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Quantitative genetics of floral characters in homostylous *Turnera ulmifolia* var. *angustifolia* Willd. (Turneraceae)

Joel S. Shore* and
Spencer C. H. Barrett

Department of Botany, University of Toronto,
Toronto, Ontario, Canada M5S 3B2.

The genetic basis of floral variation influencing the mating system of Jamaican populations of homostylous *Turnera ulmifolia* var. *angustifolia* was investigated using controlled crosses and open-pollinated families. Crosses between plants with large differences in stigma-anther separation and analysis of F_2 and backcross generations gave unimodal distributions for all floral characters. No evidence for major gene control of floral variation was obtained and results were contrary to expectations based on segregation at the distyly locus. These data and the continuous distribution of phenotypes among populations indicate that variation is polygenically controlled. Generation means from a cross between plants exhibiting extreme differences in stigma-anther separation could be accounted for by simple biometrical models. An additive-dominance model explained variation in style length while addition of a digenic epistatic parameter was required to account for variation in stamen length and stigma-anther separation. Estimation of repeatabilities and broad-sense heritability indicated genetic variation for style length, stamen length and stigma-anther separation within populations. No genetic correlation was evident for style and stamen length suggesting that selection acting on the mating system of homostylous populations would yield a response.

INTRODUCTION

Little is known of the genetic basis of mating system variation in natural plant populations other than for species with self-incompatibility systems or sexual dimorphism (Westergaard, 1958; Jain, 1976; Nettancourt, 1977). Theoretical models indicate that the genetic basis of variation plays an important role in the evolutionary dynamics of mating system change (Fisher, 1941; Moran, 1962; Nagylaki, 1976; Maynard Smith, 1978; Charlesworth and Charlesworth, 1979; Wells, 1979; Holsinger *et al.*, 1984; Lande and Schemske, 1985). Most models assume major gene control of mating system components, however, apart from polymorphic sexual systems, such as heterostyly and various forms of sexual dimorphism, few studies have revealed single gene control of mating behaviour (see Marshall and Abbott (1982) for an exception).

Polygenically controlled variation in outcrossing rate has often been inferred in plant populations but direct estimates of additive genetic variance for outcrossing are difficult to obtain since they require measurement of outcrossing rates among relatives (*e.g.*, Hauptli and Jain, 1985). The outcrossing rate must be estimated for both parents and offspring or sib families. As yet this has not been undertaken in natural plant populations.

Another approach to investigate the genetic basis of mating system variation involves determination of the amount of genetic variation for characters that are functionally associated with the mating system, such as herkogamy or dichogamy (the spatial or temporal separation of male and female reproductive organs). Breese (1959) found that artificial selection on the degree of herkogamy in *Nicotiana rustica* yielded a correlated response in outcrossing rate and degree of dichogamy. Moore and Lewis (1965) suggested that early maturation of the stigma in *Clarkia xantiana* resulted in a higher degree of selfing. Genetic data suggested that early maturation had a simple genetic basis, resulting from the effects of one or two major loci. Ennos (1981) demonstrated that a herkogamous population of *Ipomoea purpurea* had

* Present address: Department of Biology, York University, 4700 Keele Street, North York, Ontario, Canada M3J 1P3.

a higher rate of outcrossing than a sympatric non-herkogamous population of *I. hederacea*. The occurrence of additive genetic variation for herkogamy in *I. purpurea* suggested the potential for mating system modification in the species. Finally, Schoen (1982) found that the degree of protandry among populations of *Gilia achilleifolia* was correlated with outcrossing rate and that additive genetic variation for degree of protandry occurred. These studies demonstrate the occurrence of genetic variation for characters that influence mating patterns in natural plant populations. The variation may provide opportunities for evolutionary responses to natural selection.

