ISOZYMES IN PLANT BIOLOGY

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CHAPTER 5

Isozyme Variation in Colonizing Plants

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The colonization of new environments is an integral feature of the biology of most plant species. However, a relatively small number of plants, commonly referred to as colonizers, weeds, or invading species, possess attributes that enable them to establish populations continuously in areas or habitats that they have not previously occupied. In comparison with other plant life forms, and considering their number, colonizing species have received disproportionate attention from biologists. This interest is probably because some are of economic importance in agriculture and, because, from an evolutionary perspective, others provide excellent experimental systems for microevolutionary studies. The rapid life cycles of many colonizers and their ability to invade diverse environments, often in a short period, provide population biologists with a series of evolutionary experiments that are not available in most other plant groups.

Prior to the advent of enzyme electrophoretic techniques for measuring the levels of genetic variation in plant populations, much of the focus on colonizing species involved the identification of ecological attributes responsible for colonizing success. Generalizations arising from the symposium on "The Genetics of Colonizing Species" (Baker and Stebbins, 1965) stimulated comparative work on a variety of plant species to determine the adaptive significance of variation in traits such as dormancy, rate of development, phenotypic plasticity, fecundity, reproductive effort, and seed dispersal (reviewed in Baker, 1974; Harper, 1977; Grime, 1979; Jain, 1979). More recently, studies of colonizing species have compared levels of genetic diversity in related species and examined the consequences of colonizing episodes on genetic variation and opportunities for evolutionary response in novel environments. Although it is generally recognized that colonizing species employ a diverse array of ecogenetic strategies for invading unoccupied territory, several recurrent patterns have emerged from electrophoretic studies conducted during the past decade. Polyploidy, uniparental reproductive systems, depauperate levels of genetic variation, marked interpopulation differentiation, and a high degree of multilocus association have commonly been reported in colonizing species (reviewed in Brown and Marshall, 1981; Rice and Jain, 1985; Barrett and Richardson, 1986).

In this chapter we review electrophoretic evidence from isozyme surveys to evaluate whether generalizations can be made as to the processes influencing population genetic structure and evolutionary response in colonizing plants. We also assess the problems associated with determining the relative importance of historical factors, reproductive traits, and environmental heterogeneity in affecting population genetic structure. Because many successful colonizers are of polyploid origin, part of our review deals with isozyme variation in polyploid colonizers and considers how polyploidy might contribute to the evolution of colonizing ability.

MEASUREMENT OF POPULATION GENETIC STRUCTURE

The measurement of plant population genetic structure using enzyme electrophoresis has received considerable attention during the past decade (see the chapters by Hamrick and Brown et al. in this volume). Brown and Weir (1983) considered the assumptions, advantages, and pitfalls of various measures as well as formulae for obtaining estimates of the relevant parameters and their variances. Here we briefly consider the parameters commonly estimated in studies of population genetic structure with emphasis on their use in colonizing species. In addition, we briefly consider the application of the methods to populations of polyploid plants.

Estimates of within-population genetic diversity are summary measures made from a data set composed of genotype frequencies for several isozyme loci, obtained by assaying a sample of individuals from a population. As a result of codominant allelic expression at isozyme loci, the data are easily translated into allele frequencies for the isozyme loci. Brown (1975) and Brown and Weir (1983) have considered a range of experimental designs for the estimation of these genetic parameters.

Six statistics are commonly estimated from isozyme data: the percentage of loci that are polymorphic, the average number of alleles per locus, Nei's (1973) index of gene diversity, the Shannon-Weaver information index, the observed proportion of heterozygosity, and Wright's fixation index. The first four statistics are indices of genetic diversity that express, to a greater or lesser extent, the amount of allelic richness in the population and the evenness in distribution of allele frequencies (Brown and Weir, 1983). The final two statistics provide summary measures of the distribution of genotype frequencies in the population. Observed heterozygosity is the proportion of heterozygotes at each locus averaged over all loci. Wright's fixation index measures the deviation from a panmictic genotype distribution. It may be adjusted for mixed mating systems to measure the deviation from neutral inbreeding equilibrium when estimates of mating system parameters are available (Brown and Weir, 1983).

