

MALE FERTILITY AND ANISOPLETHIC POPULATION
STRUCTURE IN TRISTYLOUS *PONTEDERIA CORDATA*
(PONTEDERIACEAE)

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Mating types in most self-incompatible plants can only be determined by extensive crossing programs and hence there is little information on their number, relative frequency, and pattern in natural populations (Emerson, 1939; Wright, 1939; Campbell and Lawrence, 1981*a*, 1981*b*; Lawrence and O'Donnell, 1981). In contrast, the incompatibility types in populations of heterostylous plants are readily distinguished in the field by differences in the lengths of stamens and styles. As a result there is considerable information on the population structure of heterostylous plants. Survey data from distylous populations (e.g., Ornduff, 1970; Barrett, 1978*a*, 1978*b*) typically indicate that the long and short-styled morphs are equally frequent (isoplethy) although in some species anisoplethic population structure (unequal morph frequencies) prevails (Levin, 1972; Ornduff, 1980). Owing to the rarity of floral trimorphism there are fewer observations of tristylous species but both isoplethic (Dulberger, 1970; Barrett, 1977*a*) and anisoplethic (Ornduff, 1964; Halkka and Halkka, 1974; Barrett, 1978*b*; Weller, 1979; Barrett and Forno, 1982) populations are reported. Since populations may not have reached equilibrium when sampled, and many heterostylous species exhibit clonal growth, large numbers of populations should ideally be examined for accurate descriptions of population structure.

Fisher (1941, 1944) undertook the first theoretical analysis of equilibrium conditions in tristylous systems using known genetic mechanisms governing tristily in *Oxalis valdiviensis* and *Lythrum salicaria*. He demonstrated that isoplethy could be maintained from generation to gener-

ation by frequency dependent mating. However, his analysis did not exclude the possibility of other equilibria when all morphs are present, and for certain hypothetical mechanisms of the inheritance of self-incompatibility, other stable equilibria are possible (Finney, 1952; Spieth and Novitski, 1969; Spieth, 1971). Recently Heuch (1979*a*, 1979*b*, 1980) has developed a general theorem which must be satisfied for equilibrium populations of heterostylous plants. His analyses indicate that, provided that there are no fitness differences among the floral morphs, an isoplethic equilibrium is the only possible condition in large populations under legitimate mating.

This paper examines factors influencing population structure in the tristylous, diploid, perennial *Pontederia cordata* L. and is part of a broader study of the ecological genetics of tristily in the Pontederiaceae. Here we 1) present survey data on style morph frequency from 74 North American populations; 2) investigate by computer simulation the influence of differences in male fertility and mating system on the relative frequencies of style morphs; and 3) use experimental manipulations and progeny tests in natural populations to evaluate the hypothesis that asymmetries in mating, due to differences in pollen production among the morphs, account for observed data on population structure.

NATURAL HISTORY OF
PONTEDERIA CORDATA

Pontederia cordata, pickerelweed, is an emergent aquatic of eastern and central North America and parts of Central and South America (Lowden, 1973). Populations occur in marshlands, drainage ditch-

es, and at the periphery of lakes, rivers, and streams. They range in size from a few scattered plants to dense monospecific stands, which cover large areas, and probably contain many thousands of genotypes. Individual genets produce both vegetative and reproductive shoots, and clonal growth is by lateral expansion of the rhizome system.

Populations of *P. cordata* in North America flower for between 2 and 9 months depending on latitude. Individual flowers are borne on spicate inflorescences usually containing between 50–150 flowers. Flowers are showy, blue, last for one day, and are pollinated primarily by bees, e.g., *Bombus*, *Melissodes*, *Xylocopa* (Hazen, 1918; Price and Barrett, 1982, 1983). Experimental studies of the tristylous breeding system of *Pontederia* (Ornduff, 1966; Barrett, 1977a and unpubl.) have revealed the presence of a self- and cross-incompatibility system which results in significantly higher levels of seed production from legitimate pollinations (between anthers and stigmas at equivalent levels in flowers) compared with illegitimate pollinations. Incompatibility is strongest in the short-styled morph and weakest in the mid-styled morph (Fig. 1).

An important feature of the floral biology of *P. cordata* concerns differences in the pollen production of floral morphs. Measurements of the amounts of pollen produced by the three anther levels demonstrate that, in common with most tristylous species, pollen production is inversely proportional to stamen height (Fig. 1). However, in *P. cordata* mid-level anthers of the short-styled morph produce, on average, nearly twice as many pollen grains as mid-level anthers of the long-styled morph. This difference was found in measurements from each of 20 North American populations and appears to be a general feature of the species (Price and Barrett, 1982).

Comparison of a wide range of reproductive parameters in natural populations, including flowering phenology, bumble bee visitation levels, inflorescence production, flower production, seed fe-

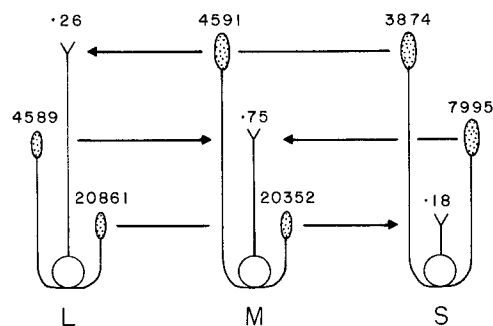


FIG. 1. Generalized diagram of the style morphs in a tristylous species. Arrows indicate legitimate pollinations. Pollen production values for each anther level are average values for *Pontederia cordata* ($N = 20$ populations). For details see Price and Barrett (1982). Self-compatibility values indicated above stigmas are those calculated from Ornduff's (1966) study of *P. cordata* by Charlesworth (1979).

cundity and germination levels, failed to detect any significant differences among the floral morphs (Price and Barrett, 1982). Tristyly is a stable feature of *P. cordata* populations, and in contrast to the closely related *Eichhornia* (Barrett, 1978b, 1979), there is no evidence of breakdown of the tristylous syndrome towards self-pollination via homostyle evolution.

