

STOCHASTIC LOSS OF STYLE MORPHS FROM POPULATIONS OF
TRISTYLOUS *LYTHRUM SALICARIA* AND
DECODON VERTICILLATUS (LYTHRACEAE)

CHRISTOPHER G. ECKERT AND SPENCER C. H. BARRETT

Department of Botany, University of Toronto, Toronto, Ontario, CANADA M5S 3B2

Abstract.—Despite the theoretical importance of stochastic processes in evolution there have been few empirical studies of the interaction between genetic drift and selection on the maintenance of polymorphisms in plant populations. We used computer models to investigate the interaction between drift and frequency-dependent selection in affecting style morph frequencies in populations of tristylous species. Drift produces a distinct pattern of morph frequency variation involving: 1) the loss of the S morph and, to a lesser extent, the M morph; 2) no consistent bias in frequencies within populations; 3) a restricted pattern of variation involving a deficiency of one morph and equal excesses of the other two. Morph frequencies were surveyed in 137 populations of *Lythrum salicaria* from both its native range in Europe ($N = 35$) and recent adventive range in Ontario ($N = 102$), and 133 populations of *Decodon verticillatus* from four regions in eastern North America with different glacial histories to assess these theoretical predictions. There was a negative relationship between morph loss and population size in both species; the relationship was weaker in *D. verticillatus* than in *L. salicaria*. Morph loss was more frequent in the adventive than native range of *L. salicaria*, and in populations of *D. verticillatus* from glaciated northern regions compared with the unglaciated southern portion of its range. Simulations incorporating variation in life history, regeneration strategy and mating patterns revealed that the degree of morph loss was strongly influenced by year to year survival, clonal propagation, self-fertilization and departures from disassortative mating. Comparing the pattern of morph frequency variation between species supported these predictions. Morph loss was lower in self-incompatible *L. salicaria* (0% in Europe; 23% in Ontario), which reproduces through seed compared to self-compatible, clonal *D. verticillatus* (52%). A stochastic model provides the most parsimonious explanation for observed patterns of morph frequency variation in both species.

Key words.—Clonal reproduction, colonization, *Decodon verticillatus*, floral polymorphism, frequency-dependent selection, genetic drift, *Lythrum salicaria*, tristily.

Received June 7, 1991. Accepted December 13, 1991.

Stochastic processes such as founder events, population bottlenecks, and genetic drift are thought to play an important role in evolution by influencing the amount and distribution of genetic variation within and among populations (Wright, 1931, 1969; Crow and Kimura, 1970; Carson and Templeton, 1984; Goodnight, 1987; Barton, 1989). Despite a growing recognition of the evolutionary significance of random processes (Wright, 1982), there are few empirical studies demonstrating the influence of drift on genetic variation maintained by selection in natural populations (Oxford and Shaw, 1986). This is, in part, because of the difficulty in arriving at specific predictions as to the patterns of genetic variation expected from the interaction between drift and selection. For example, although simply inherited polymorphisms provide useful experimental systems for the study of microevolution, patterns observed in natural populations often fail to reveal the relative

effects of drift and selection, primarily because the mode and scale of selection on these polymorphisms is often unknown (Jones et al., 1977; Endler, 1986; Crawford and Jones, 1988; Ennos, 1990; Wade and Kalisz, 1990).

Investigations of tristylous breeding systems avoid some of the difficulties inherent in ecological genetic studies of other polymorphisms. In tristylous populations, frequency-dependent selection occurs during the reproductive cycle as a consequence of disassortative mating (Barrett et al., 1987). Theoretical models indicate that this mating system leads to a single equilibrium with equal frequencies of the three floral morphs, provided that no other fitness differences occur among the morphs (Heuch, 1979a, 1979b). Moreover, stochastic models have shown that genetic drift in small populations can give rise to a characteristic pattern of morph frequency variation because of the common mode of inheritance found among

TABLE 1. Comparison of life-history, genetic, and reproductive attributes in the herbaceous wetland perennials *Lythrum salicaria* and *Decodon verticillatus* (Lythraceae).

Attribute	<i>Lythrum salicaria</i>	<i>Decodon verticillatus</i>
Breeding system	tristylous	tristylous
Incompatibility	self- and intramorph-incompatible	self- and intramorph-compatible
Ploidy level	tetraploid ¹	diploid
Primary regeneration strategy	seed	clonal
North American status	introduced to northeastern North America native to Eurasia	native to eastern North America
Typical habitat	disturbed wetlands, ditches and wet meadows	undisturbed wetlands and lake margins

¹ Diploid chromosome counts have been recorded in parts of the native range.

tristylous species (Heuch, 1980; Heuch and Lie, 1985; Morgan and Barrett, 1988; Barrett et al., 1989). Frequency-dependent selection and genetic drift, therefore, comprise the dominant forces shaping patterns of morph frequency variation in natural populations of tristylous plants. This simple model provides a general expectation against which observed patterns of morph frequency variation can be interpreted.

Surveys of morph frequencies in natural populations of tristylous species frequently show significant deviations from equal morph frequencies (e.g., Ornduff, 1974; Barrett, 1977; Weller, 1979; Barrett et al., 1983, 1989). This variation has been interpreted in terms of the ecological characteristics of species, especially their life-history and reproductive attributes. In particular, the occurrence of extensive clonal propagation in several tristylous species has led to the suggestion that skewed morph frequencies can be accounted for by founder events and limited sexual reproduction (Ornduff, 1972; Barrett and Forno, 1982). However, the extent to which ecological features of tristylous species influence the interplay of selection and drift has not been examined in detail. Here we develop a theoretical model that incorporates ecological factors in an attempt to explain the patterns of morph frequency variation observed in two tristylous species with contrasting life-history traits.

Lythrum salicaria and *Decodon verticillatus* (Lythraceae) are herbaceous perennials that inhabit a variety of wetland habitats in eastern North America. *Lythrum salicaria* is native to Eurasia but has recently

colonized disturbed wetland habitats in northeastern North America (Stuckey, 1980; Thompson et al., 1987) whereas *D. verticillatus* is native to undisturbed wetlands and lake margins in eastern North America (Graham, 1964). While the two species share some aspects of their ecology and morphology, there are several significant differences between them that could potentially influence the patterns of morph frequency variation (Table 1). Regeneration strategies of the two species are markedly different; *L. salicaria* reproduces exclusively through seed, whereas *D. verticillatus* reproduces clonally by adventitious rooting of stems. Compared to *L. salicaria*, the recruitment of sexual offspring in *D. verticillatus* is limited, although seed is produced in most populations.

In addition to these contrasts in life-history, several aspects of the floral biology of *L. salicaria* and *D. verticillatus* also differ. *Lythrum salicaria* possesses a self- and intramorph-incompatibility system found in most tristylous species (Darwin, 1877; Stout, 1923). Crosses between individuals of the same style morph and self-pollinations usually fail to set seed. In contrast, controlled self- and intramorph-pollinations in *D. verticillatus* are highly fertile (Blaisdell, 1974; C. G. Eckert and S. C. H. Barrett, unpubl. data) allowing departures from disassortative mating through both self- and intramorph-fertilizations. Finally, North American populations of *L. salicaria* appear to be uniformly tetraploid whereas those of *D. verticillatus* are diploid (Mulligan, 1957; Larsen, 1965; Tobe et al., 1986).

Here we report the results of extensive

geographical surveys of style morph frequencies in natural populations of *L. salicaria* and *D. verticillatus*. We focus particular attention on geographical patterns of variation in morph frequencies to assess the importance of stochastic processes during migration and colonization. Data from these surveys are also tested against predictions from theoretical models that examine the effects of life-history, regeneration strategy, mating system, and ploidal level on the pattern of morph frequency variation.