Multilocus measures of variation are also available but are less commonly employed. Brown et al. (1980) suggested a composite measure of multilocus organization, the standardized variance of the distribution of the number of heterozygous loci in two randomly chosen gametes. This parameter provides a measure of multilocus heterozygosity. For inbreeding or clonal species with little isozyme variation it may also be possible to enumerate the number and frequency of multilocus genotypes that occur in a population because relatively few may occur.

In colonizing species it is of interest to assess the manner in which genetic diversity is partitioned among different colonizing populations or among founding and source populations. Statistics commonly employed to assess subpopulation structure include the F-statistics developed by Wright (1951) and recently re-examined by Weir and Cockerham (1984), and the diversity analysis of Nei (1973). More recently, the spatial structure of genetic variation has been investigated using spatial autocorrelation analysis (Sokal and Wartenberg, 1983). This method is particularly useful in the study of colonizing populations and has been applied to the study of spatial pattern of flower color morphs in weedy *Ipomoea purpurea* (Epperson and Clegg, 1986).

Polyploid Populations

The types of polyploidy were originally defined using cytogenetic criteria (Kihara and Ono, 1926) but some controversy still surrounds the classification of polyploids (Stebbins, 1984; Jackson, 1984). For our purposes, we are only concerned with the influence of meiotic pairing on genetic transmission and the partitioning of genetic variation within individuals, populations, and species. We simplify a complex situation that in reality is a continuum determined by both chromosomal and genetic factors. Indeed, the chromosomal system itself evolves and cannot be treated as a static entity (Darlington, 1958). We refer to polyploid populations that exhibit preferential pairing among homologous chromosomes and show only disomic inheritance as allopolyploids. We consider autopolyploids to be euploids that possess more than two copies of each homologous chromosome, show random pairing among homologues at meiosis, and exhibit polysomic inheritance (see also Stebbins, 1950).

All the statistics considered above can be applied to polyploid populations. In addition, two