METHODS

Sampling of Style Morph Frequency

Seventy-four populations of *Pontederia cordata* were sampled in eastern North America during 1976–1980. Locality and frequency data for each population are listed in Appendix 1. Of all populations located, almost all were sampled. Available evidence suggests that clone size, inflorescence production and flowering periods of the morphs do not differ in *P. cordata* (Price and Barrett, 1982) so that a random sample of inflorescences from a population should be sufficient to determine genet morph frequencies. In small populations (up to 500 inflorescences), all inflorescences were sampled, while in large populations a random or stratified-random sample was taken.

Average frequencies were calculated for data pooled from all populations and for

proportions of each morph within populations. Average morph frequencies per population were calculated for four classes of populations to determine if there were relationships between class and morph frequencies. The classes were based on observations made at each population: 1) variety: *P. cordata* L. var. *cordata* versus *P. cordata* L. var. *lancifolia* (Muhl.) Torrey; 2) locality: northern region (Ontario, Wisconsin) versus southern region (N. and S. Carolina, Georgia, Florida, Louisiana); 3) habitat: permanent (lake, river, marsh, estuary) versus "temporary" (seasonally-flooded roadside ditches); 4) population size: large (>500 inflorescences) versus small (<500 inflorescences). *G*-tests of goodness-of-fit (Sokal and Rohlf, 1969) were used to determine levels of heterogeneity among populations and whether individual populations differed from isoplethy. The heterogeneity statistic was partitioned into that component attributable to differences between classes, and that remaining within each class (i.e., the residual or unexplained heterogeneity).

To examine spatial heterogeneity of morph frequencies, two linear roadside ditch populations were sampled near Elizabeth City (NC) on June 30, 1978. The populations were both divided into ten contiguous sections (10 m × 2 m in size) and the frequency of morphs within each section was determined. Temporal variation in morph frequency was examined by sampling two populations in Ontario (Dorset 1 and Paugh Lake NW) during August over five consecutive years.

Genetic Model

Population genetic models concerned with equilibrium frequencies of style morphs in tristylous species have assumed equal male fertility among the morphs (Charlesworth, 1979; Heuch, 1979a, 1979b, 1980). However, measurements of pollen production in tristylous species indicate that the style morphs produce different amounts of pollen (Ornduff, 1975; Weller, 1976; Price and Barrett, 1982). These differences could influence the relative male fertilities of style morphs. To

explore the effect of variation in male fertility, a deterministic computer simulation model was developed to monitor morph frequencies over generations in a hypothetical population with different patterns of mating.

The mechanism of style morph inheritance used in the model was that common to the three tristylous families (Lythraceae, Oxalidaceae and Pontederiaceae) and involves two loci, (*S*) and (*M*), with two alleles at each locus, and (*S*) epistatic to (*M*) (Charlesworth, 1979). Our studies of the genetics of tristily in *P. cordata* are not completed but this inheritance pattern occurs in *Eichhornia crassipes* and *E. paniculata* of the Pontederiaceae (Barrett, unpubl. data). Given the rarity of tristily in the angiosperms and the limited number of tristylous species in the Pontederiaceae (*Eichhornia* 3 spp., *Pontederia* 4 spp.) it seems reasonable to assume a monophyletic origin and common inheritance pattern for this polymorphism in the family.

The mating element of the model consisted of three components. A fraction of the ovules for any morph was legitimately mated, a second fraction was randomly mated, and the remaining fraction was selfed. Various types of mating systems were explored. It was assumed that: 1) selfing occurs independently of pollen production or morph frequencies; 2) male success under random mating occurs at a probability given by the pollen production of an individual divided by the total pollen pool; 3) male success under legitimate mating occurs at a probability given by the legitimate pollen production of an individual divided by the legitimate pollen pool; and 4) successful fertilization does not change the amount of pollen available for further fertilizations. Pollen production values used in the model are presented in Figure 1.

The model was run with and without linkage between the (*S*) and (*M*) loci. Identical equilibria were obtained when various recombination fractions were employed. Recombination fractions were only varied with the legitimate mating com-

ponent of the model. Different initial genotype frequencies were specified to determine the presence of a single equilibrium. Analytical solutions for the effects of differences in male fertility among the morphs were derived by modification of equations detailed in Heuch (1979b) and are presented in Appendix 2. These solutions extend the results to a range of inheritance mechanisms for legitimate and selfed matings.

Experimental Field Studies

Results from the simulation model suggest that the anisoplethic structure of many *P. cordata* populations could result from asymmetries in matings among the morphs. Owing to greater pollen production at the mid-level anthers, the short-styled morph may fertilize proportionately more ovules of the mid-styled morph than does the long-styled morph. This hypothesis was tested by analysis of stigmatic pollen loads and progeny tests of mid-styled plants in two populations.

In the first experiment two trimorphic sections of a population near Immokalee, Florida were used. The sections were equal in size (400 m²) and contained approximately the same number of inflorescences (200). A distance of 200 meters separated the sub-populations and all inflorescences were removed from a 50 meter strip around each section. Both sub-populations experienced similar weather conditions (clear, hot and humid) and pollinator activity (mostly *Xylocopa virginica* and *X. micans*) during the experimental period.