MATERIALS AND METHODS

Computer models

We modeled the dynamics of finite tristylous populations using Monte Carlo computer simulations. Each population was represented by a vector of N integers representing N individuals. At the start of each simulation, populations were founded by assigning each vector element 1 of 10 possible style morph genotypes (see below) with probabilities equal to their theoretical equilibrium frequency (Table 1 of Heuch and Lie, 1985). In going from year to year, N was held constant and each new population was made up of a proportion, I , surviving from the previous year and $N(1 - I)$ offspring, each of which was either clonal or sexual with probabilities C and M , respectively ($C + M = 1$ and $I + (1 - I)(C + M) = 1$). For each offspring, a maternal parent was randomly chosen from the previous year's population. For clonal offspring, parents were sampled with replacement so that each could potentially produce more than one clonal offspring. For sexually produced offspring, maternal parents were also sampled with replacement. The type of mating was then determined as either self-fertilization or outcrossing with probabilities s and $(1 - s)$, respectively. Outcrosses were further designated as either disassortative or random with respect to morph, with probabilities d and $(1 - d)$. Disassortative mating was achieved by randomly choosing a male parent from among all individuals in a population of a style morph different from that of the maternal parent. In populations that had lost two morphs during a simulation, all outcrossed offspring were produced by random mating because

disassortative mating was impossible. After parents were chosen, genotypes of offspring were determined by the combination of parental gametes produced through simple mendelian segregation at the style morph loci.

With this basic model both the independent and joint effects of survivorship (I), clonal propagation (C), self-fertilization (s) and disassortative mating (d) could be examined. Each simulation applied one set of the above parameters to 100 populations for 100 years (following Heuch, 1980). Running simulations for longer periods did not alter the relative effects of the parameters examined. At the end of each simulation, populations were classified as either trimorphic, dimorphic, or monomorphic depending on whether they contained three, two, or one morph. In most simulations the response variable of interest was the proportion of 100 replicate populations remaining trimorphic at the end of a simulation (T). Ninety-five percent confidence intervals for this binomial variable were calculated using Table 23 in Rohlf and Sokal (1981). Confidence intervals for a range of T values are provided in Table 2 and are applicable for all simulation results involving this variable. Computer models were coded in THINK[®] pascal (version 2.0) and run on a Macintosh SE microcomputer.

The inheritance of tristylous commonly involves two diallelic loci, S and M , with S epistatic to M (Lewis and Jones, 1992). This genetic control results in 10 possible genotypes; with the long-styled morph (L) *ssmm*, the mid-styled morph (M) *ssMm* or *ssMM*, and the short-styled morph (S) *Ssmm*, *SM/sm*, *Sm/sM*, *SsMM*, *SSmm*, *SSMm*, or *SSMM*. *Lythrum salicaria* exhibits tetrasomic inheritance at both style morph loci, with no linkage or dosage effects (Fisher and Mather, 1943; Fisher and Martin, 1947). Double reduction has been estimated at 10% for the S locus (Fyfe, 1953) and 2.5% for the M locus (Fisher, 1949). One version of our computer model simulated tetrasomic inheritance with 5% double reduction at both loci, and no linkage between them. Preliminary genetic studies in *Decodon verticillatus* indicate disomic inheritance with the S factor dominant to the M , and the M dominant to the L . However, it is not yet

TABLE 2. Average morph frequencies in simulated tristylous populations. Each row of data is from 100 populations run for 100 years with $d = 0.95$, $s = 0.01$, and $I = C = 0.00$. T is the proportion of populations including all three morphs. Ninety-five percent confidence intervals (CI) for T were calculated following Rohlf and Sokal (1981). Morph frequencies are averaged over all 100 populations and for trimorphic populations only. Style morph is denoted by L, M, and S for long-, mid-, and short-styled morph, respectively.

Population size	T	95% CI for T	Average morph frequencies					
			All populations			Trimorphic only		
			L	M	S	L	M	S
15	0.03	0.01–0.08	0.48	0.32	0.20	0.40	0.29	0.31
20	0.32	0.23–0.42	0.43	0.34	0.23	0.33	0.35	0.32
25	0.62	0.52–0.72	0.37	0.34	0.29	0.32	0.33	0.35
30	0.74	0.64–0.82	0.36	0.35	0.29	0.32	0.34	0.35
35	0.85	0.77–0.91	0.34	0.34	0.33	0.31	0.33	0.35
40	0.91	0.84–0.96	0.34	0.32	0.34	0.33	0.31	0.36
50	0.98	0.93–1.00	0.35	0.32	0.33	0.34	0.33	0.33
70	1.00	0.97–1.00	0.34	0.33	0.33	Same as all populations		
90	1.00	0.97–1.00	0.34	0.34	0.32	Same as all populations		

clear whether style morphs are controlled by one triallelic locus or by two diallelic loci; and if by two, the degree of linkage between them (C. G. Eckert and S. C. H. Barrett, unpubl. data). For the diploid case, variations of the computer model were used to simulate both one- and two-locus patterns of inheritance, and examine the effect of linkage. Neither the number of loci or degree of linkage had any significant effect on morph frequency variation. Accordingly, simulation results are only reported for the two-locus model with no linkage.

Population surveys

We estimated style morph frequencies for a total of 102 populations of *L. salicaria* from Ontario, and 133 populations of *D. verticillatus* from four different regions of eastern North America. In *L. salicaria*, we sampled 51 populations from each of two separate geographical areas corresponding to the historically older portion of the adventive range in eastern Ontario (Stuckey, 1980) and more recently colonized areas in south-central Ontario. Data from these areas were compared to a sample of 35 populations from the native European range reported in Haldane (1936), Schoch-Bodmer (1938) and Halkka and Halkka (1974). This sampling strategy allowed us to examine the effects of colonization history on morph frequency variation at both regional and continental scales.

Populations of *D. verticillatus* were sampled from four regions in eastern North

America: 21 from Ontario; 30 from the lower peninsula of Michigan; 50 from New England; and 32 from the southeastern United States. These four regions were chosen to include areas with contrasting glacial histories. All three northern regions were glaciated during the Quaternary period, thus *D. verticillatus* is likely to have had a shorter history in these areas compared to the unglaciated southeastern region. The effects of stochastic processes are likely to be more pronounced in more recently established populations. Over time, morphs lost from populations during colonization may be repatriated through immigration, and morph frequencies perturbed by stochastic events will return towards equilibrium levels. Accordingly, we predicted that the more recent migration of *D. verticillatus* to these northerly areas may be associated with greater morph frequency variation.

Style morph of flowering plants was easily determined by inspection in both species. Plants were sampled at regular intervals chosen to maximize the number of ramets sampled while minimizing the possibility of sampling the same ramet more than once. Here we define a ramet as a group of branches originating from a common rootstock. In populations of *L. salicaria*, ramets varied in size from single stems to clumps of up to 50 stems approximately one meter in diameter, thus style morph was scored at one meter intervals (following Haldane, 1936, and Halkka and Halkka, 1974). In *D. verticillatus*, ramets exhibited a greater range

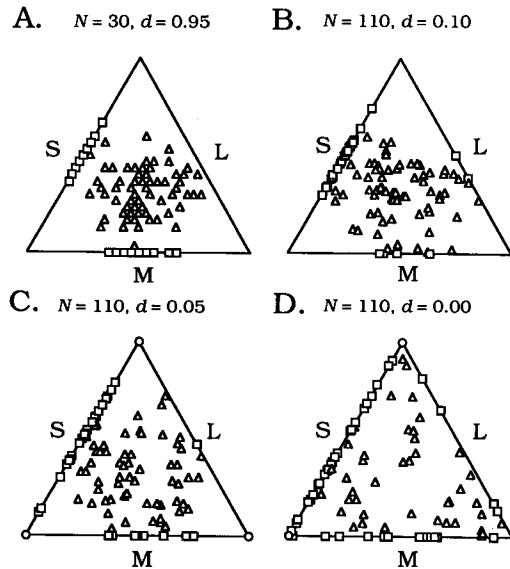


FIG. 1. The effect of genetic drift on morph frequency variation in simulated tristylous populations, with strong ($d = 0.95$), weak ($d = 0.10$), very weak ($d = 0.05$), and no ($d = 0.00$) disassortative mating among style morphs. Population size (N) is given above each figure. Otherwise, parameters were constant; $s = 0.01$, and $I = C = 0.00$. Each point represents the morph frequencies of one population after 100 years. The distance of a point from an axis is proportional to the relative frequencies of morphs (L, M, and S) in the population. Trimorphic, dimorphic, and monomorphic populations are represented by triangles, squares and circles, respectively.

of size; from those consisting of a single branch to those composed of many branches spreading up to three meters in diameter. Accordingly, style morph was scored at three meter intervals. For both species the minimum distance between populations sampled was about 1 km, though most were separated by much larger distances.