Turnera ulmifolia is a neotropical species complex of ruderal, perennial weeds. Distyly and homostyly occur within the species complex (Barrett, 1978) and are widespread breeding systems throughout the Turneraceae (Urban, 1883). *T. ulmifolia* var. *angustifolia*, is a self-compatible, hexaploid native to the Caribbean (Barrett and Shore, 1987). Inheritance studies indicate that the species is homostylous and has arisen from a distylous ancestor via crossing-over in the supergene that controls distyly (Shore and Barrett, 1985). Therefore populations of *T. ulmifolia* var. *angustifolia* lack the stamen-style dimorphism and diallelic-incompatibility system found in outcrossing distylous populations. However, unlike most homostylous taxa they exhibit marked genetic differentiation for the degree of stigma-anther separation with greater than 80 per cent of the variation in this character attributable to differences among populations (Barrett and Shore, 1987). In *T. ulmifolia* var. *angustifolia* the degree of stigma-anther separation influences outcrossing rates as determined by isozyme markers, suggesting that local selection acting on the mating systems of populations may be responsible for maintaining the observed population differences.

The genetic basis of variation in style and stamen length within and among Jamaican populations of *T. ulmifolia* var. *angustifolia*, is the subject of the current investigation. Specifically, we address the following questions. (1) What is the inheritance of floral characters among populations displaying extreme phenotypic differences in stigma-anther separation? (2) Is there evidence for major gene control of style and stamen length as occurs in distylous taxa? (3) How much genetic variation occurs within populations for floral characters that influence the mating system? (4) Are there phenotypic and genetic correlations among these floral characters?

MATERIALS AND METHODS

Methods of population sampling, plant culture, and floral measurement follow those in Barrett and Shore (1987). Each plant was individually coded, with the first letter and number corresponding to a particular Jamaican population and the second number an individual plant.

Inheritance of floral variation

One plant from each of two Jamaican populations displaying extreme phenotypic means for stigma-anther separation was randomly selected for crosses. The parental plants, A9-3 exhibiting a large stigma-anther separation (8·5 mm) and A5-28 having a small (−1·5 mm) separation, were selfed and crossed reciprocally to provide S_1 (to be called parental lines) and F_1 generations. A preliminary analysis of variance for 30 progeny within each reciprocal F_1 generation revealed a lack of reciprocal effects for style length, stamen length and stigma-anther separation. Thus reciprocals are not included in further experiments. A single plant from the F_1 was randomly chosen and selfed or crossed to both parents to yield F_2 and backcross generations (B_1 and B_2). The parental lines (P), F_1, F_2 and both backcross generations were grown in a completely randomized design under uniform glasshouse conditions. All generations were grown in a single experiment to reduce environmental variance in floral characters. For each plant, two flowers were measured for style length, stamen length and flower diameter.

Biometrical models were fitted to data for style length, stamen length, stigma-anther separation (style length − stamen length) and flower diameter, using a weighted least squares estimation procedure (Mather and Jinks, 1982). The analysis assumes that parental plants were inbred for these characters (see discussion). All calculations were performed using the mean of two flowers per plant. Initially, an additive-dominance model was fitted to the data. If the model did not fit the data digenic epistatic parameters were included in the model. To evaluate the significance of the three digenic epistatic terms, *t*-tests were used. Joint estimation of all parameters was then conducted, excluding those which did not differ significantly from zero (Mather and Jinks, 1982). Goodness of fit tests were performed to assess the adequacy of the models using a joint scaling procedure (Cavalli, 1952; Mather and Jinks, 1982).

Intra-population genetic variation

The amount of genetic variation for floral characters within 11 populations of *T. ulmifolia* var. *angustifolia* was investigated using the experimental material described in Barrett and Shore (1987). Fourteen plants from ten populations were randomized on a glasshouse bench and five flowers measured for each plant. Characters measured were style length, stamen length and flower diameter. One-way analyses of variance were performed for each character in each population and variance components calculated for the among-plant (σ_b^2) and within-plant (σ_w^2) sources of variation. A similar analysis was conducted on population A20, except that the analysis was based on 250 plants and two flowers per plant. The experimentwise error rate for the 11 hypothesis tests for each character in the analyses of variance was set to $\alpha = 0{\cdot}05$ using the Bonferroni procedure (Neter and Wasserman, 1974).

