PLANT POPULATION GENETICS, BREEDING, AND GENETIC RESOURCES

Edited by Anthony H. D. Brown
CSIRO, Canberra, Australia
Michael T. Clegg
University of California, Riverside
Alex L. Kahler
Biogenetic Services Inc., Brookings, S.D.
Bruce S. Weir
North Carolina State University, Raleigh

Sinauer Associates Inc. • Publishers
Sunderland, Massachusetts

CHAPTER 15

THE GENETICS OF PLANT MIGRATION AND COLONIZATION

Spencer C. H. Barrett and Brian C. Husband

ABSTRACT

Migration and colonization are processes shared by all organisms, yet it is unlikely that the genetic consequences are the same for all. Colonizing episodes will be important in determining population genetic structure when they occur frequently, as in species of ephemeral environments, or when as a result of long-distance dispersal, genetically isolated populations occur. The effects of small populations through founder events or bottlenecks, inbreeding, and strong directional selection in novel environments can all influence population genetic structure depending on the ecology of the species and the scale of colonization. While a theoretical framework for understanding the genetics of migration and colonization is well developed, few studies of plant populations exist that test the predictions of the models. Two particular deficiencies are evident. First, quantitative data on the significant parameters of colonization models, e.g., effective population size and migration rates, are lacking. Second, information on the effects of stochastic processes on quantitative traits is not available for plant populations; yet such traits are likely to be of major importance to survival and reproductive success. Satisfactory explanations for the success or failure of colonizing episodes will most likely come from demographic genetic studies of natural colonization events or from experimental work on artificially established colonies.

Colonization is the establishment and spread of an organism in a region or habitat not previously occupied by that species. On some spatial or temporal scale, it is an integral feature of the population biology of all plants and animals. Therefore, information on the genetic consequences of colonization is essential for understanding the population genetics and evolution of organisms. Information on the genetic structure of colonizing populations can be useful in two ways. It can be interpreted retrospectively to aid in constructing the historical processes of migration and colonization. Second, it can provide insights into the ecological persistence and evolutionary potential of populations once they have entered a new environment. To understand the evolutionary consequences of colonization, it is necessary to know the amounts, kinds, and organization of genetic variation that result from different patterns of colonization. The effects of small populations through founder events or bottlenecks, inbreeding, strong directional selection in novel environments, rapid density-independent population growth, and gene exchange with related taxa can all influence population genetic structure in colonizers depending on the species and scale of colonization.

Colonizing episodes are more likely to be important in determining population genetic structure when they occur frequently, as in many pests, weeds, and early successional species, or when, as a result of long-distance dispersal, genetically isolated populations are produced. In fact, much of the interest in the genetics of colonization has focused on species with particularly well-developed invasive powers whose populations are in a constant state of colonization, extinction, and recolonization. Such "colonizing or invading species" have provided the experimental material used to develop much of our knowledge of the evolutionary process since the modern synthesis. However, in studying the genetics of colonization it is perhaps more useful, as Lewontin (1965) originally pointed out, not to think of colonizing species as a discrete group but to consider the effects of colonizing events for any species. All organisms occur on a continuum in which the frequency of colonization of new territory or habitats varies from high to low. Differences among species in the frequency and importance of colonization for regional persistence largely depend on extrinsic ecological factors, such as the type and distribution of habitats, as well as intrinsic factors associated with the life history and reproductive system of the species in question. The development of a sound theoretical framework for the genetics of colonization necessitates the recognition that models describing the colonization process will vary for species at different positions along the continuum.

While we have made considerable progress in the past two decades in understanding the genetics of plant colonization (reviewed in Brown and Marshall 1981; Barrett and Richardson 1985; Rice and Jain 1985), there are still surprising gaps in our knowledge, particularly in relation to the dynamics of the colonization process. In most empirical studies, patterns of genetic variation are measured at one point in time and inferences are made about the processes that have led to the observed pattern, often without historical information on the populations involved. The absence of chronological genetic studies of colonizing plants severely restricts direct tests of theoretical models of the genetics of migration and colonization.

Understanding the genetics of colonization is important not only to evolutionary studies and population biology but also to agriculture and conservation. The domestication of plants and animals involved many genetic bottlenecks in both space and time and, in most cultigens, this has resulted in an erosion of genetic diversity in comparison with wild relatives (Frankel and Soulé 1981). The accidental or planned introduction of crops and weeds from one continent to another involves many of the same genetic processes that operate during colonizing episodes in wild populations. Knowledge of the migratory history of crop plants can aid in interpreting geographic patterns of genetic diversity and the sampling of germplasm. Efforts to conserve germplasm resources, either by habitat preservation or in collections, requires a knowledge of the effects of small populations on the maintenance of genetic variability and appreciation of the likely effects of prolonged inbreeding. For pest and weed species, information on the genetic diversity present in a particular area, as well as knowledge of the likely source region for a particular invasion, can be of value in devising effective methods of biological control (Marshall et al. 1980). Clearly, both theoretical and empirical studies of migration and colonization can provide basic information to applied biologists whose primary goal is the wise management of genetic resources.

In this chapter, we begin by outlining some simple theoretical concepts and models that describe how colonization affects population genetic structure. Particular attention is given to the effects of stochastic processes on different classes of genetic variation. Because of an overall paucity of empirical data on colonization in plants, most of the data relevant to the models come from species of ephemeral environments. Following a discussion of the evidence for evolutionary changes in mating systems that can accompany colonization, we conclude by suggesting the kinds of genetic studies that could be conducted profitably on plant colonization and where major gaps in our knowledge occur.

GENETICS OF FINITE POPULATIONS

Small populations are a distinct feature of most colonizing events. They are common when a population is first established (e.g., founder events) or to existing populations after disturbance (e.g., population bottlenecks). Often, only a subset of the genetic information present in the source is represented in a single migration or colonizing event. This sampling error causes random fluctuations in allele frequencies called genetic drift (Wright 1969). The genetic theory of finite populations most simply describes the effect of population size and migration on genetic drift and its consequences on population genetic structure. The models assume random mating and no selection or mutation.

Population size

At equilibrium, populations small enough to experience drift will become fixed for one of the alleles at a polymorphic locus and thereby decrease allele richness, and increase inbreeding and population differentiation. The average number of alleles per locus decreases because the probability of a rare allele occurring in a founding population decreases with population size (Nei et al. 1975). If the majority of alleles in the source population are rare, then the average number of alleles in the colonizing population will be most affected by the size of the initial genetic bottleneck, and less by the length of time a population remains small (Sirkkomaa 1983). If a population remains small over long periods, then more common alleles will be lost as random fluctuations alter allele frequencies toward 0 or 1. The frequency of homozygotes increases in small populations as a result of increased mating among relatives. The proportion of heterozygotes as a function of time is given by

$$H_{t+1} = (1 - 1/2N)H_t \tag{1}$$

indicating that the proportionate loss of heterozygosity is expected to be only $1/2N$ each generation and therefore will be substantial only if populations remain small for a number of generations (Nei et al. 1975). Not only will allele richness and heterozygosity decrease within small populations but also, if founding events are repeated in space, the variance among new colonies will depend on the average population size and the time spent at that size. Although the variance among populations increases, the expected average allele frequency among all populations will not deviate from the initial frequency in the source. Where small populations are a significant feature of the colonizing process, theory predicts that populations will exhibit low genetic variability within and a large degree of differentiation among populations. Although the theory of finite populations is well developed, it remains for empiricists to determine its significance for natural populations of plants.