Populations of both species varied greatly in size from three to tens of thousands of ramets. Population size was estimated by inspection as the number of ramets, both flowering and nonflowering. For graphical and categorical analyses, populations were grouped into six size classes: 3–50, 51–100, 101–200, 201–500, 501–1,000, and greater than 1,000. Pooling or dividing these classes had no significant effect on the results. The relationship between population size and morph loss was examined using two approaches. First, heterogeneity in the pro-

portion of populations lacking at least one morph among the six size classes was assessed using 2×6 contingency tables. Second, estimated population size was entered as explanatory variable in predicting population status (trimorphic or nontrimorphic) in a logistic regression model. Model parameters were estimated using the maximum likelihood routine of PROC CATMOD in SAS/STAT® (SAS Institute Inc., 1988).

RESULTS

Computer Models

General Results.—Basic results obtained using our models were comparable to those reported by Heuch (1980) and Barrett et al. (1989), and confirm three basic features of finite tristylous populations. First, morphs were lost rapidly through drift in small populations. The proportion of populations that still included all three morphs (T) decreased linearly with time. Second, the S morph, and to a lesser extent, the M morph were most vulnerable to loss by drift. The L morph was rarely lost (Fig. 1). The proportion of dimorphic populations that lost the S morph (LM) compared to the M morph (LS) varied among runs, but did not covary with any life-history or mating parameter examined, or with the overall strength of drift (i.e., $1 - T$). In general, the LM:LS ratio commonly varied between 80:20 and 60:40 but it was not unusual to find more extreme ratios. Finally, there was only a narrow range of population sizes in which morphs were lost. The proportion of populations remaining trimorphic (T) increased quickly with N so that populations of size 50 or more were essentially resistant to losing morphs over the time scale considered (Table 2).

Although stochastic processes have a predictable effect on the distribution of morphs among populations, average frequencies in populations that remained trimorphic at the end of a run revealed no consistent bias *within* populations (Table 2). Frequencies averaged among all populations in a given run were skewed towards an excess of the L morph and a deficiency of the S morph. However, this is simply because the S morph is most often lost and the L morph is least often lost from populations.

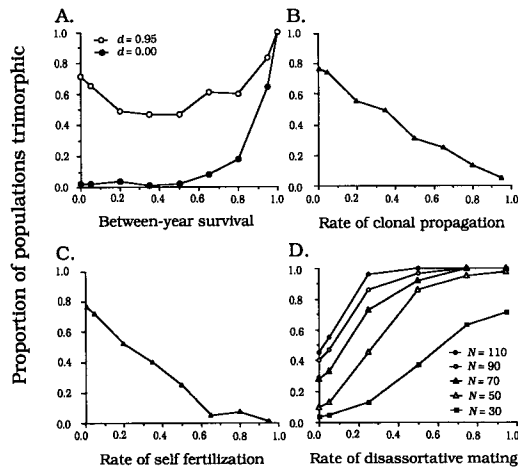


FIG. 2. The effects of year to year survival (A), clonal propagation (B), self-fertilization (C), and disassortative mating (D) on stochastic morph loss. The ordinate is the proportion of 100 populations remaining trimorphic after 100 years. When not being varied, the rates of survival (I), clonal propagation (C), and self-fertilization (s) were set at 0.00, disassortative mating (d) at 0.95, and population size (N) at 30.

Genetic drift leads to a characteristic pattern of variation in morph frequencies among populations. This pattern can be observed in Figure 1 as a marked deficiency of populations within vertices of the triangle plots. Rather than varying over the full range of possible morph frequencies, populations tended to develop a deficiency of one morph and even frequencies of the other two. Biases involving an excess of one morph and even deficiencies of the other two, or an excess of one morph and a deficiency of one other morph were rarely seen. This result was obtained over a wide range of population sizes and levels of disassortative mating. Only when the rate of disassortative mating was very low ($<1\%$) did populations exhibit the full range of morph frequencies (Fig. 1D).

Life History.—The survival of individuals from year to year is likely to preserve population structure directly, however, our simulations indicated that its interaction with drift is not straightforward. All but very high levels of I (0.05–0.80; Fig. 2A) were associated with a decrease in T . Only high levels of survivorship ($I > 0.85$) increased T beyond that in annual populations ($I = 0$). A similar effect was obtained by Heuch

TABLE 3. The joint effects of year to year survival and clonal propagation on stochastic morph loss in tristylous populations. Values are the proportion of 100 populations remaining trimorphic after 100 years with $N = 70$, $s = 0.01$, and $d = 0.95$.

Rate of clonal propagation	Rate of year to year survival			
	0.00	0.05	0.50	0.95
0.00	1.00	0.97	0.91	1.00
0.05	0.97	0.93	0.91	1.00
0.50	0.76	0.73	0.65	0.98
0.95	0.16	0.23	0.25	0.88

(1980) from his simulation of fully incompatible populations ($s = 0$, $d = 1.0$). Runs in which mating was random with respect to style morph ($d = 0$) showed that I must be greater than 0.60 before trimorphism is preserved to any significant extent by perennality per se (Fig. 2A).

Clonal propagation.—Although clonal propagation is similar to survivorship because genotypes are preserved from one generation to the next, a high rate of clonal propagation did not maintain trimorphism in our simulations. On the contrary, T declined in a linear fashion with increasing C (Fig. 2B).

Joint Effects of Survivorship and Clonal Propagation.—Clonal propagation is usually associated with perennality in plants. Results presented above indicate that both influence the probability of morph loss from populations. However, varying these parameters jointly revealed that their effects were not additive. Increasing C in annual populations ($I = 0$) resulted in a greater decrease in T than in populations with some degree of perennality (Table 3). In populations with high rates of survivorship, clonal propagation had little effect on morph loss.

Mating System.—Both the rate of self-fertilization and departures from disassortative mating had strong effects on the probability of morph loss from simulated populations. Increasing the rate of self-fertilization led to a linear decrease in T (Fig. 2C). Varying the rate of disassortative mating had the opposite effect, however, the increase in T with d was one of diminishing returns for all but the smallest population size investigated. Rates of disassortative mating above 0.70 resulted in uniformly

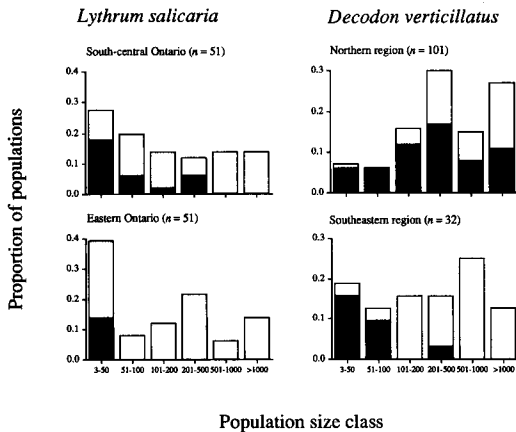


FIG. 3. The relationships between population size and region, and population size and morph loss in *Lythrum salicaria* and *Decodon verticillatus*. Height of the bars shows the distribution of population size within each region. The shaded portion of each bar represents the proportion of nontrimorphic populations within each size class. In *D. verticillatus*, northern populations include those sampled in Ontario ($N = 21$), Michigan ($N = 30$), and New England ($N = 50$).

high levels of T for populations of more than about 50 individuals (Fig. 2D).

