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The genetics of distyly and homostyly in *Turnera ulmifolia* L. (Turneraceae)

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***Turnera ulmifolia* L. is a polymorphic complex of diploid, tetraploid and hexaploid varieties. Diploids and tetraploids are distylous and hexaploids homostylous. A controlled crossing programme demonstrated that in diploids distyly is controlled by a single locus with two alleles. Long-styled plants are *ss* and short-styled plants can be either *Ss* or *SS*. In tetraploids a similar pattern occurs with short-styled plants usually *Ssss* and long-styled plants *ssss*. Tetrasomic inheritance was demonstrated by crosses with a *SSss* genotype synthesised by colchicine doubling. Double reduction could not be detected at the distyly locus. No significant deviation from a 1:1 morph ratio was observed in surveys of nine natural populations and progeny tests of 21 open-pollinated familes from Brazil. Crosses between distylous and homostylous populations were undertaken to determine the inheritance of homostyly. The results were consistent with a model of supergene control. Clear segregation of phenotypes was observed in the F_1, and the dominance relationships $S > h > s$, where *h* is an allele that determines homostyly, were obtained.**

INTRODUCTION

Distyly occurs in at least 23 flowering plant families (Ganders, 1979) and has undoubtedly evolved several times. The inheritance of distyly has been determined for species in 11 genera from nine families (Ornduff, 1979). The syndrome of floral characters, by which the long- and short-styled morphs differ, is inherited as if controlled by a single gene locus with two alleles. Except for two genera where the dominance relationships are reversed (Baker, 1966; Ornduff, 1979), the long-styled morph is homozygous (*ss*) while the short-styled morph is heterozygous (*Ss*). Evidence from the Primulaceae (Ernst 1955), and the Plumbaginaceae (Baker, 1966) suggests that distyly is controlled by a series of tightly linked genes comprising a supergene. Aberrant forms termed homostyles, with anthers and stigmas at the same level within a flower, are interpreted as recombinant phenotypes that arise by crossing over within the supergene. A recombination event resulting in homostyly has, however, never been detected in heterostylous species (Charlesworth and Charlesworth, 1979*a*). In addition, apart from a few notable exceptions (Crosby, 1949; Ernst, 1955; Ganders, 1975), homostyles are rarely observed in distylous populations, although relatives of heterostylous taxa are frequently homostylous.

Turnera ulmifolia L. is a polymorphic assemblage of perennial weeds native throughout the Neotropics. Urban (1883) described 12 varieties within the complex, six of which are distylous and the remainder homostylous. Barrett (1978) described the floral biology and breeding systems of four varieties within the complex, and a recent survey of chromosome numbers in 43 populations of *T. ulmifolia* (Shore and Barrett, 1985; and unpublished data) revealed a correlation between breeding system and ploidal level. All distylous populations are diploid or tetraploid, whereas homostylous populations are hexaploid. Here we investigate the genetics of breeding system variation in the *T. ulmifolia* complex. Specifically we: (1) determine the inheritance of distyly in diploids and tetraploids; (2) provide data on morph ratios and segregation from natural populations; (3) determine the inheritance of homostyly and discuss evidence for supergene control of distyly.

MATERIALS AND METHODS

A crossing programme was undertaken on glasshouse grown plants raised from seed collections or cuttings obtained from natural populations. Table 1 gives the locality, chromosome number and varietal status of accessions used in the study.

Table 1 Varietal status, ploidal level, and locality of *Turnera ulmifolia* accessions used in experimental studies ($X = 5$)

Population	Variety	Ploidal level	Locality	Collection No.
I1	intermedia	*2X*	Barreirinhas, Brazil	Barrett 1128
I3	intermedia	*2X*	Caracas, Venezuela	Barrett 1125
I6	intermedia	*2X*	Managua, Nicaragua	Barrett 1342
I24	intermedia	*4X*	St. Cristobal, Dominican Rep.	Barrett and Shore 1364
I32	intermedia	*2X*	Arco Verde, Brazil	Barrett and Shore 1374
E5	elegans	*4X*	Crato, Brazil	Barrett 222
E11	elegans	*4X*	Salgueiro, Brazil	Barrett and Shore 1372
A5	angustifolia	*6X*	Ochos Rios, Jamaica	Barrett 1253
A11	angustifolia	*6X*	Dragons Bay, Jamaica	Barrett 1259
A17	angustifolia	*6X*	Pelican Lake, Grand Bahama	Correll 40638
O1	orientalis	*6X*	Corrientes, Argentina	Arbo 1538
V1	velutina	*6X*	Tuxtla Gutierrez, Mexico	Koch & Fryxell 78341