On March 18, 1980, all long-styled inflorescences in the western sub-population and short-styled inflorescences in the eastern sub-population were covered with bridal-veil bags. Thus, the following day, assuming no pollen flow from outside the experimental areas, all mid-size pollen on stigmas of the mid-styled morph originated from the short-styled morph in the western sub-population and the long-styled morph in the eastern sub-population. Stigmas were collected from the mid-styled morph in the late afternoon before the flowers had withered. Two stigmas were

collected from each of 94 (east) and 44 (west) inflorescences per sub-population, one from a flower at the top of the inflorescence and one from the bottom. Stigmas from the two positions were preserved separately in fixative. After stigmas were collected, the protective bags were changed from the long- to the short-styled morph in the western section and from the short- to the long-styled morph in the eastern section. On March 19, stigmas were collected as above from 83 inflorescences (east) and 64 inflorescences (west).

Pontederia cordata exhibits a strong pollen size trimorphism which enables an unambiguous determination of the anther level from which pollen originates (Price and Barrett, 1982, 1983). Stigmatic pollen loads obtained from the two sub-populations were analyzed by acetolysis according to procedures outlined in Price and Barrett (1983). Data on the morph frequencies and pollen production of flowers in the sub-populations were estimated by field sampling and collection of buds. Stigmatic loads were then compared with expected ratios after correction for morph frequencies of the sub-population.

A more direct test of the hypothesis involves determination of the number of ovules of mid-styled plants fertilized by the short-styled morph versus the long-styled morph. Fruits of 15 open-pollinated mid-styled plants in a population at Paugh Lake NW (Ont) were collected at random during September 1979. The following spring, seeds were germinated in water (30–40 C), and raised to flowering in submersed pots under glasshouse conditions during the summers of 1980 and 1981. Progeny ratios were compared by *G*-tests with expectations based on the style morph frequencies of the population and their relative pollen production values.

RESULTS

Survey of Style Morph Frequency

Of the 74 populations of *Pontederia cordata* sampled for style morph frequency, 69 (93.2%) were trimorphic. Three populations were dimorphic and two were

TABLE 1. Average style morph frequencies in trimorphous populations of *Pontederia cordata*.

Total populations (N = 74)	Style morph		
	Long	Mid	Short
Total inflorescences (N = 20,199)	5,157	6,865	8,177
Pooled frequency	0.255	0.340	0.405
Average frequency per population	0.255	0.346	0.399

monomorphic. Based upon pooled data from all populations, the short-styled morph is most frequent, with the mid-styled morph intermediate in frequency and the long-styled morph the least frequent (Table 1). This pattern is also evident from examination of the number of populations in which each morph is most frequent, intermediate in frequency and least frequent. The short-styled morph was most frequent in 50.7% of the populations and least frequent in 5.8%. In contrast the long-styled morph was most frequent in only 14.5% of populations and least frequent in 56.5%.

To investigate anisoplethy, morph frequencies were analyzed by a replicated goodness-of-fit test (Table 2). The significant statistic for pooled data (G_p) indicates that the average frequencies deviate from isoplethy (0.333 per morph). Furthermore, populations are heterogeneous, differing from one another in their morph frequencies, as indicated by the significant heterogeneity statistic (G_h). Finally, the total statistic ($G_t = G_p + G_h$) may be partitioned into contributions by individual populations to determine the degree of departure from isoplethy of each population.

Of the 69 trimorphic populations 76.8% are significantly anisoplethic and the remainder are isoplethic (Table 2).

Analysis of the morph frequencies of populations according to the classification involving variety, locality, habitat, and population size are presented in Tables 2 and 3. In Table 2 partitioning of the heterogeneity statistic reveals that although significant heterogeneity is associated with differences between classes by far the largest proportion of the heterogeneity among populations is found within classes. The short-styled morph was the most frequent morph and the long-styled morph the least frequent morph in all classes within the classification (Table 3).

Spatial and Temporal Variation in Morph Frequencies

All sections of the two roadside ditch populations of *P. cordata* sampled for spatial heterogeneity were trimorphic (Table 4). The long-styled morph was least frequent in all sections of one population and in 80% of those in the second population. In both populations the short-styled morph was most frequent in half of the sections.

Morph frequencies were heterogeneous during the five year period in which samples were undertaken at Paugh Lake and Dorset, Ontario. At both sites and at all sampling times the short-styled morph was the predominant morph ranging in frequency from 0.363–0.502 at Paugh Lake and 0.426–0.568 at Dorset.

Simulation Model

The equilibrium style morph frequencies of a hypothetical population in which

TABLE 2. Equality of morph frequencies in 69 trimorphic populations of *Pontederia cordata*.

Test	(a) G-test summary		(b) Departure from 1:1:1	
	d.f.	G*	Populations	P
Pooled	2	694	53 (76.8%)	<.05
Heterogeneity	136	1,877	16 (23.2%)	N.S.
a) Between classes	14	442		
b) Within classes	122	1,435		
Total	138	2,571	69	

* All G values significant at $P < .001$.

TABLE 3. *Morph frequencies of Pontederia cordata by classifications involving varietal status, habitat, locality and population size. Only trimorphic populations were included.*

Classification	N	Frequency		
		Long	Mid	Short
Variety				
<i>cordata</i>	49	0.248	0.366	0.386
<i>lanceifolia</i>	20	0.278	0.281	0.441
Habitat				
Permanent	39	0.245	0.372	0.383
Temporary	30	0.272	0.302	0.426
Locality				
North	26	0.248	0.373	0.379
South	43	0.262	0.322	0.416
Population size				
Large	35	0.244	0.363	0.403
Small	34	0.268	0.318	0.414
All trimorphic populations	69	0.255	0.346	0.399

there are no differences among the morphs in pollen production are presented in Table 6a. Provided that the mating system includes some legitimate fertilizations, an isoplethic equilibrium is achieved. In the absence of legitimate mating, equilibria are dependent on the initial genotype frequencies.