When examining the genetic consequences of colonization, the critical parameter to estimate is population size. A direct count of the number of breeding individuals may be sufficient. However, in most natural populations, the number of breeding individuals does not reflect the degree of drift and inbreeding observed. In other words, the breeding population size is rarely equal to the N of the models described above. Factors that cause this disparity include gene flow over long distances, varying population size, nonrandom mating, unequal sex ratios, and age and size structure (Kimura and Crow 1963; Heywood 1986). These factors violate the assumption of the simple finite population models, that each of the N individuals has an equal probability of contributing gametes to the next generation. A better parameter is N_e, the effective population size, which represents the size of an idealized population, in which each individual contributes equally to the gamete pool, having the same variation in allele frequencies as the observed population (Wright 1931). The effective size can be derived from the actual number of breeding individuals, when factors affecting the breeding structure such as selfing rate, sex ratio, and the distribution of reproductive output are known, or can be inferred from the variance of allele frequencies at neutral loci (Kimura and Crow 1963; Nei and Tajima 1981; Pollak 1983; Crow and Denniston 1988).

Unfortunately, there are few examples where N_e has been estimated and compared to N for plant populations. Jain and Rai (1974) measured the effective population size of subpopulations of *Avena fatua* based on the number of breeding individuals, departures from random mating, and variance in seed output among plants. Since the estimates of N_e varied over the 2 years samples were taken, they calculated the harmonic mean of N_e for each population (Wright 1951). In all cases, the average effective size was less than the average number of individuals per population. Similarly, estimates of N_e based on the distribution of reproductive output within populations of *Papaver* were less than the observed number of reproductive individuals (M. Lawrence, personal communication). While N_e is less than N in these examples, the magnitude and direction of the differences will vary within and among plant species due to their diverse life histories, reproductive systems, and colonization patterns.

Colonization affects genetic structure through its influence on population size; however, there have been relatively few studies of plant colonization from this perspective. Local differentiation has been widely reported for both isozymes (Ennos 1985; Knight and Waller 1987) and life history traits (Antonovics and Primack 1982; Schemske 1984); in many cases drift has been inferred. However, differentiation can often be explained by other factors such as differences in the direction and intensity of selection among sites. To demonstrate the effects of finite population size we must at least measure the effective population size, preferably in past generations, and relate it to both the existing and expected levels of variation. Jain and Rai (1974) compared variation in morphological traits of *Avena fatua* from subpopulations in two orchards. The average effective population size for the orchards differed because of contrasting management practices. Jain and Rai related the changes in allele frequency over 2 years to population size. As predicted by theory, the average gene frequencies in both orchards did not fluctuate significantly from one year to the next, except at one locus. However, over 2 years, the subpopulations became more differentiated, particularly in the orchard with smaller subpopulations. The authors concluded that most changes in allele frequency were due to random drift or sampling errors in the survey.

Drift in small populations is also an important evolutionary force affecting differentiation in style morph diversity among populations of tristylous *Eichhornia paniculata* that inhabit N.E. Brazil. Populations vary in their morph structure, from equal morph frequencies to a single morph. In a sample of 84 populations, morph diversity increased and the variance among populations decreased with increasing plant density. This result is consistent with genetic drift since density is correlated with population size in the species (Barrett et al., in press). Measures of temporal variation in morph evenness reveal a similar pattern. Figure 1 shows changes in morph evenness between 1987 and 1988 in 34 populations of *E. paniculata* in relation to the harmonic mean of population size. Populations deviate away from (+ change) or toward (− change) equal morph frequencies to nearly the same degree (19 versus 15 populations, respectively) and the average change in morph evenness is not significantly different from zero. The largest absolute changes in diversity occur in the smallest populations, particularly those below 100 individuals (Figure 1). The observed patterns indicate that random drift in small populations is a dominant factor affecting genetic structure in *Eichhornia paniculata*.

The inheritance of traits with more obvious ecological significance, such as growth rate or reproductive effort, is not well understood and predicting the effects of small populations is difficult. While there are examples of quantitative characters under relatively simple genetic control (reviewed in Gottlieb 1984), most life history traits are likely to be controlled by many loci. When the genetic variance of polygenic traits is based on additive allele effects, variation should decrease in proportion to $1/2N_e$ after a bottleneck of N_e individuals (Lande 1980). However, if genetic variability is partly the re-

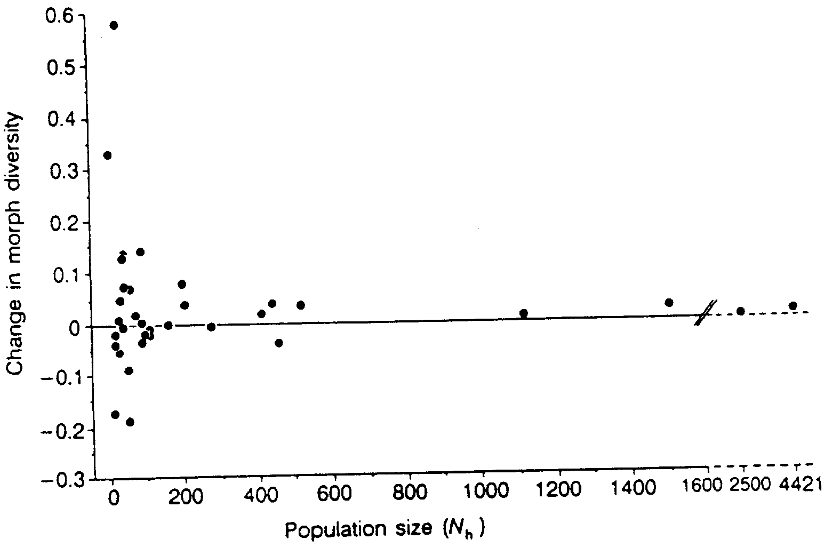

FIGURE 1. Changes in style morph diversity in relation to population size from 1987 to 1988 in 34 Brazilian populations of tristylous *Eichhornia paniculata*. Population size (N_h) is the harmonic mean of the number of reproductive individuals in each year. Style morph diversity was calculated using a modification of Simpson's index (B. C. Husband and S. C. H. Barrett, unpublished data).

sult of nonadditive allele effects (such as epistasis and dominance), the effect of small populations on genetic variation will not be a simple relationship with *N*. Recent models by Goodnight (1987, 1988) suggest that the additive genetic variance may actually increase, at least temporarily, after a bottleneck, as inbreeding converts nonadditive genetic variation from the donor population to additive genetic variation in the derived population. Figure 2 illustrates such an effect for traits related to fitness, in which 20% of the total variance in the ancestral population is additive and 80% is epistatic. If populations are kept at 16 individuals for 100 generations, the additive genetic variance increases and temporarily exceeds the total genetic variance in the ancestral population. Over the remaining period, the additive genetic variance in the derived population exceeds that in the ancestral population.

