

## Genetic modifications of dimorphic incompatibility in the *Turnera ulmifolia* L. complex (Turneraceae)

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Diploid and tetraploid populations of *Turnera ulmifolia* are distylous and exhibit a strong self-incompatibility system. Distyly is governed by a single locus with two alleles. Several self-compatible variants were, however, obtained and the nature and genetic control of self-compatibility was assessed using controlled crosses. The study documented the occurrence of self-compatible variants in four contrasting situations. These included the following. (i) Self-compatibility in a diploid short-styled variant. The gene(s) governing self-compatibility interact with the distyly locus and are expressed only in short-styled plants. When tetraploids carrying the genes were synthesized, self-incompatibility reappeared. (ii) Self-compatibility occurred in a cross between geographically separate diploid populations. Self-compatibility appeared sporadically in the F<sub>1</sub>. Crosses revealed that self-compatibility is likely under polygenic control. (iii) Low levels of self-compatibility occurred in a tetraploid population. Crosses revealed that self-compatibility was under polygenic control. A small response to selection for increased self-compatibility was observed. (iv) Hexaploids were synthesized from crosses between distylous diploids and tetraploids. All hexaploids obtained were long- or short-styled indicating that hexaploidy *per se* does not cause homostyly. A single long-styled plant showed aberrant pollen behaviour, resulting in a moderate degree of self-compatibility. All of the variants studied exhibited either aberrant pollen or stylar incompatibility responses. In no instance was the genetic control of self-compatibility solely the result of segregation at the distyly locus.

**Key words:** *Turnera*, dimorphic incompatibility, polyploidy, self-compatibility, distyly.

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Des populations diploïdes et tétraploïdes de *Turnera ulmifolia* possèdent deux styles et un système hautement auto-incompatible. La distylie est gouvernée par un seul locus avec deux allèles. Cependant plusieurs variants auto-compatibles ont été obtenus et la nature de cette auto-compatibilité, de même que son contrôle génétique, ont été évalués à l'aide de croisements contrôlés. Pour cette étude, une documentation a été obtenue sur l'occurrence des variants auto-compatibles en fonction de quatre situations contrastantes. Celles-ci incluent: (i) l'auto-compatibilité survenant chez un variant diploïde brévistyle. Le ou les gènes qui gouvernent l'auto-compatibilité ont réagi avec le locus de la distylie et ne se sont exprimés que chez les plantes brévistyles. Lorsque des tétraploïdes porteuses des gènes furent synthétisées, l'auto-incompatibilité est réapparue. (ii) L'auto-compatibilité survenant entre des populations diploïdes géographiquement séparées. L'auto-compatibilité s'est manifestée sporadiquement chez les F<sub>1</sub>. Les croisements ont révélé que l'auto-compatibilité est probablement sous contrôle polygénique. (iii) De faibles niveaux d'auto-compatibilité survenant chez une population tétraploïde. Les croisements ont révélé que l'auto-compatibilité est sous contrôle polygénique. Une faible réponse à la sélection en vue d'augmenter l'auto-compatibilité a été observée. (iv) Des hexaploïdes ont été synthétisées par des croisements entre des diploïdes et des tétraploïdes distyliques. Toutes les hexaploïdes obtenus se sont avérées brevi- ou longi-styles, ce qui indique que l'hexaploïdie, comme telle, ne cause pas l'homostylie. Une seule plante longistyle a présenté un comportement aberrant, se traduisant par un degré modéré d'auto-compatibilité. Tous les variants à l'étude ont présenté soit un pollen aberrant, soit des réponses d'incompatibilité stylaire. Le contrôle génétique de l'auto-compatibilité n'a pas été, dans aucun cas, le seul résultat de la ségrégation au locus de la distylie.

**Mots clés:** *Turnera*, incompatibilité dimorphique, polyploïdie, auto-compatibilité, distylie.

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### Introduction

Dimorphic incompatibility (distyly) is a genetic polymorphism in which populations consist of two mating groups that usually differ in style length, stamen length, and incompatibility relationships. Several other floral

traits are commonly dimorphic; these include pollen size, pollen production, pollen exine sculpturing, and stigma morphology (see Ganders (1979) for a review). The incompatibility system in distylous species enforces disassortative mating between long- and short-styled plants. In the 12 genera from 10 families where the inheritance of distyly has been investigated (Ornduff 1979), the polymorphism has been shown to be governed by segregation of two alleles at a single locus. The

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short-styled morph is most commonly determined by the dominant allele, *S*, although exceptions are known (Baker 1966; Ornduff 1979). Distyly has undoubtedly had several independent origins as it occurs in a wide range of plant taxa including both dicotyledonous and monocotyledonous families (Charlesworth and Charlesworth 1979a).

Genetic studies of natural variants in *Primula* spp. (Ernst 1933, 1936a, 1936b, 1953, 1955; Dowrick 1956) provide evidence that distyly is controlled by at least three tightly linked loci and as such represents one of the classic examples of a supergene. The supergene model of the inheritance of distyly in *Primula* may be applicable to all distylous taxa since it is difficult to envision a single gene controlling all of the complementary features that characterize the floral morphs. An additional feature of the supergene model is it predicts that certain crossovers within the supergene will generate self-compatible homostylous variants with styles and stamens of equal length. Styles of homostylous plants exhibit the incompatibility behaviour of one of the distylous morphs while the pollen has the incompatibility reaction of the alternate morph. Homostyles are found at low frequencies in distylous populations (Ernst 1936a; Crosby 1949; Charlesworth and Charlesworth 1979b; Piper et al. 1984; Curtis and Curtis 1985; Cahalan and Gliddon 1985), or more commonly as close relatives of distylous taxa (Ganders 1979). Although the supergene model adequately explains several features of the distylous syndrome and its breakdown in *Primula*, little evidence is available from other taxa with dimorphic incompatibility (although see Baker 1958, 1966; Shore and Barrett 1985a; Barrett and Shore 1987).

Homostylous variants can also arise by genetic mechanisms other than by recombination within the distyly supergene. Nonrecombinant homostyles are known in *Amsinckia spectabilis* (Ganders 1979) and nonallelic major genes as well as polygenes are known to influence stamen and style length in *Primula sinensis* (Mather and de Winton 1941; Mather 1950). To determine the mode of origin of homostyly from distyly it is necessary to have information on the genetic basis of both distyly and homostyly in the species under investigation. In addition, studies of the compatibility relationships of distylous and homostylous forms are particularly useful in distinguishing between the various genetic mechanisms responsible for homostyle formation since the crossover model predicts a specific pattern of residual incompatibility in homostyles (see Fig. 1 in Dowrick 1956).

In the *Turnera ulmifolia* L. complex (Turneraceae), dimorphic incompatibility occurs in at least four taxonomic varieties at both diploid and tetraploid levels (Barrett 1978; Shore and Barrett 1985b). Distyly is controlled by a single gene locus with two alleles (Shore and Barrett 1985a). In diploids, short-styled plants are

*Ss* and long-styled plants *ss*. Tetraploids are *Ssss* and *ssss*, respectively. The incompatibility system in *T. ulmifolia* is strongly developed and few seeds are produced by selfing or intramorph crosses (Martin 1965; Barrett 1978; Bentley 1979). In addition to the distylous varieties within the complex, at least three self-compatible homostylous varieties have been described (*T. ulmifolia* vars. *angustifolia* Willd., *orientalis* Urb., and *velutina* Urb). These are hexaploid (Shore and Barrett 1985a, 1985b; Arbo 1985). The homostylous varieties of *T. ulmifolia* are atypical in showing wide variation in the relative positions of reproductive organs and hence the facility for autogamy (Barrett and Shore 1987). While all styles are "long," anther height ranges from "short" to "long." As a result, some populations exhibit the typical long-homostyle phenotype, with long styles and stamens, while others (particularly in var. *velutina*) have phenotypes similar to long-styled plants from dimorphic populations. This variation raises the possibility that the origin of self-compatible homostyles in the *T. ulmifolia* complex occurs by at least two distinct pathways. Homostyles may arise via recombination within the distyly supergene or alternatively, through loss of self-incompatibility in long-styled plants. The occurrence of rare self-compatible variants within distylous populations of *T. ulmifolia* lends support to the latter alternative. These variants form the basis of the present study.

