

Genetic Bottlenecks in Alien Plant Species

INFLUENCE OF MATING SYSTEMS AND INTRODUCTION DYNAMICS

Stephen J. Novak and Richard N. Mack

*Small populations are prone to alterations or reductions, or both, of genetic diversity through genetic drift, founder effects, and genetic bottlenecks. Such events can reduce a population's evolutionary potential and increase the risk of extinction. In this chapter, we use plant immigrants as a model system to examine the circumstances in which genetic bottlenecks do (and do not) occur and where in the hierarchical partitioning of genetic diversity such bottlenecks take place. We assess the amount and distribution of genetic diversity among plant species in their native (or donor) and introduced ranges. Two factors are important in influencing genetic bottlenecks for alien plants: their mating system, and the circumstances of their introduction. Among outcrossing alien species (e.g., *Echium plantagineum*, *Epipactis helleborine*, *Trifolium hirtum*), the likelihood of a genetic bottleneck can be low because even a few immigrants may represent much of the species' genetic variation. Similarly, multiple introductions can reduce the likelihood and severity of bottlenecks among selfing alien species (e.g., *Bromus tectorum* and *Avena barbata*). The loss of genetic diversity most often takes place across populations and not at the within-population level. Within-population genetic diversity can be higher in naturalized than in native populations if the naturalized populations are a by-product of genetic admixtures from multiple sources. As a result, multiple in-*

troductions of different genotypes from diverse donor ranges can trigger novel outcrossing events, lead to adaptive radiation, and even initiate an invasion. Accumulating evidence suggests that many plant invasions are sparked by multiple immigrations, a large founder population, or both. Consequently, the role of putative genetic bottlenecks in affecting the fate of alien species must be evaluated in the light of the species' immigration history.

Modern evolutionary biology (referred to as the modern evolutionary synthesis) merges population genetic theory with Darwinian natural selection (Fisher 1930; Wright 1931; Haldane 1932; Dobzhansky 1937; Huxley 1942; Mayr 1942; Simpson 1944; Stebbins 1950). One goal of this modern synthesis has been to understand the factors that influence or determine the type, amount, and distribution of genetic diversity within and among populations. Genetic diversity arises through mutation and recombination and can be altered across generations through natural selection, gene flow, and random genetic drift during periods when a population is small.

Small populations can experience an alteration or a reduction, or both, in genetic diversity through genetic drift, founder effects, and genetic bottlenecks (Lande 1988). As specific examples of genetic drift, founder effects are defined as genetic changes in populations that occur when few founders establish a new colony. In contrast, genetic bottlenecks are defined as reductions in genetic diversity in populations experiencing rapid, severe reductions in the number of individuals for one to a few generations (Lande 1988; Ridley 1993).

Reduction of genetic diversity during founder events and population bottlenecks is important because it can reduce the evolutionary potential of populations (Fisher 1930; Nei et al. 1975; Falconer and Mackay 1996) and increase the risk of extinction (Frankel and Soulé 1981; Lande 1988, 1993; Frankham 1995; Saccheri et al. 1998). Loss of heterozygosity may limit a population's ability to respond rapidly to selection after a bottleneck (Maruyama and Fuerst 1985), whereas reductions in allelic richness may limit a population's long-term capacity to respond to a changing environment (Allendorf 1986). When founders establish a colony or population bottlenecks occur, genetic drift becomes a major evolutionary force. Random genetic drift, in combination with demographic stochasticity (Shaffer 1981; Menges 1991, 1998), could exert potentially powerful effects within small populations.

Our goal here is to provide an understanding of the genetic and evolutionary consequences of population bottlenecks. Specifically, we examine the circumstances in which genetic bottlenecks do (and do not) occur and where in the hierarchical partitioning of genetic diversity bottlenecks take place. In this context, plant immigrants serve as excellent model systems because reductions in population size appear as recurring aspects of their population biology (Baker 1974). Despite the negative consequences associated with these reductions, plants do not always appear to be adversely affected. How often do such

species experience genetic bottlenecks? Do they experience multiple bottlenecks during their introduction into a new territory? What are the genetic and evolutionary consequences (e.g., for hybridization, for adaptive radiation) of these events?

In exploring these questions, we first describe the results of theoretical models that predict genetic changes and responses for populations undergoing reductions in size. Next, we describe the characteristics of alien plants that make them an appropriate model system for evaluating the genetic and evolutionary consequences of population bottlenecks. We then assess the amount and distribution of genetic diversity in an array of plant species in their native and introduced ranges. These assessments provide insights into the occurrence and severity of genetic bottlenecks in alien plants and highlight the role of two factors that influence genetic bottlenecks in these plants: their mating system and specific details associated with their introduction (i.e., single compared with multiple introductions and small compared with large founder populations). Finally, in counterpoint, we provide historical evidence that many alien plant species have arrived so frequently and in such numbers as to add a caveat to explanations of the genetics of these species in their new ranges as the products of bottlenecks.

Theoretical Models

Genetic diversity can be partitioned at three hierarchical levels: the DNA sequence, Mendelian traits, and quantitative genetic traits (Hartl and Clark 1997; Futuyma 1998). Genetic diversity at the DNA sequence level is not our focus here. Rather, we examine Mendelian and quantitative genetic trait variation. A Mendelian (or discrete) trait is determined by the alleles at a single gene, or locus. In contrast, several to many genes or loci may contribute to the expression of a quantitative (or continuous) trait (Hartl and Clark 1997).

Theory that assesses change(s) in the genetic diversity of populations following a founder event or genetic bottleneck is invaluable for making formal predictions that can then be evaluated in nature with alien plant species. These models generally emphasize several factors: the effective population size of the founder or bottlenecked population (N_e), the duration of the population bottleneck (i.e., the number of generations), the number of population bottlenecks, the level of inbreeding in the post-bottleneck population, and life history traits. All these parameters can vary independently in affecting genetic diversity. In addition, Mendelian and quantitative traits would not be expected to respond to founder effects and genetic bottlenecks in the same manner, based on differences in the number of loci involved in their expression (Lewontin 1974). The circumstances associated with reductions in population size vary among species (and even among populations of the same species); consequently, these models make predictions about general, rather than specific, outcomes.

Mendelian traits

Models predicting genetic change in single-locus traits in populations experiencing founder effects and genetic bottlenecks have usually employed two parameters: average heterozygosity per locus and the mean number of alleles per locus (also referred to as allelic richness). Wright (1931) predicted that populations experiencing a sudden reduction in size would experience a reduction in average heterozygosity per locus. More recent theoretical results indicate, however, that average heterozygosity per locus may not be adversely affected by a reduction in population size (Nei et al. 1975) and so may not be as useful as allelic richness in detecting a genetic bottleneck (Allendorf 1986).