Ploidy Level.—Wright (1969) showed that polysomic inheritance should reduce the strength of genetic drift by increasing effective population size. Our simulation results indicated, however, that autotetraploidy did not lead to a substantially decreased probability of losing morphs through drift. We compared results of diploid and autotetraploid models over much of the parameter space explored above and found no consistent difference between ploidal levels. Furthermore, comparison of Heuch's (1980) autotetraploid simulations with diploid simulations from Barrett et al. (1989) also revealed no major difference in the rate of stochastic morph loss between ploidal levels.

Empirical Results

Results of our simulation studies lead to several predictions with respect to the patterns of morph frequency variation resulting from stochastic processes operating in natural populations of tristylous *Lythrum salicaria* and *Decodon verticillatus*. 1) The frequency of morph loss should decrease with increasing population size. There are

two straightforward extensions of this result. First, colonization may be associated with morph loss through founder events. Second, because trimorphism can be restored in populations over time through immigration of lost morphs, the frequency of morph loss is likely to be higher in more recently colonized areas. 2) Differences in life history between *L. salicaria* and *D. verticillatus* should be reflected in contrasting patterns of morph frequency variation. In particular, morph loss may be more frequent in clonal, self-compatible *D. verticillatus* than sexual, self-incompatible *L. salicaria*. 3) Morph loss should most frequently involve the S morph and to a lesser extent the M morph. 4) Frequencies within trimorphic populations should not be consistently biased towards any particular morph. 5) The distribution of morph frequencies among populations should be constrained such that particular patterns of variation occur infrequently (Fig. 1). Departures from these predictions indicate that other evolutionary forces associated with morph-specific fitness differences might also be influencing morph frequency variation in populations of *L. salicaria* and *D. verticillatus*.

1. Population Size and Morph Loss.—In both *L. salicaria* and *D. verticillatus*, small populations were less likely to be trimorphic than large populations (Fig. 3). The proportion of populations lacking a morph generally differed among the six size classes (*L. salicaria* $\chi^2 = 20.57$, $df = 5$, $P = 0.001$; *D. verticillatus* $\chi^2 = 17.67$, $df = 5$, $P = 0.003$). However, there was some difference between species in this pattern. The increase in the proportion of trimorphic populations with population size was much shallower for *D. verticillatus* than *L. salicaria* with the former exhibiting a higher proportion of non-trimorphic populations in all size classes. Moreover in *L. salicaria*, populations of more than 500 ramets were uniformly trimorphic and most nontrimorphic populations fell in the 3–50 size class. In *D. verticillatus*, on the other hand, nontrimorphic populations were found throughout the range of population sizes, and were quite common in the 51–100 as well as the 3–50 size class. Logistic regression of population status (trimorphic or nontrimorphic) on es-

estimated population size supported this categorical analysis. Simple logistic regression detected a significant effect of population size for populations of *L. salicaria* ($\chi^2 = 5.44$, $df = 1$, $P = 0.02$) but not for *D. verticillatus* ($\chi^2 = 2.46$, $df = 1$, $P = 0.12$).

Geographical patterns of morph loss suggest an increased rate of stochastic morph loss during colonization and migration in both species. In *L. salicaria*, 23 of 102 populations sampled in the adventive range lacked at least one morph (Fig. 4). In contrast, none of the 35 populations sampled from the native range in Europe lacked a morph. The frequency of morph loss also differed between the sample of presumably older populations in eastern Ontario (14%) and more recently established populations central Ontario (31%) ($2 \times 2 \chi^2$ corrected for continuity = 3.59, $df = 1$, $P = 0.06$). Morph loss appears to have occurred repeatedly since dimorphic and monomorphic populations are geographically dispersed in both areas of Ontario.

Data from population surveys of *D. verticillatus* suggest an increased frequency of stochastic morph loss in northern regions compared to the southeastern United States (Figs. 5 and 6). Of 32 southeastern populations, 72% included all three morphs compared to only 40% of 101 northern populations ($\chi^2 = 8.31$, $df = 1$, $P = 0.004$, Table 4). Moreover, within each northern region surveyed, the same pattern was evident;

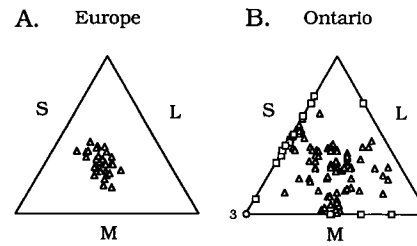


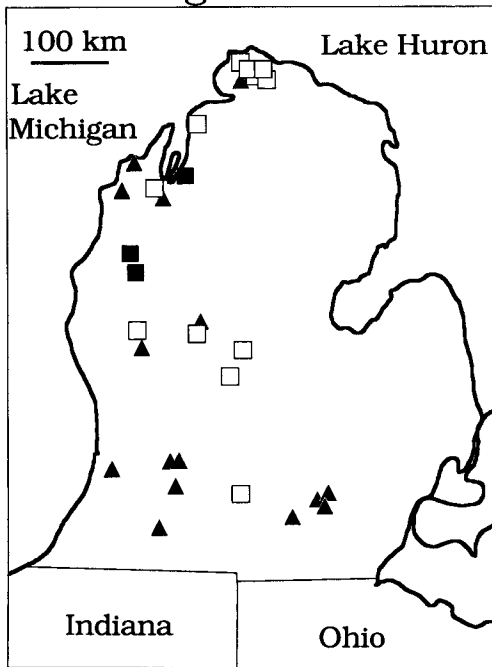
FIG. 4. Style morph frequencies in populations of *Lythrum salicaria* from Europe ($N = 35$); and Ontario ($N = 102$). See Figure 1 for details. Numbers beside vertices indicate the number of monomorphic populations overlapping on a given vertex.

northerly populations were more likely to be monomorphic or dimorphic than populations further south (Fig. 5). As in *L. salicaria*, the spatial distribution of trimorphic and nontrimorphic populations suggests that morph loss has occurred repeatedly in each region (Fig. 5). The geographical patterns of morph loss observed might be explained simply by regional differences in population size. Regions with larger average population sizes would be expected to show lower frequencies of morph loss. However, the distribution of estimated population sizes (Fig. 3) did not differ significantly between regions for either *L. salicaria* (2×6 contingency table: $G = 6.94$, $df = 5$, $P = 0.24$) or *D. verticillatus* ($G = 10.04$, $df = 5$, $P = 0.07$). Hence the patterns observed are more likely to reflect historical processes associated with

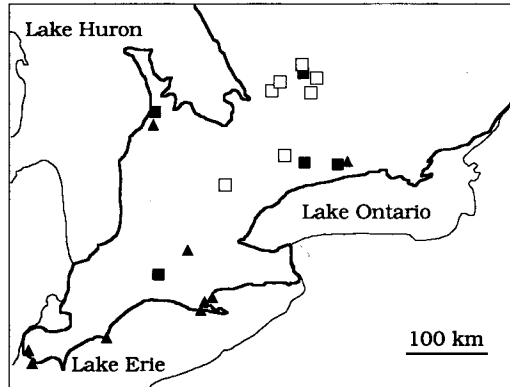
TABLE 4. Morph structure in populations of *Lythrum salicaria* in Ontario, and *Decodon verticillatus* from four regions in eastern North America. Tri, Di, and Mono are the proportion of populations in the total sample which are trimorphic, dimorphic, and monomorphic, respectively. Morph structure in dimorphic and monomorphic populations is denoted by letters representing the morphs present, with L, M, and S for the long-, mid-, and short-styled morph, respectively.