In this paper the modes of origin of self-compatibility within the *T. ulmifolia* complex are explored by examining the nature and genetic basis of self-compatibility of variants from distylous populations or that have been synthesized from interpopulation crosses. We investigate the compatibility relationships and genetic basis of self-compatibility in four contrasting situations: (i) a diploid self-compatible variant and its synthetic tetraploid derivatives; (ii) a diploid self-compatible variant derived from an interpopulation cross; (iii) naturally occurring tetraploid self-compatible variants; and (iv) hexaploids synthesized from diploid and tetraploid distylous plants. We discuss the significance of the self-compatible variants for the evolution of breeding systems in the species complex, consider the genetic bases of self-compatibility, and implications for the genetical architecture and functioning of heterostyly.

### Materials and methods

All experimental work was performed under uniform conditions in the glasshouse facility at the Department of Botany, University of Toronto. Plants were established from bulk seed collections with the exception of plant I32-1S which was obtained from field-collected stem cuttings. Plants are referred to by a code specified in Shore and Barrett (1985a); the first letter indicates the varietal status, followed by population number, the individual's number, and its style form (L, long styled; S, short styled). Detailed localities may be found in Shore and Barrett (1985a, 1985b) with the exception

of population I22 which was collected along a roadside outside the town of Lucas Diaz in the Dominican Republic (Barrett and Shore 1362 TRT). See Barrett and Shore (1985a, 1985b) for cultural and pollination methods used in this study.

#### *Self-compatibility in a diploid variant*

The short-styled variant I32-1S was the sole representative of *T. ulmifolia* var. *intermedia* in a roadside population of *T. ulmifolia* var. *elegans* at Arco Verde, N.E. Brazil. The variant has a diploid chromosome number of  $2n = 10$ , whereas var. *elegans* is tetraploid ( $2n = 20$ ) in this area (Barrett and Shore 1987). Because the variant is phenotypically most similar to plants of population I1 from Barreirinhas, N.E. Brazil ( $2n = 10$ ), plants from this population were used in crosses with I32-1S to determine the compatibility relationships and genetic basis of self-compatibility.

Compatibility relationships of the variant I32-1S were determined by selfing and crossing reciprocally to long- and short-styled plants during the summer of 1984. Capsules were harvested just prior to dehiscence and the number of seeds per pollination and the percentage fruit set recorded. To determine the genetic basis of self-compatibility, several crosses were performed as follows: the variant was selfed to generate an  $S_1$  family and a single long-styled plant (I32-2L) was selected from the progeny for further crosses. Four  $F_1$  families were produced by the crosses I32-1S  $\times$  I1-10L, I32-2L  $\times$  I1-1S, and reciprocals. Three  $F_2$  families were generated by selfing the short-styled plants, B, G, and P, selected from the  $F_1$  crosses, I1-10L  $\times$  I32-1S, I1-1S  $\times$  I32-2L, and I32-2L  $\times$  I1-1S, respectively. Progeny were screened for self-compatibility in the following manner: replicate self-pollinations were performed on each progeny individual and fruit and seed set recorded, with the exception of the four  $F_1$  families where only percent fruit set was recorded. Screening was undertaken for the selfed family using five replicate self-pollinations per plant (autumn of 1982), for the four crosses ( $F_1$ 's) (summer of 1983), the three  $F_2$  families using three replicate pollinations for the latter families (summer of 1984).

To investigate the influence of ploidal level on the compatibility behaviour of the variant, several seedlings of the cross I32-1S  $\times$  I1-10L were treated with 1% colchicine by suspending a drop of aqueous solution on the apical meristem of 2-day-old seedlings. The treatment was repeated for 2 or 3 days. Several tetraploid plants were obtained, some of which were diploid-tetraploid mosaics, with some branches possessing the diploid chromosome number,  $2n = 10$ , and others tetraploid,  $2n = 20$  (as determined from chromosome counts of meiotic material). An analysis of the compatibility behaviour of the mosaics was performed by selfing and crossing diploid and tetraploid flowers of the mosaics to long- and short-styled plants of equivalent ploidal level. In addition, interploidal crosses were also undertaken (summer of 1985).

#### *Self-compatibility in an interpopulation cross*

To investigate the influence of interpopulation crosses on the expression of self-incompatibility in *T. ulmifolia*, a wide cross involving diploid material of var. *intermedia* from Brazil and Venezuela was undertaken. The parental individuals were strongly self-incompatible. An initial screening of several  $F_1$  progeny from the cross I3-3S  $\times$  I1-10L revealed weakening of

the self-incompatibility system (summer of 1981). A single highly self-compatible long-styled plant (I113-3L) among the  $F_1$  progeny was discovered. The plant was selfed to determine the genetic basis of self-compatibility. Its progeny ( $F_2$ ) and the original  $F_1$  were screened for self-compatibility using five replicate self-pollinations for each plant (summer of 1982). In addition, the compatibility behaviour of the self-compatible plant and three of its selfed progeny were determined (summer of 1985) by selfing and crossing individuals with plants from the parental populations from which they were derived (populations I3 and I1).

#### *Self-compatibility in tetraploid variants*

Surveys of self-incompatibility in a tetraploid population of *T. ulmifolia* var. *elegans* (E5) revealed the presence of one moderately self-compatible long-styled plant (E5-1L) and a short-styled plant (E5-10S) which set a small number of seeds upon self-pollination. Plant E5-1L was originally discovered by Barrett (1978) and has been maintained clonally for 10 years, during which time it has consistently displayed a moderate degree of self-compatibility. The compatibility behaviour of both plants was determined by crossing the variants to self-incompatible plants obtained from the same population.

To examine the inheritance of self-compatibility, several crosses were performed as follows: the self-compatible plants were selfed and crossed reciprocally to generate two  $S_1$  families and an  $F_1$  family, respectively. Two highly self-compatible individuals were selected from each of the three families and selfed to generate four  $S_2$  families and two  $F_2$  families. The plants selected were LL61L and LL51L from the  $S_1$  family of E5-1L, SS3S and SS7S from the  $S_1$  family of E5-10S, and SL36L and SL34S from the  $F_1$  family of the cross E5-1L  $\times$  E5-10S. All families and the parental population were screened for self-compatibility (as above). The parental,  $F_1$ , and  $S_1$  families were screened using 10 replicate self-pollinations per plant (summer of 1981) and the  $F_2$  and  $S_2$  families were screened using five replicate pollinations (summer of 1982).

#### *Self-compatibility in synthetic hexaploids*

Because an association between hexaploidy and homostyly in *T. ulmifolia* occurs (Shore and Barrett 1985a), hexaploids were synthesized in the following manner to determine if hexaploidy causes homostyle formation. Triploid seed was produced from the tetraploid  $\times$  diploid crosses I24-2S  $\times$  I6-12L and I22-4L  $\times$  I6-31S. Seedlings were then raised and treated with colchicine, as indicated above, to produce 18 hexaploid plants, (five long- and 13 short-styled plants). Ploidal levels were verified by chromosome counts of meiotic material. Synthetic hexaploids were easily distinguished by high pollen fertility and large pollen size. In contrast, triploid plants were virtually pollen sterile. The synthetic hexaploids were screened for self-compatibility by replicate self-pollinations. A single self-compatible long-styled plant was obtained, it was selfed, and progeny were screened for self-compatibility (summer of 1985). Additionally, the hexaploid synthetic variant and its selfed progeny were crossed to diploid long- and short-styled plants of population I1 to determine their compatibility behaviour.

