

HISTORICAL FACTORS AND ANISOPLETHIC POPULATION STRUCTURE IN TRISTYLOUS *PONTEDERIA CORDATA*: A REASSESSMENT

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Abstract.—Theoretical models of floral-morph frequencies in tristylous species predict a single equilibrium with all three morphs represented in equal proportions (isoplethy). North American populations of *Pontederia cordata* exhibit considerable heterogeneity of morph frequencies between populations, with the short-styled morph often in excess of isoplethic expectations and the long-styled morph commonly underrepresented. In a previous study, it was proposed that anisoplethic population structure in *P. cordata* is the result of differential male fertility, owing to genetic differences in pollen production among the morphs. In this study, the influence of historical factors on morph frequencies prior to equilibrium was investigated using a deterministic computer model. Nonequilibrium frequencies are strongly influenced by the genotypes of founding individuals, and, because tristily is under the control of two diallelic loci, phenotypic equilibrium is approached asymptotically. The model indicates that in nonequilibrium populations the short-styled morph will be in excess and the long-styled morph will be underrepresented. This suggests that historical factors play an important role in determining population structure in *P. cordata*. Several features of the population ecology of the species lend support to this interpretation. Historical factors should be taken into account when interpreting data from population surveys of morph frequencies in tristylous species and of other genetic polymorphisms not under single-locus control.

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Tristyly is a genetic polymorphism in which plant populations are composed of three floral morphs. In each morph, styles are classified as long, mid, or short (L, M, and S, respectively), with anthers positioned at the two levels in the flower that are not occupied by the stigma. A concurrent physiological self- and intramorph-incompatibility system usually enforces disassortative mating between morphs. The most common inheritance pattern for tristily involves two diallelic gene loci, with *S* epistatic to *M* (Fisher and Mather, 1943; Weller, 1976; Barrett, unpubl.). The L morph is of genotype *ssmm*, the M morph is either *ssMm* or *ssMM*, and the S morph is *Ssmm*, *SsMm*, or *SsMM*. Polyploidy and linkage between the two loci can result in variations of the basic two-locus model. Homozygosity at the *S* locus does not usually occur, because self- and intramorph-incompatibility relations prevent $S \times S$ matings.

Theoretical interest in tristylous systems has centered on equilibrium genotype frequencies as one aspect of the general phenomenon of self-incompatibility polymorphisms (Fisher, 1941, 1944; Finney, 1952, 1983; Karlin and Feldman, 1968*a*, 1968*b*; Spieth and Novitski, 1969; Spieth, 1971; Imrie et al., 1972; Heuch, 1979*a*, 1979*b*, 1980; Karlin and Lessard, 1986). Fisher

(1944) calculated these frequencies for populations assumed to be at isoplethic equilibrium (all morphs at equal frequency) but did not provide mathematical justification for the choice of this equilibrium. Heuch (1979*a*) has shown analytically that, provided all morphs have equal fitness, isoplethy is the only possible trimorphic equilibrium.

Evidence from surveys of natural populations of tristylous species indicate that many populations are not isoplethic (Haldane, 1936; Schoch-Bodmer, 1938; Halkka and Halkka, 1974; Heuch, 1979*a*; Barrett and Forno, 1982; Barrett et al., 1983; Barrett, 1985; Weller, 1986), and researchers have attempted to explain the observed deviations. Since the morphs of heterostylous species frequently differ in reproductive traits that are likely to influence fitness, workers have investigated the effect of morph-specific fitness differences on population structure, both analytically (Heuch, 1979*a*) and by computer simulation (Charlesworth, 1979; Barrett et al., 1983). A second class of hypotheses used to explain anisoplethy involves historical factors. Genetic drift may result in the reduced frequency or loss of the S morph from populations (Heuch, 1980; Barrett, 1985), although stochastic simulation studies in-

dicates that populations composed of more than 30 individuals are likely to remain trimorphic. Since the allele frequencies for the two loci controlling the inheritance of tristylous will approach equilibrium asymptotically, anisoplethy may reflect historical factors associated with population initiation and subsequent establishment. To date, the importance of this alternative has not been investigated thoroughly.