During founder events and population bottlenecks, random sampling can alter the frequency of alleles at polymorphic loci among individuals and may result in the fixation of alleles. This process decreases allelic richness within populations and may contribute to increased genetic differentiation among populations (Brown and Marshall 1981; Barrett and Husband 1990). Alleles with the highest frequency (common alleles) have the highest probability of being sampled during a founder event or population bottleneck; rare alleles have the lowest probability of being sampled (Nei et al. 1975; Chakraborty and Nei 1977; Watterson 1984; Maruyama and Fuerst 1985). Thus, allelic richness in a population can decrease rapidly following a bottleneck through the elimination of rare alleles, unless by chance alone rare alleles are also sampled (Barrett and Husband 1990). Conversely, the frequency of heterozygotes following a bottleneck would be maintained through the union of gametes bearing the common alleles that persist in a population. The relationship between the size of a population bottleneck (N_e) and the number of alleles remaining in the population after one generation (Table 8.1) suggests that allelic richness can serve as a sensitive indicator of genetic bottlenecks (Nei et al. 1975; Allendorf 1986).

Studies of the genetic signature of population bottlenecks have contributed to conservation biology and the study of invasions (Leberg 2002). This work clearly indicates that allelic richness is more sensitive to the effects of short,

TABLE 8.1 *Relationship between effective population size (N_e) and the number of alleles remaining in a population after one generation*

N_e	Number of alleles ^a
1000	8.00
100	7.81
10	3.86
5	2.69
1	1.35

^aIn this hypothetical example, the population contained 8 alleles before a bottleneck, 7 of which were rare. For more details, see Meffe and Carroll 1997.

severe bottlenecks than is heterozygosity (Leberg 1992, 2002; Luikart et al. 1998b; Spencer et al. 2000). Approaches used to detect recent genetic bottlenecks include testing for the distortion of allele frequency distributions (Luikart et al. 1998a), assessing temporal changes in allele frequencies with repeated sampling (Waples 1989; Richards and Leberg 1996; Luikart et al. 1999), and the “variance test,” based on the standardized variance in allele frequencies (Luikart et al. 1998b). In turn, different techniques can assess genetic diversity following a bottleneck, including analyses of allozymes (Leberg 1992; Richards and Leberg 1996) and microsatellite DNA (Luikart et al. 1998b, 1999; Spencer et al. 2000). Regardless of the method used, employing loci with many alleles enhances the detection of bottlenecks. Moreover, loci with many alleles are particularly helpful for detecting cryptic genetic bottlenecks that occur in the absence of, or before the detection of, a demographic bottleneck (e.g., when there are few breeders of one sex due to a skewed sex ratio) (Luikart et al. 1998b). Recovery of both allelic richness and heterozygosity, but particularly heterozygosity, following a bottleneck will be greatest when population size increases rapidly (Nei et al. 1975). The specific circumstances associated with a founder (or colonization) event may also directly influence the amount and distribution of genetic diversity in subsequent populations.

Repeated recolonizations have genetic consequences that depend on the manner in which the emigrants are assembled and on the levels of gene flow among the resultant colonies (Slatkin 1977, 1985; Hamrick 1987; Barrett and Husband 1990; McCauley 1991). Slatkin’s (1977) “propagule pool” and “migrant pool” models are two extreme cases of colony formation. In the propagule pool model, all individuals in a colony are sampled from only one source population and thus exhibit little genetic diversity. In the migrant pool model, colonies exhibit greater genetic diversity (compared with the propagule pool model) because migrants are derived from multiple populations across the entire range of a species (Slatkin 1977; Wade and McCauley 1988; Whitlock and McCauley 1990). Under the migrant pool model, moderate to high levels of gene flow among populations would result in more genetic diversity within colonizing populations and less genetic differentiation among populations, whereas, under the propagule pool model, little gene flow would yield the opposite outcome. These two scenarios are simplifications of colonization and gene flow (Whitlock and McCauley 1990); they do, however, provide a framework for assessing the consequences of founder effects and genetic bottlenecks arising from small population size during colonization.

Quantitative genetic traits

The metric value of a quantitative (or phenotypic) trait is the result of genetic factors, environmental factors, and their interaction (Falconer and Mackay 1996). The genetic variation that contributes to the total phenotypic variation can be subdivided into additive genetic variance, dominance genetic variance, and interaction genetic variance. Additive genetic variance is determined by

the fixed value that each allele at each locus contributes to the expression of a quantitative trait; dominance genetic variance occurs when a dominant allele at a locus masks the contribution of a recessive allele. Epistasis, the interactions between genes, can influence the expression of quantitative traits. The variance that results from epistatic interactions is interaction genetic variance (Falconer and Mackay 1996).

The effects of founder events and population bottlenecks on the expression of quantitative traits depend on the underlying genetic architecture associated with each trait. For instance, if the genetic variation component of a quantitative trait is purely additive, a bottleneck will result in a decrease in additive genetic variance and decrease the total phenotypic variation for the quantitative trait (Wright 1931; Lande 1980; Carson and Templeton 1984). Theory also suggests that additive genetic variance may increase following a bottleneck. Models by Robertson (1952), Rose (1982), Willis and Orr (1993), Wang et al. (1998), and Lopez-Fanjul et al. (2002) show an increase in additive genetic variance following a bottleneck that is attributable to dominance genetic variance. Epistasis may also contribute to an increase in additive genetic variance (Goodnight 1987, 1988; Whitlock et al. 1993; Lopez-Fanjul et al. 1999, 2000, 2002), but these models of epistatic interactions are based on only two interacting loci. More recent models find that as the number of loci increases from two to three or four, additive genetic variance also increases (Naciri-Graven and Goudet 2003). This result is significant because the number of loci contributing to a quantitative trait associated with fitness is likely to be greater than two. Regardless of the underlying mechanism (dominance or epistasis), this process suggests that additive genetic variance, and therefore quantitative trait variation, can actually increase following a founder event or population bottleneck.

Increases in additive genetic variance following population bottlenecks have been demonstrated for morphometric and behavioral traits in the housefly (*Musca domestica*) (Bryant et al. 1986a,b; Bryant and Meffert 1996) and for components of fitness in *Drosophila melanogaster* (Lopez-Fanjul and Villaverde 1989; Garcia et al. 1994), *Tribolium castaneum* (Fernandez et al. 1995), *Bicyclus anynana* (Saccheri et al. 1996), and *Mus musculus* (Cheverud et al. 1999). Unfortunately, we know of no experimental studies of this type for plants (however, see Polans and Allard 1989), yet such studies are needed to determine whether the conversion of nonadditive variance to additive variance also occurs in plant populations experiencing population bottlenecks. Clearly, alien plant immigrations present ample opportunities and appropriate model systems for such investigations.

Quantitative traits are often ecologically important and can contribute directly to the components of fitness. A reduction in the additive genetic variance for a quantitative trait may lead to a reduction in fitness. In addition to reductions in genetic variation, founder effects and genetic bottlenecks can result in the fixation of deleterious alleles and contribute to inbreeding depression, thus further reducing the likelihood that a small population will persist. These issues

are examined here by assessing the response of alien plant species to these two categories of genetic drift that could arise with immigration. (For a discussion of these issues with animal invasions, see Wares et al., this volume.)

