GENETIC DRIFT AND FOUNDER EFFECT IN NATIVE VERSUS INTRODUCED POPULATIONS OF AN INVADING PLANT, *LYTHRUM SALICARIA* (LYTHRACEAE)

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Abstract.—There are few convincing examples of genetic drift at loci under selection in natural populations. The plant sexual polymorphism tristyly provides an opportunity to investigate genetic drift because stochastic processes interacting with frequency-dependent selection give rise to a diagnostic pattern of morph-frequency variation. A previous study of 102 Ontario populations of the introduced tristylous wetland herb *Lythrum salicaria* provided evidence for the role of stochastic processes during colonization. However, whether stochastic effects are greater in these recently introduced populations compared to native Eurasian populations remains unclear. The propensity of this species to invade disturbed habitats suggests that episodes of colonization and periods of small population size must also occur in the native range. A survey of 102 populations in southwestern France indicated reduced stochastic effects in native populations. Populations exhibited significantly lower morph loss than in Ontario (5% vs. 23%) and significantly higher values of morph evenness. The greater incidence of trimorphism in French populations was not associated with larger population sizes; populations were significantly smaller than those in Ontario (means: 266 vs. 487). Morph evenness was positively correlated with population size among French but not Ontario populations, providing further evidence of nonequilibrium conditions in introduced compared to native populations. The incidence of trimorphism was unexpectedly high in small native populations ($N \leq 25$; 22 of 27 populations trimorphic). Computer simulations indicated that levels of gene flow on the order of $m \geq 0.05$ can account for the maintenance of tristyly in small populations. The high connectivity of populations within the agricultural landscape typical of southwestern France may facilitate levels of gene flow sufficient to maintain trimorphism in small populations.

Key words.—Colonization, floral polymorphism, founder effect, frequency-dependent selection, gene flow, genetic drift, *Lythrum salicaria*, metapopulations, purple loosestrife, tristyly.

The expansion of a species' range may be accompanied by ecological and genetic changes of evolutionary significance, especially when it involves the movement of a species from one part of the world to another (Baker and Stebbins 1965; Parsons 1983; Mooney and Drake 1986). Recent biological invasions are of particular interest because they allow investigation of the evolutionary consequences of colonization on a historic time scale (Brown and Marshall 1981; Groves and Burdon 1986; Barrett 1992). Introduced populations may often experience novel ecological conditions, leading to alterations in their life history and demography. These ecological changes can have a direct impact on the evolutionary dynamics of populations, especially by influencing the relative importance of natural selection and stochastic processes (Mayr 1963; Templeton 1980; Carson and Templeton 1984; Stebbins 1989; Barton 1989). Empirical evidence for the evolutionary significance of stochastic processes during colonization, however, remains limited, in part because most studies on the genetic consequences of colonization have focused on genes of little selective importance, primarily allozyme loci (Brown and Marshall 1981; Berlocher 1984; Baker and Moeed 1987; Barrett and Shore 1990; Demelo and Hebert 1994). Attempts to examine the stochastic effects of colonization on adaptive traits often encounter problems teasing apart genetic changes resulting from altered selection pressures from those arising from founder effect and genetic drift

(Coyne and Barton 1988; Dennison and Baker 1991; Turner 1992).

Studies of morph-frequency variation in populations of tristylous plants have provided evidence for interactions between stochastic processes and selection in natural populations (reviewed in Barrett 1993). In tristylous populations, frequencies of the three mating types, or "style morphs," are driven towards a single stable equilibrium by frequency-dependent selection owing to disassortative mating among morphs (Heuch 1979a,b; Heuch and Lie 1985; Barrett et al. 1987). Stochastic effects can be recognized because founder effect and genetic drift in small populations produce a characteristic pattern of morph-frequency variation and morph loss (Heuch 1980; Barrett et al. 1989; Eckert and Barrett 1992; Husband and Barrett 1992). This involves random deviations from even morph frequencies plus a nonrandom pattern of morph loss owing to the pattern of dominance and epistasis at the two loci controlling the polymorphism. The inheritance of tristyly involves two diallelic loci, *S* and *M*, with the genotype of the long-styled morph (hereafter L) *ssmm*, the midstyled morph (M) *ssM–*, and the short-styled morph (S) *S––* (Lewis and Jones 1992). Consequently, the S morph is lost most often because a population that has lost the S morph has also lost the dominant *S* allele. The M morph is lost less frequently because *M* alleles may also be carried by S-morph genotypes; and the L morph is lost only rarely because recessive *s* and *m* alleles may also be carried by both S- and M-morph genotypes. These characteristic stochastic effects allow the prevalence of stochastic processes in dif-

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ferent portions of a species range to be directly assessed by examining the pattern of morph-frequency variation in large samples of populations.