In this paper, we argue that, because of the pattern of inheritance of tristylous, historical factors can be important in determining morph frequencies, even when these are calculated from surveys encompassing a large number of populations. Specifically, we 1) review data from a survey of *Pontederia cordata* populations reported in Barrett et al. (1983) and highlight features of the data that suggest the influence of historical factors in determining morph frequencies; 2) demonstrate the importance of founding genotypes in determining equilibrium population structure; and 3) develop and assess the results of a deterministic computer calculation used to follow morph frequencies in newly initiated populations. We conclude by reassessing the factors influencing anisoplethic population structure in *P. cordata* offered by Barrett et al. (1983), in light of our study.

Population Structure in *Pontederia cordata*

Morph frequencies of 74 populations of *Pontederia cordata* (reported in Barrett et al. [1983 appendix 1]) are plotted in Figure 1. Data from the survey indicate three important features of population structure in *P. cordata*. First, 69 of 74 populations are trimorphic. Second, of the 69 trimorphic populations, only 23.2% are at isoplethy, based on a replicated goodness-of-fit test (Sokal and Rohlf, 1969; see table 2 of Barrett et al. [1983] for additional information). Third, while most populations are not at isoplethy, they are also not distributed randomly throughout Figure 1. There is a paucity of populations represented by points close to the S axis and a similar but less pronounced deficiency toward the M axis. Fifty-two of the 69 trimorphic populations have an excess of the S morph, and 31 have an excess of the M morph (some popula-

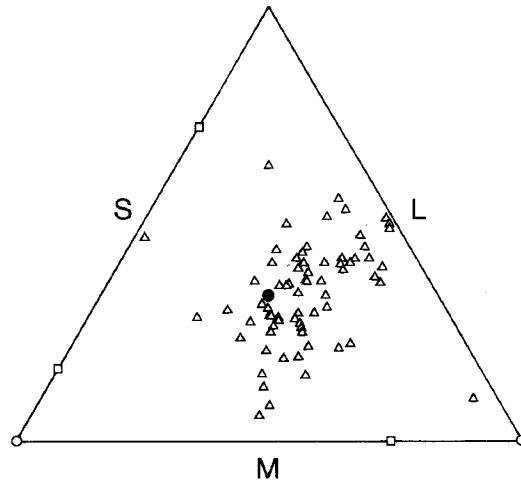


FIG. 1. Morph frequencies in 74 populations of *Pontederia cordata*. The distance of a point from each axis is proportional to the frequency of the morph in the population: points close to the L axis have a low frequency of the L morph. See Crosby (1949) for additional plotting information. Small triangles represent trimorphic populations, squares represent dimorphic populations, and open circles represent monomorphic populations. Isoplethy (filled circle) is equidistant from all axes. Morph frequencies and sample sizes for each population are detailed in Barrett et al. (1983).

tions have an excess of both morphs). The L morph was in excess in only 22 of 69 populations. Average style-morph frequencies, calculated by pooling over all tristylous populations, show a similar pattern, with the frequency of the S morph greater than that of the M morph and the frequency of the M morph greater than that of the L morph (pooled frequencies: L = 0.255, M = 0.340, S = 0.405; $N = 20,199$ flowering shoots).

In their original paper, Barrett et al. (1983) hypothesized that morph-specific differences in pollen production at mid-level anthers, a feature unique to *Pontederia* spp., could account for anisoplethy. A computer calculation was used to show that observed differences in pollen production at mid-level anthers of the S and L morphs resulted in an anisoplethic equilibrium. Morph frequencies resulting from these simulations were in close agreement with the observed survey data. We note that the model accounts for the pooled morph frequencies but not for the heterogeneity of population morph frequencies seen in Figure 1. The importance of historical factors was dis-

counted by Barrett et al. (1983), because the authors postulated that, by sampling a large number of populations, any consistent bias toward one of the morphs would be unlikely. However, historical factors will introduce bias when their effect on morph frequencies is nonrandom. Below, we demonstrate that, because of the genetic basis of tristylly, nonrandom deviations from isoplethy can be introduced during population initiation and establishment.