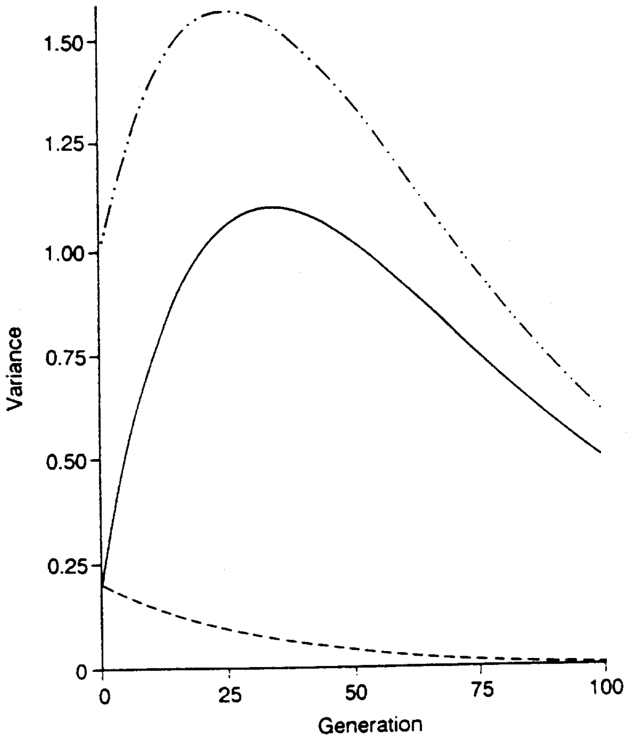

FIGURE 2. The effect of a population bottleneck of intermediate size (16 individuals) on additive genetic variance (solid line) and total genetic variance (dash/dot line) for 100 generations. The contribution of additive genetic variance in the ancestral population to additive genetic variance after the bottleneck is also indicated (dashed line). Twenty percent of the total genetic variance in the ancestral population is additive and 80% is epistatic (after Goodnight 1988).

Goodnight also shows that while epistatic variance changes to additive variation most rapidly in small populations, a greater proportion of the variance converts to additive variation over many generations in populations of moderate size. Aside from laboratory studies on houseflies by Bryant and coworkers (1986a, 1986b), there are few studies designed to test this theory and none is known from the plant literature.

Although less controlled, recent colonization events of known origin can also reveal the effect of bottlenecks on genetic variability in the field. For example, in a study of local colonization, we measured genetic variability in an isolated pair of populations of *Eichhornia paniculata* in N.E. Brazil. In 1987, one population was large and contained all three style morphs; the second population, 3 km west, was small, with only two morphs. Both populations were separated from the remaining concentration of populations by 100–200 km. Based on morph structure, size, and geographic distribution, the large trimorphic population is the most likely source of plants that established the smaller population. While enzyme variability in both populations was low relative to other Brazilian populations (see Glover and Barrett 1987), the variation in the derived population was a reduced subset of the variation in the source population (Table 1). A similar pattern was evident for quantitative

TABLE 1 Comparison of genetic variation in source and derivative populations of *Eichhornia paniculata* in N.E. Brazil.[a]

	B56	B55
Style morph structure	Trimorphic	Dimorphic
Estimated population size		
1987	2000	200
1988	775	0
Outcrossing rate (t)	0.99 ± 0.04	0.60 ± 0.14
Loci polymorphic (%)	20.8	8.3
Average number of alleles	2.3	2.0
H_{obs}	0.054	0.016
Gene diversity (h)	0.062	0.035
F	0.13	0.54
Number of traits with significant family variation	8/15	1/15

[a] The two populations were located in roadside ditches, 3 km apart, 69 km west of Campina Grande, Paraiba State (see Figure 2, Barrett et al., in press). Isozyme data are based on a survey of 24 loci from a sample of 264 plants from B56 and 64 from B55. Measures of quantitative variation in life history traits are based on comparisons of 25 open-pollinated familes of 2 individuals each, per population, grown under uniform glasshouse conditions. Variation among families was significant at the $p<0.05$ level, in a mixed model, hierarchial analysis of variance.

traits. Between-family variation was a significant component of the total variation in the source population for 8 of 15 traits. In the derived population, however, only 1 of 15 traits exhibited significant family variation and in no case did the family component of the variance exceed that in the source. While quantitative genetic variation was apparently reduced by the colonization event, genetic correlations, based on family means between all possible pairs of traits, did not change significantly between the source and derived populations. Although in this example both classes of genetic variability exhibited similar patterns, a lack of congruence between variation in quantitative traits and enzyme loci, as well as few data on the genetic basis of quantitative traits, make it all the more important that experimental studies are conducted on the effect of bottlenecks on genetic variation. If these studies are to be useful to colonization genetics they should examine traits of obvious ecological significance.

Migration

In small populations, migration moderates the random change in allele frequencies due to genetic drift. The degree to which drift occurs will depend on both the rate of migration and the genetic characteristics of the migrants. When the genotypes involved in colonization are at a constant frequency, recurrent migration will oppose the forces of drift and maintain variability within populations. The degree of differentiation among populations that have reached a drift–migration equilibrium is given by

$$V_q = pq/(4Nm + 1) \qquad (2)$$

where V_q is the variance of the frequency of allele q, and Nm is the rate of dispersion (Falconer 1981). Thus, a single migration event will have a greater influence on small populations than on large ones. However, because of drift, maintaining a given level of homogeneity requires more migration in small than large populations. In plants, migrants are commonly from neighboring populations and because of the dispersal of multiseeded fruits, are likely to be kin structured. This feature in association with variable migration rates introduces a large stochastic element and increases the potential for random differentiation of populations (Levin 1988).

In many plants species, particularly those of disturbed or ephemeral habitats, the sequence of population bottleneck and expansion, or extinction and recolonization, is repeated continuously over time. Most models of population differentiation, however, assume that each local population lasts indefinitely. Slatkin (1977) showed that without selection and mutation, the effect of local extinctions and recolonizations on genetic structure is complex and depends on the relative strengths of drift and gene flow between populations during recolonization. The impact of gene flow during recolonization depends on whether the migrants that establish new colonies are from the same population, such as the immediate seed bank or the nearest population (the propagule model), or from a random sample of populations, differing in allele frequency (migrant model). In the propagule model, drift outweighs the effect of gene flow, and, therefore, populations differentiate. Under this colonization scheme, genetic differentiation is enhanced most when the number of individuals colonizing an available site is small relative to the number entering extant sites (Wade and McCauley 1988). In the migrant model, a random sample of seeds from a collection of populations can increase variation within and reduce the levels of differentiation between populations, particularly when the number of individuals colonizing available sites is relatively large.

If selection is also considered, the theory of colonization and extinction may be analogous to the nonequilibrium theory of species diversity in communities (Huston 1979). This theory suggests that species diversity is a product of the interacting effects of disturbance and competition, both of which reduce species richness. At intermediate levels of disturbance, competition is interrupted and disturbance is not intense enough to extirpate species. At this point, disturbance is sufficient to maintain the presence of early successional species and thus diversity is higher than at low levels of disturbance (or colonization). If community diversity is comparable to genetic diversity within populations of a species, then, by analogy, variation will be a function of the effects of drift and selection. Selection will be most important in reducing variability in undisturbed populations, while drift causes fixation in frequently disturbed populations. This model predicts that variability within populations will be highest at intermediate levels of disturbance, since the effects of selection and drift are minimized. While apparently no population genetic studies address this issue, community studies on intertidal diversity (Sousa 1979) and Atlantic coast plants (Keddy 1983) appear to support this prediction.