Each individual was given a code indicating its accession, or family if applicable, followed by a numeric value specifying the particular individual within the accession, and by a letter indicating its phenotype (L = long-styled, S = short-styled, H = homostyled). All pollinations were performed in a pollinator-free glasshouse using fine forceps. Flowers were emasculated prior to cross-pollination. Pollinated flowers were individually marked and maturing capsules were wrapped with parafilm to prevent loss of seeds during dehiscence. As distylous members of the complex are strongly self-incompatible two different methods were used to obtain seeds from self- or intra-morph crosses: (1) flower buds were opened one day prior to anthesis and pollinated from an open flower of the same individual (bud-selfing), (2) plants were screened for the presence of a weakened incompatibility reaction (pseudo-compatibility) and those yielding more than three seeds per pollination were later used in the crossing programme. Progenies obtained from crosses were grown to flowering in individual pots.

To investigate the inheritance of distyly at diploid and tetraploid levels accessions comprising different varieties were employed (table 1). Reciprocal crosses were generally performed and the results pooled. Preliminary results suggested that short-styled morphs were of genotype *Ss*. To detect the occurrence of *SS* genotypes, 19 short-styled progeny derived from the self of I32-1S were selfed and at least 17 progeny from each family were grown to flowering and scored for floral morph. To investigate the possibility of tetrasomic inheritance and double reduction, the chromosome number of seedlings derived from the cross I32-1S × I1-10L, was doubled. A drop of 0·1 per cent colchicine applied to cotyledons resulted in the recovery of several tetraploid plants and a long- and a short-styled plant were selected for reciprocal crosses. To determine the inheritance of homostyly, three homostylous varieties, from five accessions of *T. ulmifolia*, were crossed to diploid long- and short-styled plants of known genotype.

To examine the equilibrium frequency in *T. ulmifolia* we extend the morph frequency data of Barrett (1978) by sampling a total of 1211 plants from nine natural populations of the tetraploid *T. ulmifolia* var. *elegans* in N.E. Brazil. Random or complete samples of populations were taken with at least 90 plants sampled per population. Further, progeny tests of 21 open-pollinated families, collected from population E11 in Brazil were performed to test for heterogeneity among families and among maternal morphs. On average 62 progeny were scored for each family.

All goodness-of-fit and heterogeneity tests were performed using the G statistic (Sokal and Rohlf, 1981).

RESULTS

Neither of the two methods employed to obtain seed from selfing long- or short-styled plants was completely successful. Bud-selfing in *T. ulmifolia* results in seed set more often in short- than long-styled individuals; only one of many long-styled plants yielded seed. In both morphs the yield of seed from bud-selfing is less than 75 per cent of that from legitimate pollinations. Screening plants for pseudo-compatibility resulted in the recovery of a few individuals that produced sufficient seed on self-pollination to be useful for genetic study. Two plants were identified among diploids (I3I1-3L and I32-1S) and two among tetraploids (E5-1L and E5-10S). Progeny (>80 per cross) derived by selfing or crossing plants E5-1L and E5-10S were

screened for self-compatibility. Six progeny yielded sufficient seed for further study.