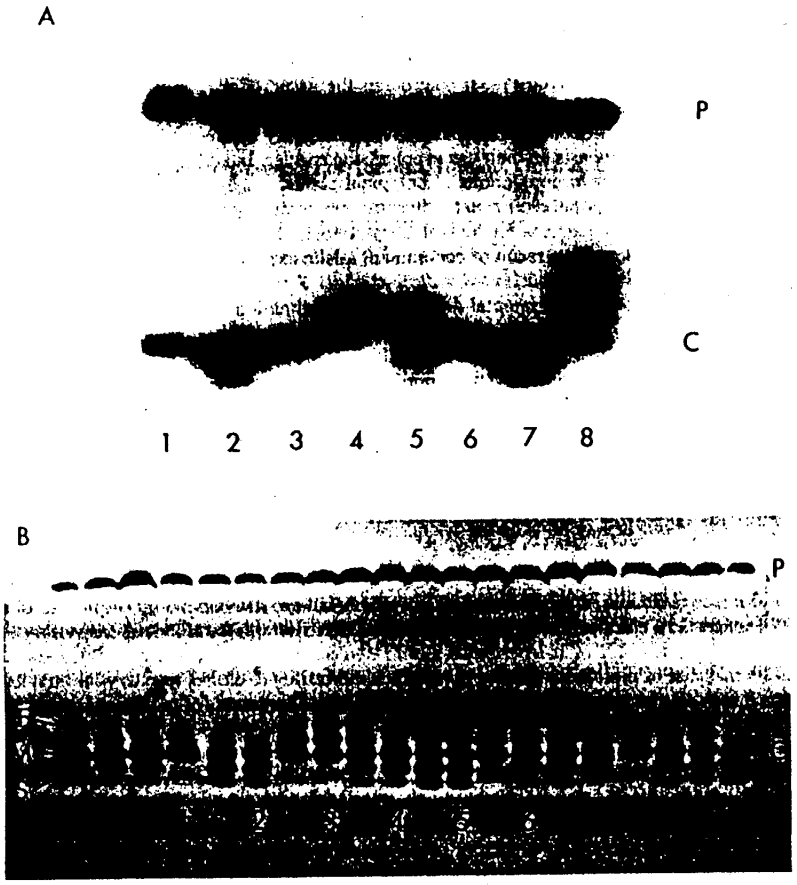

Fig. 5.1. Starch gels of *Turnera ulmifolia* assayed for glucosephosphate isomerase (GPI) activity. *GPI* is dimeric and two isozyme loci occur in diploid plants, one localized in the plastids (P) and the other in the cytosol (C). **A** For the cytosolic locus, lanes 1 and 2 are diploid homozygote and heterozygote respectively, lanes 3, 4 and 5 are three different genotypes from autotetraploid var. *elegans*, and lanes 6, 7 and 8 are three plants from different allohexaploid varieties of *T. ulmifolia*. The three genotypes in lanes 6, 7 and 8 are homozygous; no segregation is seen among selfed progeny. Genotypes in lanes 7 and 8 are "fixed heterozygotes". The number of loci coding for cytosolic GPI in the allohexaploids is not known with certainty. Lane 6 could result from one, two or three loci (having co-migrating gene products), lane 7 could be accounted for by two or three loci, and the banding pattern of lane 8 is consistent with three loci. Similarly, it is not clear how many loci code for the isozyme of *GPI* localized in the plastids of hexaploids; one, two or three loci are possible. **B** Segregation for three alleles of cytosolic *GPI* in autotetraploid *T. ulmifolia* var. *elegans*. The three alleles (*F, M, S*) code for polypeptides which, upon formation of homodimers, migrate to the positions indicated on the gel as F (fast allozyme), M (intermediate), and S (slow). Other bands are heterodimers. Six different genotypes occur on the gel for this tetrasomic locus. The lane marked 1 is a homozygous genotype, the remainder (2–6) are different heterozygotes. The genotypes are: 1-*MMMM*, 2-*MMSS*, 3-*FMMM*, 4-*MMMS*, 5-*FMSS*, 6-*FMMS*.

other measures might be useful when allopolyploids are studied. The first is the proportion of duplicate loci that exhibit "fixed heterozygosity" (e.g. Fig. 5.1A); that is, are monomorphic for different alleles. A second measure that can be employed in allopolyploids involves partitioning genetic variation into components that occur within genomes versus between homoeologous genomes (Brown and Marshall, 1981).

Few isozyme analyses have been undertaken on autopolyploid species (see below); however, all the statistics considered above can be applied to autopolyploid populations. Nei's index of gene diversity is applicable but cannot be regarded as a measure of panmictic heterozygosity, due to polysomic segregation. The extension of Wright's fixation index to autopolyploids has been considered by Wright (1969), neutral inbreeding equilibrium has been treated by Bennett (1968) and McConnell and Fyfe (1975), and mating system estimation by Bennett (1968) and Barrett and Shore (1987). Observed levels of heterozygosity may be determined by enumerating the number of heterozygotes versus homozygotes at a given gene locus.