Models of genetic structure in populations experiencing frequent colonization and extinction predict that, under certain circumstances, increasing the frequency of colonization increases the genetic diversity within populations (Wade and McCauley 1988). This is important since we regularly associate colonization and colonizing plants with low genetic diversity within populations. The results may explain why variability in disturbed populations can exceed that in stable populations, as described for ***Lupinus succulentus*** from California (Harding and Mankinen 1972). Harding and Mankinen found that disturbed populations were more variable at three flower color loci and one seed pigment locus. They suggested that contrasting selection pressures may account for the differences in genetic variation associated with disturbance. An alternate explanation, however, is that interpopulation migration plays a larger role than drift in the colonization dynamics of these populations. Unfortunately, the level of migration between populations is poorly understood and represents one of the least tractable aspects of population genetics (Levin 1988). Not withstanding this difficulty, interpretations of the genetic structure of colonizing populations cannot be made in isolation, but should be viewed in the context of the local distribution and density of populations and their dynamic interrelationships with one another.

MODELS OF COLONIZATION

Measuring and describing the genetic structure of populations, in space and time, pose no difficulties of principle. However, inferring the importance of migration and population size is difficult without knowing the dynamics of colonization. Since so few estimates of plant migration rates exist, conclusions are highly speculative. In light of this deficiency, we consider a number of colonization models, discuss their effects on genetic structure, and then summarize the empirical data available that can be interpreted within this framework. The models involve migration and finite population size, but do not deal with selection.

Continent–island model

The continent–island model is the simplest depiction of colonization, based on Wright's (1940) island model of migration. It assumes unidirectional migration from a relatively large source, with a fixed allele frequency, to small isolated colonies or islands. Wright combined the effects of population size and migration to predict whether island populations will differ from those on the continent. At equilibrium, allele frequencies in small, isolated colonies will differ significantly from their source and, depending on the rate of expansion, may differ from the genetic composition of the initial migrants due to drift (Nei et al. 1975). The distribution of allele frequencies among populations will vary, depending on their size. The frequency of populations fixed for a particular allele will be in proportion to the frequency of the allele in the migrant pool. The continent–island model can be applied to plant colonization involving long-distance dispersal and is particularly relevant to the adventive spread of weeds. Unfortunately there are relatively few examples in which genetic variation has been measured in both the source and colonial (introduced) populations of wide-ranging species and even fewer comparisons of genetic diversity between continental and island populations of plants.

In all cases where island and mainland populations have been compared, insular populations have had reduced or, in extreme cases, no measured genetic diversity (Rick and Fobes 1975; Ledig and Conkle 1983). In the former case, Galapagos Island populations of *Lycopersicon cheesmanii* are sufficiently distinct from their more variable mainland progenitor to warrant separate species status, whereas, in the latter case, both island and mainland populations of *Pinus torreyana* are genetically depauperate, suggesting that the species itself has been subject to an historical bottleneck. Two examples in which a genetic bottleneck has been associated with island colonization involve the heterostylous plants *Turnera ulmifolia* and *Eichhornia paniculata* (Table 2).

TABLE 2 Comparisons of isozyme variation in source and introduced populations of four colonizing species of plants.[a]

Region	Number of populations/loci	PLP	Average number of alleles/polymorphic locus	H_o	H
	Apera spica-venti (Warwick et al. 1987)				
Europe	6/17	0.62	2.5	0.23	0.20
Canada	9/17	0.57	2.5	0.23	0.21
	Echium plantagineum (Burdon and Brown 1986)				
Europe	2/14	0.82	2.6	0.29	0.35[b]
Australia	8/16	0.94	2.7	0.32	0.34[b]
	Eichhornia paniculata (Glover and Barrett 1987)				
Brazil	6/21	0.24	2.2	0.08	0.09
Jamaica	5/21	0.08	2.0	0.02	0.03
	Turnera ulmifolia (Barrett and Shore, in press)				
Latin America	7/14	0.46	2.1	0.11	0.12
Caribbean	16/14	0.20	2.0	0.07	0.04

[a] PLP, proportion of loci that are polymorphic; H_o, observed heterozygosity; H, gene diversity.
[b] Based on polymorphic loci.

Both taxa occur primarily in South America with isolated populations on various Caribbean islands. In the case of *E. paniculata*, island colonization is confounded with a change in mating system from outcrossing to predominant self-fertilization (see below). In contrast, both continental and island populations of *Turnera ulmifolia* var *intermedia* are self-incompatible and outbreeding, but the former populations are diploid whereas the latter are autotetraploid. Since continental autotetraploids of *T. ulmifolia* var *elegans* are highly variable, with populations more diverse than those of diploids, it is unlikely that the reduced diversity of island populations of var. *intermedia* is the result of their autotetraploid origin; more likely it is a direct result of genetic bottlenecks associated with island colonization (Barrett and Shore, in press).

Evidence from investigations of intercontinental migrations of weeds indicates that genetic variation in introduced populations can be lower or higher (reviewed in Brown and Marshall 1981) than populations from the source range. The outbreeding weeds *Apera spica-venti* and *Echium plantagineum* exhibit similar levels of variability in native and introduced populations (Table 2). Both species are native to Europe and have become established in Canada and Australia, respectively. Despite its recent introduction, *Apera* exhibits as much variability in introduced colonies as in European populations. This supports the prediction that the effects of genetic bottlenecks are reduced by factors such as outcrossing, which increase the effective size, N_e. In *E. plantagineum*, the high genetic diversity of Australian populations is in part the result of hybridization among multiple introductions of floral variants used for ornamental purposes. Without information on the source, time, and number of introductions, interpretations of the genetic effects of long-distance colonization will be difficult.

An example in which some historical information is available involves the invasion of two annual barnyard grasses [*Echinochloa microstachya* and *E. oryzoides*] into cultivated rice fields in New South Wales, Australia. Imported Californian rice varieties were used to initiate rice cultivation in New South Wales in 1922 (McIntyre and Barrett 1986). The earliest records of the two barnyard grasses in Australia were from rice fields at Leeton Rice Experiment Station in 1938, the entry point for Californian rice varieties. Comparisons of isozyme variation in North American and Australian populations of the two species indicate a major genetic bottleneck associated with introduction to Australia with Californian rice field populations the most likely source (S. C. H. Barrett and A. H. D. Brown, unpublished). In the case of *E. microstachya*, the predominant Australian genotype could be identified from among the North American sample of populations and occurred in a population from northern California close to Biggs Rice Experiment Station. Historical records suggest this site as the likely exit point for cultivated rice varieties shipped to Australia in the 1920s.

Patterns of genetic differentiation in life history attributes among populations of the two barnyard grass species from the two regions were similar to those obtained for isozyme loci. In the native *E. microstachya*, North American populations were more differentiated than Australian populations with two populations clustered with the Australian sample (Figure 3). Once again this points to northern California as the likely source region for the Australian invasions. Population samples of the crop mimic *E. oryzoides* showed little differentiation between California and Australia. The lack of differentiation may result from the similar cultural conditions for rice growing in the two regions (McIntyre and Barrett 1986) as well as restricted amounts of genetic variations present in the founding stocks.