The recent invasion of North American wetlands by the Eurasian, self-incompatible, tristylous herb *Lythrum salicaria* L. (Lythraceae) provides an opportunity to examine the importance of stochastic processes during colonization. In 102 populations from southern Ontario, Canada, Eckert and Barrett (1992) found a pattern of morph loss consistent with the operation of stochastic processes. These results support the widely held expectation that stochastic processes are particularly prevalent during colonization in invading species. However, whether the intensity of stochastic processes is indeed greater in these introduced populations compared to those in the native range remains uncertain. The ability of this species to invade disturbed habitats in both native and adventive regions suggests that colonizing episodes and periods of small population size must also be a feature of European populations. In contrast, the scattered data available for European populations reported in the literature (Darwin 1877; von Ubisch 1925; Haldane 1936; Schoch-Bodmer 1938; Fisher and Mather 1943; Halkka and Halkka 1974; Andersson 1994; Ägren and Ericson 1995) suggest only minor deviations from equilibrium morph frequencies. As noted by Eckert and Barrett (1992), variation in sampling strategies among these European workers makes comparison with the Ontario sample difficult, weakening any assessment of the relative importance of stochastic processes in the native versus introduced range.

To investigate the role of stochastic processes in European populations, we sampled populations of *L. salicaria* from a central portion of the native range in southwestern France. By comparing this sample with our earlier study of Ontario populations, we also determined the extent to which differences in population size may account for differences in morph-frequency variation between native and adventive regions. Our survey of French populations revealed unexpectedly high levels of trimorphism in small populations. In addition, we observed that native populations occurring in the highly disturbed agricultural habitats typical of southern France were usually situated relatively close together and were often "connected" by individuals scattered in intervening habitats. These observations suggest that gene flow might be important in contributing to the maintenance of trimorphism in native populations. We therefore investigated the potential effects of gene flow on the pattern of morph-frequency variation using computer simulations.

MATERIALS AND METHODS

Population Surveys

We sampled 102 populations from two areas in southwestern France separated by approximately 400 km. These included 50 populations from an area bounded by the Camargue wetlands to the east, the Hérault Valley to the west, and the Cévennes to the north; and 52 populations from the Gascony-Landes-Médoc area around Bordeaux (total: 14,621 plants). Both areas were characterized by agricultural landscapes, with *Lythrum salicaria* occurring along irrigation ditches, river banks, and moist creek beds. Populations were

selected for sampling following criteria outlined in Eckert and Barrett (1992). All populations were separated by at least 800 m, although most were separated by much larger distances.

Morph frequencies were estimated for individual populations from large random samples of flowering plants scored for style morph. Individual plants were usually easy to distinguish, and we saw no evidence of extensive clonal propagation in any population. In very dense patches where it was not easy to distinguish individuals, flowering spikes were sampled at 1 m intervals (following Haldane 1936; Halkka and Halkka 1974; Eckert and Barrett 1992). In populations with fewer than 200 individuals, we censused almost all flowering plants.

To assess deviations from equal frequencies of the three morphs expected at equilibrium, we calculated the index of morph evenness (O) developed by Husband and Barrett (1992). This index is based on the triangle plot commonly used to present morph frequencies in tristylous populations (see Fig. 1). Each side of the triangle represents a different morph, and the distance a point is plotted from a given side is proportional to the frequency of that morph in a population. The center of the triangle is the expected phenotypic equilibrium, with equal frequencies of the three morphs. The evenness of a population's morph frequencies can, therefore, be indexed by the Euclidean distance of a given point from the center, normalized by the maximum possible distance. Hence, O ranges from zero for monomorphic populations to unity in trimorphic populations with even morph frequencies.