(i) Inheritance of distyly in diploids

The inheritance of distyly in diploid *T. ulmifolia* var. *intermedia* was determined using three long- and six short-styled plants, from four different accessions, and one long-styled plant (I3I1-3L), from the cross I3-3S × I1-10L. Bud pollinations were used for all illegitimate crosses except those involving individuals I3I1-3L and I32-1S which yielded sufficient seed on selfing. The data presented in table 2 are consistent with the common

Table 2 Style morphs in progeny of crosses of *Turnera ulmifolia* var. *intermedia* ($2n = 10$)

Cross	Style morphs of progeny: Long	Short	G	P
(a) Legitimate crosses				
I6-12L × I6-19S	34	58	6·33	0·01
I6-12L × I6-31S	65	53	1·22	0·27
I6-12L × I3-3S	90	78	0·86	0·36
I3-3S × I3-4L	16	23	1·26	0·26
I3-24S × I3-4L	9	9	0·00	—
I1-2S × I1-10L	26	18	1·46	0·23
Deviation from 1:1	$G = 0·002$, $P = 0·96$			
Heterogeneity	$G = 11·138$, $P = 0·05$			
(b) Illegitimate crosses of the short-styled morph				
I6-19S × I6-31S	4	29	3·40	0·07
I6-19S selfed	3	15	0·73	0·39
I6-31S selfed	5	18	0·13	0·71
I3-24S selfed	5	13	0·07	0·79
I3-3S selfed	21	52	0·54	0·46
I32-1S selfed	33	109	0·24	0·63
Deviation from 1:3	$G = 0·58$, $P = 0·45$			
Heterogeneity	$G = 4·52$, $P = 0·50$			
(c) Illegitimate crosses of the long-styled morph				
I6-12L selfed	52	0	—	—
I3I1-3L selfed	156	0	—	—

genetic model of the inheritance of distyly. Short-styled plants are heterozygous (*Ss*), yielding both morphs on selfing, and long-styled plants are homozygous (*ss*) with only long-styled plants in selfed progeny. Heterogeneity was apparent among legitimate crosses. This was largely the result of the cross (I6-12L × I6-19S); the only example showing heterogeneity among reciprocals. When the short-styled morph was used as the pollen parent a large excess of short-styled progeny was observed. Further we note that all crosses involving plant I6-19S yielded an excess of short-styled plants.

Four of 19 short-styled plants, derived by selfing plant I32-1S, yielded no long-styled progeny upon selfing. At least 34 selfed progeny were scored for each of these four plants. The probability of observing no long-styled plants among the progeny of a heterozygous parent for a sample size of 34 is less than 6×10^{-5}. Hence these individuals are likely to be short-styled plants of genotype *SS*. Among the segregating progenies, 105 long-styled and 326 short-styled plants were obtained and no deviation from 1:3 or heterogeneity, was observed ($G_{dev} = 0·09$, $P = 0·76$; $G_{het} = 17·8$, $P = 0·22$). The occurrence of four non-segregating plants as well as the absence of a deficiency in short-styled progeny from selfs of short-styled plants indicates that *SS* genotypes are viable.

(ii) Inheritance of distyly in tetraploids

At the tetraploid level plants from two accessions were used, one each from vars. *elegans* and *intermedia*. Bud-selfing was employed for individual I24-1S only. All other plants were selfed. Individuals SS3S and SS77S are self-fertile sibs obtained by selfing E5-10S and screening several of its progeny for pseudo-compatibility. Plants SL34S and SL36L were similarly obtained from the cross E5-10S × E5-1L and plants LL61L and LL51L from the self of E5-1L. Data in table 3 indicate that short-styled plants are heterozygous and long-styled plants are homozygous. Aberrant ratios were obtained in four crosses. The parental short-styled plant E5-10S yielded an extreme deficiency of short-styled progeny on selfing, as did two of its three progeny (SS77S and SL34S).

To account for the aberrant ratios from these three selfs, three models with different expectations were investigated. Since the crosses gave homogeneous segregations ($G = 0·58$, $P > 0·5$) results were pooled, giving a ratio of 1 long:1·23 short. The models evaluated were: (1) a model assuming a maximum amount of double reduction, corresponding to random chromatid segregation (Allard, 1960), with an expectation of 1 long:2·48 short ($G = 52·7$, $P < 0·001$); (2) a model assuming lethality of zygotes containing more than one *S* allele giving an expectation of 1 long:2 short ($G = 25·8$, $P < 0·001$); (3) a model assuming both a maximum amount of double reduction and lethality of zygotes carrying more than one S allele, with an expectation of 1 long:1·6 short ($G = 7·72$, $P < 0·01$). None of the models accounts for the extreme deficiency of short-styled plants, but the third comes closest to the observed ratio. Evidence reviewed below, however, indicates that double