Population Initiation

Populations of tristylous species that are initiated by a limited number of genotypes will not necessarily contain all four alleles required for the presence of the three morphs at equilibrium. In this section, we ask what morphs will be present in populations initiated by different combinations of the six genotypes present in a hypothetical reference population. We assume that this source population is isoplethic, that it is undergoing disassortative mating only, and that the dispersal of genotypes is proportional to their frequency in the population (Heuch and Lie, 1985). We consider two mating systems in populations initiated in this way and assume that populations may persist for long periods of time through clonal propagation. The first mating system consists of disassortative mating only, while the second involves a change in the mating system at the time of population initiation, with a mixture of disassortative, assortative, and self mating. For brevity, we refer to the second mating system as the "varied-mating" model. The varied-mating model assumes that some outcrossing occurs and that matings between plants of different morphs are more likely to be successful than are matings between plants of the same morph. Under these assumptions, the rate of assortative or self mating does not affect the number of morphs present at equilibrium.

If new populations founded by two individuals chosen randomly from the reference population are maintained through disassortative mating only, 35.0% will be monomorphic, 32.6% dimorphic, and 32.4% trimorphic. The value for monomorphic populations assumes that they will persist through clonal propagation. Because only one morph is present in these popu-

lations, no sexual reproduction is possible under the disassortative-mating model. If the varied-mating model is assumed, 11.2% of the populations are monomorphic, 48.5% are dimorphic (33.2% L and M, 15.1% L and S, 0.2% M and S), and 40.4% are trimorphic. Trimorphic populations can be initiated by seven different pairs of genotypes when only disassortative mating is permitted and by eleven pairs under the varied-mating model. Increasing the number of genotypes initiating a population decreases the probability of monomorphic and dimorphic populations and increases the probability of the population's becoming trimorphic. This is shown in Table 1 and is particularly apparent under the varied-mating model.

Table 1 indicates the frequency with which monomorphic and dimorphic populations consisting of different morphs should be observed when gene flow between populations is rare. Under the disassortative-mating model, monomorphic populations must be maintained through vegetative propagation and are likely to be of limited duration. These populations would consist of the L, M, or S morph with approximately equal probability. However, when varied mating is assumed, over 99% of the monomorphic populations consist of the L morph. Dimorphic populations containing only the M and S morphs should be rare (less than 0.5%), regardless of the mating system. Populations composed of the L and M morphs are expected to be approximately twice as frequent as populations with the L and S morphs.

The proportion of populations with all three morphs will be influenced by the extent of gene flow between populations. Monomorphic and dimorphic populations were infrequently encountered in the survey by Barrett et al. (1983), suggesting that gene flow is common in *P. cordata*. Furthermore, the frequency of these populations is consistent with the above predictions, with dimorphic populations containing only the L and M morphs (L-M populations) more frequent than L-S populations, which in turn are more frequent than M-S populations. However, because only five dimorphic populations were encountered in the survey, it is not possible to test these observations statistically. More extensive sampling is re-

TABLE 1. The influence of different patterns of mating and number of initiating individuals on equilibrium population structure in a tristylous species. Values are the percentages of populations with a particular structure when all combinations of initial genotypes are drawn from an isoplethic source population.