FACTORS INFLUENCING POPULATION GENETIC STRUCTURE

The spatial and temporal organization of genetic variation within plant populations results from the joint action of mutation, migration, selection, and genetic drift. In colonizing species certain historical, life history, and ecological factors play a prominent role in determining the patterns of genetic diversity within and among populations. Because repeated colonizing episodes are a feature of invading species, genetic bottlenecks, founder effects, and drift are likely to play a more significant role in influencing genetic diversity than in many other plant life forms. Bottlenecks associated with long-distance founding events, the absence of repeated migration as a source of genetic enrichment, and the possibility of novel selection pressures in new environments are all likely to lead to a loss of genetic variation during colonizing events, particularly those that involve long-distance migration (Clegg and Brown, 1983; Barrett and Husband, 1989). In addition, demographic, life history, and reproductive features play an important role in influencing levels of genetic variation, as does the environment that a population occupies (Hamrick et al., 1979; Barrett, 1982; Loveless and Hamrick, 1984; Brown and Burdon, 1987). The complex forces that act upon genetic variation in populations of colonizing plants make it difficult to disentangle the relative importance of individual factors. Below we review several isozyme studies that have attempted to do so, and in addition, examine both large scale surveys of isozyme variation and studies of individual taxa to see whether recurrent patterns of genetic organization emerge.

Historical Factors

Migration and population establishment in colonizing species often involve a small number of immigrants. In theory this can lead to a loss of genetic variation through sampling effects. A small sample of individuals is unlikely to contain all of the variation present in the source population. Nei et al. (1975) studied the theoretical consequences of this process on genetic diversity and concluded that the level of variability declines, but that this depends not only on the number of immigrants involved, but also on the frequency of bottlenecks following establishment. Much of the literature on bottleneck effects relates to outbreeding organisms and considers the influence of small population size on levels of heterozygosity and the loss of rare alleles. However, in self-fertilizing plants with little heterozygosity, of more significance is the number of different populations in the source region that have supplied immigrants to the newly colonized area and the likelihood of cross-fertilization between them. Since many successful plant colonizers are primarily self-fertilizing, and single propagules are capable of founding populations following long-distance dispersal, genetic bottlenecks should be a standard expectation, particularly in cosmopolitan weeds.

Intercontinental migration of the annual tetraploid barnyard grass *Echinochloa microstachya* from North America to Australia provides evidence of the importance of genetic bottlenecks in selfing species. A survey of genetic variation in 20 North American populations of the species revealed a high degree of interpopulation genetic differentiation for isozymes and quantitative life

history traits (S. C. H. Barrett and A. H. D. Brown, unpublished data). Each population was largely composed of a unique multilocus isozyme genotype. This pattern of genetic differentiation is anticipated in wide-ranging, selfing species. *Echinochloa microstachya* was introduced during this century to rice fields in New South Wales, probably as a contaminant of imported rice stocks from California (McIntyre and Barrett, 1985; Barrett, 1988a). Since introduction, *E. microstachya* has spread throughout the rice-growing area as a weed of rice. A survey of isozyme variation in Australian populations revealed a very different pattern from that observed in the native North American range. Of the 20 populations assayed, 18 were genetically uniform and composed of the same multilocus genotype. Two variant loci (*HK, Lap*) were evident in the remaining populations. Clearly, migration of *E. microstachya* to Australia from North America has been associated with a major genetic bottleneck, because Australian populations are almost entirely devoid of isozyme variation. Of particular interest was the finding that the predominant Australian genotype could be identified from among the North American sample of populations. The genotype occurred in a population from northern California close to Biggs Rice Experiment Station, the major exit point of cultivated rice varieties shipped to Australia in the 1920s. This illustrates the utility of isozymes as genetic markers for testing historical hypotheses concerned with migration and founder effects.