Population size was estimated by inspection as the number of mature plants, most of which were flowering at the time of our surveys. For graphical and categorical analyses, populations were grouped into seven size classes: 3–25, 26–50, 51–100, 101–200, 201–500, 501–1000, and greater than 1000. Morph evenness (O) was much more variable for small than large populations, resulting in strong heterogeneity in sample variances for O among population size classes, which could not be remedied by standard transformations. The relationship between population size and O could be assessed for the Ontario and French samples separately using the one-way Welch ANOVA, which weights each group mean by the reciprocal of its respective sample variance (Welch 1951). A nonparametric two-way analysis with region and population size class as main effects applied to rank transformed data (Conover 1980) was inappropriate because the rank transform tends to obscure interaction between main effects (Seaman et al. 1994), which was of particular interest in this case. Consequently, we performed a cruder test for interaction by comparing O between regions for each population size class separately using t-tests.

Computer Simulations

We investigated the theoretical effect of gene flow on morph-frequency variation in tristylous populations using a modification of the stochastic Monte Carlo simulation described in Eckert and Barrett (1992). The model incorporates the two-locus pattern of inheritance shown for most tristylous species (see above; Lewis and Jones 1992), including *L. salicaria* (Fisher and Mather 1943). Although *L. salicaria* shows

France
102 populations

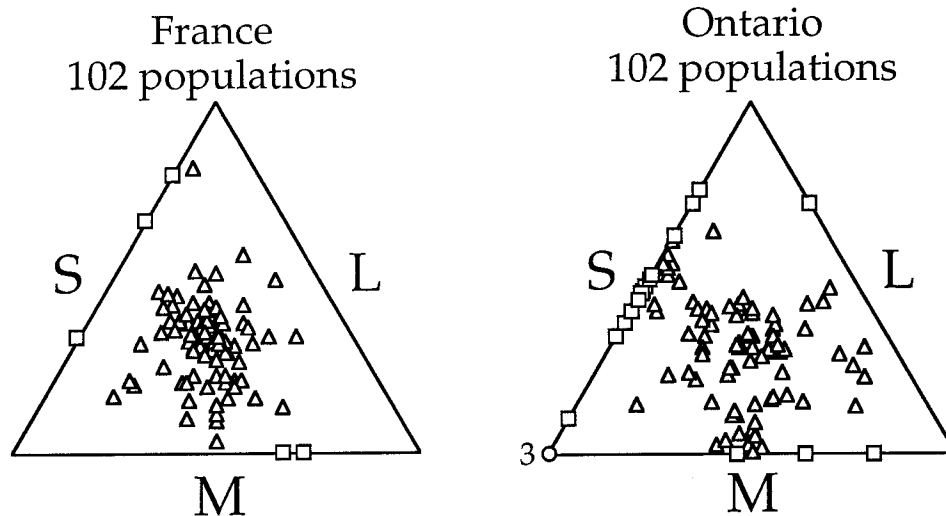## Ontario
102 populations

FIG. 1.   Style-morph frequencies in populations of *Lythrum salicaria* from southwestern France and southern Ontario. Each side of the triangle represents one of the three style morphs, and each point represents the morph frequencies of one population. The distance of a point from a side is proportional to the frequency of that morph in that population. Points in the center of the triangle have even morph frequencies. Trimorphic, dimorphic, and monomorphic populations are represented by triangles, squares, and circles, respectively. Numbers beside vertices indicate the number of monomorphic populations overlapping on a given vertex. Data from Ontario after Eckert and Barrett (1992).

tetrasomic inheritance of tristyly at both loci (Fisher and Martin 1947; Fisher 1949; Fyfe 1953), we simulated a diploid genetic system for the sake of generality. Ploidy, however, does not affect the theoretical dynamics of tristylous populations because, with only two alleles per locus and strong disassortative mating among morphs, autotetraploid tristyly loci effectively behave as diploid loci (Heuch and Lie 1985; Eckert and Barrett 1992).

The rates of self-fertilization (s), disassortative mating among morphs (d), and year-to-year survival (I) were set to values likely for populations of species like *L. salicaria* with high levels of perenniality and strong self-incompatability and intramorph-incompatibility ($s = 0.01$, $d = 0.95$ and $I = 0.80$; see Eckert and Barrett 1992). For comparison, we also included simulations with nonoverlapping generations ($I = 0$). At the start of each simulation run, an array of 100 populations was set up as 100 vectors of N individuals, each represented by an integer denoting its genotype at the two style-morph loci. The nine possible style-morph genotypes were assigned with probabilities equal to their equilibrium frequencies (Heuch and Lie 1985, table 1). As a result, all populations initially contained all three morphs.