Sample	Proportion of total sample			Proportion of dimorphic populations			Proportion of monomorphic populations			Number of populations sampled
	Tri	Di	Mono	LM	LS	MS	L	M	S	
<i>Lythrum salicaria</i>										
Eastern Ont.	0.86	0.12	0.02	0.67	0.17	0.17	1.00	0.00	0.00	51
Central Ont.	0.69	0.27	0.04	0.79	0.21	0.00	1.00	0.00	0.00	51
Total	0.77	0.20	0.03	0.75	0.20	0.05	1.00	0.00	0.00	102
<i>Decodon verticillatus</i>										
Ontario	0.43	0.24	0.33	0.40	0.60	0.00	0.42	0.29	0.29	21
Michigan	0.50	0.10	0.40	0.33	0.33	0.33	0.33	0.25	0.42	30
New England	0.34	0.22	0.44	0.27	0.55	0.18	0.50	0.04	0.46	50
Southeast USA	0.72	0.25	0.03	0.50	0.25	0.25	0.00	1.00	0.00	32
Total	0.48	0.20	0.32	0.37	0.44	0.19	0.43	0.17	0.40	133

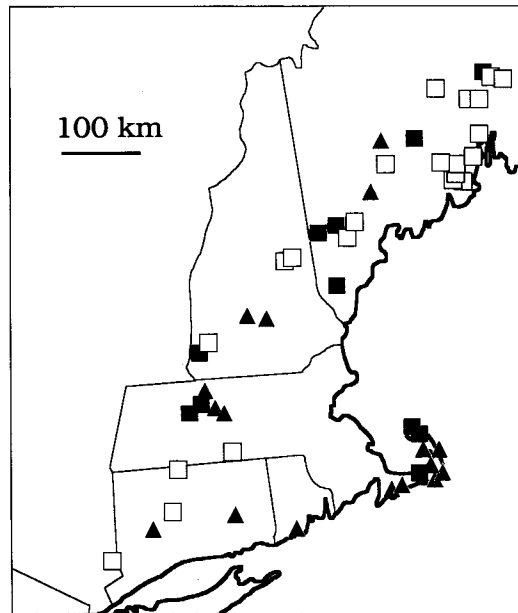
A. Michigan



B. Ontario



C. New England



D. Southeast USA

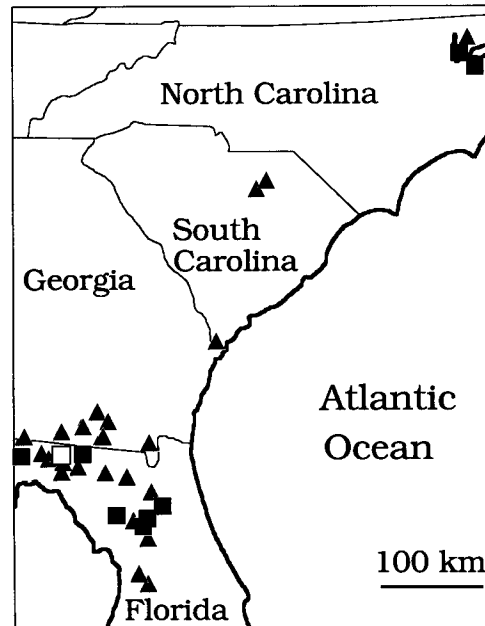


Fig. 5. Location and morph structure of 133 populations of *Decodon verticillatus* from the Michigan lower peninsula ($N = 30$), Ontario ($N = 21$), New England ($N = 50$), and the southeastern United States ($N = 32$). Trimorphic, dimorphic, and monomorphic populations are plotted as solid triangles, solid squares, and open squares, respectively.

migration and colonization rather than the effect of contemporary population size.

2. *Life-History Traits and Morph Loss.* — Comparing *L. salicaria* and *D. verticillatus*

lends support to theoretical predictions concerning the effects of various life-history traits on morph loss. Fifty-two percent of the 133 populations of *D. verticillatus* sam-

pled lacked at least one morph (Table 4). In contrast, none of 35 populations of *L. salicaria* sampled in its native range lacked a morph.

3. Which Morph is Lost?—Stochastic processes should lead to the loss of the S morph most frequently and the L morph least frequently. Data from both Ontario samples of *L. salicaria* closely fit this pattern (Table 4). Seventy-five percent of the 20 dimorphic populations surveyed lacked the S morph, 20% the M morph, and only 5% the L morph. All three monomorphic populations contained only the L morph. In *D. verticillatus*, the frequencies with which each of the morphs were lost did not closely match those expected from stochastic processes interacting with frequency-dependent selection alone (Table 4). Overall, 37% of the 33 dimorphic populations surveyed lacked the S morph, 44% the M morph, and 19% the L morph. Of the 45 monomorphic populations, 43% were monomorphic for the L morph, 17% for the M morph, and 40% for the S morph. Furthermore, the pattern of morph loss varied among the four regions surveyed (Table 4).

4. Morph Frequencies within Populations.—While there are differences in the probability that each of the style morphs will be lost from populations, our simulations indicated that this should not be reflected by consistent biases in morph frequency within trimorphic populations. However, averaging morph frequencies of trimorphic populations in both species revealed some biases. In *L. salicaria*, data from both Ontario samples showed an excess of the L morph and a deficiency of the M morph (Table 5). European samples also showed an excess of the L morph but this is associated with a deficiency of the S morph rather than the M morph (Table 5). In *D. verticillatus*, average frequencies among trimorphic populations indicated a slight excess of the S morph and deficiencies of the L and M morphs. However, there was much heterogeneity in the degree and direction of skew among the four regions surveyed suggesting that the bias in overall frequencies may have little biological significance (Table 5).

5. Patterns of Morph Frequency Variation.—Stochastic processes alone should

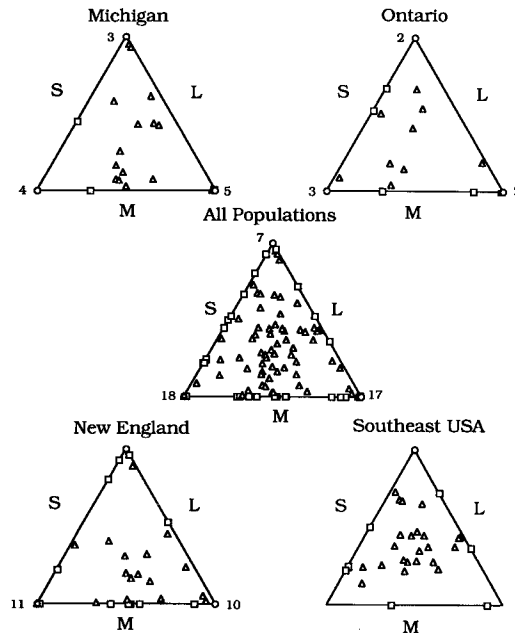


FIG. 6. Style morph frequencies in populations of *Decodon verticillatus* from Michigan ($N = 30$), Ontario ($N = 21$), New England ($N = 50$), the southeastern United States ($N = 32$), and for all samples pooled ($N = 133$). See Figures 1 and 4 for details.

produce a restricted pattern of morph frequency variation, except under very low levels of disassortative mating (Fig. 1D). When populations are plotted in trivariate morph frequency space the vertices of the triangle should remain largely unoccupied (Fig. 1A, B, and C). Inspection of the triangle plots based on our population surveys indicates that this prediction is fulfilled in *L. salicaria*. The plot of morph frequencies for the Ontario sample of *L. salicaria* (Fig. 4B) bears a strong resemblance to the simulation results illustrated in Fig. 1A and B. In contrast, the pattern of morph frequency variation observed in *D. verticillatus* (Fig. 6) exhibits a stronger resemblance to that expected under negligible levels of disassortative mating (Fig. 1D).