Colonization events may be associated with mating system shifts, and can complicate attempts to determine the influence of historical factors on the patterns of genetic variation in source and colonial populations (Brown and Marshall, 1981). This difficulty was encountered in a study of continental and island populations of *Eichhornia paniculata*, a short-lived annual or perennial, diploid emergent aquatic that colonizes seasonal pools, ditches, and rice fields in northeastern Brazil, Cuba, and Jamaica (Barrett, 1985; Glover and Barrett, 1987). A survey of isozyme variation in 11 populations from northeastern Brazil and Jamaica indicated the importance of both founder effects and increased levels of self-fertilization on genetic diversity. Populations from Jamaica were genetically depauperate with respect to isozyme variation, containing a significantly lower number of polymorphic loci, number of alleles per locus, mean observed heterozygosity, and genetic diversity than Brazilian populations (Table 5.1). These measures were significantly correlated with the outcrossing rate (t) of populations. Brazilian populations contained significantly more variation within populations than between populations, whereas the reverse situation occurred among Jamaican populations. This pattern is largely the result of differences in the mating systems of populations in the two regions (Glover and Barrett, 1986). The relatively low levels of isozyme variation in Jamaican populations of *E. paniculata*, compared to those in northeastern Brazil, probably result from a limited number of long-distance dispersal events to the island. However, following establishment, genetic drift and the primarily selfing habit of Jamaican plants probably contributed to reduced levels of genetic variation within populations.

Table 5.1. *Comparisons of genetic variation in continental (Brazil) and island (Jamaica) populations of* Eichhornia paniculata *based on a survey of 21 isozyme loci. After Glover and Barrett (1987)*

Parameter	Symbol	Brazil	Jamaica
% loci polymorphic per population	P	23.8	7.6
Observed % loci heterozygous	H_O	7.8	2.0
Total gene diversity	H_T	0.15	0.06
Gene diversity within populations	H_S	0.091	0.027
Gene diversity between populations	G_{ST}	0.40	0.57
Inter- to intra- population ratio	R_{ST}	0.81	1.7
Average genetic distance	d	0.085	0.049

Brazil N = 6 populations, Jamaica N = 5 populations

Recent studies of multilocus organization within and among Jamaican populations of *E. paniculata* provide evidence of the role of genetic drift in structuring genetic diversity in colonizing species (B. C. Husband and S. C. H. Barrett, unpublished data). Among five populations examined, 38 multilocus genotypes were identified with different genotypes predominating within each population

(Figure 5.2). The relatively small number of multilocus genotypes occurring in the five populations and their uneven distribution on the island suggest that populations have been founded by a small number of individuals, and restricted gene flow and inbreeding have preserved the specific allelic combinations found within each population.

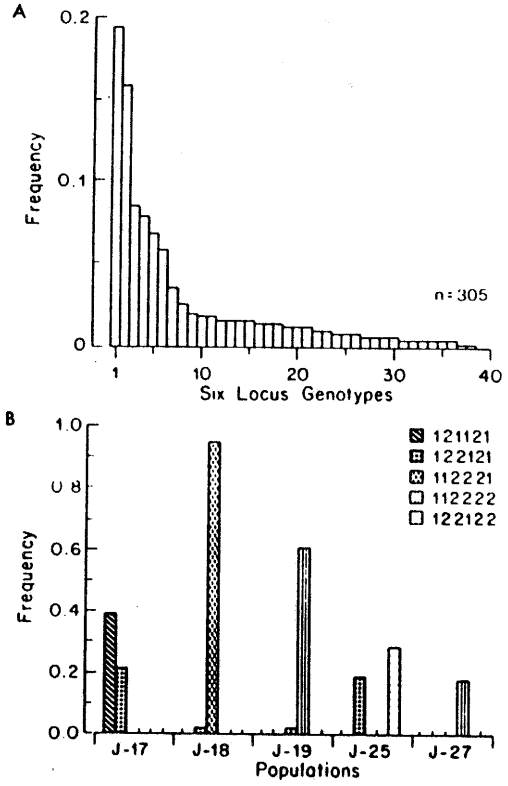

Fig. 5.2. Frequencies of multilocus genotypes in Jamaican populations of *Eichhornia paniculata*. **A** Frequency distribution of 38 six locus isozyme genotypes in five populations (n = 305 plants). **B** Frequencies of the five most common six locus genotypes in each of five Jamaican populations. Sample sizes for each population are 56, 43, 66, 68, 62 for J-17, J-18, J-19, J-25, and J-27 respectively. Polymorphic loci are *Got-1, 2, 3; Pgm-1, GPI-2; Per-1*. The five populations are different from those surveyed in Table 1.