We simulated three different models of gene flow that together encompass the standard population-genetic models of migration (Hedrick 1985). In the equilibrium-dispersal model, immigrants were drawn from an infinite source population with equilibrium genotype frequencies. This model is essentially the continent-island model of migration. In the random-dispersal model, immigrants were drawn with replacement from a large propagule pool consisting of five seeds sampled randomly from each of the 100 populations in the metapopulation array. With realistic levels of gene flow ($m \leq 0.10$) this simulates the random-dispersal of propagules between populations within the entire metapopulation, and is analogous to the island model of migration. In the local-dispersal

model, populations were grouped into 10 sets of 10 populations and immigrants were drawn with replacement from a more restricted pool consisting of five seeds randomly sampled from each of the populations within each group. This is a more realistic metapopulation model in that migration tends to occur between groups of closely situated populations. Immigration was modeled as seed dispersal, with immigrants being recruited along with resident seeds to fill vacancies created by mortality occurring between years. Gene flow via pollen dispersal was not examined here. Pollen dispersal should have a qualitatively similar, although perhaps reduced, effect compared to seed dispersal. Moreover, it is difficult to model for tristylous populations with intramorph incompatibility without specifying the probabilities of long-distance transfer of pollen between the three different levels of anthers and stigmas (e.g., Charlesworth 1979). At any given year, t, populations were composed of a proportion I consisting of individuals surviving from the previous year, $t - 1$, and $(1 - I)$ consisting of new recruits, of which m were immigrants and $(1 - m)$ were residents. We used three values of m (0.005, 0.01, 0.05) encompassing much of the range of migration rates reported for natural plant populations (Hamrick 1987). Results of the three simulation models were very similar. Hence, we present results from the equilibrium-dispersal model only.

We applied each set of parameters to 10 replicate metapopulation arrays of 100 populations of constant size, and recorded population morph frequencies throughout each simulation run. The results reported below are means of the 10 replicates. In runs with gene flow, populations arrived at a rough drift-migration equilibrium. We determined these equilibria by running simulations until the proportion of populations remaining trimorphic consistently fluctuated around a constant value (usually 100–300 yr). For consistency with previous simulation results (Barrett et al. 1989; Eckert and
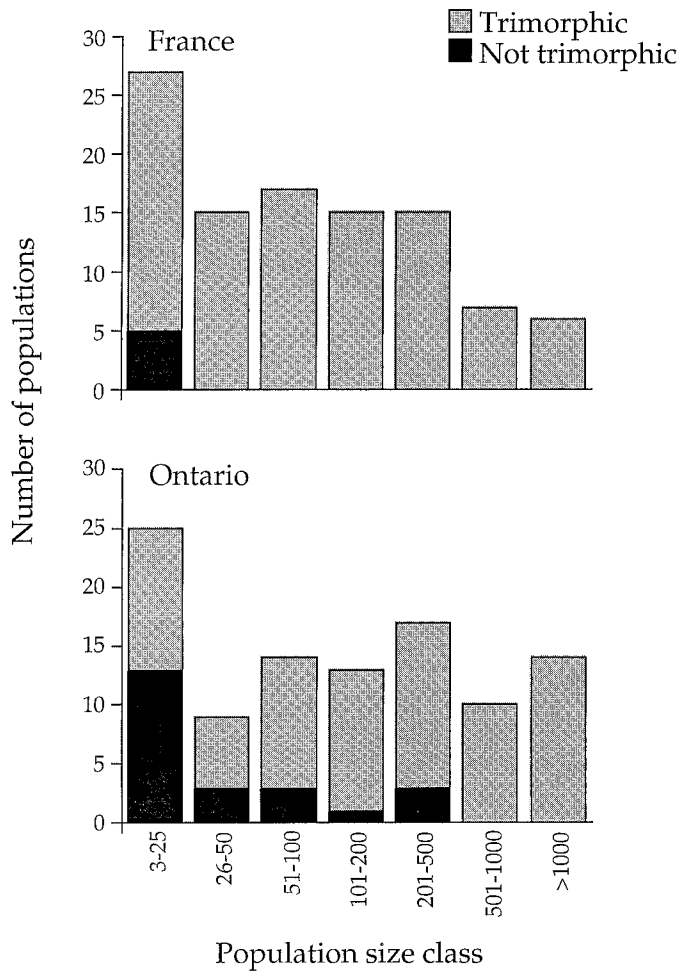
FIG. 2. The relationship between population size and morph loss in native populations of *Lythrum salicaria* from southwestern France and introduced populations from southern Ontario. Data from Ontario after Eckert and Barrett (1992).