Alien Plant Species as Model Systems

Humans have become increasingly adept at transporting plants into new ranges, often far removed from the species' native range (Mack et al. 2000). Although plants are routinely dispersed accidentally (as contaminants in seed lots or as hitchhikers in or on cargo), a huge number of species have been introduced deliberately to new ranges (Bryant 1998). The fates of such deliberately introduced species vary widely (Ridley 1930). These species' seeds or other dispersal units are not only protected in transit from environmental hazards, but are also usually cultivated upon entry into the new range. Cultivation of deliberately introduced aliens is key to their survival and eventual persistence, as it effectively buffers the immigrants and their descendants from many forms of environmental stochasticity (Mack 2000). Equally important is the opportunity for repeated deliberate introductions of these alien species, regardless of the fate of the initial founders. Not surprisingly, then, the largest fraction of the naturalized flora in the United States and elsewhere has arisen from deliberately introduced species (Mack and Erneberg 2002, and see references therein). Cultivation and the likelihood of repeated introduction enhance the opportunity for a deliberately introduced alien species not only to become naturalized (i.e., persistent in a new range), but also to proliferate, spread, and cause damage (Mack 2000). At this point in its history in the new range, the species is termed an invader.

The characteristics that correlate with invasions vary substantially, and the epidemiology of biological invasions is not easily categorized. For example, naturalized plant species often exhibit uniparental reproduction, either self-pollination (selfing) or some form of asexual (or clonal) reproduction (Mulligan and Findlay 1970; Baker 1974; Price and Jain 1981). As a result, Baker (1967, 1974) suggested that uniparental reproduction would be an advantage during colonization. Furthermore, there may be selection for selfing during colonization, even in alien species that display an outcrossing mating system in their native range. Primarily selfing alien species typically exhibit low amounts of genetic diversity across and within populations and a high level of genetic differentiation among populations (Barrett and Richardson 1986; Barrett and Husband 1990; Hamrick and Godt 1990; Schoen and Brown 1991). Uniparental reproductive systems do, however, free a plant from dependence on the proximity of mates (Baker 1955), can confer reproductive success even under unfavorable environmental conditions (Stebbins 1957), and preserve adaptive gene complexes (Antonovics 1968; Brown 1979)—all potential advantages for an immigrant population. But many invasive species are not selfers. *Apera spica-venti* (Warwick et al. 1987), *Echium plantagineum* (Brown and Burden 1983; Bur-

don and Brown 1986), *Epipactis helleborine* (Squirrell et al. 2001), and *Trifolium hirtum* (Molina-Freaner and Jain 1992) all have become invasive, yet these species exhibit outcrossing mating systems.

The range of characteristics that invasive plant species exhibit probably reflects the range of characteristics exhibited by vascular plants in general. Variation in the invasion process and in the characteristics of invasive species has resulted in our inability to predict accurately which species will become invasive. As a result, a comprehensive list of the characteristics of invasive species remains elusive (National Research Council 2002) and may not be feasible (Williamson 1998).

Alien plants have served as model systems for studying the genetic and evolutionary consequences of dispersal and colonization (Baker and Stebbins 1965; Brown and Marshall 1981; Clegg and Brown 1983; Barrett and Husband 1990). In the remainder of this chapter, we discuss specific examples of genetic diversity in alien plant species. To this end, we attempt to provide a thorough assessment of the amount of genetic diversity reported for these species and how it is partitioned within and among populations. Such detail allows us to determine the presence of genetic bottlenecks and their extent (i.e., where in the hierarchical partitioning of genetic diversity they take place). Finally, this examination provides insights into the factors that influence the genetic and evolutionary consequences of founder events and population bottlenecks for plants in new ranges (Box 8.1).

Case Studies

Assessments of the genetic and evolutionary consequences of founder events and population bottlenecks for alien plants should include a comparison of populations from introduced and native ranges, thereby providing a relevant gauge of changes in genetic diversity among the immigrants (Barrett and Husband 1990; Novak et al. 1991, 1993; Novak and Mack 1993, 2001). Unfortunately, few studies include this comparison. Additionally, such assessments should document the size of the species' native and introduced ranges and its introduction history. Knowing the ranges for alien species can guide population sampling so that the breadth of the species' genetic diversity can be determined. Dates and locations of early collection sites and the circumstances of introduction (e.g., accidental or deliberate) provide evidence on which introduction scenarios can be based and by which the genetic consequences of founder effects and genetic bottlenecks can be evaluated (Bartlett et al. 2002).

The studies we review here collectively meet several criteria: (1) they include several plant families (to minimize taxonomic bias), (2) they involve plants introduced in widely separated parts of the world (to minimize geographic bias), (3) they include analysis of both native and introduced populations within the same design, (4) they employ species that vary from highly outcrossing to highly selfing, (5) they assess both the amount and the distribution

BOX 8.1 *Insights Alien Plants Yield about Genetic Bottlenecks*

1. For outcrossing alien plants, a few immigrants may represent a significant amount of the genetic variation in the species, reducing the likelihood of genetic bottlenecks following introduction.
2. Even for selfing alien plants, multiple introductions can reduce the expected loss of genetic variation with immigration, reducing the likelihood that genetic bottlenecks will occur.
3. Loss of genetic variation with introduction appears to occur most often across populations and not at the within-population level.
4. Within-population genetic diversity is sometimes higher in naturalized than in native populations, particularly when naturalized populations are formed as a by-product of genetic admixtures from multiple native populations.
5. Within-population genetic diversity may contribute directly to initiating an invasion and may also set the stage for evolutionary change.
6. Multiple introductions of different genotypes allow outcrossing events, even if rare, to give rise to adaptive radiations that have not occurred in the native range (e.g., *Avena barbata* in different climatic regimes in California).
7. Many plant invasions, including those of ruderals and deliberately introduced species, are sparked by multiple immigrations (which can span centuries) or large founder populations, or both.
8. Consequently, the results of putative bottleneck effects in an alien species must be evaluated in the light of the species' immigration history.
9. Both current theory and empiricism fail to adequately examine the level of genetic variation associated with failed (extirpated) populations in new ranges. As a result, the extent to which bottlenecks characterize the obvious alternative outcome to immigration is unknown.

of the species' genetic diversity, and (6) they provide at least some historical context for the species' entry and spread in the new range.

Outcrossing mating system

Despite the prediction that plants exhibiting uniparental reproduction, including a selfing mating system, would be at an advantage during colonization, a number of plants with an outcrossing mating system have become invasive (Brown and Burdon 1987, see also Rice and Sax, this volume). Here we compare the results of studies of genetic diversity in native and introduced populations of *Echium plantagineum* (Burdon and Brown 1986), *Epipactis helleborine* (Squirrell et al. 2001), and *Trifolium hirtum* (Molina-Freaner and Jain 1992). In general, these studies reveal that alien plant species with an outcrossing mating system do not always experience the reduction in genetic diversity antic-

ipated with founder events or population bottlenecks. If a reduction does occur, it is not severe. Additionally, these results suggest that the circumstances associated with the introduction of alien plant species can also mitigate the effects of population bottlenecks.