The continent–island model of colonization is applicable to many examples in the plant literature, although few workers have explicitly tested the relationships between migration and genetic structure as defined by Wright (1969). It is difficult to evaluate the predictions of the model when the appropriate variables are not known. Estimates of the number of introductions, founder size, and levels of migration are required to predict differences between colonial and source populations. While there is increased interest in estimating levels of interpopulation gene flow using the methods of Wright

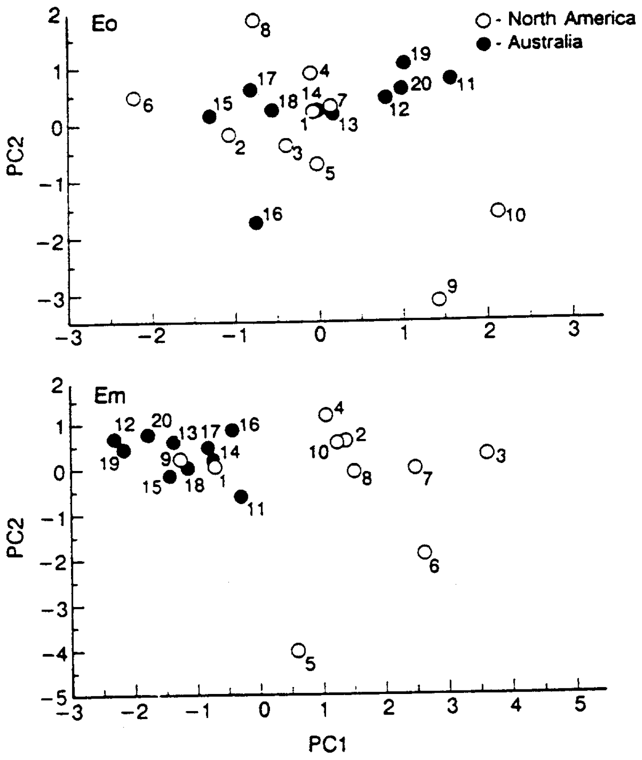

FIGURE 3. Principal components analysis of quantitative variation in 12 life history traits in populations of *Echinochloa oryzoides* (Eo) and *E. microstachya* (Em) from North America (open circles, 1–10) and Australia (closed circles, 11–20). The 20 populations of each species were grown under uniform glasshouse conditions. Note the absence of differentiation between populations from the two regions in *E. oryzoides* and the occurrence of two population of *E. microstachya* (1,9) from northern California that cluster with the Australian sample (S. C. H. Barrett and A. H. D. Brown, unpublished).

(1969) and Slatkin (1985), no studies have as yet examined this in relation to colonization history in plants.

Island model

Island models of colonization assume that migration occurs among subpopulations. In contrast to the continent–island model, migration is multidirectional because the subpopulations are assumed to be of the same effective size. We will describe the botanical evidence for two spatial patterns of population differentiation in the context of the island model. First is the random pattern, in which migration among populations is essentially random. Second is the stepping stone pattern, where migration occurs only between adjacent subpopulations, in one or two dimensions.

The island model has been used as a theoretical framework for interpreting spatial patterns of population structure on a quantitative as well as a qualitative basis. The degree that populations differentiate will depend on the effective population size of each subpopulation. If N_e is small, drift will maintain a random pattern of variation in gene frequencies. In the *Avena* study, discussed earlier, Jain and Rai (1974) compared the observed local differentiation to quantitative predictions of the island model. Using estimates of N_e, migration, and selfing rates, they found that differentiation among subpopulations was consistent with that expected by the island model. That is, the degree of similarity in allele frequencies among subpopulations was not correlated with the distance separating them. Also, the variance in allele frequencies expected based on this model was similar to that observed. Similar spatial patterns of genetic structure have been reported in *Oenothera* (Levin 1975), *Clarkia* (Soltis and Bloom 1986), and *Impatiens* (Knight and Waller 1987). In each case, the genetic distance among populations was not correlated with geographic distance. These species are annual and occur in ephemeral habitats. This suggests that, where habitats are disturbed and extinction and colonization occur frequently, populations rapidly differentiate and a clear source-derivative relationship within a local area may not be maintained.

Not all species from ephemeral environments display a random distribution of alleles among populations. In a recent study of isozyme variation in 12 Jamaican populations of *E. paniculata* sampled throughout the island, genetic distances among populations were significantly correlated with geographic distance (B. C. Husband and S. C. H. Barrett, unpublished). Two spatial patterns are evident from the isozyme survey: (1) central populations on the island are differentiated from populations toward the east and west (Figure 4A,B), and (2) populations in the west are differentiated from those throughout the rest of the island (Figure 4C). These patterns may reflect the initial location of two separate introductions to Jamaica and subsequent diffusion from these points. This hypothesis is supported by both the presence of unique alleles at the loci *Pgi* and *Pgm* and associated differences in floral traits and life history in populations from the western end of the island.

Migration restricted primarily to adjacent populations results in a pattern of genetic variation described as either stepping stone, in patchily distributed species, or clinal, in continuously distributed species. The stepping stone model, first described by Kimura and Weiss (1964), predicts that when migration is restricted in this way, populations will diverge and the correlation among populations will decrease with the distance separating them. A stepping stone model may explain the pattern of variation at neutral loci, for populations that have diffused from a single site of colonization and where