Table 3 Style morphs in progeny of crosses of *Turnera ulmifolia* vars. *elegans* and *intermedia* ($2n = 20$)

Cross	Style morphs of progeny: Long	Short	G	P
(a) Legitimate crosses				
E5-1L × E5-10S	91	76	1·35	0·25
I24-3L × E5-10S	71	96	3·76	0·05
Deviation from 1:1	$G = 0{\cdot}30$, $P = 0{\cdot}58$			
Heterogeneity	$G = 4{\cdot}81$, $P = 0{\cdot}03$			
(b) Illegitimate crosses of the short-styled morph				
I24-1S selfed	8	31	0·44	0·51
E5-10S selfed	79	100	30·89	<0·001
SS3S selfed	29	66	1·48	0·22
SS77S selfed	56	61	28·38	<0·001
SL34S selfed	67	87	24·94	<0·001
Deviation from 1:3	$G = 70{\cdot}90$, $P < 0{\cdot}001$			
Heterogeneity	$G = 15{\cdot}23$, $P = 0{\cdot}004$			
(c) Illegitimate crosses of the long-styled morph				
E5-1L selfed	130	0	—	—
SL36L selfed	147	0	—	—
LL61L selfed	14	0	—	—
LL51L selfed	6	0	—	—
(d) Legitimate cross of synthetic tetraploids				
SN1S × LN1L	35	208	—	—
Deviation from 1:5	$G = 0{\cdot}93$, $P = 0{\cdot}33$			

reduction may not occur at the distyly locus and hence the model may be inappropriate.

The synthetic tetraploids produced by somatic chromosome doubling had genotypes *SSss* (short-styled) and *ssss* (long-styled). On crossing, the progeny showed no deviation from the expected 5 short:1 long tetrasomic ratio (table 3(d)). A maximum likelihood estimate and standard error of the double reduction parameter a was obtained jointly from these data and the pooled data from open-pollinated families of var. *elegans* (table 4). The estimation procedure yielded a value not significantly different from zero ($a = -0{\cdot}045$, s.e. = 0·044). Hence double reduction could not be detected at the distyly locus.

Style morph frequencies in natural populations of var. *elegans* in Brazil were homogeneous ($G_{het} = 7.23$, $P = 0.51$) and reveal no significant deviation from 1:1 expectation ($G_{dev} = 0{\cdot}07$, $P = 0{\cdot}79$). The 21 open-pollinated families sampled from a natural population in Brazil (E11) of var. *elegans* ($2n = 20$) provided no evidence of deviation from 1:1 expectation or heterogeneity among morphs or families within morphs (table 4).

(*iii*) *The inheritance of homostyly*

All F_1 progeny obtained from crosses between homostylous hexaploids and distylous diploids were highly sterile. Sterility precluded the possibility of examing further generations. However, clear floral dimorphism was evident among progenies (fig. 1(a), (b)), despite morphological divergence and sterility barriers among the diploid and hexaploid varieties. In each of the three homostylous varieties that were examined, no long-styled plants were obtained in crosses. However, crosses that involved short-styled plants always segregated both short-styled plants and homostylous plants at equal frequencies (table 5). On the basis of these patterns of segregation an apparent homostyle allele (h), which is dominant to the long-styled allele (s), but recessive to the short-styled allele (S), governs the homostylous phenotype in *T. ulmifolia*.

All homostyles of *T. ulmifolia* that we have examined exhibit the floral phenotype of a long-homostyle, with long styles and long-level anthers. However, considerable variation occurs in the relative lengths of reproductive organs among populations, with some displaying a considerable degree of herkogamy. Further details on the nature of the variation and its genetic basis will be presented elsewhere.