When the observed pollen production differences among the morphs of *P. cordata* are incorporated into the model, strikingly different equilibria arise, with the exception of runs involving complete

selfing (Table 6b). This latter condition occurs because the model assumes selfing is independent of pollen production. In the absence of legitimate mating, and provided that some random mating occurs, the morph with the highest total pollen production spreads to fixation. In our case this involves the long-styled morph. With a mixed mating system, with increases in the random component and decreases in the legitimate component, equilibria become more skewed towards predominance of the long- and mid-styled morphs. As the

TABLE 4. *Spatial variation in morph frequencies in two linear, roadside ditch populations of Pontederia cordata near Elizabeth City, North Carolina.*

Section	Population 1, $G_h = 4.51^1$				Population 2, $G_h = 35.0$			
	L	M	S	N	L	M	S	N
1	0.22	0.49	0.29	45	0.12	0.43	0.44	72
2	0.15	0.30	0.55	47	0.06	0.38	0.56	63
3	0.16	0.44	0.41	32	0.22	0.43	0.35	49
4	0.14	0.53	0.33	94	0.12	0.57	0.31	49
5	0.17	0.27	0.55	40	0.26	0.43	0.31	54
6	0.27	0.23	0.49	51	0.09	0.37	0.54	56
7	0.24	0.41	0.35	66	0.16	0.44	0.40	63
8	0.32	0.42	0.25	59	0.21	0.43	0.36	42
9	0.28	0.31	0.41	54	0.17	0.31	0.52	52
10	0.13	0.24	0.62	53	0.10	0.27	0.62	56
\bar{x}	0.21	0.38	0.41	541	0.15	0.41	0.45	556

¹ Heterogeneity statistic for comparison among sections.

TABLE 5. Yearly variation in morph frequencies in natural populations of *Pontederia cordata*.

Population	Year	Long	Mid	Short	N
Paugh Lake NW (Ontario) $G_h = 25.0^1$ $P < .005$	1978	0.303	0.274	0.423	274
	1979	0.291	0.238	0.471	361
	1980	0.281	0.217	0.502	301
	1981	0.299	0.338	0.363	512
	1982	0.324	0.276	0.400	377
Dorset (Ontario) $G_h = 95.0$ $P < .005$	1978	0.188	0.284	0.528	261
	1979	0.245	0.187	0.568	294
	1980	0.311	0.263	0.426	631
	1981	0.423	0.126	0.451	539
	1982	0.223	0.249	0.528	265

¹ Heterogeneity statistic for comparison among years.

level of legitimate mating decreases the short-styled morph may be lost altogether because of its low total pollen production in comparison with the other morphs (Fig. 1).

If all mating is legitimate, the morph frequencies that result are very close to the observed average values from the population survey (observed frequencies: Long

0.255, Mid 0.346, Short 0.399; model frequencies: Long 0.267, Mid 0.354, Short 0.379). Similar results can be obtained analytically from the equations detailed in Appendix 2. It should be noted that the anisoplethic equilibrium which results is primarily due to the near two-fold difference between the pollen productions of the mid-level anthers of the long- and short-styled morph (Fig. 1). Runs which were undertaken with equal *within* level pollen production between floral morphs always gave an isoplethic equilibrium despite the overall differences in *total* pollen production among the morphs.

TABLE 6. Equilibrium style morph frequencies in a tristylous population with various mating systems and male fertilities. Pollen production values used in the model are those in Figure 1.

Mating system (%) ¹			Equilibrium frequencies		
Legitimate	Random	Self	Long	Mid	Short
a) Equal male fertility					
100	0	0	0.333	0.333	0.333
0	100	0	0.372	0.322	0.306 ²
0	0	100	0.610	0.223	0.167 ²
20	80	0	0.333	0.333	0.333
20	0	80	0.333	0.333	0.333
0	80	20	0.397	0.313	0.290 ²
0	20	80	0.528	0.259	0.213 ²
20	40	40	0.333	0.333	0.333
b) Differential male fertility					
100	0	0	0.267	0.354	0.379
0	100	0	1.0	0	0
0	0	100	0.610	0.223	0.167 ²
20	80	0	0.510	0.490	0
20	0	80	0.267	0.354	0.379
0	80	20	1.0	0	0
0	20	80	1.0	0	0
20	40	40	0.440	0.463	0.097

¹ Style morphs exhibit the same mating pattern for each run.

² Equilibrium frequencies dependent on initial genotype frequencies. Values above were from runs using genotype frequencies of an isoplethic population (see Fisher, 1941 p. 36 for these values).

Tests of the Differential Pollen Production Hypothesis

Field studies provided only limited evidence to suggest that preferential pollination and fertilization of the mid-styled morph by the short-styled morph may contribute to anisoplethy in populations of *P. cordata*.

In the eastern sub-population of the pollen flow experiment (Immokalee, Florida), the observed pollen loads (attributable to mid-level anthers of the short- and long-styled morph) of the top and bottom flowers were not significantly different from predictions based upon the known differential mid-level anther production values for the sub-population (Table 7). In contrast, loads of mid-size pollen differed significantly from those predicted based on equal pollen production at mid-level anthers. In the western sub-population,

TABLE 7. Pollination test of the effect of differential mid-level anther pollen production on pollen flow to mid-level stigmas of *Pontederia cordata* at Immokalee, Florida (March 19–20, 1980).