Repeatability, the proportion of total phenotypic variance not attributable to within-plant variation, was calculated for each character in each population using variance components from the analysis of variance. Repeatability (R) was calculated as $R = 1 - \sigma_w^2/\sigma_t^2$, where $\sigma_t^2 = \sigma_b^2 + \sigma_w^2$ is the total phenotypic variance (Falconer, 1981). R was expressed as a percentage.

A more detailed analysis was undertaken on open-pollinated families of population A20 to further partition variation in floral characters. Ten families of 25 progeny each and two flowers per plant were measured and analysed. A nested analysis of variance was performed and variance components calculated for the among-family (σ_f^2), among-plants within families (σ_i^2) and within-plant (σ_w^2) sources of variation. The among-family components of variation were used as estimates of broad-sense heritability.

Phenotypic correlations were calculated among pairs of characters for population A20. Genetic correlations were approximated by calculating the correlation among family means for each pair of characters (Gale and Eaves, 1972).

Preliminary analyses on all data were undertaken to explore the effects of different transformations. No transformation improved the adequacy of the fit to the models, nor were the results of analyses using transformed data very different from those using untransformed data. Accordingly, all analyses presented were conducted on untransformed data.

RESULTS

Inheritance of floral variation

The distributions of floral characters in crosses between parental plants with large differences in stigma–anther separation were unimodal (fig. 1). Means and variances for all distributions are presented in table 1. While there were large discontinuities in the distributions between parental lines, particularly for stigma–anther separation, there was no evidence that a single major gene controls the inheritance of the floral characters that were examined.

Results of the biometrical analyses of generation means are presented in table 2. Estimates of m (the mid-parent value in the absence of epistasis), the additive ($[d]$), dominance ($[h]$) and digenic epistatic parameters (epistatic interactions between additive effects $[i]$, between additive and dominance effects $[j]$, and between dominance effects $[l]$), are presented along with goodness of fit tests of the models, where appropriate (table 2). An additive-dominance model adequately describes the data for style length (table 2). Dominance occurs and the estimate of $[h]$ is larger than $[d]$. The F_1 mean for style length ($\bar{x} = 24{\cdot}6$ mm) exceeds the value for the higher parental line (A9-3, $\bar{x} = 23{\cdot}8$ mm). The analysis indicates that on

Table 1 Sample sizes (N), means (mm) and variances (in parentheses) for style length, stamen length, stigma–anther separation (style length-stamen length) and flower diameter for parental lines (A9-3 and A5-28), F_1, F_2, and backcross generations of *Turnera ulmifolia* var. *angustifolia*

Generation	N	Style length	Stamen length	Stigma–anther separation	Flower diameter
A9-3	33	23·8 (1·42)	15·3 (0·72)	8·48 (0·35)	48·2 (9·5)
A5-28	34	19·9 (1·23)	21·5 (0·78)	−1·54 (1·21)	48·7 (7·1)
F_1	35	24·6 (0·87)	20·6 (0·50)	4·04 (0·36)	54·6 (13·6)
F_2	79	23·2 (2·81)	19·2 (1·78)	4·02 (3·17)	49·7 (18·3)
A9-3 × F_1	78	24·3 (1·96)	17·7 (1·76)	6·59 (2·54)	50·3 (11·5)
A5-28 × F_1	103	22·4 (1·50)	20·7 (0·93)	1·69 (1·59)	50·6 (10·3)