## Results

### *Self-compatibility in a diploid variant*

Compatibility behaviour of the short-styled variant I32-1S is presented in Table 1. The plant is highly self-compatible, setting an average of 30 seeds/fruit when self-pollinated, and a full complement of seed when used as the female parent in crosses with long- and short-styled plants. However, the plant is only successful as a pollen parent in crosses with long-styled individuals. These data indicate that the variant possesses aberrant stylar behaviour. Its style will not reject pollen from short-styled plants, while its pollen exhibits the normal incompatibility response.

The genetic basis of self-compatibility in the stylar variant was evaluated in several crosses (Table 2). A large number of progeny from the S<sub>1</sub> family of I32-1S (136) were screened for self-compatibility. A striking pattern emerged with all long-styled progeny showing virtually complete self-incompatibility, while short-styled plants were self-compatible to varying degrees (Table 2 and Fig. 1). A continuous distribution of selfed seed set was exhibited among short-styled progeny. These data are consistent with a single-locus model of the control of self-compatibility. A modified allele at the distyly locus (*Sc*), which is dominant to *s*, confers self-compatibility upon short-styled plants. The continuous distribution of selfed seed set among short-styled progeny may result from segregation of genes with minor effects on the expression of self-incompatibility as well as environmental effects.

To test the hypothesis of a single allele, *Sc*, governing self-compatibility in the stylar variant, the following crosses were performed: (i) the variant I32-1S was crossed reciprocally with I1-10L to test for maternal effects; (ii) a single long-styled plant (I32-2L) obtained from the selfed progeny of the variant I32-1S was crossed reciprocally with a self-incompatible short-styled plant from population I1 (I1-1S). If the hypothesis is correct, all progeny from the latter cross (and reciprocal) should be self-incompatible, as neither I32-2L or I1-1S would carry the *Sc* allele. Data from the cross I32-1S × I1-10L and reciprocal are consistent with the hypothesis of a single dominant *Sc* allele governing self-compatibility in the variant (Table 2). However, data from the cross I32-2L × I1-1S falsify the hypothesis since all long-styled progeny exhibit self-incompatibility, while short-styled plants are largely self-compatible (Table 2). Neither cross shows reciprocal effects. Thus, self-compatibility in the stylar variant is not determined by a single dominant allele segregating at the distyly locus, nor is a cytoplasmic factor involved.

An alternative hypothesis consistent with these data is that self-compatibility in the diploid stylar variant is controlled by a nonallelic dominant gene possibly linked

TABLE 1. Compatibility behaviour of I32-1S in crosses with plants from population I1. All plants are from diploid ( $2n = 10$ ) populations of *Turnera ulmifolia* var. *intermedia*. The number of plants of population I1 used is indicated

Cross	No. of plants	No. of pollinations	Mean seeds/pollination ± SD	% fruit set
I32-1S × short	7	35	36.0 ± 5.7	100.0
I32-1S × long	5	14	36.5 ± 6.2	100.0
Short × I32-1S	7	35	0.1 ± 0.2	8.6
Long × I32-1S	5	14	28.9 ± 6.6	100.0
I32-1S selfed	—	5	30.0 ± 8.3	100.0

TABLE 2. Comparison of selfed fruit set among eight families derived from crosses involving plant I32-1S. Results are based on three replicate pollinations per plant with the exception of the I32-1S selfed family for which five replicate pollinations were performed. I32-2L is a long-styled plant from the selfed progeny of I32-1S

Cross	Long-styled progeny		Short-styled progeny	
	No. of plants	% fruit set	No. of plants	% fruit set
I32-1S self (S <sub>1</sub> )	31	1.9	105	92.4
I32-1S × I1-10L	18	0.0	18	83.3
I1-10L × I32-1S	18	0.0	23	84.1
I32-2L × I1-1S	20	0.0	22	83.3
I1-1S × I32-2L	34	0.0	27	90.1
B selfed (F <sub>2</sub> ) <sup>a</sup>	6	5.6	35	83.8
G selfed (F <sub>2</sub> ) <sup>b</sup>	11	3.0	33	87.9
P selfed (F <sub>2</sub> ) <sup>c</sup>	1	0.0	41	70.7

<sup>a</sup>Derived from cross I1-10L × I32-1S.

<sup>b</sup>Derived from cross I1-1S × I32-2L.

<sup>c</sup>Derived from cross I32-2L × I1-1S.

to the distyly locus. The gene exhibits an epistatic interaction with the distyly locus with self-compatibility only expressed in the presence of the *S* allele. Three short-styled individuals, B, G, and P (obtained from the F<sub>1</sub> crosses I1-10L × I32-1S, I1-1S × I32-2L, and I32-2L × I1-1S, respectively), heterozygous for the putative gene were selfed and their F<sub>2</sub> progeny screened for self-compatibility. Under the above hypothesis (and in the absence of linkage) we would expect three-quarters of the short-styled progeny to be self-compatible, while the remaining quarter should be self-incompatible; all long-styled progeny should be self-incompatible. In the presence of linkage there are different expectations for the selfed families of B versus G and P and these will vary with the recombination frequency. For the family of B, we expect all short-styled plants to exhibit

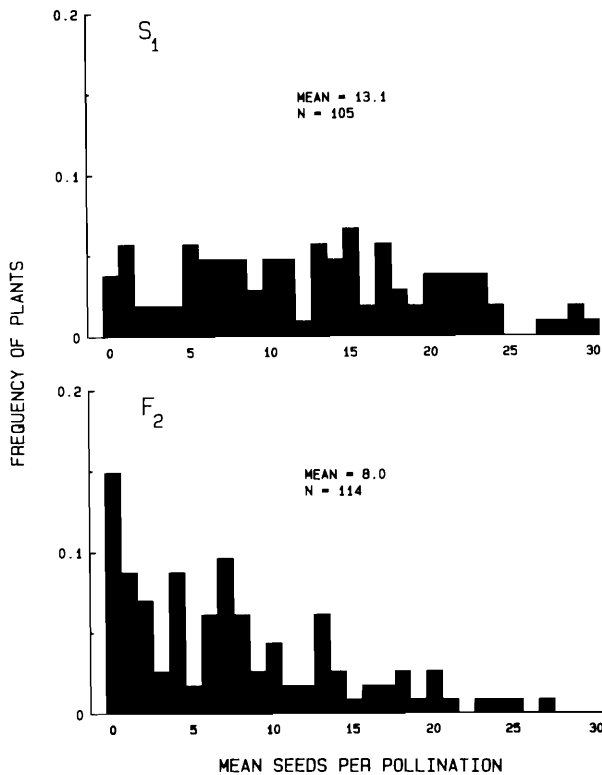


FIG. 1. The distributions of mean seed set per self-pollination among short-styled progeny of  $S_1$  and  $F_2$  families of *T. ulmifolia* var. *intermedia* ( $2n = 10$ ). The  $S_1$  family was derived by selfing the diploid self-compatible styler variant I32-1S. The  $F_2$  distribution was obtained by pooling short-styled progenies of the selfed families of plants B, G, and P. These were derived from the crosses I1-10L  $\times$  I32-1S, I1-1S  $\times$  I32-2L, and I32-2L  $\times$  I1-1S, respectively. Five replicate self-pollinations were used for each  $S_1$  plant and three for each  $F_2$ . The mean selfed seed set, mean percent fruit set, and number of plants used are indicated.

self-compatibility in the absence of recombination and for families of G and P, we expect two-thirds of the three short-styled progeny to be self-compatible.