Table 4 Style morphs in progeny of open-pollinated families of *Turnera ulmifolia* var. *elegans* ($2n = 20$) from Brazilian population (E11)

Family	Style morphs of progeny: Long	Short
S1	39	43
S2	12	7
S3	25	27
S4	10	15
S5	39	34
S6	29	22
S7	6	8
S8	10	9
S9	23	27
S10	29	23
S11	49	52
L1	1	1
L2	63	69
L3	46	49
L4	38	42
L5	35	30
L6	9	16
L7	8	14
L8	57	63
L9	39	35
L10	71	72

	df	G	P
Deviation from 1:1	1	0·31	0·58
Between morph heterogeneity	1	0·48	0·49
Between family heterogeneity	19	9·68	0·94

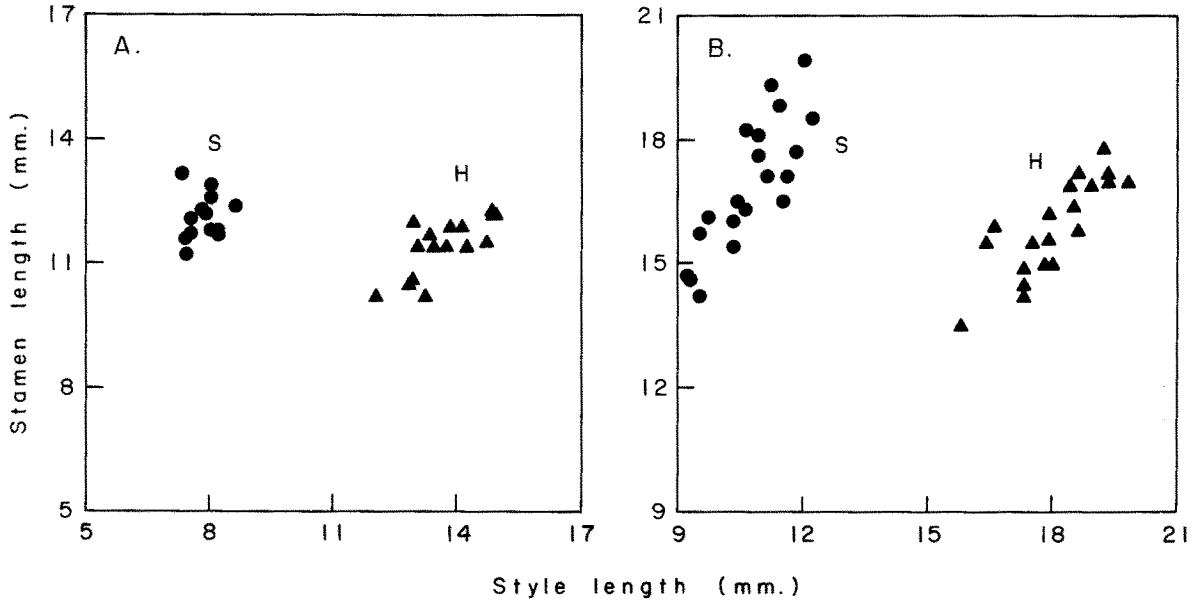

Figure 1 Distribution of floral phenotypes in crosses between distylous and homostylous populations of *Turnera ulmifolia* (a) O1-21H×I6-19S (b) A11-12H×I32-1S.

Table 5 Style morphs in progeny of crosses of distylous *Turnera ulmifolia* var. *intermedia* ($2n = 10$) with three homstylous varieties ($2n = 30$)

	Style morphs of progeny		
Cross	Long	Short	Homostyle
(a) crosses with var. *angustifolia*			
(i) Homostyle×Short			
A11-12H×I32-1S	0	54	46
A11-12H×I6-19S	0	17	14
A11-12H×I6-31S	0	11	18
A11-14H×I32-1S	0	10	3
A11-14H×I6-19S	0	7	9
A5-28H×I32-1S	0	3	5
Deviation from 1S:1H	$G = 0{\cdot}25$, $P = 0{\cdot}62$		
Heterogeneity	$G = 7{\cdot}12$, $P = 0{\cdot}21$		
(ii) Long×Homostyle			
I6-12L×A11-12H	0	0	4
I6-12L×A11-14H	0	0	4
I6-12L×A17-1H	0	0	7
(b) crosses with var. *orientalis*			
I6-12L×O1-21H	0	0	80
O1-21H×I6-19S	0	40	36
Deviation from 1S:1H	$G = 0{\cdot}21$, $P = 0{\cdot}65$		
(c) crosses with var. *velutina*			
V1-3H×I32-1S	0	2	2
V1-3H×I6-19S	0	0	1
I1-10L×V1-3H	0	0	4