To distinguish between the relative importance of historical factors and effects of the mating system on multilocus organization, examination of the degree of linkage disequilibrium among loci is required. This approach has been employed in both inbreeding and outcrossing colonists (reviewed in Brown, 1984). Isozyme surveys of inbreeders have generally revealed a limited number of multilocus associations with certain genotypes occurring more frequently than would be expected if alleles at different loci occurred at random with respect to one another (Allard et al., 1972; Brown et al., 1980; Warwick, 1989). In contrast, in *Echium plantagineum*, an insect-pollinated, outcrossing, annual weed introduced to Australia, only small, nonsignificant multilocus associations were detected (Brown and Burdon, 1983). In this species it appears that cross-pollination encourages sufficient recombination to remove any transient disequilibrium that might arise from bottlenecks in population size during early founding events.

Not all long-distance colonizing events result in reduced levels of genetic diversity in colonial populations in comparison with source populations. In outcrossing weeds that expand rapidly following establishment, differences in population genetic structure between the native and introduced range may be less marked. Warwick et al. (1987a) found little difference in the levels and patterns of genetic diversity among native European and introduced Canadian populations of the self-incompatible, annual *Apera spica-venti* (silky bentgrass) (Table 5.2).

A difficulty in comparing native and introduced populations of colonizing plants arises out of the choice of material sampled from the presumed source region. When the species in question has a widespread distribution, as in many cosmopolitan weeds of Eurasian origin, problems of sampling inevitably occur unless historical information on the source of immigrants is available. Ideally, chronological genetic studies of introduced populations into new habitats or regions should be conducted so that the dynamics of evolutionary change under colonization can be studied more precisely.

Table 5.2. *Comparisons of genetic variation in native European and introduced Canadian populations of* Apera spica-venti *(silky bentgrass) based on a survey of 12 isozyme loci. After Warwick et al. (1987)*

Region	N (pops)	P	A	H_O	H_T	H_S	G_{ST}
Europe	6	0.62	2.5	0.23	0.21	0.20	0.01
Canada	9	0.57	2.5	0.23	0.21	0.21	0.02

Reproductive Systems

Flowering plants display a wide range of reproductive systems, with colonizing species forming a diverse but distinctive sample. Most annual weeds are predominantly self-fertilizing and are incapable of clonal propagation. Perennial species display a diversity of reproductive systems, including selfing, outcrossing, and apomixis. Many successful perennial colonizing species possess well-developed clonal propagation and, particularly in aquatic weeds, sexual reproduction occurs only rarely (Barrett, 1982; Wain et al., 1985). As is true of all plants, the variety of reproductive modes in colonizing species is paralleled by differences in population genetic structure. This is because the mating system governs the character of genetic transmission in populations, and the occurrence of sexual reproduction provides opportunities for recombination and genetic experimentation (see the chapters by Brown et al. and Hamrick in this volume).

Large-scale surveys of isozyme variation in plants with differing reproductive systems have provided evidence of the important role of the mating system in influencing the amount of genetic variation and its organization within and among populations (Loveless and Hamrick, 1984, see chapter by Hamrick in this volume). Inbreeding species exhibit lower polymorphism, lower heterozygosity, and more pronounced interpopulation differentiation than outcrossers. In clonal and apomictic plants a range of population genetic structures is evident. In a review of 27 studies, Ellstrand and Roose (1987) found that multiclonal populations of intermediate diversity and evenness were most commonly found. Among several of the colonizing species in their sample (e.g., *Taraxacum* spp., *Cyperus* spp.), however, populations containing little or no genetic diversity were encountered (Van Oostrum et al., 1985; Horak and Holt, 1986).