Echium plantagineum (Patterson's curse) is native to the western Mediterranean region, and it has become invasive in regions with Mediterranean-like climates. *Echium plantagineum* was initially introduced into Australia in the mid-nineteenth century both accidentally, as a contaminant of seed and livestock feed, and deliberately, as an ornamental (Piggin 1982). Burdon and Brown (1986) analyzed allozyme diversity in ten populations of *E. plantagineum*: two from the native European range and eight from the introduced range in Australia. Both across and within populations, the populations of *E. plantagineum* from Australia exhibit more alleles per locus and a higher percentage of polymorphic loci than European populations (Table 8.2). In addition, expected heterozygosity (i.e., the heterozygosity expected under Hardy-Weinberg equilibrium) levels are virtually the same among introduced and native populations (0.34 and 0.35, respectively); introduced populations possess a slightly higher value for observed heterozygosity than those sampled in the native range (0.32 and 0.29, respectively) (Table 8.2). Values for total allelic diversity (H_T) for introduced and native populations of *E. plantagineum* are similar, as is the manner in which genetic variation is partitioned within and among populations (Table 8.3). For both introduced and native populations, most of the allozyme diversity is partitioned within rather than among populations (G_{ST} values were 0.12 and 0.08, respectively).

Australian populations of *E. plantagineum* do not appear to exhibit a reduction in genetic diversity associated with long-distance dispersal and subsequent spread (e.g., in the number of alleles across and within populations). Burdon and Brown (1986) suggested that this lack of reduction in genetic diversity is due to high levels of outcrossing and genetic recombination in *E. plantagineum*. Additionally, introductions of this species probably occurred over many years (Piggin 1982; Burdon and Brown 1986). Furthermore, either the size of founder populations or the number of introductions, or both, must have been sufficiently large to prevent any reduction in genetic diversity with introduction. The reported population sample sizes of *E. plantagineum* are small, especially the number of native populations analyzed ($N = 2$) (Burdon and Brown 1986), and may bias the comparison of genetic diversity between native and introduced populations. Fortunately, sample sizes are larger in other studies assessing genetic diversity in primarily outcrossing alien plants.

The pattern of genetic diversity in *Epipactis helleborine* (broad-leaved helleborine) reflects less outcrossing than in *E. plantagineum*. *Epipactis helleborine* is a multiflowered, wasp-pollinated, self-compatible terrestrial orchid native to Europe and Asia that has become invasive in North America. It was first recorded near Syracuse, New York, in 1879 and soon thereafter near Toronto, Ontario (1890), and Montreal, Quebec (1892). The plant spread rapidly across North America (Squirrell et al. 2001).

TABLE 8.2 Amount of genetic diversity across and within native and introduced populations of alien plant species

Species/Region	N	A_a	P_a	A_w	P_w	H_o	H_e	Source
<i>Echium plantagineum</i>								
Europe (native)	2	2.86	86%	2.61	82%	0.29	0.35	Burdon and Brown 1986
Australia (alien)	8	3.56	100%	2.72	94%	0.32	0.34	Burdon and Brown 1986
<i>Epipactis helleborine</i>								
Europe (native)	35	2.33	78%	1.77	55%	-0.019*	0.230	Squirrel et al. 2001
Canada (alien)	12	2.22	78%	1.90	58%	0.068*	0.232	Squirrel et al. 2001
<i>Trifolium hirtum</i>								
Eurasia (native)	22	1.62	38%	1.07	5%	—	0.01	Molina-Freaner and Jain 1992
California (alien)	22	1.29	19%	1.18	14%	—	0.05	Molina-Freaner and Jain 1992
<i>Bromus tectorum</i>								
Eurasia (native)	51	1.64	52%	1.01	2%	0.0001	0.005	Novak and Mack 1993
North America (alien)	60	1.32	28%	1.05	5%	0.0000	0.012	Novak et al. 1991
Eastern North America (alien)	38	1.08	16%	1.01	1%	0.0000	0.002	Bartlett et al. 2002
Other ranges (alien)	19	1.28	24%	1.03	4%	0.0002	0.008	Novak and Mack 2001
<i>Avena barbata</i>								
Mediterranean (native)	51	2.40	100%	1.04	4%	—	—	Clegg and Allard 1972
California (alien)	16	2.20	100%	1.24	23%	—	—	Clegg and Allard 1972

Note: N refers to the number of populations sampled, A_a and P_a refer to the number of alleles per locus and the percentage of polymorphic loci across populations, A_w and P_w refer to the average number of alleles per locus and percentage of polymorphic loci within populations, and H_o and H_e refer to the observed and expected heterozygosity. An asterisk indicates values for the fixation index, which was reported in this study rather than observed heterozygosity.

Squirrel et al. (2001) used allozyme and chloroplast DNA markers to assess the amount and distribution of genetic diversity in native and European populations of *E. helleborine*. They analyzed the allozyme diversity in 35 European populations and 12 introduced populations from Ontario and Quebec. Allelic composition and the level of allelic diversity across native and introduced populations of *E. helleborine* are similar, although the value for the latter is slightly higher in the native range: European and Canadian populations average 2.33

TABLE 8.3 *Distribution of genetic diversity*

Species/Region	N	H_T	H_S	D_{ST}	G_{ST}	Source
<i>Echium plantagineum</i>						
Europe	2	0.381	0.351	0.030	0.080	Burdon and Brown 1986
Australia	8	0.388	0.341	0.047	0.120	Burdon and Brown 1986
<i>Epipactis helleborine</i>						
Europe	35	—	—	—	0.200*	Squirrel et al. 2001
Canada	12	—	—	—	0.090*	Squirrel et al. 2001
<i>Trifolium hirtum</i>						
Eurasia	22	0.082	0.014	0.068	0.824	Molina-Freaner and Jain 1992
California	22	0.078	0.055	0.024	0.300	Molina-Freaner and Jain 1992
<i>Bromus tectorum</i>						
Eurasia	51	0.087	0.009	0.077	0.754	Novak and Mack 1993
North America	60	0.115	0.046	0.069	0.478	Novak et al. 1991
Eastern North America	38	0.075	0.014	0.061	0.560	Bartlett et al. 2002
Other ranges	19	0.117	0.033	0.084	0.321	Novak and Mack 2001

Note: Distribution of genetic diversity using Nei's gene diversity statistics (Nei 1977), where H_T is the total gene diversity, H_S is the portion of the total diversity distributed within populations, D_{ST} is the portion of the total diversity distributed among populations, and G_{ST} is the proportion of the total diversity distributed among populations. An asterisk indicates values for F_{ST} , which was reported in this study rather than G_{ST} .

and 2.22 alleles per locus, respectively. The percentage of polymorphic loci (78%) is the same across both native and introduced populations (see Table 8.2). Within populations, this pattern is reversed, as plants from Canada have more alleles (1.90 vs. 1.77), slightly more polymorphic loci (58% vs. 55%), and a slightly higher value of expected heterozygosity (0.232 vs. 0.230) than plants from Europe. Observed heterozygosity was not reported, but the fixation index (f) for each population was provided (see Table 8.2). Fixation index values for both native and introduced populations are not significantly different from zero and indicate random mating in both regions. The level of genetic differentiation among introduced populations of *E. helleborine* is much less ($F_{ST} = 0.090$) than the level reported for native populations ($F_{ST} = 0.200$) (see Table 8.3).