DISCUSSION

The genetic control of distyly was first elucidated by Bateson and Gregory (1905), although Darwin (1877) undertook the necessary crosses. In all cases, the syndrome of characters that comprises the polymorphism is controlled by a single gene locus with two alleles. Recently, Schou and Philip (1984) have identified a second genetic system where the floral polymorphism and incompatibility system are apparently uncoupled, and possibly controlled by unlinked loci. A similar system may operate in *Narcissus* (Dulberger, 1964). Evidence for supergene control of distyly has been obtained for species in the Primulaceae (Ernst, 1955) and Plumbaginaceae (Baker, 1966). Preliminary data is also available for the Rubiaceae (Baker, 1958). In *Amsinckia spectablis* of the Boraginaceae, Ganders (1979) has shown that homostylous phenotypes are not the result of recombination within a supergene. This does not exclude the possibility of supergene control of the polymorphism in this species, but indicates that genes other than those of the supergene are responsible for homostyle formation. Indeed, two such genes are known to occur in *Primula sinensis* (Mather, 1950).

The *Turnera ulmifolia* complex exhibits distyly, with reciprocal lengths of styles and stamens, pollen size dimorphism, and a strong self- and intramorph incompatibility system (Barrett, 1978). In

diploids, we have shown that distyly is controlled by a single locus with two alleles. Long-styled plants are *ss* and short-styled plants can be either *Ss* or *SS*. However, homozygous shorts, although viable, will not generally occur in natural populations, as disassortative mating, enforced by diallelic incompatibility, will prevent their formation. In tetraploids of *T. ulmifolia* a similar pattern of inheritance is observed. Short-styled plants are of genotype *Ssss* and long-styled plants are *ssss*. A short-styled plant of genotype *SSss* was synthesised by colchicine doubling and presumably short-styled genotypes with 3–4 doses of the *S* allele could be synthesised by the appropriate procedures.

A large deficiency in the number of short-styled progeny was obtained on selfing short-styled plants of the tetraploid *T. ulmifolia* var. *elegans*. This occurred in a self-compatible short-styled plant and two of its progeny. None of the three models considered gave a satisfactory fit to the data. We suggest that the aberrant ratios may be the result of the self-compatibility gene(s) imparting a selective advantage to male gametophytes of genotype *ss*. This hypothesis could be tested by performing the appropriate crosses. Aberrant ratios and their possible causes have been considered for other heterostylous taxa (Mather and de Winton, 1941; Baker, 1975; Weller and Ornduff, 1977; Ganders, 1979).

Casper and Charnov (1982) argue, based on sex allocation theory, that the 1:1 morph ratio found in most distylous populations is an evolutionary stable state. Further, under their model "autosomal" genes can cause the ratio to deviate from 1:1 given the appropriate selection pressures. In nine populations of *T. ulmifolia* var. *elegans* we found no evidence of deviation from a 1:1 morph ratio. In addition, progeny tests of 21 open-pollinated families revealed no deviation from 1:1, or heterogeneity among families. These data suggest that no significant genetic variation for morph ratio occurs within these populations of *T. ulmifolia* var. *elegans*, and isoplethy is a simple outcome of disassortative mating and Mendelian segregation at the distyly locus.

The three homostylous varieties of *T. ulmifolia* that we have studied experimentally are morphologically differentiated, allopatric, intersterile, and occur at different margins of the range of the species complex. This suggests that heterostyly has broken down to homostyly on at least three occasions in the species complex, always in association with the hexaploid condition (Shore and Barrett, 1985; and unpubl. data). All three varieties were used to determine the inheritance of homostyly and provide evidence for supergene control of distyly. Based on a hypothesis of supergene control of distyly we can predict (1) discrete phenotypic segregation and (2) specific dominance relationships of alleles governing control of the alternative floral phenotypes. Under the model we expect the following dominance relationships: $S > h > s$, where h is an allele determining homostyly. This pattern of dominance was observed for crosses involving all three varieties, although for var. *velutina* few progeny were raised. The clear segregation of floral phenotypes in the F_1 and pattern of dominance is consistent with the hypothesis that distyly is controlled by a supergene (composed of at least two loci) in *T. ulmifolia*.