Investigation of the reproductive systems of colonizing species is critical to understanding population genetic structure. A recent study (Wolf et al., 1988) of Bracken Fern, *Pteridium aquilinum*, one of the world's most widespread plant species, indicates how earlier misinterpretation of its reproductive biology led to a false picture of the clonal structure of populations. Although clonal propagation is a prominent feature of bracken populations, a survey of genetic variation at 13 isozyme loci in four geographically distinct populations (two in the U.K. and two in the U.S.A.) points to the importance of sexual reproduction. The survey revealed a high level of genetic diversity with 61% of loci polymorphic and an average of 3.5 alleles per locus. The results caution against the assumption that plants with prolific clonal propagation, such as bracken, will necessarily form vast areas of genetic monotony.

Isozyme studies have also challenged the assumption that reduced levels of genetic diversity are likely to occur in asexual plants (Richards, 1986). A particularly intriguing example concerns the sterile triploid grass, *Puccinellia* × *phryganodes*, a widely distributed colonizer of Arctic coastal wetlands. Although plants undergo vigorous clonal growth, flowering is infrequent, and seed set has never been reported in North American populations. Jefferies and Gottlieb (1983) therefore predicted that low levels of genetic variability would occur both within and between populations. Unexpectedly, an examination of isozyme patterns in clones from three widely separated populations in Arctic Canada indicated high levels of genetic diversity with many clones genetically unique. Jefferies and Gottlieb (1983) suggest that, despite triploidy, some residual fertility and occasional seed production may occur in Arctic populations of *P. phryganodes*. It is also possible that sexual tetraploids reported from northern Europe occur in North America and have contributed to the patterns of genetic variation observed. Regardless of the origins of genetic diversity in *P. phryganodes*, it appears that local triploid populations in the Hudson Bay Lowlands may contain sufficient genetic variation for adaptive responses to the impact of geese grazing (Sadul, 1987).

A significant number of isozyme surveys of primarily selfing colonizing species has revealed populations that are either genetically uniform or contain very low levels of polymorphism and heterozygosity (Table 5.3; see also Brown and Marshall, 1981; Barrett, 1982; Barrett and Richardson, 1986). Most studies were conducted in the introduced rather than the native range of colonizers, and

Table 5.3. *Taxa of colonizing plants displaying extensive monomorphism at isozyme loci both within and among populations*

Taxon	Life history	Ploidal level	Region sampled	Major habitat	Source
Abutilon theophrasti	A	P	E. Canada	agrestal	Warwick, 1988
Avena barbata	A	P	S. California	ruderal	Allard et al., 1978
Bromus tectorum	A	D	N.W. U.S.A.	rangelands	S. Novak and R. Mack (unpubl. data)
Chenopodium spp.	A	D	W. U.S.A.	ruderal	Crawford and Wilson, 1979
Datura stramonium	A	D	E. Canada	agrestal	Warwick, 1988
Echinochloa spp.	A	P	Australia	agrestal	S. C. H. Barrett and A. H. D. Brown (unpubl. data)
Emex spinosa	A	D	Australia	agrestal	Marshall and Weiss, 1982
Erodium spp.	A	P	California	ruderal	S. Novak (unpubl. data)
Hordeum murinum	A	D	Europe	ruderal	Giles, 1983
Hydrocharis morsus-ranae	P	D	E. Canada	aquatic	Scribailo et al., 1984
Panicum miliaceum	A	P	S. Ontario	agrestal	Warwick, 1988
Polygonum lapathifolium	A	P	E. Canada	ruderal	L. Consaul (unpubl. data)
Salicornia spp.	A	D(P	N. temperate	salt marsh	Wolff and Jefferies, 1987a, b
Senecio viscosus	A	P	N. Europe	ruderal	Koniuszek and Verkeij, 1982
Setaria faberi	A	P	E. Canada	agrestal	Warwick, 1988
Sorghum halepense	A	P	E. Canada	agrestal	Warwick, 1988
Taraxacum obliquum	A	P	N. Europe	sand dunes	Van Oostrum et al., 1985
Typha spp.	P	P?	E. U.S.A.	wetlands	Sharitz et al., 1980
Xanthium spp.	A	P	Australia	ruderal	Moran and Marshall, 1978

Life history—annual (A) or perennial (P); Ploidy—diploid (D) or polyploid (P)

the majority of species occurred in either agrestral or ruderal habitats.