Twenty-nine populations (17 European and 12 Canadian populations) of *E. helleborine* were analyzed for their chloroplast DNA haplotypes through the presence (or absence) of a 10-bp duplication in the *trnL* intron. Only 4 of 17 populations from Europe exhibited this polymorphism, whereas 11 of 12 populations from North America were polymorphic. Similar to the results reported for the allozyme data, values of F_{ST} for chloroplast DNA polymorphism indicate less genetic differentiation among introduced populations than among those from the native range ($F_{ST} = 0.367$ and 0.506, respectively).

Thus, allozyme and chloroplast DNA genetic markers both reveal that *E. helleborine* has apparently not undergone a reduction in genetic diversity

upon introduction into North America (Squirrell et al. 2001). In fact, the average level of genetic diversity within introduced populations is higher, and the level of genetic differentiation is lower, than in native populations. These data did not allow Squirrell et al. (2001) to determine whether single or multiple introductions had occurred, but they do suggest that the introduction was sufficiently large to include much of the genetic diversity in the native range. Given the outcrossing mating system of *E. helleborine*, its level of heterozygosity, and its genetic structure, a founder population with as few as five individuals would have been sufficient to maintain this genetic diversity, provided that large population sizes were rapidly restored following introduction (Squirrell et al. 2001).

Unlike *E. plantagineum* and *E. helleborine*, *Trifolium hirtum* (rose clover) does appear to have experienced a reduction in genetic diversity upon its introduction into California. However, this reduction occurs at the among-population level and not within introduced populations. *Trifolium hirtum* is an annual legume native to the Mediterranean region. It was deliberately introduced into California in 1944 as livestock forage (Love and Sumner 1952) by seeds collected in 1936 in the Adana Province, Turkey. By the late 1960s, *T. hirtum* had invaded highway roadside habitats (Jain and Martins 1979).

Genetic and demographic studies assessed the clover's spread (Jain and Martins 1979; Martins and Jain 1979, 1980), and more recently Molina-Freaner and Jain (1992) compared allozyme diversity in native and introduced populations of *T. hirtum*. Twenty-two populations from Eurasia and the same number from California were included; 14 of the Eurasian populations were collected in Turkey. Across populations, Eurasian populations exhibit higher levels of genetic diversity than Californian populations (1.62 and 1.29 alleles per locus, and 38% and 19% polymorphic loci, respectively) (see Table 8.2). In contrast, genetic diversity at the within-population level is, on average, higher for Californian populations (1.18 alleles per locus and 14% polymorphic loci) than that reported within Eurasian populations (1.07 alleles per locus and 5% polymorphic loci). In addition, expected heterozygosity for introduced populations is five times greater than the value for native populations. Values for total allelic diversity (H_T) for introduced and native populations of *T. hirtum* are similar; however, the manner in which genetic variation is partitioned within and among populations is very different (see Table 8.3). Genetic differentiation among native populations is nearly three times greater than that among introduced populations (G_{ST} values were 0.824 and 0.300, respectively). Thus, *T. hirtum* appears to have experienced a reduction in genetic diversity across introduced populations in California, but within populations the Californian plants exhibit higher levels of genetic diversity, and have much less genetic structure, than populations in Eurasia.

Molina-Freaner and Jain (1992) contend that these results are a product of the outcrossing mating system of *T. hirtum*; that is, that even a few founding individuals would possess a high proportion of the species' genetic diversity. Alternatively, given that the species was deliberately introduced for forage, the

founding population may have been large and may even have been composed of admixtures of genotypes derived from multiple source populations in Turkey. This introduction scenario is similar to the migrant pool model described by Slatkin (1977). Moreover, Turkey includes the most polymorphic portion of the clover's native range: 72% of all polymorphic loci detected across native populations were found in the Turkish samples. Differences in the distribution of genetic diversity between European and Californian populations of *T. hirtum* may also be due to a shift toward a mixed mating system with colonization of roadside habitats in California. This shift could have resulted in higher outcrossing rates and an intermixing of genetic diversity (Molina-Freaner and Jain 1992).

Assessments of the amount and distribution of genetic diversity in other primarily outcrossing alien plant species are generally in keeping with the results for these species (e.g., Warwick et al. 1987; Balfourier and Charmet 1994; Meekins et al. 2001); that is, evidence for genetic bottlenecks is not apparent. Genetic bottlenecks were observed, however, in a comparison of continental and island populations of *Turnera ulmifolia*, a herbaceous perennial native to the New World tropics, including the Caribbean region (Barrett and Shore 1989; Barrett and Husband 1990). The species' continental and island populations are both self-incompatible and outcrossing. Despite its outcrossing mating system, *T. ulmifolia* exhibits a marked reduction in genetic diversity within Caribbean populations. For example, the value for the percentage of polymorphic loci across Caribbean populations (20%) is less than half the value (46%) in South American populations (Barrett and Shore 1989; Barrett and Husband 1990). Additionally, average genetic diversity within South American populations is threefold greater than genetic diversity within island populations (0.12 and 0.04, respectively). Colonization of islands can impose demographic constraints on populations that often lead to genetic bottlenecks (Barrett and Husband 1990). However, evidence from *Rubus alceifolius* suggests that these demographic constraints can be overcome by multiple introductions.

Rubus alceifolius (blackberry) is native to Southeast Asia and has been introduced onto Madagascar and other Indian Ocean islands, including Mayotte, Réunion Island, and Mauritius. Amsellem et al. (2000) determined the genetic diversity in native and introduced populations of *R. alceifolius* using amplified fragment length polymorphic (AFLP) markers. Genetic diversity within native populations is high, while the diversity in Madagascar is somewhat lower. In contrast, populations from Mayotte, Réunion, and Mauritius are each composed of a single genotype, all of which are similar to genotypes on Madagascar. Amsellem et al. (2000) proffer that *R. alceifolius* was initially introduced onto Madagascar multiple times, and then spread to the other Indian Ocean islands from Madagascar (rather than directly from the native range). Thus, the high level of diversity within Madagascan populations probably stems from multiple introductions, whereas subsequent founder events resulted in a reduction in genetic diversity on each of the other islands.

Another consequence of the introduction of *R. alceifolius* onto Madagascar and Réunion Island is an apparent shift from sexual reproduction in its native range to predominantly asexual reproduction (apomixis) (Amsellem et al. 2001). Although plant species exhibiting apomixis are typically expected to possess extremely low genetic diversity, recent findings reveal that such species vary widely in the amount and distribution of diversity within and among populations (Ellstrand and Roose 1987; Hamrick and Godt 1990). In fact, occasional sexual reproduction (especially outcrossing) in a species that reproduces predominantly through asexual means may generate unique, highly adapted, or aggressive genotypes that are subsequently conserved through apomixis (Novak and Mack 2000). Amsellem et al. (2001) suggest that just such a mechanism may have contributed to the invasion of *R. alceifolius* on Madagascar and the other Indian Ocean islands.