DISCUSSION

The main issue that this study addressed is whether stochastic processes influence the frequencies of alleles under selection in natural populations. Simulation studies incorporating several ecological variables allowed us to make predictions against which

TABLE 5. Style morph frequencies in population samples of *Lythrum salicaria* from Ontario and Europe, and *Decodon verticillatus* from four regions in eastern North America. Frequencies (\pm SD) have been averaged for all populations sampled, and for trimorphic populations only.

Sample	Morph frequency			Number of pops. sampled	Number of plants sampled
	Long	Mid	Short		
<i>Lythrum salicaria</i>					
All populations					
Eastern Ont.	0.40 \pm 0.17	0.30 \pm 0.19	0.30 \pm 0.17	51	7,474
Central Ont.	0.43 \pm 0.18	0.31 \pm 0.18	0.26 \pm 0.22	51	7,941
Average	0.41 \pm 0.18	0.31 \pm 0.18	0.28 \pm 0.20	102	15,415
Europe	0.37 \pm 0.04	0.33 \pm 0.07	0.30 \pm 0.07	35	12,202
Trimorphic populations only					
Eastern Ont.	0.39 \pm 0.12	0.29 \pm 0.15	0.32 \pm 0.14	44	7,372
Central Ont.	0.36 \pm 0.13	0.31 \pm 0.15	0.33 \pm 0.19	35	6,775
Average	0.38 \pm 0.13	0.30 \pm 0.15	0.33 \pm 0.16	79	14,147
Europe	As above				
<i>Decodon verticillatus</i>					
All populations					
Ontario	0.40 \pm 0.36	0.28 \pm 0.34	0.32 \pm 0.37	21	5,039
Michigan	0.31 \pm 0.35	0.29 \pm 0.37	0.41 \pm 0.38	30	4,863
New England	0.41 \pm 0.40	0.17 \pm 0.29	0.42 \pm 0.40	50	9,191
Southeast USA	0.33 \pm 0.24	0.39 \pm 0.22	0.28 \pm 0.22	32	2,942
Average	0.37 \pm 0.35	0.26 \pm 0.31	0.37 \pm 0.35	133	22,031
Trimorphic populations only					
Ontario	0.41 \pm 0.26	0.30 \pm 0.22	0.29 \pm 0.22	9	1,828
Michigan	0.26 \pm 0.20	0.34 \pm 0.31	0.39 \pm 0.23	15	3,053
New England	0.33 \pm 0.26	0.22 \pm 0.23	0.45 \pm 0.27	17	4,795
Southeast USA	0.30 \pm 0.18	0.39 \pm 0.16	0.30 \pm 0.16	23	2,632
Average	0.32 \pm 0.22	0.32 \pm 0.23	0.36 \pm 0.22	64	12,308

surveys of morph frequency variation in natural populations of tristylous plants could be compared. To assess the influence of ecological features on morph frequency variation we deliberately chose two tristylous species with contrasting life-history and reproductive traits.

Data from *Lythrum salicaria* provide strong evidence for the importance of stochastic forces influencing style morph frequencies in populations from the adventive range of the species. Twenty percent of populations sampled in Ontario were dimorphic. An additional three percent were monomorphic. As predicted by our model, the likelihood of loss varied among morphs; the S morph was most frequently absent, whereas the L morph was rarely lost. In Europe, on the other hand, populations surveyed were uniformly trimorphic. One interpretation of this difference is that the recent invasion of North America by *L. salicaria* has been associated with repeated

founder events and periods of small population size, leading to the loss of style morphs from populations. Stochastic processes have also been invoked to account for the loss of the S morph from populations of tristylous *Eichhornia paniculata* (Barrett et al., 1989).

Colonization episodes, however, must also be a feature of the biology of European populations. This suggests alternative interpretations: The absence of morph loss in the European sample may be associated with the small number of populations involved and/or differences in sampling strategy. The sampling scheme we used was motivated by our simulation studies and those of Heuch (1980), both of which indicated that morph loss was most likely in populations of fewer than 50 individuals. Moreover, data from Ontario indicated a relationship between population size and morph loss. European workers may have excluded very small populations, thereby potentially underestimating the frequency of morph loss. Haldane

(1936) and Halkka and Halkka (1974), the source of much of the European data, both pointed out the significance of small populations to morph loss. However, we note that of the 35 populations sampled in Europe only 14% were comprised of fewer than 50 plants compared to 33% of 102 sampled in Ontario. Whether this reflects the rarity of small populations in Europe or, more likely, differences in the scale that various workers sampled morph frequencies is not known. Reliability of the European sample also affects our conclusion that interspecific differences in life-history and mating system contribute to the higher rate of morph loss in *Decodon verticillatus* compared to *L. salicaria*. However, even if the rate of morph loss has been underestimated for *L. salicaria* in its native range, adventive populations in Ontario show significantly lower rates of morph loss (33%) than observed among populations of *D. verticillatus* (52%, Table 4, $2 \times 2 \chi^2 = 7.33$, $df = 1$, $P = 0.007$). Clearly, a sample of European populations spanning the full range of sizes is required to confirm the geographical patterns of morph frequency variation revealed by our comparison. Because the range of *L. salicaria* is rapidly expanding in North America and elsewhere, surveys of morph frequency in other parts of the adventive range would be valuable in evaluating the effects of repeated colonization episodes on morph loss.

Patterns of morph frequency variation in *D. verticillatus* exhibited considerable heterogeneity among the four geographic regions sampled. Interpreting this pattern in light of the simple model developed here is, therefore, not straightforward. The existence of a large stochastic element in the population biology of *D. verticillatus* is suggested by the high frequency of monomorphic and dimorphic populations. This is expected to arise through repeated founder events in a highly clonal species with limited sexual recruitment. A similar pattern has been observed in the widespread, clonal weed *Eichhornia crassipes* (Barrett and Forno, 1982). The frequency of morph loss was greatest in northern populations of *D. verticillatus*, suggesting stochastic effects have been especially important during postglacial migration of the species. In contrast to the predictions of our model, however, morph

loss involved the M morph slightly more often than the S morph, and a substantial proportion of dimorphic (18.5%) and monomorphic (57.2%) populations lacked the L morph. The absence of the L morph, and to a lesser extent the M morph, from some populations may be explained by a lack of sexual reproduction in these populations. Without recombination, recessive style morph alleles remain hidden in heterozygous genotypes. Our simulations, however, always included some degree of sexual recruitment. Differences in morph structure between northern and southern populations support this interpretation. Data from southern populations, where conditions allowing sexual reproduction are more likely to occur, fit the predictions of our model fairly well; whereas at the northern limits of the range, where ecological conditions may be marginal, the data were less in accord with the model (Table 4). This explanation would be supported if northern populations monomorphic for the S and M morphs segregated missing morphs following controlled self- and cross-pollinations.

The contrasting patterns of morph frequency variation in *L. salicaria* and *D. verticillatus* may be accounted for by differences in life history and mating system between the two species (Table 1). In our simulations, clonal propagation, self-fertilization, and deviations from disassortative mating all increased the rate of morph loss. This is because increases in these parameters reduced the recruitment of offspring resulting from disassortative mating. It is disassortative mating that provides the frequency-dependent selection that prevents the loss of style morphs from populations. The combination of clonal propagation and self-compatibility in *D. verticillatus* is likely to result in considerable self-fertilization, particularly in populations composed of large continuous clones. Under these conditions the strength of frequency-dependent selection is likely to be much lower than in populations of *L. salicaria*. This prediction is supported by both a higher level of morph loss and wider morph frequency variation in *D. verticillatus* compared to *L. salicaria*.

Our computer model simulated genetic drift in small populations of constant size.