Population size class

FIG. 3. The relationship between population size and morph evenness (O) in trimorphic populations of *Lythrum salicaria* from southwestern France and southern Ontario. Bars are means $\pm$ 1 SE. Sample sizes are indicated in Figure 2. Results of t-tests comparing mean evenness between France and Ontario for each population size class are shown above the bars: ns: $P > 0.20$, $* P < 0.05$, $**$ $P < 0.01$, $*** P < 0.001$. Data from Ontario after Eckert and Barrett (1992).

Barrett 1992), we report the results obtained after 100 yr as well as the equilibrium results for runs with nonzero migration rates.

RESULTS AND DISCUSSION

Morph-Frequency Variation in Native versus Introduced Populations

There was a low incidence of morph loss among populations of *Lythrum salicaria* from both areas of southwestern France. Only 5 of the 102 populations were lacking a morph. Although the number of dimorphic populations is small, the pattern of morph loss is in accord with theoretical expectations: three populations were lacking the S morph, two the M morph, and none were missing the L morph (Fig. 1). These results contrast sharply with those from the Ontario study (Eckert and Barrett 1992) in which 23% of the 102 populations surveyed lacked a morph (2 × 2 contingency table $\chi^2 = 13.4$, df = 1, $P = 0.0002$). In addition to the loss of morphs from populations, stochastic processes are expect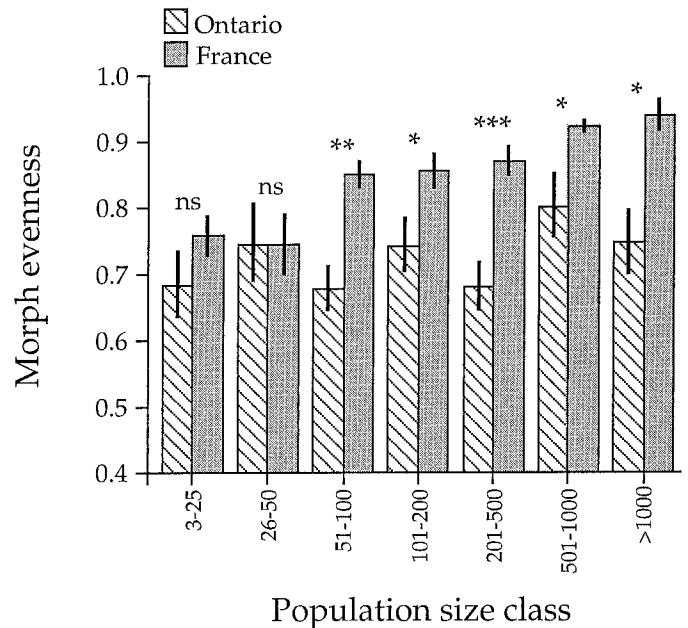ed to increase the degree of morph-frequency variation among trimorphic populations. Estimates of morph evenness (O) were significantly higher for trimorphic populations in France (mean $\pm$ SE = 0.83 $\pm$ 0.01) compared to those in Ontario (0.72 $\pm$ 0.02; $t = 4.9$, df = 174, $P < 0.0001$).

Data from French populations support our previous results from Ontario showing a negative relationship between morph loss and population size (Fig. 2). In both Ontario and France, small populations were significantly more likely to lack a morph than larger populations (2 × 6 contingency table, df = 6; France: $G = 14.0$, $P = 0.029$; Ontario: $G = 25.4$, $P = 0.0003$). This effect was particularly pronounced in the French sample, where all populations lacking a morph contained fewer than eight plants. In Ontario, style morphs were also missing from moderate-sized populations (range: 3–500; median: 24). Not all small populations, however, lacked a morph. In the French sample, more than half (7) of the 12 populations containing 10 or fewer plants contained all three morphs. On the other hand, small populations from Ontario ($N \leq 10$) usually (10 of 14) lacked a morph, although this difference between native and adventive samples was not significant (2 × 2 contingency table $\chi^2 = 2.3$, df = 1, $P = 0.126$).