These studies collectively provide insight into the fates of alien plants with an outcrossing mating system: such species may undergo little or no reduction in genetic diversity with founder events or population bottlenecks. Furthermore, if a genetic bottleneck does occur in these alien plants, it is most likely to occur at the across-population level (as seen with *T. hirtum*, and to a lesser degree with *E. helleborine*). These conclusions stem directly from an additional insight provided by these studies: several of the outcrossing species described above were deliberately transported to their new range(s), and such deliberate introductions often involve multiple introductions and founder populations with many individuals. This observation runs contrary to conventional wisdom and suggests that multiple introductions may be more common among plants than previously thought. Moreover, in at least one instance (*T. hirtum*), immigrants appear to have been drawn from multiple source populations, suggesting that these results are in keeping with the migrant pool model of Slatkin (1977). These alien plant species possess an outcrossing mating system in their native range, so in most cases, the majority of their genetic diversity is partitioned within rather than across populations. These studies also reveal that even a small number of founding individuals or founder events will probably sample much of an outcrossing species' genetic diversity (Warwick 1990). Thus, a reduction in genetic diversity with founder events or population bottlenecks is not a certainty for naturalized species with an outcrossing mating system. Any reduction depends on the degree to which genetic diversity is partitioned within native range populations and on the specific details associated with a species' introduction (the number of introduction or colonization events and the size of the founder populations).

Selfing mating system

We next examine the influence of primarily selfing mating systems on the amount and distribution of genetic diversity following immigration. Results from these studies also illustrate the post-immigration genetic consequences of multiple introductions.

Bromus tectorum (cheatgrass) is a predominantly selfing annual grass with wide distribution in temperate grasslands (Upadhyaya et al. 1986). Its native range includes most of Europe, the northern rim of Africa, and southwestern Asia (Pierson and Mack 1990). The grass has been accidentally introduced into many temperate environments worldwide (Upadhyaya et al. 1986; Stace 1997).

The amount and distribution of genetic diversity within and among native and introduced populations of *B. tectorum* have been compared, and the introduction and spread of the plant in North America and around the world evaluated, using genetic markers. The dynamics of introduction and spread have been explored by combining historical information with the detection of the same geographically restricted multilocus genotypes in populations from both the native and introduced ranges. This protocol has allowed assessment of the genetic and evolutionary consequences of the founder effects and genetic bottlenecks associated with the grass's introduction and invasion.

In total, 51 Eurasian populations, 94 North American populations, and 19 populations from other naturalized ranges of this species (Canary Islands, Argentina, Chile, Hawaii, and New Zealand) have been analyzed (Novak et al. 1991, 1993; Novak and Mack 1993, 2001; Bartlett et al. 2002). Based on multilocus genotype distributions, source populations for the introduction of *B. tectorum* into North America and its other naturalized ranges appear to have been drawn exclusively from populations in either central Europe or the western Mediterranean region. For instance, the multilocus genotype characterized by the allele *Got-3c* has been detected in only two central European populations (Bayreuth, Germany, and Libochovice, Czech Republic), yet this genotype is now widespread throughout the grass's range in western North America, Argentina, Hawaii, and New Zealand. In contrast, the *Pgi-2b* multilocus genotype is the most widespread of any genotype detected so far in the native range (e.g., France, Spain, and Morocco); it is, however, restricted to the western Mediterranean region. This genotype has been detected in widely separated populations across the introduced range of *B. tectorum*, including three from Nevada, one from California (Truckee, CA), four from the Canary Islands, and two from Chile, confirming that emigrants of *B. tectorum* departed from at least two European regions.

Genetic markers also prove their efficiency in determining the dynamics of introduction and spread. The pattern of genetic markers for *B. tectorum* in its introduced range supports historical evidence that its invasion in western North America stems from multiple introductions (Novak et al. 1993; Novak and Mack 1993, 2001). Diagnostic genetic markers were detected for populations in six locales in western North America, indicating a minimum of six independent founder events. Conversely, only two genetic markers were detected among the 38 eastern North American populations of *B. tectorum* that have been analyzed; 33 of these 38 populations exhibit the most common genotype (Bartlett et al. 2002). Thus, populations from eastern North America do not appear to have had the same history of introductions as seen in the West. Furthermore, the detection of more diagnostic genetic markers in western

North America suggests that its populations were derived directly via introductions from the native range (Novak and Mack 2001). However, the distribution of one multilocus genotype (*Pgm-1a* and *Pgm-2a*) in several populations across the United States suggests that the descendants of some plants introduced into eastern North America were subsequently transported westward.

Multiple introductions may have also occurred in the other naturalized ranges of *B. tectorum*. For instance, the occurrence of different marker genotypes in Argentinean (*Pgm-1a* and *Pgm-2a*) and in Chilean (*Pgi-2b*) populations suggests that separate introductions occurred in each country (Novak and Mack 2001). Likewise, the distribution of multilocus genotypes in populations in the Canary Islands suggests that multiple introductions from populations in Europe and North Africa led to the grass's establishment there (Novak and Mack 2001). Despite cheatgrass having been introduced almost exclusively by accident, multiple introductions occurred repeatedly.

Populations of *B. tectorum* from Eurasia exhibit more alleles and polymorphic loci than populations from any of the species' introduced ranges (see Table 8.2). *Bromus tectorum* has apparently undergone a reduction in genetic diversity with introduction, but this reduction has not been detected within all introduced populations. Based on genetic markers, populations of *B. tectorum* in western North America and other naturalized ranges appear to have been established through a more complicated introduction history than has been the case for populations in eastern North America. On average, populations from western North America and other naturalized ranges contain more alleles and polymorphic loci than populations from eastern North America and even more than native Eurasian populations (see Table 8.2). *Bromus tectorum* is reportedly a highly selfing species (Upadhyaya et al. 1986). Heterozygosity levels in this grass are indeed exceedingly low: only a handful of heterozygotes have been detected in the plant's native and introduced ranges (see Table 8.2). As with alien plants with an outcrossing mating system, the genetic signature of founder effects and population bottlenecks may vary among the hierarchical levels at which genetic variation can be partitioned.

The loss of genetic diversity across introduced populations of *B. tectorum* is, in part, a consequence of the manner in which genetic diversity is partitioned within and across its native populations. Most of the genetic diversity in its native range is partitioned across rather than within populations ($G_{ST} = 0.754$) (see Table 8.3). Thus, during the "random sampling" of individuals upon emigration, many alleles or genotypes were not represented, especially rare ones. This situation is exacerbated for those selfing species for which the emigrants are drawn from only a small portion of an enormous native range. In the case of *B. tectorum*, levels of genetic differentiation across populations are lower in the introduced ranges than in the native range (see Table 8.3). Even the few introductions that occurred in eastern North America reduced the level of genetic differentiation among populations compared with the level in the native range.