Data from the three selfed families ( $F_2$ ) indicate that long-styled progeny are largely self-incompatible exhibiting only 3% fruit set from self-pollination in all families (Table 2). Among the short-styled progeny 84, 88, and 71% of the progeny from the three selfed families of B, G, and P, respectively, set fruit. The similar levels of fruit set among the selfed families of B and G indicate that the single unlinked gene model may be more appropriate. However, a continuous distribution of selfed seed set is observed among the short-styled progeny from all families in which it was evaluated (Fig. 1). Thus, although the data are consistent with a single gene model, the model does not readily explain the continuous distribution of selfed seed set among

short-styled progeny. It is possible that more than one gene is involved in determining self-compatibility in the styler variant and that these interact with the *S* locus so that self-compatibility is only exhibited by short-styled plants.

To investigate the effect of polyploidization on the compatibility behaviour of the variant, tetraploids were synthesized. Eight diploid-tetraploid mosaics were obtained by colchicine doubling, of which six were short-styled and two were long-styled. Polyploid shoots could be readily distinguished from diploid shoots by pollen size. In the short-styled mosaics, diploid shoots had a mean pollen length of  $77.3 \pm 0.7 \mu\text{m}$  and tetraploid shoots  $95.2 \pm 2.8 \mu\text{m}$ . Diploid shoots of long-styled mosaics had a mean pollen length of  $65.1 \pm 0.6 \mu\text{m}$  and tetraploid shoots  $83.8 \pm 2.6 \mu\text{m}$ . Meiotic counts from shoots classified as diploid or tetraploid based on pollen size confirmed the ploidal level of shoots in the five instances where it was examined. Pollen fertility (assessed by scoring the stainability of 100 pollen grains from each ploidal level on each of six mosaics) was lower for tetraploid shoots than diploid ( $75.7 \pm 9.2$  vs.  $95.6 \pm 5.5$  mean % pollen stainability). Other "gigas" features shown by tetraploid shoots included, greater floral diameter, stamen length, and style length (about 1 mm larger).

The seven mosaic plants and three synthetic nonmosaic tetraploids, all derived from the same family, were tested for their compatibility behaviour (Tables 3 and 4). Remarkably, tetraploid sectors of short-styled plants are largely self-incompatible, while diploid shoots on the same plant are highly self-compatible. Both diploid and tetraploid shoots of long-styled plants remained self-incompatible. Legitimate crosses of tetraploid short-styled shoots exhibit a lower seed set than diploids, however, the reduction is insufficient to account for the low degree of selfed seed set in tetraploids. Thus self-compatibility seems to have reappeared in the synthetic tetraploids. Interestingly, crosses between diploid and tetraploid short-styled plants reveal that the styler modification remains in the synthetic tetraploids. Ample seed is set when the tetraploid short-styled plants are crossed with pollen of diploid short-styled plants; the reverse pattern does not occur (Tables 3 and 4).

The synthetic tetraploid short-styled plants are of genotype  $SSss$  as a result of somatic chromosome doubling. To examine whether dosage effects involving the *S* allele are responsible for reemergence of self-incompatibility, several short-styled progeny obtained from the cross of a synthetic tetraploid long- and short-styled plant (LN1L  $\times$  SN1S and reciprocal) were screened for self-compatibility. Short-styled progeny from this cross will be of genotype  $Ssss$ . A total of 106 plants was screened for self-compatibility using three replicate pollinations per plant. The combined selfed

TABLE 3. Compatibility behaviour of diploid-tetraploid mosaics derived from I32-1S. Mean seed set/pollination  $\pm$  SD (number of pollinations) are provided

Plant	Ploidal level	Self	Legitimate cross as egg parent	Legitimate cross as pollen parent
S1	4x	0.2 $\pm$ 0.6(15)	10.0 $\pm$ 7.5(5)	12.6 $\pm$ 12.6(6)
	2x	4.0(1)	31.0(1)	65.0(1)
S2	4x	0.5 $\pm$ 1.1(8)	18.5 $\pm$ 2.1(2)	24.0 $\pm$ 24.0(2)
	2x	21.0 $\pm$ 11.5(8)	34.0 $\pm$ 2.5(5)	49.4 $\pm$ 4.2(4)
S3	4x	0.6 $\pm$ 1.2(31)	8.0 $\pm$ 5.7(2)	17.0 $\pm$ 9.9(2)
	—	—	—	—
S4	4x	5.1 $\pm$ 4.7(9)	13.0 $\pm$ 18.4(2)	35.0 $\pm$ 2.8(2)
	2x	24.5 $\pm$ 7.2(19)	24.2 $\pm$ 1.5(5)	44.0 $\pm$ 21.2(5)
S5	4x	2.7 $\pm$ 3.1(3)	14.3 $\pm$ 5.7(3)	26.5 $\pm$ 16.3(2)
	2x	11.7 $\pm$ 6.8(23)	17.0 $\pm$ 10.4(3)	37.0 $\pm$ 32.1(3)
S6	4x	0.0 $\pm$ 0.0(12)	35.7 $\pm$ 4.5(3)	24.7 $\pm$ 6.7(3)
	—	—	—	—
S7	4x	5.2 $\pm$ 3.7(5)	32.0(1)	28.0(1)
	2x	28.8 $\pm$ 15.9(14)	49.0(1)	41.0(1)
S8	4x	0.7 $\pm$ 1.0(15)	23.5 $\pm$ 13.2(4)	24.3 $\pm$ 16.4(4)
	—	—	—	—
Mean	4x	1.9 $\pm$ 2.2(8)	19.4 $\pm$ 10.2(8)	24.0 $\pm$ 6.8(8)
	2x	18.0 $\pm$ 10.0(5)	31.0 $\pm$ 12.0(5)	47.3 $\pm$ 10.9(5)
L1	4x	0.0 $\pm$ 0.0(18)	21.6 $\pm$ 12.9(18)	18.4 $\pm$ 13.1(18)
	—	—	—	—
L2	—	—	—	—
	2x	0.7 $\pm$ 1.5(17)	32.0 $\pm$ 13.9(3)	33.0 $\pm$ 13.9(3)
L3	4x	0.0 $\pm$ 0.0(4)	32.7 $\pm$ 8.5(3)	22.0 $\pm$ 3.5(3)
	2x	0.1 $\pm$ 0.3(13)	46.0 $\pm$ 7.8(4)	31.5 $\pm$ 5.7(4)
L4	4x	0.0(1)	15.0(1)	8.0(1)
	2x	0.1 $\pm$ 0.2(17)	50.5 $\pm$ 21.8(8)	24.7 $\pm$ 9.4(8)
Mean	4x	0.0 $\pm$ 0.0(3)	23.1 $\pm$ 8.9(3)	16.1 $\pm$ 7.3(3)
	2x	0.3 $\pm$ 0.3(3)	42.8 $\pm$ 9.7(3)	29.7 $\pm$ 4.4(3)

seed set data yielded a mean of  $0.3 \pm 0.7$  seeds/self-pollination. Of the 16 long-styled plants in the progeny, none set seed. Further, the compatibility behaviour of 10 short-styled progeny were assessed in crosses with diploid short-styled plants. When used as females in crosses to diploid short-styled males, these plants set  $12.9 \pm 9.0$  seeds/pollination while the reciprocal cross yielded  $2.9 \pm 1.7$ . Hence, *SSss* and *Ssss* short-styled synthetic tetraploids exhibit similar compatibility behaviour indicating no dosage effects of the *S* allele on self-incompatibility.