Morph evenness in trimorphic populations increased significantly with population size (Fig. 3) in French populations (one-way ANOVA: $F = 5.0$, df = 6,90, $P = 0.0002$, $r^2 = 24.9\%$) but not adventive populations from Ontario ($F = 1.0$, df = 6,72, $P = 0.426$). Determining the statistical significance of this apparent population size-×-region interaction was hampered by strongly heterogeneous sample variances for O (see Methods). Some statistical support for this effect

was provided by *t*-tests comparing *O* between regions for each population size class separately. Significant differences were observed in the five largest but not the two smallest size classes (Fig. 3).

The lower frequency of morph loss and higher evenness values in native compared to introduced populations of *L. salicaria* were not associated with larger population sizes in France than Ontario (Fig. 2). On the contrary, the mean size of introduced populations was 80% larger than native populations (Ontario = 487 ± 902 SD; France = 266 ± 499; *t* = 2.17, df = 202, *P* = 0.031). This difference in mean size is also reflected by a similar, but only marginally significant, difference in median size (France = 80; Ontario = 125; Wilcoxon rank sums test: *Z* = 1.73, *P* = 0.084).

It is significant that this contrast in the magnitude of stochastic effects between regions occurs despite the larger size of introduced populations. Presumably the larger size of Ontario populations is a result of altered ecological circumstances in the adventive range. Our field observations suggest that the availability of suitable wetland habitats, as well as the absence of competitors, herbivores, and pathogens, may largely account for the explosive spread of this species in North America (and see Stuckey 1980; Thompson et al. 1987; Malecki et al. 1993). Although much of the theory on stochastic population processes emphasizes the importance of small population size and population bottlenecks (e.g., Nei et al. 1975; Mayurama and Fuerst 1984, 1985a, 1985b; Watterson 1984), range expansion by weedy plant species is often accompanied by rapid population growth following introduction to a new region leading to larger populations than occur in the native range (Elton 1958; Sculthorpe 1967; Baker 1972; Mack 1981; Barrett 1992).

The higher rate of morph loss in adventive compared to native populations of *L. salicaria* could be accounted for if the strength of self-incompatibility had declined during colonization. Shifts in mating pattern, from outcrossing to selfing, commonly occur following long-distance migration (Baker 1955; Brown and Burdon 1987; Barrett 1989). Weakening of self-incompatibility could result in increased self-fertilization and reduced disassortative mating among morphs. Computer simulations indicate that both these mating system changes make small populations more vulnerable to stochastic morph-frequency variation (Barrett et al. 1989; Eckert and Barrett 1992). However, experimental pollinations involving native and introduced populations of *L. salicaria*, including populations from southwestern France and southern Ontario grown in a common glasshouse environment, have not revealed differences in the expression of incompatibility in plants from the two regions (D. Manicacci and S. C. H. Barrett unpubl. data; see also O'Neil 1994; Ottenbreit and Staniforth 1994). Hence, changes in mating pattern in introduced populations are unlikely to have contributed to the differences in morph-frequency variation between native and adventive regions.

Collectively, these results strongly indicate that the influence of stochastic processes is greater in introduced populations of *L. salicaria* from Ontario than in native populations from southwestern France. To our knowledge, this study constitutes one of the first attempts to compare the strength of stochastic processes between native and introduced popula-

tions, and provides strong evidence for the importance of nonequilibrium population structure during rapid territorial expansion of an invading species.

Although stochastic effects are particularly evident in the Ontario sample, this does not imply that they are nonexistent in native populations. There are three aspects of our data that point to the operation of genetic drift in populations of *L. salicaria* from southwestern France. First, morph loss was entirely restricted to populations of fewer than eight individuals. Second, the evenness of morph frequencies in trimorphic populations was strongly related to population size. Finally, the pattern of morph loss was consistent with theoretical expectations based on a simple interaction between genetic drift and frequency-dependent selection. The results from the native range are not entirely unexpected, given that reductions in population size are likely to occur frequently in this species because of its ability to invade disturbed habitats. What is perhaps more remarkable is the stability of floral trimorphism in the face of these ecological pressures. This is in contrast to several self-compatible tristylous taxa in which extensive genetic modifications to the sexual polymorphism have been documented in association with colonization of marginal or disturbed environments (Ornduff 1972; Barrett 1979; Barrett et al. 1989; Eckert and Barrett 1994). It seems likely that the maintenance of a strong trimorphic incompatibility system in *L. salicaria* serves to buffer the mating system against inbreeding and consequent opportunities for the spread of recessive mutations modifying the sexual polymorphism (Charlesworth 1992; Fenster and Barrett 1994).