Mid-size pollen from	Sub-population					
	Date	East		Date	West	
		Flower position			Flower position	
		Bottom	Top		Bottom	Top
Short morph	20th	155 ¹	154	19th	93	80
Long morph	19th	108	96	20th	127	61
Observed ratio S:L		1.43:1	1.60:1		0.73:1	1.31:1
Expected ratio ²		1.70:1			1.43:1	
Goodness of fit tests						
a) Assuming no pollen production differences at mid-level anthers		<i>G</i> 8.445 <i>P</i> < .025	13.579 > .197		<i>G</i> 5.276 <i>P</i> < .025	2.568 > .1
b) Assuming pollen production as observed at mid-level anthers		<i>G</i> 1.807 <i>P</i> > .1	0.197 > .5		<i>G</i> 24.484 <i>P</i> < .005	0.262 > .5

¹ Number of mid-size pollen grains on mid level stigmas.

² Based upon pollen production of mid-level anthers of long- and short-styled morphs, corrected for morph frequencies of the sub-populations.

flowers from the top of inflorescences exhibited stigmatic pollen loads that were intermediate between predictions of the two hypotheses. The trial involving bottom flowers from the western sub-population was the only one in which mid-size pollen from the long-styled morph was more frequent on mid-level stigmas than pollen from the short-styled morph.

A total of 76 flowering progeny were obtained from the 15 open-pollinated mid-styled families from the Paugh Lake (NW) population. Low germination levels and seedling mortality reduced the potential number of flowering individuals. The observed segregation of short-styled versus non-short-styled plants (L or M) was identical to that predicted from the differential male fertility hypothesis, but with a sample size of $N = 76$ the expected segregation from an hypothesis of equal male fertility is not significantly different from the observed values (Table 8). More extensive progeny testing is required to fully distinguish between the two hypotheses.

DISCUSSION

Style morph frequencies in populations of tristylous species can deviate from 1:1:1 for a variety of reasons. Founder effects

can account for anisoplethy in populations of recent origin or in those in which sexual reproduction is restricted (Ornduff, 1964; Barrett, 1977b). In small populations, genetic drift may favor the allele for long style (*m*) and the allele for non-short style (*s*), since they may be carried by genotypes of all three style morphs. Such random processes could result in populations with

TABLE 8. Fertilization test of the differential male fertility hypothesis. Segregation of style morphs in open-pollinated progenies of the mid-styled morph of *Pontederia cordata* at Paugh Lake (NW), Ontario, 1979.

	Long	Mid	Short	<i>N</i>
Flowering progeny	25	23	28	76
Observed	48.0		28.0	76
Expected ¹				
1) Assuming no pollen production differences at mid-level anthers	52.5		23.5	76 ²
2) Assuming pollen production ratio as observed (1.66:1)	48.3		27.7	76 ³

¹ For calculations of expectations see Appendix III.

² $G = 1.21, P > .1$.

³ $G = 0.00527, P > .9$.

an excess of the long-styled morph, and to a lesser extent the mid-styled morph, since these forms can be produced by segregation (Heuch, 1980). Inbreeding may favor morphs determined by genotypes which are homozygous at the two loci, usually the long-styled morph (Mulcahy, 1964). Differential mating success involving pollen or ovules may tend to eliminate a morph, as has been hypothesized for the mid-styled form in several species of *Oxalis* (Mulcahy, 1964; Ornduff, 1964; Weller, 1976). Finally, morph-specific differences in self-fertilization resulting from differential self-compatibility (Stout, 1923; Esser, 1953; Ornduff, 1966; Barrett, 1977a) and self-pollination (Barrett, 1979; Charlesworth, 1979), may lead to a predominance of the mid-styled morph.

The only other tristylous species for which there exists a large body of data on style morph frequencies in natural populations is *Lythrum salicaria*. The data, collected in various European localities by Darwin (1877), Haldane (1936), Schoch-Bodmer (1938), Høeg (1944) and Halkka and Halkka (1974) have been recently summarized by Heuch (1979a). Average morph frequencies are in the reverse sequence to those of *P. cordata*, with frequencies of Long 0.364, Mid 0.331, and Short 0.305. The results of the surveys by Haldane (1936) in England, Schoch-Bodmer (1938) in Switzerland and Halkka and Halkka (1974) on Finnish islands were in close agreement suggesting that the anisoplethic frequencies are the result of fitness differences among the style morphs (Heuch, 1979a).

Although most populations of *P. cordata* are anisoplethic, the morph frequencies are heterogeneous, perhaps because most populations have not reached equilibrium. In any given population morph frequencies may not be similar to the anisoplethic prediction of our genetic model because of historical factors associated with dispersal, disturbance and establishment. However, in a large sample of populations, a bias toward any of the morphs due to historical events alone would be unlikely. Thus, it seems more probable that

selection is responsible for the predominance of the short-styled morph and deficiency of the long-styled morph in our samples.

Similar morph ratios may be typical of populations of the closely related *Pontederia sagittata* Presl. In a taxonomic revision of the genus, Lowden (1973) listed, but did not analyze, frequency data from nine populations sampled from Mexico, Guatemala, and Honduras. The average frequencies (Long, 0.279, Mid 0.339, Short 0.389; $N = 314$) are very similar to those obtained from our survey of *P. cordata*. Interestingly, pollen production at mid-level anthers of the short-styled morph of *P. sagittata* is twice that of mid-level anthers of the long-styled morph (Glover and Barrett, unpubl. data). The population structure and pattern of style morph distribution in the related *Eichhornia crassipes* contrast sharply with *Pontederia* spp. Of 196 New World populations sampled by Barrett and Forno (1982), 77.0% were monomorphic, 18.4% were dimorphic and only nine populations contained the three style morphs. Clonal growth, the high dispersability of the free-floating life form and limited sexual reproduction favor establishment of monomorphic populations in *E. crassipes* (Barrett 1977b, 1979). In *Pontederia* regular seed dispersal among aquatic habitats and frequent recruitment from seed contributes to the maintenance of trimorphic population structure.