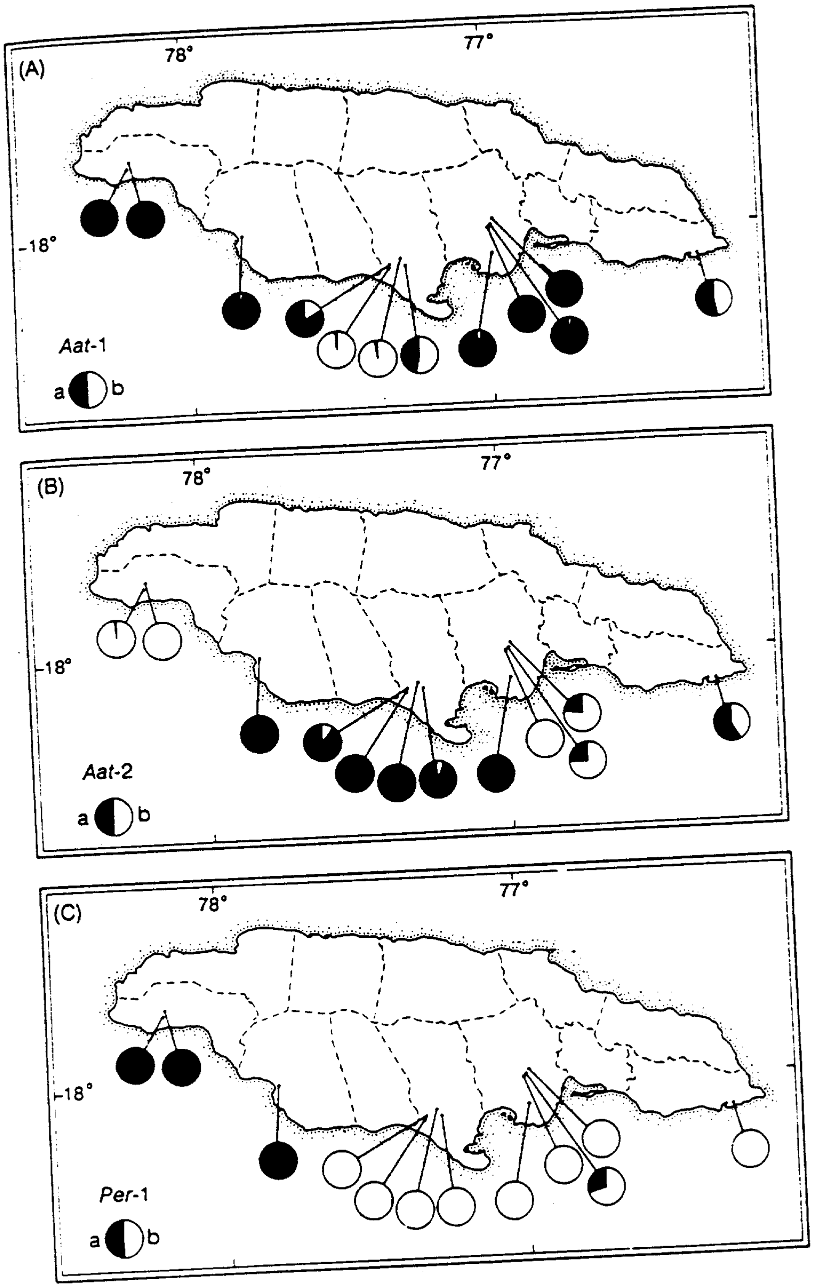

FIGURE 4. Geographic patterns of variability at three isozyme loci in Jamaican populations of *Eichhornia paniculata*. The number of polymorphic loci per population ranged from 0 to 3 of 24 loci screened. A–C, allele frequencies at the loci *Aat*-1, *Aat*-2, and *Per*-1, respectively; a represents the fastest migrating allele and b the slowest (B. C. Husband and S. C. H. Barrett, unpublished).

migration is primarily outward from the source. There are several examples of plant species with populations whose genetic similarity, based on isozymes, is significantly correlated with geographic separation (Lundkvist and Rudin 1977; Yang et al. 1977; Bergmann 1978; Yeh and O'Malley 1980). In contrast to species with random patterns of genetic differentiation (see above), most examples involve tree species from relatively stable habitats. One exception is described by Weber and Stettler (1981), who found a weak but nonsignificant correlation between genetic and geographic distance in *Populus trichocarpa*. Like the annuals that tend to exhibit random variation, *Populus trichocarpa* is an opportunist from ephemeral habitats.

These results suggest that island models of migration may be suitable for predicting the geographic patterns of genetic differentiation throughout the range of a species. Whether a species exhibits regional patterns of differentiation among populations may depend on the direction and frequency of colonization. These are likely to differ among species with contrasting life histories such as long-lived trees and annual plants of ephemeral habitats.

Central–marginal model

The central–marginal model of colonization has provided an important framework for investigating the processes of microevolution (Antonovics 1976). The model assumes that central habitats are environmentally more benign and less isolated than marginal ones. If marginal sites are colonized by migrants from a central source, the model predicts they should be genetically differentiated and less variable than those at the center. Lower genetic variation in marginal populations may be due to genetic drift and/or strong directional selection. The relative importance of these forces is likely to depend on whether central–marginal classifications are based on geographic or ecological criteria.

Empirical studies have not consistently supported predictions of the central–marginal model, regardless of the criteria used to evaluate marginality. Populations in marginal sites may have lower (Farris and Schaal 1983; Silander 1984), similar (Tigerstedt 1973; Levin 1977), or higher (Keeler 1978; Schumaker and Babbel 1980) variability than central sites. These results are not altogether unexpected, however, since most of these studies were conducted across ecological gradients but involved isozyme surveys. Variability at isozyme loci is unlikely to be under strong selection and may be selectively neutral. There are relatively few studies of quantitative genetic variability within central and marginal populations of plants. In *Veronica peregrina* (Linhart 1974) and *Spartina patens* (Silander 1985), the expected decrease in genetic variability in ecologically marginal environments was observed. However, in *Danthonia spicata*, there was no consistent difference between central and marginal populations (Scheiner and Goodnight 1984). These authors suggest that *D. spicata* has only recently colonized the marginal sites they studied and, as a consequence, selection has had little time to operate.

Most comparisons of central and marginal populations lack information on the historical relationships among the populations examined. An exception involves the postglacial migration of *Pinus contorta* in northern Canada (Cwynar and MacDonald 1987). Palynological studies from lakes throughout the northern range of *P. contorta* suggest that the species migrated from southern refugia to the Yukon Territory in the last 12,000 years. Cwynar and MacDonald (1987) compared the date of colonization with genetic diversity, for 42 isozyme loci and several quantitative traits, at 15 locations along a north–south transect through its distribution. The average number of alleles per population decreased from the center to the northern periphery of the range (Figure 5A). However, levels of heterozygosity remained constant. While the effects of selection cannot be completely discounted, the fact that populations with the least genetic diversity are also the youngest supports the hypothesis that the observed central–marginal cline results from drift occurring during the colonization process. Several quantitative traits were also correlated with the time since populations were founded. Cwynar and MacDonald (1987) suggest that selection in peripheral populations on characters conferring greater dispersal ability, such as seed mass and wing loading, may have occurred (Figure 5B). Palynological approaches combined with isozyme studies may prove valuable for determining the colonization history of species for which there is a reliable pollen record.

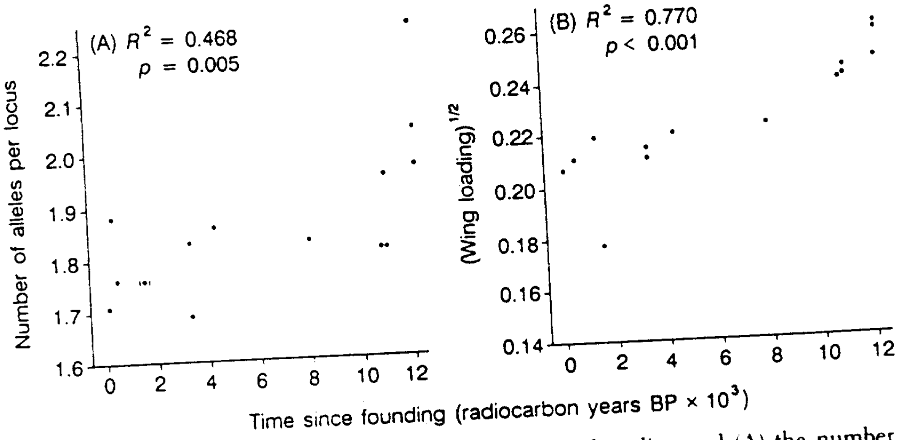

FIGURE 5. The relationship between the time since founding and (A) the number of alleles per locus and (B) the square root of wing loading, an index of seed dispersal, in populations of *Pinus contorta* ssp. *latifolia* from N.W. Canada. Values for time of founding were obtained from palynological records and radiocarbon dating (after Cwynar and MacDonald 1987).