#### *Self-compatibility in an interpopulation cross*

To examine the influence of interpopulation crosses on the expression of self-incompatibility, an  $F_1$  was produced by crossing plants from geographically sepa-

rate populations. An initial screening of the  $F_1$  revealed the presence of a plant (I113-3L) which set an average of 13 seeds upon self-pollination (Table 5). An  $F_2$  family was produced by selfing this plant; all progeny, as expected, were long styled. The compatibility relationships of individual I113-3L and three of its selfed progeny indicate that they are pollen variants. Pollen from the plants effects fertilization on both long- and short-styled maternal plants. The styles, however, retain the expected incompatibility reactions of long-styled morphs in typical distylous populations (Table 5). The distributions of self-compatibility in the original  $F_1$  population and among the  $F_2$  generated by selfing I113-3L are presented in Fig. 2. A single generation of selection yielded a small positive response in the family means. The mean degree of self-compatibility, as

TABLE 4. Summary of compatibility behaviour among diploids ( $2n = 10$ ) and synthetic tetraploids ( $2n = 20$ ) derived from the cross I32-1S  $\times$  I1-10L of *T. ulmifolia* var. *intermedia*. Mean seeds/pollination  $\pm$  SD (no. of male parents) are presented

Female parent		Male parent			
Style morph	Ploidal level	Short (4x)	Short (2x)	Long (4x)	Long (2x)
Short	4x	2.0 $\pm$ 2.1(7) 30*	21.3 $\pm$ 9.2(7) 30	22.7 $\pm$ 11.6(3) 7	26.2 $\pm$ 8.1(3) 4
Short	2x	1.4 $\pm$ 0.5(4) 30	20.9 $\pm$ 6.5(4) 26	17.8 $\pm$ 10.3(2) 3	21.0(1) 1
Long	4x	24.4 $\pm$ 1.6(2) 7	35.0 $\pm$ 4.2(2) 3	0.0 $\pm$ 0.0(3) 23	0.0 $\pm$ 0.0(2) 14
Long	2x	17.8 $\pm$ 4.7(1) 4	37.0(1) 1	0.0 $\pm$ 0.0(2) 13	0.3 $\pm$ 0.3(3) 47

\*Number of pollinations.

TABLE 5. Compatibility behaviour of I311-3L (derived from the cross I3-3S  $\times$  I1-10L) and three of its selfed progeny ( $F_2$ ) in crosses with plants from the parental populations I1 and I3 of *T. ulmifolia* var. *intermedia* ( $2n = 10$ )

Cross	No. of pollinations	Mean seeds/pollination $\pm$ SD	% fruit set
I311-3L selfed	8	13.3 $\pm$ 4.7	100.0
I311-3L $\times$ short	5	11.0 $\pm$ 7.1	100.0
I311-3L $\times$ long	7	0.0 $\pm$ 0.0	0.0
Short $\times$ I311-3L	3	20.3 $\pm$ 5.1	100.0
Long $\times$ I311-3L	7	4.1 $\pm$ 4.9	57.1
$F_2$ selfed	8	6.6 $\pm$ 5.3	87.5
$F_2$ $\times$ short	3	15.3 $\pm$ 1.1	100.0
$F_2$ $\times$ long	9	0.0 $\pm$ 0.0	0.0
Short $\times$ $F_2$	6	21.0 $\pm$ 5.1	100.0
Long $\times$ $F_2$	10	9.3 $\pm$ 12.7	60.0

measured by the number of seeds per self-pollination, increased from 0 in the parental populations (see data in Barrett 1978) to 1.1 in the  $F_1$ , and 6.1 in the selected  $F_2$ .

The genetic basis of self-compatibility in this material is not readily interpretable. The  $F_2$  shows a continuous distribution of seed set on self-pollination suggesting polygenic control. The limited appearance of self-compatibility in the  $F_1$  and its retention in the  $F_2$  suggests that some unique combination of genes may have been brought together in the  $F_1$ , resulting in the sporadic occurrence of self-compatibility.

#### Self-compatibility in tetraploid pollen variants

Occasional individuals in tetraploid *T. ulmifolia* var. *elegans* possess a small degree of self-compatibility (Barrett 1978). The compatibility relationships of two

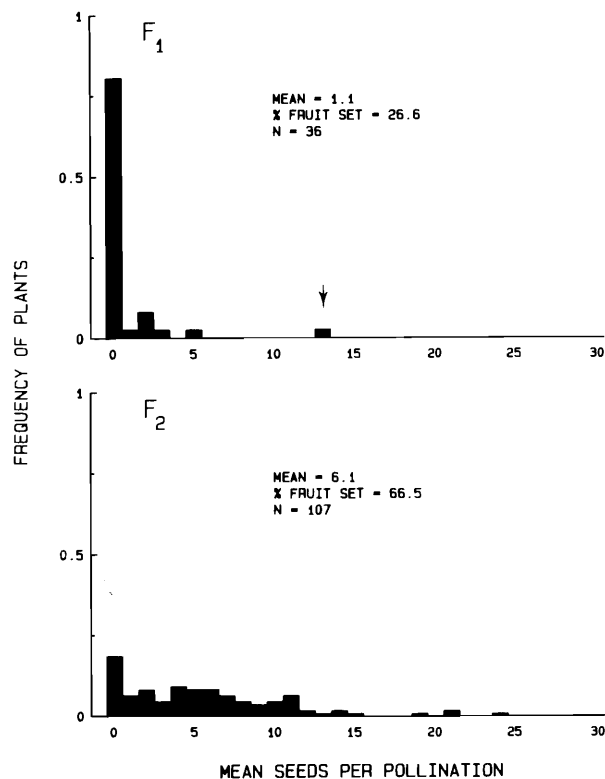


FIG. 2. The distributions of mean seed set per self-pollination among progeny of  $F_1$  and  $F_2$  families of an interpopulation cross of *T. ulmifolia* var. *intermedia* ( $2n = 10$ ). The  $F_1$  family was derived by the interpopulation cross I3-3S  $\times$  I1-10L. The  $F_2$  family was obtained by selfing the most highly self-compatible  $F_1$  plant, I311-3L, indicated by the arrow. Five replicate pollinations were used for each plant screened. The mean selfed seed set, mean percent fruit set, and number of plants used are indicated.

TABLE 6. Compatibility behaviour of two self-compatible plants from population E5 of *T. ulmifolia* var. *elegans* ( $2n = 20$ ), in crosses with self-incompatible plants from the same population. The number of self-incompatible plants used is indicated

Cross	No. of plants	No. of pollinations	Mean seeds/ pollination $\pm$ SD	% fruit set
E5-1L $\times$ long	5	50	0.0 $\pm$ 0.0	0.0
E5-1L $\times$ short	4	7	24.6 $\pm$ 6.8	100.0
Long $\times$ E5-1L	5	50	16.6 $\pm$ 4.4	98.0
Short $\times$ E5-1L	4	8	25.4 $\pm$ 8.0	100.0
E5-1L selfed	1	10	16.2 $\pm$ 6.3	100.0
E5-10S $\times$ long	4	13	28.4 $\pm$ 6.1	100.0
E5-10S $\times$ short	5	50	0.0 $\pm$ 0.0	0.0
Long $\times$ E5-10S	4	13	27.1 $\pm$ 9.5	100.0
Short $\times$ E5-10S	5	50	3.6 $\pm$ 6.1	78.0
E5-10S selfed	1	10	2.7 $\pm$ 2.6	80.0

variants studied here revealed that self-compatibility is the result of aberrant pollen behaviour. Intramorph pollinations as well as intermorph pollinations yield seed when the variants are used as pollen donors. Styles of the pollen variants exhibit normal incompatibility responses (Table 6). The amount of selfed seed set in both plants is lower than that obtained by legitimate pollination. However, the long-styled variant shows a greater degree of self-compatibility than the short-styled variant.

The inheritance of self-compatibility in tetraploid individuals of *T. ulmifolia* var. *elegans* is likely to be polygenic. Several crosses were conducted and the results are presented in Fig. 3. Results for the two families have been pooled for each generation since they were not significantly different. Additionally, long- and short-styled progeny in segregating families exhibited little variation in the degree of self-compatibility and accordingly only pooled results are shown. Low germination percentage of  $S_2$  families derived from E5-1L resulted in limited numbers of progeny for this cross.