While hypotheses exist to explain anisoplethy in other tristylous species (see above), the survey data and theoretical models of anisoplethy published to date do not involve a Short-Mid-Long sequence for tristylous species. Charlesworth's (1979) models of the evolution and breakdown of tristily predict many anisoplethic equilibria but none involve predominance of the short-styled morph or deficiency of the long-styled morph. The remainder of this discussion will therefore evaluate hypotheses which could account for this pattern of population structure in *P. cordata* populations.

Examination of a range of vegetative

and reproductive parameters in the three floral morphs of *P. cordata* failed to detect significant differences which might influence fitness, with the exception of comparisons involving pollen production and self-compatibility (Price and Barrett, 1982, and unpubl.). The floral morphs produce varying amounts of total pollen because of production differences between the three anther levels (see Fig. 1), but these differences are irrelevant to morph frequencies when all matings are legitimate. Of greater significance, however, is the considerable disparity in pollen production at mid-level anthers, since as the simulation studies indicate, this feature could result in deviations from isoplethy similar to those observed in nature. While an hypothesis involving mating asymmetries among the morphs, based on differential male fertility, seems most plausible because of the consistent and unique nature of the pollen production data in *P. cordata*, other explanations require discussion.

If the mechanism of inheritance of tristily was atypical in *P. cordata* and the short allele was recessive, then Heuch's (1980) hypothesis that genetic drift favors the recessive genotype could be invoked. For reasons discussed earlier (see Methods) this explanation seems unlikely but cannot be rejected until a complete genetic analysis of style length has been completed in *P. cordata*. Controlled pollination studies of *P. cordata* indicate that the expression of self-incompatibility varies among the style morphs. In common with several other tristylous species, self-compatibility is most pronounced in the mid-styled morph and weakest in the short-styled morph (Ornduff, 1966). These differences could influence the mating systems of the style morphs and in particular the degree of self-fertilization.

By using the genetic model it is possible to compare the effect of varying selfing rates of the morphs on equilibrium frequencies. If it is assumed that the selfing rate of a morph is proportional to its degree of self-compatibility, then the known compatibility data for *P. cordata* (see Fig.

1) can be used in the model. When this is done, the mid-styled morph predominates due to its much higher level of self-compatibility. Similar results were obtained by Charlesworth (1979) in her theoretical studies of tristylous systems. By adjusting the mating systems of the morphs to include various proportions of legitimate, random and selfed matings and assuming equal male fertilities, it is possible to produce an anisoplethic population structure similar to that observed in *P. cordata*. However, the selfing rates that are required to obtain such effects are not in accord with the known compatibility data available for the species.

Experimental tests of the differential male fertility hypothesis were inconclusive. Demonstrating preferential pollination of the mid-styled morph by the short-styled morph is complicated by the uniform size of mid-level pollen. More trials involving manipulations of population structure, as were employed, would seem to offer the best experimental approach to the problem unless other forms of pollen marking (e.g., dyes or isotopes) are employed. Extensive progeny testing of the mid-styled morph in natural populations provides a more direct test of the hypothesis. Large sample sizes are, however, required to distinguish differences in male fertility among the style morphs.

A final question concerns the basis of the difference in pollen production at mid-level anthers of *P. cordata*. It has been suggested elsewhere (Price and Barrett, 1982) that this feature of the species may have no direct adaptive value but is the inevitable outcome of differences in floral development among the style morphs. In tristylous species the insertion patterns of the two sets of stamens usually differ within a flower (Barlow, 1923). In *P. cordata* the long-level stamens of mid- and short-styled flowers and the short-level stamens of long- and mid-styled flowers have identical patterns of insertion on the perianth tube, while the arrangement in mid-level stamens differs between short- and long-styled flowers. In the short-styled flowers, mid-level stamens are the lower

set and their filaments are inserted on the adaxial side of the perianth tube while in the long-styled flowers they are the upper set and are inserted on the abaxial side of the perianth tube. These structural differences are associated with an anther size dimorphism, with the anthers of the long-level stamens of mid- and short-styled plants and mid-level stamens of the short-styled morph being significantly larger than the anthers of short-level stamens of long- and mid-styled plants and the mid-level stamens of the long-styled morph (Price and Barrett, 1982). The size dimorphism of the anthers is correlated with pollen production. Thus the larger of the two mid-level anther sets in *P. cordata* produces the greatest amount of pollen. It is possible that these patterns are the result of differences in the timing of development of anthers in the two style morphs. An analysis of stamen development in *P. cordata* should resolve this point.

SUMMARY

Populations of *Pontederia cordata* L. (Pontederiaceae) in the North American range are typically trimorphic. The average frequencies of the long-, mid- and short-styled morphs in a survey of 74 populations are 0.255, 0.346 and 0.399, respectively. Populations are heterogeneous for morph frequency and 76.8% of the 69 trimorphic populations displayed significant anisoplethy. Populations most frequently exhibit a predominance of the short-styled morph and a deficiency of the long-styled morph, irrespective of locality, habitat type or population size. The pattern is also evident at a spatial scale of 20 m² in two linear roadside ditch populations in North Carolina and may be typical of populations of the related *P. sagittata* of Central America.