Population structure	Disassortative-mating model: Initial number of individuals			Varied-mating model: Initial number of individuals		
	2	3	4	2	3	4
Monomorphic	35.0	11.96	4.10	11.2	3.69	1.23
L	11.1	3.69	1.23	11.1	3.69	1.23
M	12.7	4.55	1.63	0.1	0.00	0.00
S	11.2	3.72	1.24	0.0	0.00	0.00
Dimorphic	32.6	30.47	22.36	48.5	35.60	24.08
L, M	20.6	21.30	16.82	33.2	25.80	18.44
L, S	11.9	9.16	5.54	15.1	9.72	5.64
M, S	0.1	0.01	0.00	0.2	0.01	0.00
Trimorphic	32.4	57.57	73.54	40.4	60.72	74.68

quired to verify the predictions of the model.

Approaches to Isoplethy

This section describes a computer calculation used to investigate the dynamics of trimorphic-population establishment in greater detail. We assume that the parental generation is determined by selection of genotypes from an ancestral population as described in the previous section. Genotype frequencies of successive generations are calculated from the expected segregation of genotypes resulting from a fixed rate of prior selfing (denoted as $1 - t$) and outcrossing. Outcrossed matings occur in proportion to genotype frequencies and are either assortative or disassortative. Only a fraction a (less than 1) of the assortative matings are successful. This parameter reflects the decreased probability of successful pollen transfer and fertilization associated with assortative mating in a tristylous breeding system. All genotypes of a given morph are assumed to have identical mating systems, and progeny from all classes of mating have equal fitness. In some instances, we use a simple modification that incorporates overlapping generations but maintains discrete reproductive intervals. This modification of the calculation can be written as

$$\mathbf{g}_{t+1} = (1 - I)\mathbf{g}'_{t+1} + I\mathbf{g}_t \quad (1)$$

where I is the proportion of plants surviving from generation t to generation $t + 1$, \mathbf{g}_t is the vector describing genotype frequencies after t generations, and \mathbf{g}'_{t+1} is the vector describing genotype frequencies following

disassortative, assortative, and self mating in the t th generation. Populations were followed until the square of the deviation from isoplethic expectation summed over all morphs in all populations was less than 0.001. For brevity, we discuss general results obtained with the varied-mating model only.

Trajectories of Morph Frequencies During Population Establishment. — Two genotypes arriving simultaneously will result in trimorphic populations for eleven different genotype pairs. Changes in morph frequencies in the four most likely populations over time are presented in Figure 2a, with $t = 0.9$, $a = 0.0$, and $I = 0.5$. Lines in the figure connect successive generations of a given population following initiation. The lines represent 81% of all possible trajectories; remaining populations follow similar paths. As predicted by Heuch (1979a), all paths lead to populations at isoplethic equilibrium. The number of generations required for a population to reach isoplethy is dependent on the founding genotypes. Inspection of Figure 2a indicates that all combinations of founding genotypes result in paths in which the S morph is overrepresented, with frequencies greater than 33%. Understanding the genetic basis of this result rests on the observation that trimorphic populations must include the S morph among the initial genotypes, as this is the only morph that carries the dominant S allele. As the source population was assumed to be maintained through disassortative mating only, the S morph will be heterozygous at this locus. Thus the ratio of short-styled to non-short-