However, stochastic morph loss may result from one, or some combination of, drift, founder effect and population bottlenecks. What are the relative contributions of each of these processes to morph frequency variation in *L. salicaria* and *D. verticillatus*? Simulating founder effect by using small initial population sizes in our computer model demonstrated that morphs can be lost only if the number of founders is quite small. A sample of eight founders drawn at random from a large tristylous population at equilibrium produced a trimorphic population 94% of the time. Even a sample of only two founders included all three style morph alleles 43% of the time. Trimorphic populations can even arise from a single founder if it is heterozygous at both style morph loci (13% of all possible founders) and capable of some degree of self-fertilization. Similar results were also obtained by Heuch and Lie (1985) and Morgan and Barrett (1988). The likelihood of losing a morph through founder effect will be higher if morph frequencies in source populations are unequal (Heuch and Lie, 1985). This effect will be ameliorated, however, if founders originate from several source populations (Slatkin, 1985).

It is difficult to infer the relative contributions of each kind of stochastic process to morph frequency variation from population survey data alone. However, both founder effects and genetic drift are likely to have been important in *L. salicaria* and *D. verticillatus*. Many populations of both species were small enough ($N < 50$) to lose morphs through drift (33.3% and 9.8% in *L. salicaria* and *D. verticillatus*, respectively). In addition, negative correlations between population size and the proportion of populations lacking a morph bolsters the interpretation that drift is a major cause of morph loss. However, such a correlation, though supportive, is neither necessary nor sufficient evidence for the operation of drift. Drift during early population growth may not result in a negative correlation, because population size at the time of surveying may not accurately reflect the size when morphs were lost. Similarly, morph loss by founder effect could produce a negative correlation between population size and morph loss if the smallest of the populations surveyed were also the youngest and, consequently,

had less opportunity for immigration of morphs absent when populations were founded. While founder effect has undoubtedly contributed to morph loss in both *L. salicaria* and *D. verticillatus*, it should have more profound consequences on population structure in the latter species because the genetic composition of founders can be preserved by clonal propagation.

Although the three morphs differ in the likelihood of being lost from populations, our simulations indicated that this asymmetry was not associated with a consistent bias in frequencies of trimorphic populations. Survey data from trimorphic populations of *L. salicaria* and *D. verticillatus*, however, showed some biases in both species. In *L. salicaria*, trimorphic populations sampled in both eastern and central Ontario showed, on average, an excess of the L morph and a deficiency of the M morph. Uneven morph frequencies within populations may stem from natural selection involving other fitness differences among morphs (Charlesworth, 1979; Barrett et al., 1983). For example, in *L. salicaria* both Darwin (1877) and Stout (1923) provide evidence for weak self-incompatibility in the M morph compared to the L or S morphs. A higher selfing rate in the M morph combined with strong inbreeding depression could explain low frequencies of this morph observed in some Ontario populations (see Charlesworth, 1979). Although estimates of the relative reproductive success of each morph are required to directly test a selection hypothesis, the wide variation in morph frequencies among populations with no consistent skew suggests that if fitness differences among morphs do occur, they are likely to be weak relative to stochastic effects.

Biased morph frequencies may also result from stochastic processes operating on a local scale within populations (Heuch, 1980). Large populations may be subdivided such that drift leads to the loss of morphs within subpopulations. Morph frequencies estimated at the population level would combine these stochastic effects among subpopulations and result in an excess of the L morph and deficiencies of the S morph and, to a lesser extent, the M morph. Average morph frequencies in the European sample

are consistent with this explanation (Heuch, 1980). However in Ontario populations, an average excess of the L morph was associated with a deficiency of the M morph not the S morph, suggesting interactions between "micro-stochastic" forces and selection.

In *D. verticillatus*, heterogeneity in average morph frequencies among regions complicates an interpretation involving selection because it requires regional variation in morph-specific fitnesses. Regional variation in ecological conditions, particularly pollinator service, is likely in this widespread species. In addition, disequilibrium between style morph alleles and loci affecting fitness generated through drift and inbreeding in small populations may result in fitness asymmetries among morphs. As of yet, we have no evidence to assess these possibilities. Alternatively, this variation in morph frequencies may be the result of sampling error owing to the relatively few populations surveyed within each region. Morph frequencies of herbarium specimens (Table 6), however, mirror the pattern of variation revealed by population surveys (Table 5), suggesting that the particular biases detected may be a real feature of populations in each region. These regional biases may be accounted for by stochastic processes operating on a geographic scale. Because highly clonal, perennial populations will progress very slowly towards any deterministic equilibrium, populations or groups of populations that acquire skewed morph frequencies through founder effect may bear the imprint of historical accident for a long time. The founding of new populations from skewed source populations may further amplify the initial founder effect.

Although conspicuous, simply inherited polymorphisms are easily studied, Wright (1978) pointed out that their usefulness is compromised by "their somewhat peripheral role in evolution." Polymorphisms controlling the mating system, however, are an obvious exception to this generalization because patterns of mating greatly affect the distribution of genetic variation in populations and hence their evolutionary dynamics (Robertson, 1952; Allard, 1975; Hamrick and Godt, 1990; Charlesworth, 1992). Stochastic morph loss may have most

TABLE 6. Morph frequencies from herbarium specimens of *Decodon verticillatus* collected in Ontario, New England, the southeastern United States and the entire species' range. Replicate sheets from a single collection were counted as one record. Herbarium specimens are from CAN, DAO, DUKE, FLAS, FSU, GH, MO, NY, TRT, and US.

Sample	Morph frequency			No. of localities	No. of records
	Long	Mid	Short		
Ontario	0.44	0.17	0.39	82	82
New England	0.34	0.24	0.42	57	66
Southeast					
USA	0.30	0.41	0.29	47	61
Entire range	0.40	0.25	0.39	399	430

evolutionary significance when it is associated with long-distance dispersal events. Geographical isolation restricts opportunities for the reestablishment of floral polymorphism, leading to the potential for evolutionary modifications in the breeding system. The stochastic loss of the S morph appears to have initiated such modifications in tristylous *Eichhornia paniculata* (Barrett et al., 1989), and may have also influenced the course of floral evolution in New World *Lythrum* section *Euhysopifolia*. North American members of this section are uniformly distylous and likely derived from a tristylous Eurasian ancestor. Comparative morphological evidence suggests that the morphs in distylous taxa correspond most closely to the L and M morphs of a tristylous species (Ornduff, 1979) implying that the S morph has been lost during the migration of *Lythrum* to North America. Phylogenetic analysis of this group would be useful in assessing whether this interpretation is correct. If true, it would suggest that the interaction of stochastic processes with constraints imposed by inheritance has guided macroevolutionary pathways of floral evolution that have occurred within the genus.

ACKNOWLEDGMENTS

We thank the Ontario Ministry of Natural Resources, the United States Fish and Wildlife Service, and the Michigan, Georgia, and Florida Departments of Natural Resources for their cooperation; C. Campbell, T. Gooch, S. Graham, D. Hall, F. Phelan, A. Reznicek, E. Voss, J. Weimar, and S. Weller

for their help in finding populations; K. Du-four, D. Hoysak, B. Husband, J. Magwood, and I. Robertson for help collecting *Lythrum* morph frequencies; and especially Robert and Eleanor Godfrey for their generous hospitality in the southeast. Discussion with B. Husband and M. Morgan helped refine the computer models. A. Baker, M. Gross, B. Husband, R. Lenski, and M. Morgan made helpful comments on earlier versions of this paper. The Natural Sciences and Engineering Research Council of Canada (NSERC) provided fellowship support for Eckert and funded this work through an operating grant to Barrett.