MATING SYSTEMS AND COLONIZATION

Populations colonizing new territory are often confronted with novel environments, particularly after long-distance dispersal. In most cases, the environments are unsuitable and founding colonies are soon extirpated. Unfortunately, we know almost nothing about the causes of failure of most introductions so, for particular colonization models, it is difficult to evaluate the relative importance of factors such as chance, low genetic variation, or difficulties in finding mates. When individuals are preadapted to the new environment, colonizing populations may spread and are then often exposed to a set of conflicting demands. There may be strong selection pressures on the genetic system for phenotypic innovation. This requires mobilization of genetic variability and a flux of new genotypes. It may be achieved by genetic changes in the breeding system through increased levels of outcrossing. However, if, as is often the case during early stages of colonization, population sizes are small and plant density low, mating between individuals may be difficult. Under these circumstances, assured reproduction through self-fertilization or apomixis may be selectively advantageous. The particular solution to the conflicting demands of genetic experimentation on the one hand and assured reproduction on the other may depend largely on the position of a species on the colonization continuum, and the levels and organization of genetic variation in introduced populations.

Among plants characterized by frequent colonizing episodes and severe fluctuations in population size, uniparental reproductive systems tend to predominate (Baker 1955; Allard 1965; Brown and Marshall 1981). A variety of ecological and genetic factors influence the evolution of self-fertilization and apomixis (Jain 1976; Brown and Marshall 1981). Hence it is not clear for most colonizers whether outcrossing systems based on self-incompatibility or dioecism are maladaptive because they impose too severe a constraint on mating during colonization, or because they fail to suppress genotypic diversity and perpetuation of successful genotypes. Experimental studies on the effects of low density on mating success in outbreeding plants would be useful in assessing the role of reproductive assurance in colonizing plants, since it is often argued that, in general, seed set in plants is rarely pollen limited.

An example of the disruptive effects of frequent colonizing episodes and small population size on the maintenance of outcrossing occurs in tristylous *Eichhornia paniculata*. Populations of this species inhabit seasonal pools and ditches in arid N.E. Brazil where the size and life history of populations are largely determined by available moisture (Barrett 1985). Since the region has one of the most unpredictable rainfall regimes in the world, colonization–extinction cycles are a prominent feature of this annual or short-lived perennial aquatic. In N.E. Brazil, *E. paniculata* populations display a wide range of mating systems from large tristylous outcrossing populations that contain high levels of genetic diversity to semihomostylous selfing populations with low levels of genetic polymorphism (Glover and Barrett 1986, 1987). The evolution of selfing in *E. paniculata* is associated with colonization of ecologically and geographically marginal sites and involves changes in population structure from stylar trimorphism through dimorphism to monomorphism. The breakdown of tristyly is occurring in contemporary populations of *E. paniculata* in both N.E. Brazil and Jamaica, enabling examination of the microevolutionary processes responsible for the evolution of self-fertilization (Barrett et al., in press).

Dissolution of the tristylous genetic polymorphism in *E. paniculata* occurs in two stages involving the sequential loss of alleles at the two diallelic loci (*S*,*M*) that govern the inheritance of the polymorphism. Loss of the *S* allele and hence the S morph converts trimorphic populations to dimorphic populations. This process appears to occur by both random and deterministic processes. Stochastic fluctuations in population size and founder events are more likely to result in a loss of the *S* allele from populations than the three remaining alleles at the *S* and *M* loci (Heuch 1980; Barrett et al., in press). In addition, selection mediated by pollinators may also lead to a loss of the S morph from populations. Where specialist long-tongued pollinators are absent, such as in small or isolated populations, the seed set of the S morph suffers, in comparison with the L and M morphs, because of its concealed female reproductive organs. The decline in frequency of the S morph occurs more rapidly when mating patterns change from disassortative to random mating. Such an effect is more likely in small colonizing populations serviced by generalist pollinators (Barrett et al., in press).

Loss of the L morph from dimorphic populations of *E. paniculata* accompanies the spread of genes altering stamen position in the M morph. The genes that are recessive in nature modify the mating system, resulting in high levels of self-fertilization. Their origin in dimorphic populations may be associated with their low density and small size in comparison with trimorphic populations. Recessive genes are more likely to be exposed to selection through inbreeding in small populations than in large outcrossing populations. Once selfing variants arise, they appear to be favored over the L and unmodified M plants through reproductive assurance under conditions of low pollinator service (Barrett et al., in press). However, even where pollinator service is reliable, the automatic selection of the M morph, leading to the origin of floral monomorphism, can occur as a result of mating asymmetries between the morphs. Under this model of mating system evolution, a negative relationship should exist between the frequency of the L morph and of selfing variants of the M morph in dimorphic populations. Surveys of morph frequencies in N.E. Brazil provide evidence for this association (Figure 6). As in many of the cases discussed previously, however, samples collected over space rather than through time can at best give only indirect evidence of the dynamic processes responsible for evolutionary change within populations. This problem is particularly acute in colonizing species where populations are

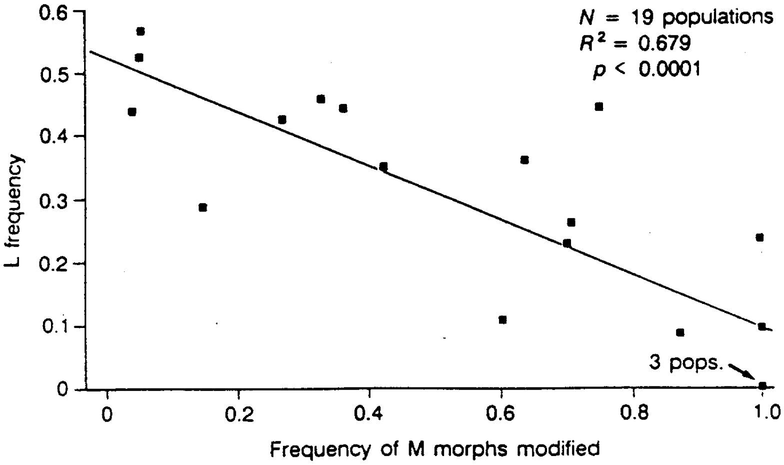

FIGURE 6. The relationship between the frequency of the long-styled morph (L) and the frequency of mid-styled (M) plants that were self-pollinating variants in 19 dimorphic and monomorphic populations of *Eichhornia paniculata* from N.E. Brazil (after Barrett et al., in press).

often short-lived and rarely at equilibrium. Accordingly, it is often difficult to study temporal changes in gene frequencies for any extended period of time and samples in space are likely to be subject to large variances due to genetic drift.