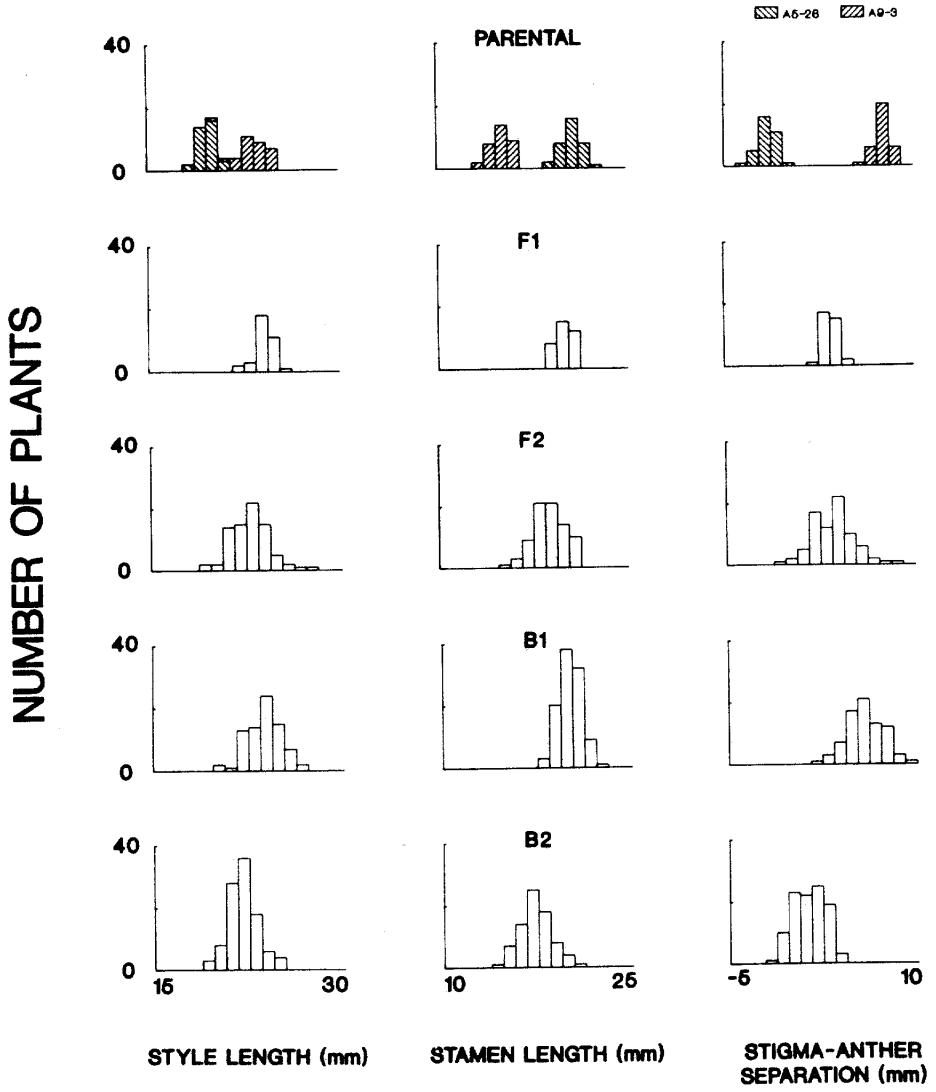

Figure 1 Phenotypic distributions of parental lines A9-3 and A5-28, and their F_1, F_2 and backcross generations for style length, stamen length, and stigma-anther separation in *Turnera ulmifolia* var. *angustifolia* from Jamaica.

Table 2 Parameter estimates and their standard errors from a biometrical analysis of generation means of parental, F_1, F_2, B_1, and B_2 generations. Style length, stamen length, stigma-anther separation and flower diameter (mm) were analysed. Goodness of fit tests and associated degrees of freedom (df) are provided

Parameters	Style length	Stamen length	Stigma-anther separation	Flower diameter
m	21·91 ± 0·12	18·41 ± 0·11	3·48 ± 0·10	44·58 ± 1·09
$[d]$	1·93 ± 0·14	3·04 ± 0·09	4·98 ± 0·10	—
$[h]$	2·75 ± 0·21	0·93 ± 0·45	2·02 ± 0·51	9·98 ± 1·57
$[i]$	—	—	—	3·90 ± 1·16
$[l]$	—	1·23 ± 0·43	−1·46 ± 0·48	—
$\chi^2(P)$	0·45 (0·93)	0·25 (0·88)	0·61 (0·74)	1·06 (0·79)
df	3	2	2	3

average, alleles resulting in longer styles are dominant to those that produce shorter styles.