The similar behaviour of homostylous varieties, in crosses with heterostylous populations, suggests that they have arisen via the same genetic mechanism involving recombination within the distyly supergene. Charlesworth and Charlesworth (1979*a*) modelled the breakdown of distyly and found that if the allele determining the short-styled morph is dominant, as in *T. ulmifolia*, long-homostyles are likely to spread to fixation with greater probability than other self-compatible phenotypes. Data from *T. ulmifolia* provide support for the model since each breakdown event has resulted in fixation of the long-homostyle phenotype.

In our surveys and experimental work of distylous populations in *T. ulmifolia* we have not observed the occurrence of homostylous plants. Mather (1950) proposed that the supergene controlling distyly in *Primula* might be contained within an inversion and as a result was protected from recombination. However, no firm evidence that such an inversion occurs in *Primula* species has been found and we have no cytological evidence for inversion polymorphisms in *T. ulmifolia*. De Winton and Haldane (1935) found no evidence for double reduction in *P. sinensis* and Dowrick (1956) detected a low frequency of occurrence in *P. obconica*. Since this may indicate that the distyly locus is linked to the centromere, Dowrick (1956) suggested that centromere interference might prevent crossing-over from occurring within the supergene of some *Primula* species.

We have demonstrated tetrasomic inheritance of distyly in tetraploid *T. ulmifolia*, however, we did not detect double reduction. The frequency of double reduction is an increasing function of the frequency of quadrivalent formation and recombination between the locus and centromere. Quadrivalent formation has been documented in tetraploid *T. ulmifolia* (Raman and Kesavan, 1964;

Arbo and Fernandez, 1983; Shore and Barrett, unpublished data) and we estimate the frequency of quadrivalent formation to be about 50 per cent. If we assume that quadrivalents are distributed at random among all sets of homologous chromosomes and that the distyly locus is not linked to the centromere, then $a = 0{\cdot}07$, approximately (Allard, 1960). Hence, given the sample sizes used in our estimate of double reduction and the frequency of quadrivalent formation in *T. ulmifolia*, we cannot detect the effect of linkage to the centromere, if it occurs (the smallest a we can detect is approximately 0·08). Thus, in addition to tight linkage among loci controlling distyly, centromere interference remains a tenable yet untested hypothesis for the apparent absence of recombinant homostyles in distylous populations of *T. ulmifolia*.

In *T. ulmifolia* there is an association between homostyly and hexaploidy. Cytological studies indicate that while all tetraploids form quadrivalents, and may be autopolyploids, the three hexaploid varieties form only bivalents at first metaphase, and are therefore likely to be allopolyploids (Shore and Barrett, unpublished data). In other heterostylous families, although there is a tendency for homostyly to occur at higher ploidy levels, no clear pattern emerges (Baker, 1966; Ockendon, 1968; Charlesworth and Charlesworth, 1979*b*). Dowrick (1956) argued that chromosome doubling may change the position of chiasma formation and result in an increased frequency of recombination within the distyly supergene. This, however, does not explain why recombinant, polyploid, homostyles should preferentially spread through distylous populations following their origin. Several authors have modelled the spread of homostylous phenotypes in distylous populations (Crosby, 1949; Dowrick, 1956; Bodmer, 1960; Charlesworth and Charlesworth, 1979*a*). Current models of the evolution of selfing propose that inbreeding depression is the most important factor restricting the spread of selfers in outcrossing populations (Maynard Smith, 1978; Charlesworth and Charlesworth, 1979*a*; Lloyd, 1979; Lande and Schemske, 1985). It is possible that recombinant homostyles might spread more easily in hexaploid populations, as a result of a reduction in the magnitude of inbreeding depression associated with hexaploidy.

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