A computer simulation model was used to explore the effects of variations in pollen production and mating system on style morph frequencies. The model suggests that known differences in pollen production at mid-level anthers of the long- and short-styled morphs could account for the

observed anisoplethic population structure in *P. cordata* as a result of mating asymmetries among the morphs. An hypothesis which predicts preferential pollination and fertilization of mid-styled ovules by the short-styled morph was tested by experimental manipulation of a natural population and by progeny tests. Data from the experiments provided limited evidence in support of the hypothesis. It is proposed that variation in pollen production between the mid-level anthers of the long- and short-styled morphs arises because of differences in floral development between the forms and may have no direct adaptive value.

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APPENDIX 1. *Style morph frequencies in N. American populations of Pontederia cordata.*

Population	Style morph			N
	Long	Mid	Short	
1) Trimorphic				
a) var. <i>cordata</i>				
i) Permanent habitats				
Dorset 1, Ont.	0.354	0.292	0.354	48
Dorset 2, Ont.	0.225	0.228	0.547	614
Balsam L. 1, Ont.	0.128	0.518	0.354	517
Balsam L. 2, Ont.	0.240	0.370	0.390	246
Balsam L. 3, Ont.	0.077	0.401	0.522	456
Balsam L. 4, Ont.	0.082	0.560	0.358	441
Ceddar Creek, Ont.	0.153	0.397	0.450	1,410
Cache L., Ont.	0.225	0.391	0.384	276
Algonquin West R., Ont.	0.264	0.442	0.294	129
Margaret L., Ont.	0.216	0.500	0.284	102
Saskatchewan L., Ont.	0.342	0.368	0.289	76
Pog L., Ont.	0.015	0.500	0.485	274
Moon R. 1, Ont.	0.221	0.336	0.443	122
Moon R. 2, Ont.	0.340	0.289	0.372	253
Boot L., Ont.	0.244	0.372	0.385	538
Mississauga R., Ont.	0.396	0.277	0.327	606
Paugh L. NW, Ont.	0.303	0.274	0.423	274
Paugh L. SW, Ont.	0.370	0.253	0.377	1,094
Paugh L. SE, Ont.	0.509	0.473	0.018	55
McQuire L., Ont.	0.244	0.400	0.356	90
Paugh-McQuire Cr., Ont.	0.307	0.255	0.438	192
Dwight, Ont.	0.360	0.267	0.373	75
Shoe L., Ont.	0.285	0.414	0.301	355
Echo Bay, Ont.	0.086	0.448	0.466	163
Whitefish, Ont.	0.133	0.412	0.455	369
Manitowish, Wis.	0.271	0.342	0.387	225
Wilmington, N.C.	0.354	0.316	0.329	158
Osborn, S.C.	0.229	0.310	0.461	297
Darien Altamaha S, Ga.	0.300	0.359	0.341	337
Darien Altamaha N, Ga.	0.225	0.412	0.363	430
Kenwood 1, Fla.	0.184	0.413	0.403	315
Kenwood 2, Fla.	0.213	0.437	0.350	366
Ft. McCoy, Fla.	0.431	0.302	0.267	232
ii) Temporary habitats				
Elizabeth City 1, N.C.	0.156	0.409	0.435	738
Elizabeth City 2, N.C.	0.213	0.368	0.419	530
Askin, N.C.	0.237	0.421	0.342	38
Parkers Ferry, S.C.	0.200	0.450	0.350	20
Pocataligo, S.C.	0.182	0.636	0.182	11
Waycross, Ga.	0.091	0.424	0.485	99
Waycross, Ga.	0.296	0.296	0.409	115
Fish Hall Rd., Ga.	0.354	0.289	0.357	1,396
84 e. of 99-1, Ga.	0.434	0.242	0.324	302
St. Marks, Fla.	0.256	0.217	0.528	180
Lake George, Fla.	0.081	0.535	0.384	86
Greenville, Fla.	0.456	0.087	0.456	103
East Crowley, La.	0.011	0.516	0.473	91
Crowley, La.	0.099	0.380	0.521	192
Thibodeaux, La.	0.447	0.130	0.423	246
Morgan City, La.	0.262	0.297	0.441	512

APPENDIX 1. *Continued.*

Population	Style morph			N
	Long	Mid	Short	
b) var. <i>lancifolia</i>				
i) Permanent habitats				
Tifton, Ga.	0.145	0.424	0.431	413
Statenville E., Ga.	0.083	0.475	0.442	120
Myakkahatchee R., Fla.	0.096	0.368	0.537	136
Immokalee, Fla.	0.285	0.360	0.355	445
Felda, Fla.	0.280	0.363	0.357	336
Palmdale, Fla.	0.306	0.285	0.409	526
ii) Temporary habitats				
Centenary, S.C.	0.352	0.155	0.493	71
Britton's Neck, S.C.	0.400	0.211	0.389	95
Edisto Beach, S.C.	0.500	0.286	0.214	70
Ridgeland 1, S.C.	0.305	0.263	0.431	167
Ridgeland 2, S.C.	0.314	0.221	0.465	331
Ridgeland 3, S.C.	0.489	0.063	0.448	96
Hardeeville, S.C.	0.346	0.197	0.456	309
Clyo, Ga.	0.017	0.492	0.492	59
Brunswick 1, Ga.	0.372	0.196	0.432	285
Brunswick 2, Ga.	0.339	0.280	0.381	307
Brunswick 5, Ga.	0.045	0.102	0.852	88
Brunswick 6, Ga.	0.434	0.159	0.407	113
Hoboken, Ga.	0.351	0.306	0.343	379
Statenville W., Ga.	0.119	0.424	0.458	59
2) Dimorphic				
a) var. <i>cordata</i>				
Permanent habitats				
Rice Lake 1, Ont.	0.260	—	0.740	146
Kenwood, Fla.	0.276	0.724	—	58
b) var. <i>lancifolia</i>				
Temporary habitat				
Kingstree, S.C.	0.833	0.167	—	6
3) Monomorphic				
var. <i>cordata</i>				
Permanent habitats				
Barry's Bay, Ont.	—	—	1.000	28
Rice Lake 2, Ont.	1.000	—	—	42