For stamen length and stigma–anther separation an additive-dominance model did not explain the data. However, the addition of a digenic epistatic parameter [*l*], resulted in a model that fits the data (table 2). For stamen length, the F_1 mean ($\bar{x} = 20{\cdot}6$ mm) is nearer to the parent with longer stamens (A5-28, $\bar{x} = 21{\cdot}5$ mm) and [*h*] is positive. This indicates that alleles that increase stamen length, on average, are dominant to alleles that decrease the length of stamens. Epistatic interactions are, however, required to account for the data. Estimates of the parameters [*h*] and [*l*] have the same sign suggesting that the predominant interaction among loci is of the complementary type (Mather and Jinks, 1982). For stigma–anther separation, dominance occurs as [*h*] is positive. The F_1 mean is closer to the parental line with the larger stigma–anther separation (table 1, fig. 1). The occurrence of opposite signs for [*h*] and [*l*] suggests that the predominant inter-locus interaction is of the duplicate type (Mather and Jinks, 1982).

Analysis of data for flower diameter by ANOVA indicates that this character displays heterosis in crosses between the parental lines. The mean of the F_1 significantly exceeds the diameter of the larger parent (mean flower diameter (mm) A5-28 = 48·7, A9-3 = 48·3, $F_1 = 54{\cdot}6$, $P < 0{\cdot}05$). The additive-dominance model did not fit the data, but addition of a digenic epistatic parameter [*i*] resulted in an adequate fit.

Genetic variation within populations

Results of analysis of variance and repeatabilities for floral characters within eleven populations of *T. ulmifolia* var. *angustifolia* are presented in table 3. Twenty-one of 44 *F*-values are statistically significant suggesting that genetic variation for floral traits is widespread in Jamaica, occurring within nine of the eleven populations studied. Populations A7, A8 and A20 exhibited significant *F*-values for all traits examined. Population A13 was obtained from an abandoned garden at the University of West Indies and contained plants originally collected from different populations.

Repeatability contains several confounded sources of variation including a genetic component and a component of environmental variation (*i.e.*, general enviromental variance, see Falconer, 1981). We therefore provide data on repeatability only to serve as a survey of the upper limits to within-population genetic variation since this provided the only means of estimating levels of genetic variation for several populations sampled. Most notable among the data are the large repeatabilities obtained for population A20. Since open-pollinated families were available for this population a more detailed analysis was performed to further partition the observed variation in floral characters.

Table 3 Repeatabilities (per cent) of floral characters from 11 populations of *T. ulmifolia* var. *angustifolia* in Jamaica obtained from glasshouse grown plants. Significance of *F*-values from one-way ANOVAs are indicated, otherwise values are non-significant

Population	Style length	Stamen length	Stigma–anther separation	Flower diameter
A4	3·6	17·8	24·0	33·7*
A5[a]	0·6	16·2	45·1*	11·4
A6	16·3	8·1	1·7	11·0
A7	39·3*	27·8*	36·9*	63·5*
A8	56·9*	51·6*	31·2*	30·0*
A9[a]	6·2	0·0	5·1	8·8
A10	38·3*	24·4	63·8*	3·5
A11	20·0	23·9	6·9	29·2*
A12	17·2	20·0	42·3*	18·4
A13[b]	54·5*	36·9*	69·8*	16·2
A20[c]	75·4*	55·6*	75·8*	73·6*

* $P < 0{\cdot}05$.
[a] Populations used in biometrical analysis.
[b] Population sampled from a garden collection.
[c] Population used in family sampling.

Population A20 exhibits a mixed mating system ($\bar{t} = 0{\cdot}19$, S.E. = 0·03, range 0·04–0·79) with outcrossing rate heterogeneity among maternal plants (Barrett and Shore, 1987). As a result, each family contains different proportions of selfed and outcrossed offspring. Narrow-sense heritability (the proportion of phenotypic variance attributable to additive genetic variance within a population) cannot be adequately estimated from these open-pollinated data in the absence of additional assumptions or information about the mating system (Squillace, 1974). However, the among-family variance components from a nested analysis of variance (table 4) provides an estimate of broad-sense heritability for population A20. The among-family source of variation is statistically significant indicating the presence of genetic variation for the characters examined (table 4). Stigma–anther separation has the largest among-family variance component (57·2 per cent) indicating that a substantial proportion of variation for this character is genetically based.