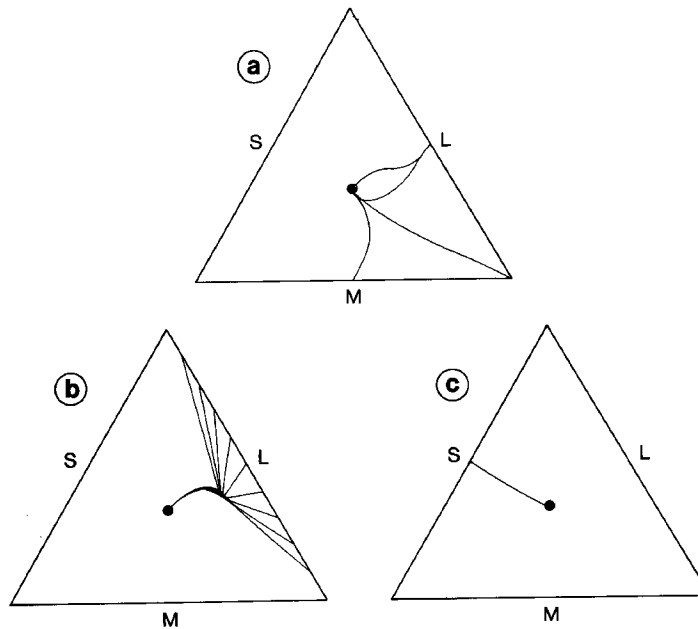


FIG. 2. Changes in morph frequencies of populations initiated by genotypes selected from an isoplethic source population. Lines in each figure connect frequencies in successive generations following initiation. a) Paths followed by four initial genotype combinations leading to trimorphic populations, assuming varied mating with $t = 0.9$, $a = 0.0$, and $I = 0.5$. b) Paths followed by a population initiated with genotypes $ssMm$ and $SsMm$ when each genotype is represented at different initial frequencies; $t = 0.9$, $a = 0.0$, and $I = 0.0$. c) Path followed by a dimorphic population containing the L and M morphs, when a third genotype, containing an S allele, is introduced; $t = 0.9$, $a = 0.0$, and $I = 0.0$. The solid circle represents isoplethy.

styled progeny from an S morph that mates disassortatively will be 1:1. When selfing occurs, the ratio will be 3:1. For this reason, the S morph predominates in the early generations of population establishment. Increasing levels of assortative or self mating or increasing the proportion of individuals surviving between generations tends to decrease changes in morph frequencies between successive generations and to increase the time required to reach isoplethy.

Simultaneous arrival of two genotypes is one method by which a trimorphic population can be initiated. Alternatively, two genotypes might arrive sequentially or a dimorphic population might be invaded by a genotype carrying the allele necessary for the population to become trimorphic. The sequential arrival of two genotypes can be simulated in the model by constructing populations with each genotype of the initiating pair originally represented at different frequencies. Lines in Figure 2b trace paths followed by populations initiated by an illustrative pair of genotypes, assuming $t = 0.9$,

$a = 0.0$, and $I = 0.0$. Each line represents the establishment of a single population. The collection of lines in the figure indicates paths followed by populations when the two genotypes are represented at nine different initial frequencies. After very few (2–5) generations, morph frequencies under this model are indistinguishable from those observed when populations originate with the simultaneous arrival of two genotypes. Calculations for cases in which dimorphic populations are invaded by a third genotype, resulting in trimorphic populations, can result in novel paths. For instance, when the third genotype to enter the population contains the S allele, the population will approach equilibrium with the L and M morphs at equal, but decreasing, frequencies. This is shown in Figure 2c.

Expected Morph Frequencies. — Trimorphic populations approach isoplethy following paths such as those in Figure 2a. The expected morph frequencies at a given time after population initiation can be calculated by determining the weighted mean

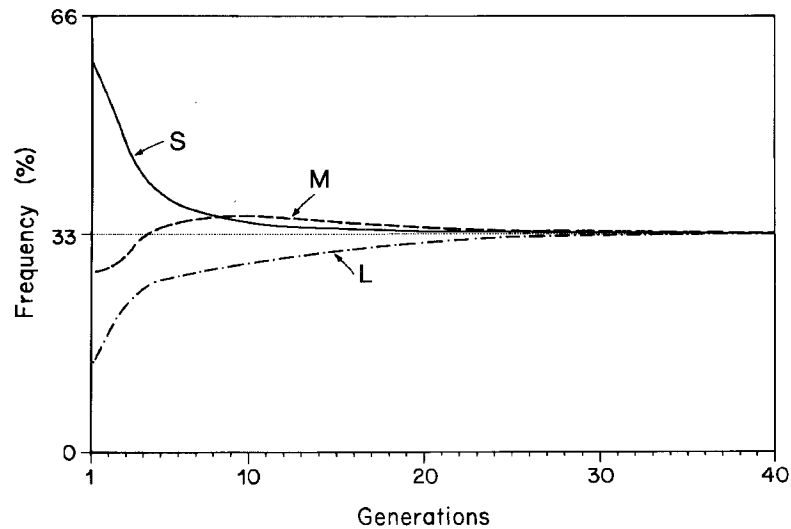


FIG. 3. Changes in the weighted mean morph frequencies of all pairs of initiating genotypes resulting in trimorphic populations, from population initiation to isoplethy, with $t = 0.9$, $a = 0.0$, and $I = 0.0$.