The most striking feature of the data obtained from selfs and crosses of the pollen variants is the occurrence of a large number of self-incompatible progeny that have arisen from selfing plants that exhibit moderate levels of self-compatibility (e.g., E5-1L selfed). However, an increase in the mean seed set per self-pollination and percent fruit set occurred in successive generations (Fig. 3). The mean seed set in the parental population was 0.7 (11% fruit set) and increased to a maximum of 2.5 seeds/pollination (41% fruit set) in the  $S_2$  family with the highest mean level of self-compatibility.

Plant E5-1L was the most self-compatible individual in the parental population. None of its selfed progeny exhibited as large a degree of self-compatibility. In

TABLE 7. Compatibility behaviour of synthetic hexaploids of *T. ulmifolia* var. *intermedia* ( $2n = 30$ ), a self-compatible plant, and four of its  $S_1$  progeny (SYN6XL) in crosses with diploid plants from population I1 ( $2n = 10$ ). The number of plants from populations I1 used is provided

Cross	No. of plants	No. of pollinations	Mean seeds/ pollination $\pm$ SD	% fruit set
SYN6XL $\times$ short	4	8	17.0 $\pm$ 6.3	100.0
SYN6XL $\times$ long	5	17	0.2 $\pm$ 0.2	23.5
Short $\times$ SYN6XL	3	8	19.9 $\pm$ 6.3	75.0
Long $\times$ SYN6XL	4	18	11.0 $\pm$ 1.2	88.8
SYN6XL selfed	5	28	13.1 $\pm$ 4.7	100.0
SYN6XS selfed	13	49	0.0 $\pm$ 0.0	0.0
SYN6XL selfed <sup>a</sup>	4	20	0.0 $\pm$ 0.0	0.0

<sup>a</sup>These are the synthetic hexaploids originally generated excluding the self-compatible long-styled variant.

contrast, selfed progeny from E5-10S were more highly self-compatible than the original parent, with one plant setting a mean of 27 seeds/self-pollination. The data suggest that several genes are segregating in the population and these confer varying degrees of self-compatibility upon both style morphs, via aberrant pollen compatibility behaviour.

#### *Self-compatibility in synthetic hexaploids*

All hexaploid varieties of *T. ulmifolia* that have been studied are self-compatible. To evaluate whether hexaploidy *per se* might result in a weakening of the incompatibility system, synthetic hexaploids were generated from self-incompatible distylous plants. Five long- and 13 short-styled hexaploids were synthesized. All individuals were strongly self-incompatible with the exception of a single long-styled plant which produced moderate amounts of seed upon self-pollination (Table 7).

The compatibility relationships of the long-styled variant and four of its selfed progeny were assessed (Table 7). All progeny were moderately self-compatible. Pollen from these plants was capable of fertilizing either style form. However, their styles exhibited the usual incompatibility response. Thus the plant and its progeny exhibit aberrant pollen behaviour similar to that observed in the natural tetraploid variants and the diploid variant derived from an interpopulation cross, both discussed above.

#### Discussion

The present study documents the occurrence of self-compatible distylous variants in diploid and tetraploid populations of the *Turnera ulmifolia* complex. All plants are either long- or short-styled. None of the

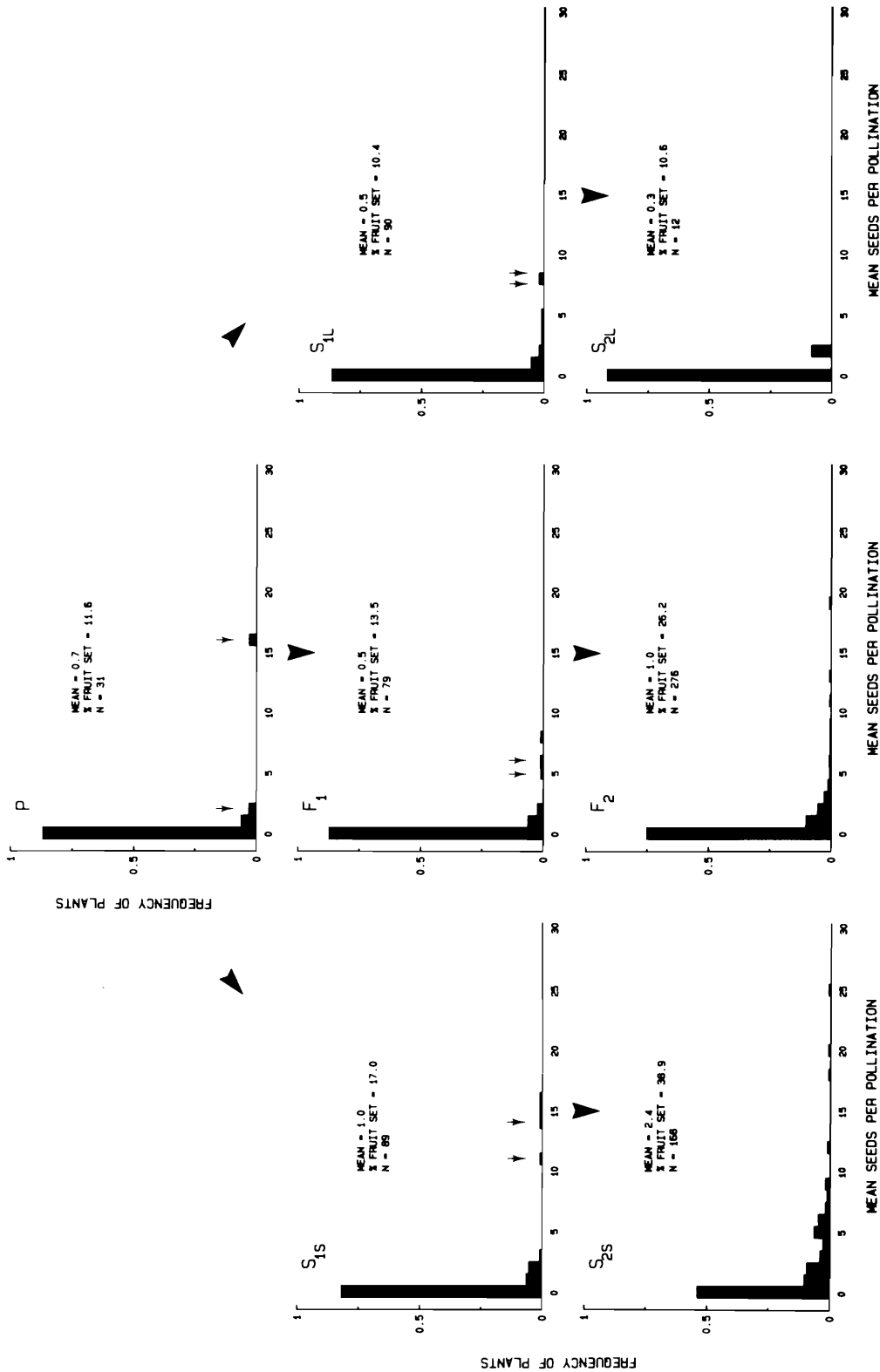


FIG. 3. The distributions of mean seed set per self-pollination among the parental population (P), F<sub>1</sub>, F<sub>2</sub>, S<sub>1</sub>, and S<sub>2</sub> families of *T. ulmifolia* var. *elegans* (2n = 20) obtained from population E5. The arrows indicate the plants used in generating subsequent populations. For the parental distribution (P) the arrow at the right indicates the mean selfed seed set of E5-1L, which was selfed to generate the S<sub>1L</sub> family. Two plants from this family (S<sub>1L</sub>), indicated by the arrows, were selfed (LL51L and LL61L) to generate the S<sub>2L</sub> family. Similarly, the most self-compatible short-styled plant in the parental population was selfed (indicated by the arrow on the far left in P) to generate the S<sub>1S</sub> family. Two individuals from this family (S<sub>1S</sub>), indicated by the arrows, were selfed (SS77S and SS3S) to generate the S<sub>2S</sub> families. The two parental individuals were crossed to generate the F<sub>1</sub>. Two plants in the F<sub>1</sub>, indicated by the arrows (SL36L and SL34S), were selfed to generate the F<sub>2</sub>. The mean selfed seed set, mean percent fruit set, and number of plants used are provided.

variants display the compatibility relationships expected of self-compatible recombinants generated by crossing-over within the supergene controlling distyly. Instead, they behave as though either their pollen or stylar incompatibility function has been abolished or weakened in strength. Recombinants of the distyly supergene are expected to show both pollen and stylar incompatibility reactions. The variants observed in the present study are perhaps best described as genetically pseudo-compatible (East 1927; Pandey 1959; Mulcahy 1984), although the term encompasses a range of different compatibility phenomena and several different genetic mechanisms. In this discussion, the implications of the occurrence of self-compatible variants for the evolution of breeding systems within the *T. ulmifolia* complex is considered. Specifically, we address the question of whether similar variants could have given rise to the self-compatible varieties that occur within the species complex (Urban 1883; Barrett 1978; Shore and Barrett 1985a, 1985b). Additionally, the genetic basis of the observed patterns of self-compatibility are discussed and the possible implications for the genetical architecture and function of distyly are also considered.