Identification of source populations for the introduction of *B. tectorum* worldwide reveals that immigrants were drawn from at least two regions in the

native range: Central Europe and the western Mediterranean. Similarly, the geographic distribution of marker genotypes suggests that multiple introductions have occurred across much of the species' naturalized range. Furthermore, the genetic diversity within introduced populations of *B. tectorum* is, on average, higher, and the level of genetic differentiation among introduced populations lower, than in native populations. As in our examination of alien plants with an outcrossing mating system, these findings are consistent with the migrant pool model of Slatkin (1977). These findings for *B. tectorum* are revealing: multiple introductions, even in a highly selfing plant species, appear to partially offset the reduction in genetic diversity associated with founder events and population bottlenecks.

Avena barbata (slender wild oat), which is naturalized in California, presents an alternative genetic outcome of immigration. *Avena barbata* is an annual, predominantly selfing, diploidized tetraploid grass (i.e., a tetraploid plant with gene expression similar to that of a diploid) whose native range extends from the Mediterranean basin to southwestern Asia and eastward to Nepal (Marshall and Allard 1970; Allard et al. 1993). In Eurasia, *A. barbata* persists in a wide range of environments (Allard et al. 1993). The grass has become a successful colonizer of Mediterranean-like climates worldwide and was accidentally introduced to California from the western Mediterranean basin in a large number of independent introductions extending over more than a century (Kahler et al. 1980). *Avena barbata* spread rapidly upon introduction and is now a major component of grasslands and grass-oak savanna habitats (Marshall and Allard 1970; Clegg and Allard 1972).

Clegg and Allard (1972) described the allozyme diversity in 16 Californian populations of *A. barbata*. Of these 16 populations, 9 were sampled from the Central Valley and adjacent foothills (region I), and 7 were sampled from the intermontane regions of the coastal strip and higher-elevation foothills of the Sierra Nevada (region II). The diversity of *A. barbata* in California was compared with that of 51 populations in 9 areas in the Mediterranean region. Only a portion of the data can be summarized in the format we use above. However, one goal of the investigators was to compare the allelic compositions of native and introduced populations. Consequently, their data do reveal genetic consequences of this species' introduction into California.

The extent of genetic diversity across native and introduced populations of *A. barbata* is similar. The number of alleles per locus and the percentage of polymorphic loci across populations are 2.40 and 100% in native populations and 2.20 and 100% in introduced populations for five allozyme loci (see Table 8.2). In contrast, genetic diversity within Californian populations (1.24 alleles per locus and 23% polymorphic loci) is, on average, higher than the values within the Mediterranean populations (1.04 alleles per locus and 4% polymorphic loci) (see Table 8.2). Thus, Californian populations do not appear to have experienced a severe genetic bottleneck, either at across-population or within-population levels (Clegg and Allard 1972). Similar results were reported for populations of *A. barbata* from the Mediterranean region and central Cali-

fornia (see Singh and Jain 1971). This close correspondence in the amount of genetic diversity and in allelic composition between populations from the western Mediterranean region and California is probably a result of multiple introductions from Spain.

A more comprehensive analysis of Spanish populations of *A. barbata* subsequently compared the allelic and genotypic composition of native and introduced gene pools (Garcia et al. 1989). Plants from 42 populations across southern and western Spain were analyzed for genetic diversity at 15 loci. Once again, Spanish and Californian gene pools were found to be similar. The similarity is especially high for populations sampled from southwestern Spain, a likely point of embarkation for ships to the New World, including California (Garcia et al. 1989). However, the level of allelic diversity in Spain is lower than the level observed elsewhere in the native range, such as Israel (Kahler et al. 1980). Similar to many other species in Europe with cryptogenic origin (Kornas 1990), *A. barbata* may have evolved in the eastern Mediterranean region and southwestern Asia and subsequently spread across the Mediterranean basin. As a consequence, neither Spanish nor Californian populations are likely to reflect all the genetic diversity of this species across its native range (Kahler et al. 1980; Garcia et al. 1989).

The multilocus structure of Californian populations of *A. barbata* is quite different from that of populations in the native range, despite the similarity of allelic composition in native and introduced populations (Clegg and Allard 1972; Kahler et al. 1980; Garcia et al. 1989; Perez de la Vega 1991). For instance, 80% of populations in region I of California are fixed or nearly fixed for the "xeric" multilocus genotype, while 10% are fixed or nearly fixed for the "mesic" genotype (found in region II); few populations are polymorphic. Spanish multilocus genotypes are intermediate between the xeric and mesic Californian genotypes (Garcia et al. 1989; Perez de la Vega 1991). As a result, overall genetic diversity is generally higher within Spanish than within Californian populations, and the genetic diversity of Californian populations is distributed mainly among populations—the opposite of the patterns seen in the species' native and introduced populations discussed thus far.

Such a pattern of genetic diversity could be attributed to founder effects or genetic bottlenecks associated with introduction. Alternatively, these patterns could result from natural selection for locally adapted genotypes within xeric and mesic habitats (Clegg and Allard 1972)—selection that could spark an "adaptive radiation" in the introduced range. The implication of this scenario is potentially far-reaching: it suggests that a combination of sufficient genetic variation in introduced populations together with novel selection regimes can set the stage for adaptive evolution, as suggested by Ellstrand and Schierenbeck (2000). Invasions, then, need not proceed only through the introduction of preadapted genotypes (*sensu* Futuyma 1998); the genetic raw material originally introduced can be reorganized into more invasive genotypes. Consequently, a species' performance in other ranges may not serve as the sole indicator of its invasiveness, if novel genetic recombination can occur anywhere

in a new range (National Research Council 2002). How these events may relate to the potential for speciation is unresolved, but they do appear to set the stage for the diversification of genotypes between native and introduced populations. These issues can be resolved through detailed genetic analysis of both native and introduced populations, followed by comparisons of the performance of these novel genotypes in their new ranges.

A variety of other genetic diversity patterns are observed in predominately selfing plant invaders, particularly when (in contrast to *B. tectorum* and *A. barbata*) introduced populations are a consequence of fewer introduction events. For example, *Capsella bursa-pastoris* (shepherd's purse) has experienced an overall reduction in genetic diversity in its introduced range, presumably as a consequence of few introduction events (Neuffer and Hurka 1999). In other cases, some highly selfing alien species that occupy large naturalized ranges are apparently represented by only one or a few genotypes: *Xanthium strumarium* (Moran and Marshall 1978), *Emex spinosa* (Marshall and Weiss 1982), and *Emex australis* (Panetta 1990) in Australia and *Sorghum halepense* (Warwick et al. 1984) in Canada. Similar findings have been reported for alien species that reproduce clonally, such as the highly apomictic *Chondrilla juncea* (Chaboudez 1994). In these cases, naturalization stems from few introductions. As a consequence, genetic diversity is sharply reduced in the introduced range.

Do Deliberate Introductions Mitigate Genetic Drift?