APPENDIX 2

Heuch (1979a, 1979b) derived a relation which must be satisfied at equilibrium for the style morphs in tristylous systems. This relation can be modified to include pollen production data in the following manner.

Let P_{ij} ($i \neq j$) be the pollen production of the i th morph at its j th stamen level.

For tristily, $i = l, m, s$ $j = l, m, s$.

Let the selfing rates of long-, mid-, and short-styled plants be A_l, A_m, A_s , respectively. They are constants, independent of pollen production and morph frequency.

Let the frequencies of the long-, mid-, and short-styled morphs be L, M, S , respectively.

The probability of each of the three legitimate and three self matings can be written.

e.g.,

$$\text{Prob. (long} \times \text{mid)} = \frac{LMP_{ml}(SP_{sl} + MP_{ml})^{-1} + MLP_{lm}(SP_{sm} + LP_{lm})^{-1}}$$

$$\text{Prob. (long} \times \text{long)} = A_l L$$

Setting $R_l = P_{sl}/P_{ml}$, $R_m = P_{sm}/P_{lm}$, $R_s = P_{ms}/P_{ls}$, the probability that a random parent plant is long (Q_l), mid (Q_m) or short (Q_s) is

$$\begin{aligned}
 Q_l &= A_l L + \frac{1}{2} L [1 - A_l + M(1 - A_m)] \\
 &\quad \times (SR_m + L)^{-1} + S(1 - A_s) \\
 &\quad \times (MR_s + L)^{-1} \\
 Q_m &= A_m M + \frac{1}{2} M [1 - A_m + L(1 - A_l)] \\
 &\quad \times (SR_l + M)^{-1} + SR_s(1 - A_s) \\
 &\quad \times (MR_s + L)^{-1} \\
 Q_s &= A_s S + \frac{1}{2} S [1 - A_s + LR_l(1 - A_l)] \\
 &\quad \times (SR_l + M)^{-1} + MR_m(1 - A_m) \\
 &\quad \times (SR_m + L)^{-1}.
 \end{aligned}$$

Proposition 1 from (Heuch 1979a) states that at equilibrium $Q_l = L$, $Q_m = M$, $Q_s = S$, thus:

1. $1 - A_l = \frac{M(1 - A_m)(SR_m + L)^{-1} + S(1 - A_s)(MR_s + L)^{-1}}{L}$
2. $1 - A_m = \frac{L(1 - A_l)(SR_l + M)^{-1} + SR_s(1 - A_s)(MR_s + L)^{-1}}{M}$
3. $1 - A_s = \frac{LR_l(1 - A_l)(SR_l + M)^{-1} + MR_m(1 - A_m)(SR_m + L)^{-1}}{S}$

If selfing rates among morphs are equal (i.e., $A_l = A_m = A_s = A$), a constant factor $(1 - A)$ may be removed from each term of equations 1, 2 and 3. Thus, the equilibrium morph frequency is identical to that for legitimate mating only. Further, if pollen productions at equivalent stamen levels are equal (i.e., $R_l = R_m = R_s = 1$), the equations reduce to those of Heuch (1979a), which imply a 1:1:1 morph frequency.

For zero or equal selfing rates, equations 1, 2, and 3 may be solved to obtain expressions for equilibrium morph frequencies solely in terms of the pollen production ratios R_l , R_m and R_s . The solution and expressions are complex. However, in *P. cordata* only R_m is significantly different from a value of one. Thus setting $R_l = R_s = 1$ we obtain the following expressions for equilibrium morph frequencies:

$$\begin{aligned}
 L &= (2 + R_m)^{-1} \\
 M &= 1 - (2 + R_m)^{-1} - R_m(1 + 2R_m)^{-1} \\
 S &= R_m(1 + 2R_m)^{-1};
 \end{aligned}$$

alternatively

$$R_m = (M - L)(S - M)^{-1} \text{ at equilibrium.}$$

The analytical results are identical with those obtained by computer simulation (Table 6a, b), and will differ only where we have made the simplifying assumption that $R_s = R_l = 1$, or where the simulation includes a random mating component. The analytical solutions, however, imply that identical equilibria are achieved for a large range of inheritance mechanisms. For details concerning conditions for the existence of equilibria under the model of self and legitimate mating see Heuch (1979b).

APPENDIX 3

Let S_e be the expected number of short-styled plants in open pollinated mid-styled plants and P_{sm} and P_{tm} the pollen productions of the mid-level anther of short- and long-styled flowers, respectively. S and L are the frequencies of the short- and long-styled morphs in the population. N is the number of progeny which are scored. Under the assumption of legitimate mating, short-styled plants are heterozygous, thus the expected number of shorts in the progeny of mids =

$$S_e = 1/2 N \left[\frac{(P_{sm})(S)}{(P_{sm})(S) + (P_{tm})(L)} \right].$$

The number of non-shorts in the progeny of mids = $N - S_e$.