In this study an unusual diploid short-styled stylar variant was identified. The plant cannot be interpreted as having arisen via recombination within the distyly supergene as its style exhibits null activity, accepting pollen from either long- or short-styled plants. Crosses were performed to see if a modified *S* allele was responsible for self-compatibility. The results indicate that the gene(s) responsible for self-compatibility are not allelic to the distyly locus. Self-compatibility may be the result of a single dominant gene, or more likely several genes, which interact with the distyly locus and result in self-compatibility in the presence of at least one *S* allele. Shore and Barrett (1985a) demonstrated the occurrence of four self-compatible *SS* short-styled plants among 19 short-styled progeny examined from the self of this variant. The compatibility behaviour of the variant indicates that genes at other loci may modify the incompatibility response, as has been documented in *Primula sinensis* (Beale 1938; Mather and de Winton 1941; Mather 1950).

Synthetic diploid-tetraploid mosaics were produced from the stylar variant. The plants carry the gene(s) conferring self-compatibility. Surprisingly, tetraploid short-styled shoots exhibited a high degree of self-incompatibility, while diploid shoots on the same plants were highly self-compatible. The phenomenon is not the result of a reduced fertility of the tetraploids as legitimate crosses set ample seed and pollen fertility is only 20% lower than that of the diploids. This is possibly the first report of a transition from a self-compatible to a self-incompatible condition via polyploidy. It is the exact reversal of the situation in dicotyledonous species

with gametophytic incompatibility. In these plants polyploidy results in loss of self-incompatibility (Stout and Chandler 1942; Lewis 1947; Brewbaker 1954, 1958; Annerstedt and Lundqvist 1967; de Nettancourt 1977).

Further crosses involving the synthetic tetraploids, with pollen derived from diploids, revealed that the stylar modification remained. Pollen obtained from short-styled diploid shoots gave abundant seed. The significance of these findings to the operation of the incompatibility system is not immediately apparent. As pollen size in synthetic tetraploids is larger than in diploids, it is possible that the variant style only allows pollen that is below some threshold size to achieve fertilization. Alternatively, some correlate of pollen size may differ between the ploidal levels and may be responsible for the observed effect.

All remaining self-compatible variants of *T. ulmifolia* that we examined show aberrant pollen behaviour, with pollen exhibiting a weakened incompatibility response in self- and own-form pollinations. The appearance of self-compatibility in the  $F_1$  progeny of a cross between two geographically separated diploid populations and the continuous distribution of self-compatibility in the  $F_2$  suggests that polygenic modification of the self-incompatibility system is involved. Self-compatibility may result from disruption of the genetic background in which the *S* alleles normally function. That other loci or polygenes can modify the strength of self-compatibility in distylous taxa has been demonstrated (see above), and ample evidence of such effects are available for homomorphic gametophytic and sporophytic systems (Mather 1943; Nasrallah and Wallace 1968; Richards and Thurling 1973; Henny and Ascher 1976; Sharma and Murty 1979; Litzow and Ascher 1983). The interpopulation cross performed here is likely to have given rise to unique combinations of genes. In this background the *S* alleles may not function with complete efficiency resulting in varying levels of self-compatibility. The occurrence of natural and artificial self-compatible polyploids may also result from similar processes. Polyploidy may lead to the origin and establishment of self-compatible taxa that arise by hybridization between differentiated population systems through disruption of genetic backgrounds.

The occurrence of dimorphic incompatibility in synthetic hexaploids demonstrates that hexaploidy, at its inception, does not disrupt the genes governing distyly. However, it should be noted that it was possible to establish a self-compatible line from a single long-styled synthetic hexaploid pollen variant. The self-compatible plants do not, however, exhibit the compatibility relationships shown in natural hexaploids (Barrett and Shore 1987).

Some progress was made in selecting for increased

self-compatibility in pollen variants from a tetraploid population. However, the increase in strength of self-compatibility was not marked, and the most striking feature of the data was the high proportion of self-incompatible plants in the selfed progeny of highly self-compatible parental plants. It is important to note that the  $F_1$  and  $S_1$  populations were screened in a different year than the  $F_2$  and  $S_2$  populations. Thus, while every effort was made to ensure that screening was carried out under similar environmental conditions, the possibility exists that the observed response was partly environmental in origin. Additionally, if inbred progeny show a reduction in seed set as a result of inbreeding depression, then the measure of self-compatibility used here will underestimate the true value. The bias, if such an effect occurs, is towards reducing the possibility of detecting a selective response. Mather and de Winton (1941) have suggested that selection for increased self-compatibility has occurred in horticultural strains of *Primula sinensis*. This is presumably the result of polygenic modification of the strength of self-incompatibility.

The evolutionary significance of the low levels of self-compatibility observed in natural populations is not clear. Genes determining self-compatibility may rarely be exposed to selection owing to the prevalence of disassortative mating in populations. However, on rare occasions, as a result of colonizing episodes, the small amount of seed that can be produced on self-fertilization may lead to the establishment of self-compatible populations (Baker 1955; Jain 1976). The data further suggest that if two previously isolated populations hybridize, genetic variation for self-compatibility could be exposed to selection.

Natural hexaploid populations of *T. ulmifolia* are self-compatible and commonly homostylous although some populations are phenotypically similar to the long-styled morphs of distylous populations. The incompatibility behaviour of these plants is not like that exhibited by long-styled self-compatible variants described in this study. Instead they show the incompatibility response of recombinant homostyles derived by crossing-over within the distyly supergene (Barrett and Shore 1987). Thus, while the self-compatible variants described here provide an alternate pathway for the evolution of self-compatibility within the *T. ulmifolia* complex, this seems not to have been the route followed by homostylous taxa. That modifiers can lead to the evolution of self-compatibility in distylous species has been treated theoretically by Charlesworth and Charlesworth (1979b), and Lande and Schemske (1985) have modelled the evolution of selfing based on polygenic variation.

The demonstration of self-compatible variants of two types, pollen and stelar, both of which exhibit null or reduced activity, may shed light on the genetic architec-

ture and functioning of dimorphic incompatibility. Charlesworth and Charlesworth (1979a) and Ganders (1979) argue that the incompatibility system in distylous species is not homologous with the *S* loci found in taxa with homomorphic incompatibility systems (although see Muenchow (1981) for an alternative view). An important issue in this debate is whether null style or pollen activity mutants are controlled by the distyly locus (Charlesworth 1982). While variants of both types were identified in this study, neither appeared to be controlled by the distyly locus. Self-compatibility in the variants varies quantitatively, and genetic background is important in regulating the expression of the self-incompatibility system.