We opened this chapter with questions about the consequences of founder events and genetic bottlenecks for alien plants as well as the larger question of the extent to which immigrant plants face these potentially severe constraints. While the examples cited above provide a mixed answer, the general conclusion would be "yes, sometimes plant immigrants do experience a reduction in genetic variation." Left largely unaddressed, however, is whether most other naturalized and invasive species stem from large, not small, immigrant populations and from multiple (even many) introductions, not a single introduction. Unlike other large taxonomic groups of immigrants, such as insects (Simberloff 1989), plants may not routinely experience these hazards because opportunities for founder events and population bottlenecks have been rendered moot by immigrant plants' prevalence as seed contaminants in imported seeds and as deliberate commodities in international trade. As a consequence, founder and bottleneck events may be infrequent. Hundreds, and possibly thousands, of plant species have importation histories that exceed 100 years (Rehder 1940; Mack 1991); that is, they were not simply imported once, nor were they always imported in small numbers (Box 8.2; Mack 1991). Furthermore, as the international exchange in all manner of horticultural species has grown since 1800 (McCracken 1997), the potential donor ranges have also grown, providing an increase in the opportunity for selection in another naturalized range before entry into the United States. Future comprehensive examinations of the genetic

BOX 8.2 *A History of Seed Contamination in the United States*

Long after U.S. agriculture became based largely on crops of foreign origin, much, if not all, of the seed sown for these crops was annually imported from Europe. Hicks (1895) provided a detailed account of the total dependence on imported seeds for crops that included alfalfa, beet, broccoli, cress, endive, radish, spinach, and turnip, as well as many forage grasses (e.g., *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Festuca ovina*), and substantial importation for many others (cabbage, carrot, leek, onion, pepper, parsley). Such massive and prolonged importation of these species created opportunities for two categories of naturalized species. Some of these imports have become naturalized themselves (e.g., *A. odoratum*, *F. ovina*), but more likely their importation enormously facilitated the entry and cultivation of other alien species that were seed contaminants.

Extraneous, potentially invasive seeds were a routine component of these seed imports. The inclusion of the seeds of ruderal or otherwise unwanted species would have been a common by-product of harvesting seed crops before the development of effective seed sieving procedures in the late nineteenth century. Consequently, many of the ruderal species now naturalized in the United States had probably arrived there repeatedly before 1800

(Mack 2003). But the genetic diversity of these species' gene pools in the U.S. would have been bolstered by the huge volume and extent of European seed sources that entered the trade post-1865. Unfortunately, the U.S. government placed few, if any, safeguards on seed purity in that era, and some unscrupulous European seed merchants took full advantage of this regulatory gap by shipping extensively contaminated seeds to the U.S., even while their own nations were mandating the purity of seeds for domestic trade (Hicks 1895).

Newly created seed testing laboratories in the United States chronicled the extent and diversity of seed contamination in the late nineteenth century. In one extreme case, 90% of the seed sold as clover was extraneous and nonindigenous (Hicks 1895). Moreover, the sources of imported seeds spanned Western Europe, thereby ensuring that a wide breadth of the genotypic diversity among European ruderals was annually sampled and transported to the U.S. For some of the most widespread naturalized species in the U.S. (e.g., *Capsella bursa-pastoris*, *Nepeta cataria*, *Plantago lanceolata*, *Rumex acetosella*, *Rumex crispus*, *Verbascum thapsus*), any constraints imposed by genetic drift would have been eliminated via these massive immigrations (Mack and Erneberg 2002).

diversity and origins of naturalized and invasive horticultural species in the United States may well reveal that any latent constraints arising from founder effects and population bottlenecks are the exception, not the rule.

Conclusions

An abundance of theory predicts reductions in genetic diversity following founder events or population bottlenecks (e.g., Wright 1931; Nei et al. 1975; Chakraborty and Nei 1977; Watterson 1984; Maruyama and Fuerst 1985; Lande

1993). Although such reductions have indeed occurred among some alien plants, the extent of reduction and its location can vary substantially within the hierarchical partitioning of genetic diversity. Additionally, the mating system and history of introduction appear to influence the likelihood of any reduction in diversity (see Box 8.1). For instance, outcrossing species partition most of their diversity within rather than among populations. Consequently, only a few immigrants could represent a significant amount of the genetic diversity of native populations. With multiple introductions, the probability of a reduction in genetic diversity among alien outcrossing species appears to decline further.

Genetic diversity in highly selfing (and primarily clonal) plant species is mostly partitioned among rather than within populations, and a few immigrants would probably incorporate little of the diversity in the species' native range. However, multiple introductions of even selfing aliens may include much genetic diversity, especially if individuals are drawn from across a species' native range. This scenario closely resembles the "migrant pool" model of Slatkin (1977). As reflected in a growing body of examples for both outcrossing and selfing alien plant species, multiple introductions appear to be the rule rather than the exception (Novak et al. 1993; Mack and Erneberg 2002). Either as deliberate introductions or as seed contaminants, large numbers of propagules can be drawn repeatedly from much of the donor range (Mack and Erneberg 2002). Consequently, the prevalence of genetic bottlenecks following a founder event or a population bottleneck, at least for plants (for data on animals see Wares et al., this volume), may be much less than once envisioned and should be evaluated in light of each species' immigration history.

When genetic diversity is lost upon introduction, the loss most often occurs across populations and not at the within-population level. This observation is important because the maintenance of genetic diversity within populations may directly foster an invasion and also sets the stage for evolutionary change. In fact, multiple introductions can result in the establishment of populations that contain admixtures of genotypes from the native range; these naturalized populations may contain far greater within-population diversity than occurs in the native range. Furthermore, outcrossing events in the naturalized range, even if rare, would lead to recombination and the creation of novel genotypes. The emergence of such genotypes would provide opportunities for adaptive radiation that could not occur in the native range (as seen with *A. barbata* in the different climatic regimes of California).

The discrepancy between the predictions of theory and the empirical evidence needs to be resolved. Future investigations should include direct side-by-side comparisons of the performance of native and introduced populations, wide sampling across a species' native and introduced range, and identification of as many genetic markers as possible, and should incorporate historical information for evaluation of introduction dynamics (Novak and Mack 2001; Bartlett et al. 2002). Based on recent models for detecting genetic bottlenecks (Luikart et al. 1998b, 1999), highly polymorphic genetic markers should be employed in which individual alleles (and heterozygous individuals) can

be identified. Microsatellite DNA analysis is often well suited for this task (Parker et al. 1998; Sunnucks 2000). Investigations that assess the effects of population bottlenecks on the additive genetic variance in alien plants are especially needed, in contrast to the bulk of investigations that have assessed the effects of genetic bottlenecks with single-locus genetic markers.

Many aspects of the population biology of plants, especially the production of many progeny, make plants particularly suitable as models in quantitative genetics. Identifying the underlying genetic controls of ecologically important traits will be key; these identifications will contribute substantially to understanding the consequences of introduction events and to predicting invasive potential. Finally, we need to apply the same diligence to deciphering explanations for plant introductions that fail that we now do to those that persist (Harper 1982): for example, do failures stem more from genetic, demographic, or environmental limitations, or from some combination of these factors? The study of alien species has already fulfilled much of their promise to serve as natural experiments in evolution (Waddington 1965) and population biology (Mack 1985). Much more has yet to be discovered.

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