LITERATURE CITED

- ALLARD, R. W. 1975. The mating system and microevolution. *Genetics* 79:115-125.
- BARRETT, S. C. H. 1977. Tristyly in *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth). *Biotropica* 9:230-238.
- BARRETT, S. C. H., A. H. D. BROWN, AND J. S. SHORE. 1987. Disassortative mating in tristylous *Eichhornia paniculata* (Pontederiaceae). *Heredity* 58:49-55.
- BARRETT, S. C. H., AND I. W. FORNO. 1982. Style morph distribution in New World populations of *Eichhornia crassipes* (Mart.) Solms-Laubach (water hyacinth). *Aquat. Bot.* 13:299-306.
- BARRETT, S. C. H., M. T. MORGAN, AND B. C. HUSBAND. 1989. The dissolution of a complex genetic polymorphism: The evolution of self-fertilization in tristylous *Eichhornia paniculata*. *Evolution* 43:1398-1416.
- BARRETT, S. C. H., S. D. PRICE, AND J. S. SHORE. 1983. Male fertility and anisoplethic population structure in tristylous *Pontederia cordata* (Pontederiaceae). *Evolution* 37:745-759.
- BARTON, N. H. 1989. Founder effect speciation, pp. 229-256. *In* D. Otte and J. A. Endler (eds.), *Speciation and Its Consequences*. Sinauer, Sunderland, MA USA.
- BLAISDELL, S. E. 1974. The biology of *Decodon verticillatus* (Lythraceae) in Michigan. Masters Thesis, Michigan State University, East Lansing, USA.
- CARSON, H. L., AND A. R. TEMPLETON. 1984. Genetic revolutions in relation to speciation: The founding of new populations. *Annu. Rev. Ecol. Syst.* 15:97-131.
- CHARLESWORTH, B. 1992. Evolutionary rates in partially self-fertilizing species. *Am. Nat.* *In press*.
- CHARLESWORTH, D. 1979. The evolution and breakdown of tristily. *Evolution* 33:486-498.
- CRAWFORD, T. J., AND D. A. JONES. 1988. Variation in the colour of the keel petals in *Lotus corniculatus* L. 4. Morph distribution in the British Isles. *Heredity* 61:175-188.
- CROW, J. F., AND M. KIMURA. 1970. *An Introduction to Population Genetics Theory*. Harper & Row, N.Y., USA.
- DARWIN, C. 1877. *The Different Forms of Flowers on Plants of the Same Species*. John Murray, London, UK.
- ENDLER, J. A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ USA.
- ENNOS, R. A. 1990. Detection and measurement of selection: Genetic and ecological approaches, pp. 200-214. *In* A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*. Sinauer, Sunderland, MA USA.
- FISHER, R. A. 1949. The linkage problem in a tetrasomic wild plant, *Lythrum salicaria*. *Proc. 8th Int. Congr. Genetics, Hereditas* suppl. pp. 223-233.
- FISHER, R. A., AND V. C. MARTIN. 1947. Spontaneous occurrence in *Lythrum salicaria* of plants duplex for the short-style gene. *Nature* 160:541.
- FISHER, R. A., AND K. MATHER. 1943. Inheritance of style length in *Lythrum salicaria*. *Ann. Eugen.* 12:1-23.
- FYFE, V. C. 1953. Double reduction at the mid locus in *Lythrum salicaria*. *Heredity* 7:285-292.
- GOODNIGHT, C. J. 1987. On the effect of founder events on epistatic genetic variance. *Evolution* 41:80-91.
- GRAHAM, S. A. 1964. The genera of Lythraceae in the southeastern United States. *J. Arnold Arbor. Harv. Univ.* 45:235-250.
- HALDANE, J. B. S. 1936. Some natural populations of *Lythrum salicaria*. *J. Genet.* 32:393-397.
- HALKKA, O., AND L. HALKKA. 1974. Polymorphic balance in small island populations of *Lythrum salicaria*. *Ann. Bot. Fenn.* 11:267-270.
- HAMRICK, J. L., AND M. J. GODT. 1990. Allozyme diversity in plant species, pp. 43-63. *In* A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds.), *Plant Population Genetics, Breeding, and Genetic Resources*. Sinauer, Sunderland, MA USA.
- HEUCH, I. 1979a. Equilibrium populations of heterostylous plants. *Theor. Popul. Biol.* 15:43-57.
- . 1979b. The effect of partial self-fertilization on type frequencies in heterostylous plants. *Ann. Bot.* 44:611-616.
- . 1980. Loss of incompatibility types in finite populations of the heterostylous plant *Lythrum salicaria*. *Hereditas* 92:53-57.
- HEUCH, I., AND R. T. LIE. 1985. Genotype frequencies associated with incompatibility systems in tristylous plants. *Theor. Popul. Biol.* 27:318-336.
- JONES, J. S., B. H. LEITH, AND P. RAWLINGS. 1977. Polymorphism in *Cepaea*: A problem with too many solutions? *Ann. Rev. Ecol. Syst.* 8:109-143.
- LARSEN, K. 1965. IOPB chromosome reports IV. *Taxon* 14:86.
- LEWIS, D., AND D. A. JONES. 1992. The genetics of heterostyly, pp. 129-150. *In* S. C. H. Barrett (ed.), *Evolution and Function of Heterostyly*. Springer-Verlag, Berlin, Germany.
- MORGAN, M. T., AND S. C. H. BARRETT. 1988. Historical factors and anisoplethic population structure in tristylous *Pontederia cordata*: A reassessment. *Evolution* 42:496-504.
- MULLIGAN, G. L. 1957. Chromosome numbers in Canadian weeds I. *Can. J. Bot.* 35:779-789.
- ORNDUFF, R. 1972. The breakdown of trimorphic incompatibility in *Oxalis* section *Corniculatae*. *Evolution* 26:52-65.

- . 1974. Heterostyly in South African flowering plants: A conspectus. *J. S. Afr. Bot.* 40:169–187.
- . 1979. The morphological nature of distyly in *Lythrum* section *Euhyssopifolia*. *Bull. Torrey Bot. Club* 106:4–8.
- OXFORD, G. S., AND M. W. SHAW. 1986. Long-term variation in colour-morph frequencies in the spider *Enoplognatha ovata* (Clerk)(Araneae: Theridiidae): Natural selection, migration and intermittent drift. *Biol. J. Linn. Soc.* 27:225–249.
- ROBERTSON, A. 1952. The effect of inbreeding on the variation due to recessive genes. *Genetics* 37:189–207.
- ROHLF, F. J., AND R. R. SOKAL. 1981. *Statistical Tables*. 2nd ed. W.H. Freeman and Co., N.Y., USA.
- SAS INSTITUTE, INC. 1988. *SAS/STAT® User's Guide*, Release 6.03 Edition. SAS Institute Inc., Cary, NC USA.
- SCHOCH-BODMER, H. 1938. The proportion of long-, mid-, and short-styled plants in natural populations of *Lythrum salicaria*. *J. Genet.* 36:39–43.
- SLATKIN, M. 1985. Gene flow in natural populations. *Annu. Rev. Ecol. Syst.* 16:393–430.
- STOUT, A. B. 1923. Studies of *Lythrum salicaria*. I. The efficiency of self-pollination. *Am. J. Bot.* 10:440–449.
- STUCKEY, R. L. 1980. The distributional history of *Lythrum salicaria* (purple loosestrife) in North America. *Bartonia* 100:3–30.
- THOMPSON, D. Q., R. L. STUCKEY, AND E. B. THOMPSON. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. U.S. Fish and Wildlife Service. NTIS, 2.
- TOBE, H., P. H. RAVEN, AND S. A. GRAHAM. 1986. Chromosome counts for some Lythraceae Sens. Str. (Myrtales), and the base number of the family. *Taxon* 35:13–20.
- WADE, M. J., AND S. KALISZ. 1990. The causes of natural selection. *Evolution* 44:1947–1955.
- WELLER, S. G. 1979. Variation in heterostylous reproductive systems among populations of *Oxalis alpina* in southeastern Arizona. *Syst. Bot.* 4:57–71.
- WRIGHT, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- . 1969. *Evolution and the Genetics of Populations*. Volume 2. *The Theory of Gene Frequencies*. University of Chicago Press, Chicago, IL USA.
- . 1978. *Evolution and the Genetics of Populations*. Volume 4. *Variability Within and Among Natural Populations*. University of Chicago Press, Chicago, IL USA.
- . 1982. The shifting balance theory and macroevolution. *Annu. Rev. Genet.* 16:1–19.

Corresponding Editor: R. Lenski