morph frequencies of all paths at that time. Each path is weighted by the probability of drawing the requisite initial genotypes for the path from the source population. In Figure 3, the expected morph frequencies are plotted against generation number following population establishment, with $t = 0.9$, $a = 0.0$, and $I = 0.0$ and assuming that populations are initiated by two individuals arriving simultaneously. For all points from population establishment to isoplethy, the S morph is in excess of the isoplethic frequency of the morph. In early generations, this excess is substantial. The L morph, on the other hand, is always deficient, relative to its isoplethic frequency, until isoplethy is reached. The M morph is initially deficient but, by the fourth generation, becomes more frequent than at equilibrium and reaches a maximum frequency after eight generations. Thereafter, the frequency of the M morph closely tracks that of the S morph. Isoplethy is reached after 32 generations. The model predicts an initial period during which the S morph is in excess of isoplethic frequency, followed by a protracted period characterized by a less marked excess of both the S and M morphs, which occur in approximately equal frequencies.

Similar results are obtained when parameters of the models are altered. Decreasing the value of t or increasing the value of a or I lengthens the number of generations

required to reach isoplethy, as indicated in Table 2. When two genotypes are assumed to arrive sequentially, populations approach isoplethy along paths similar to those followed by trimorphic populations initiated by the simultaneous arrival of two genotypes, as shown in Figure 2b. In all cases, however, the pattern discussed above is repeated: the S morph is always in excess of isoplethic frequencies, and the L morph is always less frequent than at isoplethy.

Predictions of the model change if monomorphic and dimorphic populations are in-

TABLE 2. Number of generations until isoplethy is reached under various patterns of mating in a tristylous species. All pairs of individuals resulting in trimorphic populations were included, and isoplethy was reached when the square of the deviation from isoplethic expectation summed over each morph in all populations was less than 0.001. Each population was weighted by the probability of drawing the pair from an isoplethic source population.

Outcrossing rate (t)	Ratio of assortative : disassortative matings (a)	Overlapping generations (I)	Generations to isoplethy
1.0	0.0	0.0	26
1.0	0.0	0.5	50
1.0	0.1	0.0	31
1.0	0.1	0.5	60
0.9	0.0	0.0	26
0.9	0.0	0.5	51
0.9	0.1	0.0	32
0.9	0.1	0.5	61

cluded when calculating expected morph frequencies. Including these populations results in an overall deficiency of the S morph and excesses of the L and M morphs, relative to isoplethic frequencies. This follows from Table 1, where the L and M morphs have greater representation than the S morph in monomorphic and dimorphic populations. However, invasion of dimorphic populations by the third morph, resulting in trimorphic populations, moderates this effect. Expected morph frequencies are also sensitive to the nature of population initiation. Increasing the number of genotypes arriving before populations become well established decreases the disparity between initial and isoplethic morph frequencies in trimorphic populations. The model successfully accounts for morph-frequency deviations from those expected at isoplethy when a small number of genotypes is responsible for population initiation.

DISCUSSION

In their original paper, Barrett et al. (1983) recognized that many of the populations of *Pontederia cordata* they sampled were unlikely to have reached equilibrium and that historical factors associated with population establishment would influence morph frequencies. However, they discounted the possibility of a consistent bias toward any of the morphs as a result of historical factors alone, because of the large number of populations involved in their survey. Instead, they interpreted the anisoplethic population structure of *P. cordata* as the result of male-fertility differences among the floral morphs. In *Pontederia* spp. the mid-level anthers of the S morph produce an average of two times the amount of pollen produced by the corresponding anthers of the L morph. Preferential fertilization of M ovules by pollen of the S morph could lead to the consistent excess of the S morph and deficiency of the L morph observed in natural populations.