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- ANERSTEDT, I., and A. LUNDQVIST. 1967. Genetics of self-incompatibility in *Tradescantia paludosa* (Commelinaceae). *Hereditas* (Lund, Swed.), **58**: 13–30.
- ARBO, M. M. 1985. Notas taxonómicas sobre Turneráceas Sudamericanas. *Candollea*, **40**: 175–191.
- BAKER, H. G. 1955. Self-compatibility and establishment after long-distance dispersal. *Evolution* (Lawrence, Kans.), **9**: 347–348.
- . 1958. Studies in the reproductive biology of West African Rubiaceae. *J. West African Sci. Assoc.* **4**: 9–24.
- . 1966. The evolution, functioning and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceae. *Evolution* (Lawrence, Kans.), **20**: 349–368.
- BARRETT, S. C. H. 1978. Heterostyly in a tropical weed: the reproductive biology of the *Turnera ulmifolia* complex (Turneraceae). *Can. J. Bot.* **56**: 1713–1725.
- BARRETT, S. C. H., and J. S. SHORE. 1987. Variation and evolution of breeding systems in the *Turnera ulmifolia* L. complex (Turneraceae). *Evolution* (Lawrence, Kans.). In press.
- BEALE, B. H. 1938. Further studies of pollen-tube competition in *Primula sinensis*. *Ann. Eugenics*, **9**: 259–268.
- BENTLEY, B. L. 1979. Heterostyly in *Turnera trioniflora*, a roadside weed of the Amazon basin. *Biotropica*, **11**: 11–17.
- BREWBAKER, J. L. 1954. Incompatibility in autotetraploid *Trifolium repens*. I. Competition and self-compatibility. *Genetics*, **39**: 307–316.
- . 1958. Self-incompatibility in tetraploid strains of *Trifolium hybridum*. *Hereditas* (Lund, Swed.), **44**: 547–553.
- CAHALAN, C. M., and C. GLIDDON. 1985. Genetic neighbourhood sizes in *Primula vulgaris*. *Heredity*, **54**: 65–70.
- CHARLESWORTH, D. 1982. On the nature of the self-incompatibility locus in homomorphic and heteromorphic systems. *Am. Nat.* **119**: 732–735.
- CHARLESWORTH, B., and D. CHARLESWORTH. 1979a. The

- maintenance and breakdown of distyly. *Am. Nat.* **114**: 499–513.
- CHARLESWORTH, D., and B. CHARLESWORTH. 1979*b*. A model for the evolution of distyly. *Am. Nat.* **114**: 467–498.
- CROSBY, J. 1949. Selection of an unfavourable gene-complex. *Evolution* (Lawrence, Kans.), **3**: 212–230.
- CURTIS, J., and C. F. CURTIS. 1985. Homostyle primroses re-visited. I. Variation in time and space. *Heredity*, **54**: 227–234.
- DOWRICK, V. P. J. 1956. Heterostyly and homostyly in *Primula obconica*. *Heredity*, **10**: 219–236.
- EAST, E. M. 1927. Peculiar genetic results due to active genetic gametophytic factors. *Hereditas* (Lund, Swed.), **9**: 49–58.
- ERNST, A. 1933. Weitere Untersuchungen zur Phänanalyse zum Fertilitätsproblem und zur Genetik heterostyler Primeln. 1. *Primula viscosa*. Arch. Julius Klaus-Stift. Vererbungsforsch. Sozialanthropol. Rassenhyg. **8**: 1–215.
- 1936*a*. Heterostylie-forschung. Versuche zur genetischen Analyse eines Organisations- und “Anpassungs” merkmals. *Z. Indukt. Abstamm. Vererbungsl.* **71**: 156–230.
- 1936*b*. Weitere Untersuchungen zur Phänanalyse zum Fertilitätsproblem und zur Genetik heterostyler Primeln. II. *Primula hortensis* Wettstein. Arch. Julius Klaus-Stift. Vererbungsforsch. Sozialanthropol. Rassenhyg. **11**: 1–280.
- 1953. Primärer und sekundärer Blütendimorphismus bei Primeln. *Oesterr. Bot. Z.* **100**: 235–255.
- 1955. Self-fertility in monomorphic *Primulas*. *Genetica* (The Hague), **27**: 91–148.
- GANDERS, F. R. 1979. The biology of heterostyly. *N.Z. J. Bot.* **17**: 607–635.
- HENNY, R. J., and P. D. ASCHER. 1976. The inheritance of pseudo-self-compatibility (PSC) in *Nemesia strumosa* Benth. *Theor. Appl. Genet.* **48**: 185–195.
- JAIN, S. K. 1976. The evolution of inbreeding in plants. *Annu. Rev. Ecol. Syst.* **7**: 469–495.
- LANDE, R., and D. W. SCHEMSKE. 1985. The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* (Lawrence, Kans.) **39**: 24–40.
- LEWIS, D. 1947. Competitor and dominance of incompatibility alleles in diploid pollen. *Heredity*, **1**: 85–108.
- LITZOW, M. E., and P. D. ASCHER. 1983. The inheritance of pseudo-self-compatibility (PSC) in *Raphanus sativus* L. *Euphytica*, **32**: 9–15.
- MARTIN, F. W. 1965. Distyly and incompatibility in *Turnera ulmifolia*. *Bull. Torrey. Bot. Club*, **92**: 185–192.
- MATHER, K. 1943. Specific differences in *Petunia*. I. Incompatibility. *J. Genet.* **45**: 215–235.
- 1950. The genetical architecture of heterostyly in *Primula sinensis*. *Evolution* (Lawrence, Kans.), **4**: 340–352.
- MATHER, K., and D. DE WINTON. 1941. Adaptation and counter-adaptation of the breeding system in *Primula*. *Ann. Bot. N.S.* **5**: 297–311.
- MULCAHY, D. L. 1984. The relationships between self-incompatibility, pseudo-compatibility, and self-compatibility. In *Plant biosystematics*. Edited by W. F. Grant. Academic Press, Toronto.
- MUENCHOW, G. 1981. S-locus model for the distyly supergene. *Am. Nat.* **118**: 756–760.
- NASRALLAH, M. E., and D. H. WALLACE. 1968. The influence of modifier genes on the intensity and stability of self-incompatibility in cabbage. *Euphytica*, **17**: 495–503.
- NETTANCOURT, D. DE. 1977. Incompatibility in angiosperms. Springer-Verlag, Berlin.
- ORNDUFF, R. (1979). The genetics of heterostyly in *Hypericum aegypticum*. *Heredity*, **42**: 271–272.
- PANDEY, K. K. 1959. Mutations of the self-incompatibility gene (S) and pseudo-compatibility in angiosperms. *Lloydia*, **22**: 222–234.
- PIPER, J. G., B. CHARLESWORTH, D. CHARLESWORTH. 1984. A high rate of self-fertilization and increased seed fertility of homostyle primroses. *Nature* (London), **310**: 50–51.
- RICHARDS, R. A., and N. THURLING. 1973. The genetics of self-incompatibility in *Brassica campestris* L. ssp. *oleifera* Metzg. I. Characteristics of S-locus control of self-incompatibility. *Genetica* (The Hague), **44**: 428–438.
- SHARMA, J. R., and B. R. MURTY. 1979. Changes in genetic background under selection influencing the expression of self-incompatibility in *Brassica campestris* var. Brown Sarson. *Genetica* (The Hague), **51**: 45–53.
- SHORE, J. S., and S. C. H. BARRETT. 1985*a*. Morphological differentiation and crossability among populations of the *Turnera ulmifolia* L. complex (Turneraceae). *Syst. Bot.* **10**: 308–321.
- 1985*b*. The genetics of distyly and homostyly in *Turnera ulmifolia* L. (Turneraceae). *Heredity*, **54**: 167–174.
- STOUT, A. B., and C. CHANDLER. 1942. Hereditary transmission of induced tetraploidy and compatibility in fertilisation. *Science* (Washington, D.C.), **96**: 257.
- URBAN, I. 1883. Monographie der Familie der Turneraceen. Berlin, Gebrüder Borntraeger.