Although it is difficult to determine the relative importance of various stochastic population processes from patterns of morph-frequency variation alone (Eckert and Barrett 1992), our comparison of native and introduced populations indicates regional differences in the relative importance of founder effect versus genetic drift. The relationships between population size and both the probability of morph loss and morph evenness were much stronger for native than introduced populations. Only very small native populations (*N* < 10) lacked a morph, suggesting that morphs were lost through genetic drift. This idea is further supported by the positive relationship between morph evenness and population size in native trimorphic populations. In our Ontario study areas, *L. salicaria* is only recently established and many of the populations were fewer than 10 or 20 yr old and are currently growing rapidly (Eckert et al. 1996). In this region, dimorphic populations were sometimes quite large (*N* = 100–500), and there was no correlation between morph evenness and population size in trimorphic populations. The absence of morphs and large deviations from equal morph frequencies in large populations are more likely to have occurred through founder effect than genetic drift (Eckert and Barrett 1992).

Gene Flow and the Maintenance of Tristyly in Small Populations

Our observations of the spatial dispersion of populations in southwestern France suggested that gene flow may be partly responsible for the maintenance of tristyly in small native populations. Halkka and Halkka (1974) and Andersson

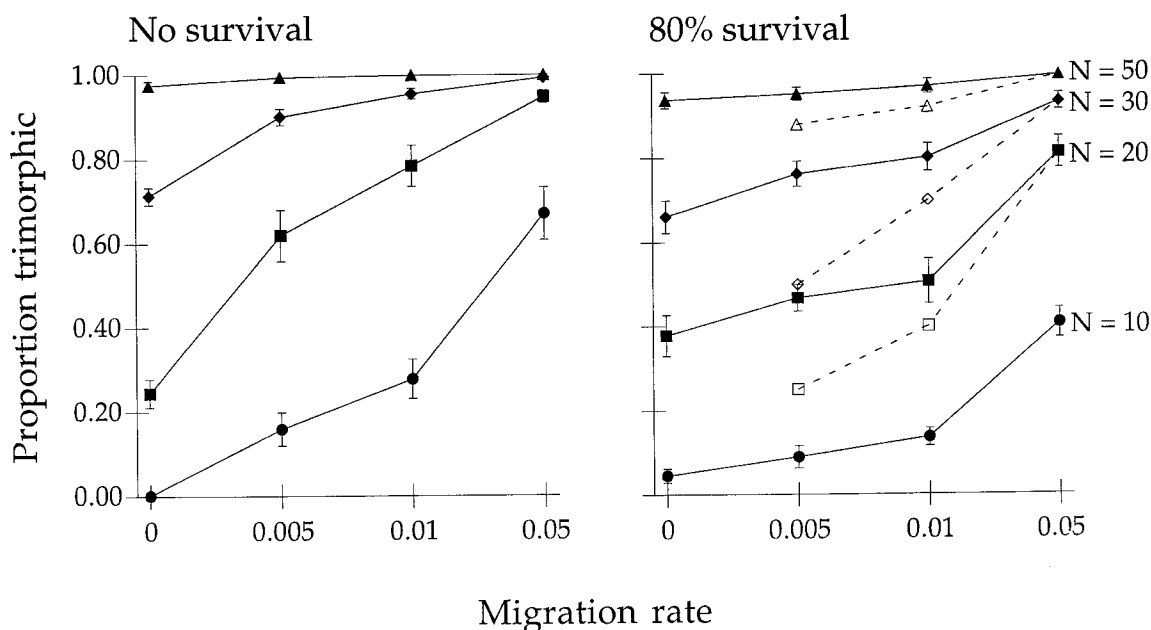## No survival 80% survival

Migration rate

FIG. 4. The theoretical relationship between morph loss and gene flow in annual (no survival) and perennial (80% survival) tristylous metapopulations. The results were produced using the equilibrium-dispersal model (see Methods). Values shown by solid symbols and lines are mean proportions of subpopulations remaining trimorphic in each metapopulation after 100 yr averaged across 10 replicate runs (± 1 SD). For nonzero migration rates, these values usually represent a drift-migration equilibrium. In cases where equilibrium was reached after 100 yr, equilibrium values are shown using open symbols and broken lines. For simulations with no migration, all subpopulations eventually become monomorphic; hence, equilibrium values are zero. Note that the abscissa is not a linear scale.