Selfing variants of *E. paniculata* predominate on the island of Jamaica. This is in accord with Baker's Law (Baker 1955, 1967) that establishment following long-distance dispersal favors self-compatible (and in this case autogamous) colonists. Once self-compatible plants have established on islands, however, it is of interest to examine whether their mating systems can evolve in response to new selective pressures. In *E. paniculata*, high levels of self-fertilization are typical of all Jamaican populations that we have examined. This is probably because they occur in highly disturbed, ruderal habitats subject to frequent local extinctions. However, maintenance of high levels of self-fertilization is not typical of all island colonists, particularly those that have undergone ecological diversification. A considerable literature has developed in recent years concerning mating system evolution and patterns of genetic differentiation of island plants (e.g., Lowry and Crawford 1983; Baker and Cox 1984; Helenurm and Ganders 1985; Barrett and Shore 1987; Witter and Carr 1988). While the necessity of self-compatibility and even autogamy for insular establishment is generally recognized, it appears that the autochthonous development of outcrossing mechanisms has occurred in many groups of island plants. This pattern is particularly associated with adaptive radiation into new habitats (Carlquist 1974; Ehrendorfer 1979; Baker and Cox 1984).

A particularly good example of mating system change in island colonists is evident in the genus *Bidens* on the Hawaiian islands (Sun and Ganders 1988). All 19 endemic species are thought to have originated from adaptive radiation of a single ancestral species following long-distance dispersal, probably from the American mainland. All taxa on Hawaii are interfertile but exhibit more morphological and ecological diversity than the remaining 200 species in the genus on five continents. Gynodioecy occurs in nine of the Hawaiian species but is unknown in non-Hawaiian taxa. Genetic and developmental studies indicate that the origin of male sterility is homologous in all Hawaiian *Bidens*, suggesting that gynodioecy most likely evolved during adaptive radiation of an initial colonizer after arrival in the oceanic islands (Sun 1987; Sun and Ganders 1987). The frequencies of females in gynodioecious populations of Hawaiian *Bidens* are positively correlated with the selfing rate of hermaphrodites suggesting that gynodioecy has evolved in response to increased levels of inbreeding in hermaphrodite populations (Sun and Ganders 1986). This is likely to have occurred in *Bidens*, since population sizes of many of the Hawaiian species are extremely small (Helenurm and Ganders 1985) favoring increased inbreeding. Other examples of the autochthonous development of outcrossing mechanisms in island plants include the evolution of dioecism in Hawaiian *Wikstroemia* (Mayer 1987) and the evolution of herkogamy in homostylous *Turnera ulmifolia* var *angustifolia* in the Caribbean (Barrett and Shore 1987).

CONCLUSIONS

In the two decades since the symposium volume on the Genetics of Colonizing Species (Baker and Stebbins 1965), much descriptive information has been amassed on the mating systems and population genetic structure of colonizing plants (reviewed by Brown and Burdon 1987; Barrett and Shore, in press). This has enabled some generalizations to be made concerning the genetic characteristics of species with well-developed colonizing abilities. While stressing that colonizing species are by no means a homogeneous group, Brown and Marshall (1981) identified several recurrent patterns in successful colonizers. Shared features often included fixed heterozygosity through polyploidy, propagation by self-fertilization or asexual means, genetically depauperate populations with respect to isozyme variation, high levels of multilocus association, marked population differentiation, and high levels of phenotypic plasticity. Knowledge of the shared attributes of successful colonizers provides useful information for studies of plant colonization, since it enables us to make educated guesses as to which genetic and ecological features of populations are likely to be important to colonizing success. However, beyond the generalities, there are the specific details of individual colonizing episodes and these are likely to vary with species and environment. Satisfactory explanations for the success or failure of colonizing episodes are most likely to be obtained from detailed observations of natural colonization events or from experimental studies of artificially established colonies.

It is remarkable that, considering the ease with which many plant colonizers can be grown, measured, crossed, and manipulated, so few experimental studies have been conducted on the genetic aspects of plant colonization. Agricultural weed populations in particular offer attractive opportunities for experimental studies since, in comparison with plants of natural communities, they inhabit relatively uniform environments in which the selection pressures are more easily identified and controlled (Barrett 1988). One of the few attempts to examine the genetic consequences of colonization by experimental means are the studies by S. K. Jain and colleagues at Davis. In a series of long-term experiments involving establishment of artificial colonies of known genetic composition in *Trifolium hirtum* and *Limnanthes* spp. they have examined the importance of mating systems and levels of genetic variation for colonizing success (Jain and Martins 1979; Martins and Jain 1979; Jain 1984). Because of the long-term nature of these experiments, few clear answers have been obtained to date, although there is some evidence that variable colonies of *T. hirtum* establish more successfully than less variable colonies. In the future, more widespread use of genetic markers in experimental demographic studies (Ritland, this volume) may enable workers to measure parameters required to test various colonization models and to determine the relative importance of stochastic versus deterministic processes to evolutionary change in colonizing populations.

While experimental studies that involve the founding and manipulation of colonies may enable us to test hypotheses concerned with colonization, there is still need for comparisons of the spatial and temporal patterns of genetic diversity between colonizing and noncolonizing populations within species. As mentioned above, little is known about genetic changes that occur within plant populations through time, and yet these are critical for understanding the effects of population size. In the few studies where investigators have followed genes, genotypes, or phenotypes through time, either within or between seasons, significant changes have been reported and important insights have been obtained into the stages in the life cycle where selection is most intense (Clegg et al. 1978; Gray 1987; Allard 1988). Of particular value in these types of studies would be to examine the patterns of variation exhibited by different classes of genetic variation (e.g., isozymes versus quantitative traits) following colonizing episodes that involve periods of small population size.

Our understanding of the genetic consequences of colonization in natural populations is largely based on the patterns of isozyme variability, as measured by electrophoresis. Yet, levels of isozyme variation may not accurately reflect variability elsewhere in the genome (Giles 1984). Isozymes are well suited to indexing levels of genetic variation and relationship among individuals and among populations (Brown and Burdon 1987). Many quantitative traits have direct effects on survival and reproductive success. Therefore, investigating the effects of colonization on such characters may provide more meaningful insights into the biological significance of colonization and its effect on evolutionary potential subsequent to colonization.

Theories of speciation through genetic bottlenecks are based on the assumption that the genetic architecture of species results from multilocus epistasis (Mayr 1970; Templeton 1980). In these models, speciation occurs through the breakdown and reassembly of this multilocus structure, by founder events. In contrast, models of the effects of small population size within species are often based on single loci with additive gene effects. Although few empirical studies have examined the effects of colonization on multilocus structure, there is some evidence that genetic correlations between quantitative traits are altered by small population size (Mitchell-Olds 1986), inbreeding (Rose 1984), and novel selective pressures (Silander 1984). However, it is not known how often colonizing ability is constrained by negative genetic correlations between fitness components. Future analysis of genetic correlations will likely shed light on the constraints to evolution after colonization as well as allowing a more realistic assessment of speciation models invoking founder effects (Carson and Templeton 1984; Barton and Charlesworth 1984).

From this review, it is clear that the scale and pattern of colonization have profound effects on the organization of genetic variation in plant populations. The genetic theory of finite populations has defined, mathematically, how small populations cause reductions in variation through drift. In addition, simple models of colonization and migration help us to predict the spatial patterns of genetic differentiation among populations. Despite these theoretical foundations, few studies of natural populations exist to evaluate their predictions and many of the critical parameters (e.g., migration rates, effective population sizes) are unmeasured. At best, we can examine the qualitative predictions of the models. Colonization is a process shared by all species. Yet it is unlikely that the genetic implications are the same for all. In order to understand the genetic consequences of migration and colonization for different species, we must acquire better ecological and genetical explanations for the factors regulating their distributions.

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