Phenotypic and genetic correlations were calculated among pairs of floral characters measured in population A20 and are presented

Table 4 Variance components (per cent) of floral characters in a population of *T. ulmifolia* var. *angustifolia* from Jamaica. Ten families of 25 progeny and two replicate flowers were measured for each plant. Plants were grown under uniform glasshouse conditions in a randomized design. Significance of *F*-values from a nested ANOVA are provided

Source of variation	Style length	Stamen length	Stigma–anther separation	Flower diameter
Among family	44·3***	32·9***	57·2***	43·3***
Within family	31·1***	22·7***	18·6***	30·3***
Within plant	24·6	44·4	24·2	26·4

*** $P < 0.001$.

in table 5. All phenotypic correlations were significant and positive; however, none of the genetic correlations were significant (table 5). Genetic correlations between style length and stamen length and between style length and flower diameter were very small ($r = 0.05$). The genetic correlation between stamen length and flower diameter was larger and positive ($r = 0.52$) although not significant.

Table 5 Phenotypic (above diagonal) and genetic (below diagonal) correlations for floral characters in population A20 of *Turnera ulmifolia* var. *angustifolia*

	Style length	Stamen length	Flower diameter
Style length	—	0·35***	0·40***
Stamen length	0·05	—	0·53***
Flower diameter	0·05	0·52	—

*** $P < 0.001$.

DISCUSSION

The application of quantitative genetic methods to the study of floral variation is necessary if progress in understanding the genetic basis of mating system variation is to be made. Studies in species of agronomic importance (Breese, 1959; Rick and Dempsey, 1969; Manshardt and Bassett, 1984; Hauptli and Jain, 1985), as well as limited work on natural populations (*e.g.*, Ennos, 1981; Schoen, 1982; Macnair and Cumbes, 1989), have demonstrated the presence of quantitative genetic variation for floral characters that influence mating patterns. The use of quantitative genetic methods for natural plant populations is complicated by the wide range of mating systems exhibited among plant species (reviewed by Schemske and Lande, 1985). Plant populations deviate from random mating as a result of selfing or mating among relatives in substructured populations. This makes quantitative genetic analyses based on families sampled from natural populations difficult (Mitchell-Olds and Rutledge, 1986), particularly in the absence of quantitative data on the mating system of populations. In this study, the analysis of genetic variation for floral characters was undertaken using biometrical methods that depend to varying degrees on knowledge of the mating system and extent to which parental plants are inbred.

The biometrical analyses conducted on generation means assume that the parental lines used in this study were homozygous at loci which influence the characters of interest. We believe this assumption may be approximated in the parental plants chosen for analysis for several reasons: First, genetic variation for floral characters within the population from which the parental plant A9-3 was obtained was not detected (table 3). For parental plant A5-28, the homostylous phenotype and high degree of autogamy of this population suggest the occurrence of a high degree of selfing. This would increase the likelihood that individuals are highly inbred. A nested analysis of variance that compared populations A5 and A9 demonstrated that 97·3 per cent of the phenotypic variance in stigma–anther separation is due to the among-population source while only 0·7 per cent of the variance was due to individuals within populations. This analysis therefore suggests that even if small amounts of residual heterozygosity at loci influencing stigma–anther separation occurs within the parental individuals it would likely be overwhelmed by the large genetic differences between parental individuals chosen for the study.

Crosses performed among extreme phenotypes to examine the inheritance of floral variation gave unimodal distributions in segregating generations. The data provide no evidence of a single major gene controlling variation in the floral characters examined. This suggests that the major gene loci governing the inheritance of the distylous polymorphism play no significant role in controlling the patterns of floral variation that occur in homostylous populations (see below). Simple biometrical models could explain the generation means obtained from controlled crosses. An additive-dominance model adequately described the data for style length, while a digenic epistatic parameter was required in the model to describe the means for stamen length and stigma–anther separation.