(1994) also invoked gene flow to account for the high frequency of trimorphic populations of *L. salicaria* in Scandinavia. However, the quantitative effect of gene flow on the maintenance of tristyly has not been investigated theoretically, making it difficult to evaluate these inferences based on natural history. Given the stability of trimorphism in isolated populations modeled in previous simulations (Eckert and Barrett 1992, fig. 2), we anticipated that low levels of gene flow would be sufficient to maintain trimorphism, even in very small populations. However, the main conclusion from our simulation results described below is that although gene flow can protect small populations against stochastic morph loss to some extent, the effect depends strongly on the life history of the species in question.

The joint effect of migration rate, population size, and year-to-year survival on the maintenance of trimorphism is illustrated in Figure 4. In simulations without gene flow, all populations eventually lose one or two style morphs. The rate at which trimorphism decays depends strongly on population size. With small population sizes ($N \leq 10$), all populations lost at least one morph within 100 yr, whereas in larger populations ($N \geq 50$), this process requires 1000 yr or more. With gene flow, metapopulations arrived at a drift-migration equilibrium.

Migration had a much greater effect on annual populations (no survival) than on perennial populations (80% survival). This is expected because the establishment of immigrant genotypes should vary directly with the rate of seedling recruitment. In perennial populations, moderate levels of immigration (0.5–1% immigrants among new recruits) did not significantly reduce the incidence of morph loss. For ex-

ample, in perennial populations of size 20, 1% immigration had a much smaller effect than increasing population size to 30 individuals. Only high rates of immigration (5%) afforded much protection against morph loss.

Although our ecological observations suggested that gene flow may be enhanced by high levels of connectivity among populations and the frequent disturbance that characterize the habitats in which *L. salicaria* occurs, empirical estimates of migration rates are required to support this hypothesis. High levels of gene flow (5–15%) have been demonstrated in small populations of a few insect-pollinated, outcrossing species (Ellstrand and Marshall 1985; Ellstrand et al. 1989; Broyles and Wyatt 1991). However, it has proven notoriously difficult to predict rates of gene flow based on life history and mating system parameters (Hamrick 1987; Ellstrand and Elam 1993). Therefore, it would be premature to assume that extensive gene flow is solely responsible for the maintenance of floral trimorphism in native populations of *L. salicaria*.

Biased Morph Frequencies and Natural Selection

Stochastic variation in morph frequencies among trimorphic populations should be strictly random and not associated with consistent biases in average morph frequencies (Eckert and Barrett 1992, table 2). In contrast, surveys of morph frequencies from Ontario, France and elsewhere in Europe have consistently shown biases involving an excess of the L morph and deficiencies of either the S or M morphs (Table 1; and see Heuch 1979a; Eckert and Barrett 1992; Andersson 1994; Ågren and Ericson 1995). Moreover, the biases shown by our data were the same or larger when morph frequencies

TABLE 1. Average style morph frequencies (± SE) in trimorphic populations of *Lythrum salicaria* from southwestern France and southern Ontario. Morph frequencies were also calculated with weighting by estimated population size. Data from Ontario after Eckert and Barrett (1992).

Region	Morph frequency		
	L	M	S
Average frequencies			
France	0.36 ± 0.01	0.33 ± 0.01	0.31 ± 0.01
Ontario	0.37 ± 0.01	0.30 ± 0.01	0.33 ± 0.01
Weighted by population size			
France	0.36 ± 0.01	0.33 ± 0.01	0.31 ± 0.01
Ontario	0.41 ± 0.01	0.23 ± 0.02	0.36 ± 0.01

were weighted by estimated population size (Table 1), indicating that they are a feature of large populations and not the result of chance skew in particularly small populations. The consistent occurrence of an excess in the frequency of the L morph across the geographical range of *L. salicaria* and in a variety of ecological settings strongly implicates natural selection in causing this pattern. Short-term studies in *L. salicaria* (Ågren and Ericson 1995) and other tristylous species exhibiting biased morph frequencies (Weller 1986; Eckert and Barrett 1995) have failed to provide evidence of fitness differences among morphs. In contrast to the pervasive effects of stochastic processes demonstrated here, selection on morph frequencies may be subtle and only detectable by long-term demographic investigations into the dynamics of tristylous populations.

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