The results of the present study indicate that historical factors can have an important influence on morph frequencies in tristylous populations to the extent that biases may be evident even when large samples are employed. Excess of the S morph and a deficiency of the L morph were observed in early generations of the model when popu-

lations were founded by the entire range of genotype combinations that occur under the two-locus (*S*, *M*) model of the inheritance of tristylity. This suggests that the observed anisoplethy in *P. cordata* is attributable, in part, to the inclusion in the sample of many populations that were not at equilibrium.

The present study has focused on trimorphic populations initiated by a small number of individuals. However, the large proportion of trimorphic populations observed in the survey suggests that the number of individuals responsible for population initiation is relatively high. When more individuals are responsible for population initiation, the difference between initial and isoplethic morph frequencies in trimorphic populations declines, and the ability of the model to explain the observed anisoplethy decreases. Several considerations help to ameliorate this inconsistency. The survey might have overestimated the proportion of trimorphic populations. While virtually all populations encountered were surveyed (Barrett et al., 1983), it is possible that small populations were overlooked. Smaller populations are more likely to be recently initiated and, therefore, to be monomorphic or dimorphic. In addition, we have assumed that all populations were initiated by individuals drawn from an isoplethic equilibrium population. However, new populations can be initiated by individuals that originate from populations that have not reached isoplethy. Under this scenario, deviations from isoplethy during the early stages of population establishment are greater than those shown in Figure 3.

While information concerning the exact nature of population initiation and establishment in *P. cordata* is not available, several features of the population ecology of *P. cordata* lend support to this interpretation. Seedling and juvenile establishment in this long-lived emergent aquatic are largely regulated by water depth, and recruitment is highly episodic in nature. Our field observations suggest that many populations, particularly those in lake shore habitats, are initiated following bursts of establishment as a result of low water levels. Relatively little recruitment occurs in the intervening periods, when higher water levels prevail.

As a result of the episodic nature of seedling establishment, populations may frequently be composed of a restricted number of genotypes that are the descendants of the initial founding morphs. Subsequent clonal growth by these genotypes increases the physical size of populations, but, because of restrictions on further establishment, the progress toward equilibrium is likely to be retarded. The sampling procedure adopted by Barrett et al. (1983) involved the random sampling of reproductive shoots within populations. Although sample sizes were generally high (mean number of shoots per population = 273), the number of genotypes represented in the samples may have been considerably smaller, particularly in populations with large clone size.

Our results do not refute the hypothesis of differential male fertility as a factor contributing toward anisoplethic population structure in *P. cordata*. Many of the populations sampled were large, sampling was extensive, and a high degree of intermixing among morphs was evident. Morph frequencies in large populations (>500 inflorescences) revealed that the S morph was overrepresented and the L morph was underrepresented, in comparison with isoplethic expectations (Barrett et al., 1983). If only historical factors were involved and we assume that at least some of the large populations are at equilibrium, then average morph frequencies should be closer to isoplethy in the sample of large populations. This was not the case, suggesting that male fitness differences play a role in determining the relative frequency of morphs under certain conditions. Extensive progeny testing of the morphs and the use of genetic markers are required to measure the extent of male fertility variation in *P. cordata* populations.

The models developed here indicate that a considerable range of morph frequencies can arise owing to historical factors associated with the number and time of arrival of different combinations of genotypes. The models help to explain both the observed deviations from isoplethy and the significant heterogeneity in morph frequencies among populations. Morph-specific fitness differences are more appropriately invoked when populations show a highly consistent

structure (Weller, 1986), when the observed morph ratios are different from those predicted by the current model (e.g., *Lythrum salicaria*; see Heuch, 1979a), or when populations can be shown through long-term censusing to have reached an anisoplethic equilibrium.

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