While unimodality among segregating generations alone cannot be taken as evidence of a polygenic system (Thoday and Thompson, 1976), the continuous range of floral phenotypes exhibited among populations (Barrett and Shore, 1987) as well as the unimodal distribution of phenotypes among segregating generations, provide strong support for the hypothesis that variation in stigma-anther separation in *T. ulmifolia* var. *angustifolia* is polygenic in nature. A very approximate estimate of the minimum number of genes contributing to quantitative variation in stigma-anther separation can be calculated using the weighted estimation procedure of Cockerham (1986). The analysis indicated that a *minimum* of $4{\cdot}5 \pm 0{\cdot}6$ genes contribute to the difference in stigma-anther separation between the extreme parental lines. Lande (1981) provides assumptions of this analysis which are only approximately met by our data owing to the occurrence of non-additive gene effects.

Few data comparable to those presented here are available in the literature. Recently, however, Macnair and Cumbes (1989) have examined the genetic architecture of differences in floral variation between *Mimulus guttatus* and a putatively derived selfing species, *M. cupriphilus*. Several results they obtained are similar to ours. No evidence was found for major gene control of style length, stamen length or stigma-anther separation. Biometrical analyses gave a lack of fit of the additive-dominance models for style length, stamen length and stigma-anther separation indicating epistasis occurs for these characters. In *Mimulus* the direction of dominance exhibited for stigma-anther separation was, however, the reverse of that observed in our study. Estimates of minimum gene numbers indicated that between 3 and 7 genes account for genetic variation in floral characters between the two *Mimulus* species. However, as noted above, application of techniques for estimating the minimum number of genetic factors assume additive gene action and this assumption was also not met in the *Mimulus* data (see table 2, Macnair and Cumbes, 1989). Accordingly, the estimates of gene number for floral characters in *Turnera* and *Mimulus* should be treated with caution and are presented here simply for comparative purposes.

What factors account for the maintenance of genetic variation observed for floral characters within populations of *T. ulmifolia* var. *angustifolia* in Jamaica? At least two possibilities occur: (1) polygenic mutation is sufficient to maintain the levels of variation observed (Lande, 1977), and (2) migration and hybridization among differentiated populations maintains intra-population variation. At present we do not have enough information to address these hypotheses. However, given the weedy colonizing habit of the species (Barrett, 1978), periodic disturbance may result in contact among differentiated populations and recurrent hybridization may provide opportunities for selection to re-shape floral architecture.

The role of the former distyly supergene in contributing to variation among homostylous populations of *T. ulmifolia* for style and stamen length remains obscure. In distylous populations the locus has a major effect on floral architecture and maintains a reciprocal positioning of reproductive organs between the long- and short-styled morphs. Following recombination and the origin of homostyly, polygenic modifiers appear to have become exposed to selection in homostylous taxa of *T. ulmifolia* resulting in alterations in the lengths of reproductive organs. The distyly locus can still function, however, since controlled crosses between distylous and homostylous plants result in the expression of residual incompatibility reactions in the styles and pollen of homostyles (Barrett and Shore, 1987).

If major gene segregation at the distyly locus had a major influence on floral variation in *T. ulmifolia* var. *angustifolia* we would expect the following dominance relationships to pertain. Alleles determining short styles, long stamens and a small stigma-anther separation would be dominant to those determining long styles, short stamens and a large stigma-anther separation. While the direction of dominance for stamen length is in the predicted direction, for the remaining two pairs of traits the pattern is the reverse of that predicted by segregation at the distyly locus (table 2). Thus, although the physiological effects associated with dimorphic incompatibility persist in homostylous plants, there is no evidence that this locus has a major effect on morphological variation in floral characters observed among Jamaican populations of *T. ulmifolia* var. *angustifolia*. Mutation and selection of polygenes appear to govern the process of mating system evolution in homostylous populations via their effects on changing style and stamen lengths.

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