280 | 17.77*** |
| <i>H</i> | Tiny Tim | 2, 3, 4 | 184 | 172 | 51 | 30 | 437 | 2.94 |
| <i>a</i> | Marker stocks | 4 | 34 | 24 | 3 | 3 | 64 | No analysis possible |
| <i>c</i> | Marker stocks | 4 | 23 | 35 | 2 | 4 | 64 | No analysis possible |
| <i>l</i> | Marker stocks | 4 | 29 | 29 | 1 | 5 | 64 | No analysis possible |
| <i>sp</i> | Tiny Tim | 4 | 45 | 56 | 21 | 18 | 140 | 0.63 |

linkage group. Necrotic (*Nec*) does not appear to be identical to necrosis (*ne*), a gene which in recessive condition, causes the development of a necrosis in *Cladosporium fulvum* resistant plants (LANGFORD 1948). The tentative relative positions of these five genes on the second chromosome are summarized in Figure 3.

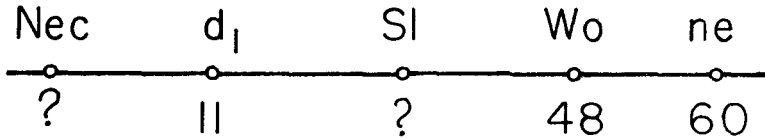


FIGURE 3.—Linkage map of chromosome 2 of the tomato showing relative positions of genes determining Necrosis and self-incompatibility.

Preliminary measurements of seven characteristics of the inflorescence and flowers of the hybrids and parent materials gave some indication that length of style, width and length of corolla segments might be associated with self-incompatibility. Length of peduncle, width and length of anther column and number of flowers per inflorescence showed no signs of such an association. Accordingly more extensive measurements were taken of the first three characteristics in a large family of the fourth backcross generation. Measurements were made of all 39 of the self-incompatible plants and of 68 of the self-fertile plants taken at random. In addition, the ratio of corolla segment width to length was calculated. The data were subjected to analyses of variance to determine the association of these characteristics with self-incompatibility and with the two linked genes, dwarf and Necrotic. The first analyses showed that Necrotic did not influence the traits in question. The data were then grouped into four phenotypic classes determined by self-incompatibility and dwarf and were reanalyzed. All analyses showed highly significant differences. Paired comparisons were then made of classes differing with respect to only one character (Table 5).

It is evident from the table that both self-incompatibility and dwarf are associated with the floral differences. Dwarf tends to shorten and narrow flower parts whereas self-incompatibility shows the opposite effects. However, the effects are by no means clear cut and interactions appear to occur. Linkage and crossing over are probably the main causes of the apparent interaction.

In the fifth and sixth backcross generations, a few self-incompatible plants occurred free of d_1^+ , *Nec*, and the flower characteristics of *L. chilense*. These plants bore a striking resemblance to Tiny Tim. Evidently the quantitative characters studied above were associated with self-incompatibility by linkage rather than pleiotropy.

DISCUSSION

The persistence of self-incompatibility in the backcrosses to Tiny Tim is without parallel in genetic literature. A strong resemblance of the background genotypes of *L. esculentum* and *L. chilense* is thus suggested. The chief difference with respect to incompatibility in crosses to Tiny Tim appears to reside in two

TABLE 5

Results of the analyses of variance of four flower characteristics

| Classes | Mean style length (mm) | Mean corolla segment width (mm) | Mean corolla segment length (mm) | Mean corolla segment ratio |
|--|------------------------|---------------------------------|----------------------------------|----------------------------|
| Comparison of phenotypic classes differing in compatibility reaction | | | | |
| SI + | 9.10 | 6.32 | 9.84 | 0.644 |
| SF + | 8.86 | 5.67 | 10.53 | 0.552 |
| Difference | 0.24 | 0.65** | -0.69* | 0.092** |
| SI d_1 | 8.42 | 5.62 | 8.89 | 0.646 |
| SF d_1 | 7.06 | 4.91 | 8.07 | 0.619 |
| Difference | 1.36** | 0.71* | 0.82* | 0.027* |
| Comparison of phenotypic classes differing at the d_1 locus | | | | |
| SF + | 8.86 | 5.67 | 10.53 | 0.552 |
| SF d_1 | 7.06 | 4.91 | 8.07 | 0.619 |
| Difference | 1.80** | 0.76** | 2.46** | -0.067** |
| SI + | 9.10 | 6.32 | 9.84 | 0.644 |
| SI d_1 | 8.42 | 5.62 | 8.89 | 0.646 |
| Difference | 0.68* | 0.70* | 0.95* | -0.002 |

genes of major effect. The evidence that other major genes may be present in other *L. esculentum* stocks is of the utmost importance and suggests a method of tracing the phylogeny of the forms of this diverse species. Many minor genes undoubtedly affect the strength of reaction, witnessed, as backcrossing proceeded, by the increased length of pollen tubes after self-pollination and by the limited self-fertility of the F_2 . In contrast to these results, MATHER (1943) found a rapid loss of self-incompatibility in two backcrosses of *Petunia axillaris* \times *P. violacea*. He attributed his results to a well-developed polygenic difference between the species which controlled the incompatibility reaction.

The establishment of an outbreeding *L. esculentum* population at the present time appears to be difficult if not impossible, for plants of the *L. esculentum* type which carry different *S* alleles seldom cross. The barrier to the cross, manifested in poor pollen germination and embryo abortion, appears to be due to the *L. esculentum* genotype. MCGUIRE and RICK (1954) attributed the barrier found in backcrosses of F_1 hybrids to *L. peruvianum* to a few genes with sporophytic affect. In this case, however, the wide differences in crossability point to a multi-genic control.

The association by linkage of self-incompatibility with a variety of marker genes as well as polygenes affecting the very morphological features leading to successful outcrossing (long, exerted style, and showy flowers) may not be wholly fortuitous. Such linkage associations have been shown to occur in *Primula* (ERNST 1936). Recently RICK (1959) has shown non random gene distribution among tomato chromosomes. An unexpectedly large number of marker genes were found on chromosome two, the chromosome on which one gene controlling self-incompatibility lies. The perpetual heterozygosity for *S* alleles in an outcrossing species such as *L. chilense* may very well lead to the development of

linked adaptive gene combinations. Both the linkage associations found here and those found by RICK (1959) could thus be easily explained.

The fact that all self-incompatible plants showed the secondary property of inhibiting the pollen of self-fertile species is consistent with the concepts of unilateral interspecific incompatibility as developed by LEWIS and CROWE (1958). Furthermore, no self-fertile plant showed this phenomenon, even among those known to carry an *S* allele. In plants with weak self-incompatibility the unilateral reaction was always present and was usually stronger than self-incompatibility. Inspection of the styles from such crosses always showed a pollen tube inhibition similar in appearance to that of self-incompatibility. Thus it appears that the two phenomena, self-incompatibility and unilateral incompatibility were properties of the same genetic and physiological system in this study.

This triple nature of the reproductive isolating barriers between the two species deserves mention here. The superficial barrier resembling self-incompatibility and preventing hybridization of *L. chilense* by *L. esculentum* was relatively easily removed by transferring *S* alleles into *L. esculentum*. A second, more potent multigenic barrier was then evident in failure of pollen germination and embryo abortion. Finally, a third, relatively simply controlled barrier, necrosis, was deleterious to hybrid survival. It is interesting that only the first of these barriers is unilateral. The more complexly controlled barrier on the other hand, was evident in reciprocal crosses. It is tempting to think that it is therefore the oldest barrier and that unilateral interspecific incompatibility is a more recent acquisition which accompanied the evolution of *L. esculentum* from a self-incompatible progenitor, via the scheme of LEWIS and CROWE (1958). It is evident that the question cannot be answered in this material for the necessary intermediate types may no longer be extant.

SUMMARY

Evidence was collected indicating that the self-incompatibility in *L. chilense* is of the *Nicotiana* type.

The inheritance of self-incompatibility in hybrids of *L. esculentum* and *L. chilense* was studied in F_1 , F_2 , and backcross hybrids. Self-incompatibility appears to be controlled by two or more dominant genes of major action in the hybrids. A difference in *L. esculentum* stocks with respect to these genes was found. Unilateral interspecific incompatibility was shown to have the same genetic control in these materials as self-incompatibility. In addition, evidence was found of a polygenic difference between the two species affecting the strength of the incompatibility reaction. A polygenic barrier was shown to underlay the barrier due to the *S* genes. This resulted in poor pollen germination and extreme embryo abortion. A necrotic condition acting as a physiological breakdown was found among the hybrids.

Self-incompatibility was found to be associated by linkage to three genes on chromosome two and several quantitative traits. A tentative linkage map of tomato chromosome two was constructed.

Self-incompatibility was transferred from *L. chilense* to the *L. esculentum* variety Tiny Tim by six backcrosses.

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