Agricultural weeds are especially susceptible to the processes that lead to a loss of genetic variation in populations. Introduction of crop weeds most commonly results from contamination of seed lots with weed seeds. Often few propagules are introduced, and where long distance shipments are involved, the likelihood of recurrent invasion is low. The selfing habit of many weeds enables establishment after long distance dispersal, resulting in the build-up of highly homozygous populations in the introduced range. In addition, the transient nature of many weed populations, particularly those subject to eradication by weed control practices, can prevent the build-up of large, stable population systems capable of maintaining large stores of genetic variation. Some of the factors influencing the population genetics and evolution of agricultural weeds are reviewed by Barrett (1988a).

A recent survey (Warwick, 1989) of isozyme variation in five agricultural weeds in Canada clearly illustrates that high levels of genetic variation are not a prerequisite for colonizing success. *Abutilon theophrasti, Datura stramonium, Panicum miliaceum, Setaria faberi,* and *Sorghum halepense* are weeds of maize and soybean fields in the corn belt region of the U.S.A. During the past 15–20 years they have extended their ranges northward into southern Ontario, in association with the expansion of maize and soybean production. All species are self-pollinating annuals that display a high degree of phenotypic plasticity, and four of the five are polyploid. Electrophoretic surveys of populations revealed a striking lack of genetic polymorphism at isozyme loci in all five species. Most populations were composed of one, or more rarely, several multilocus genotypes (Table 5.4).

Table 5.4. *Comparisons of isozyme variation in five annual, self-fertilizing weeds of corn and soybean from southern Ontario, Canada. After Warwick (1989)*

	Abutilon theophrasti	*Panicum miliaceum*	*Setaria faberi*	*Sorghum halepense*	*Datura stramonium*
Chromosome number	2n = 24	2n = 36	2n = 36	2n = 40	2n = 24
Number of populations	39	39	8	13	9
Number of loci	27	19	24	21	22
Number (%) of loci monomorphic	25 (93%)	18 (95%)	21 (88%)	18 (86%)	22 (100%)
Number (%) of loci polymorphic	2 (7%)	1 (5%)	3 (12%)	3 (14%)	0
Number (%) of duplicated loci with enzyme multiplicity	14 (52%)	8 (42%)	13 (54%)	3 (14%)	2 (9%)
Number of multilocus genotypes	4	2	9	10	1

Not all cases of isozyme uniformity in colonizing species involve weeds of agricultural or ruderal habitats. Several aquatic and wetland species with depauperate levels of isozyme variation have been reported, including *Typha* spp. (Mashburn et al., 1978) and *Hydrocharis morsus-ranae* (Scribailo et al. 1984). The general topic has recently been reviewed by Les (1988). Although *Typha* and *Hydrocharis* are both capable of extensive clonal propagation, the observed genetic uniformity is unlikely to be due entirely to an absence of sexual reproduction, because seedlings derived from populations are also largely devoid of isozyme variability.

One of the most striking examples of genetic uniformity in wetland species involves the annual halophyte *Salicornia*, which colonizes bare sediments in coastal salt marshes, brackish pools, and inland saline lakes throughout the north temperate zone. Jefferies and Gottlieb (1982) and Wolff and Jefferies (1987a, b) surveyed electrophoretic variation in a large number of European and North American populations of diploid and tetraploid taxa within the *Salicornia europaea* species complex. They found an almost complete absence of isozyme variation within taxa, although different species were fixed for different alleles at several loci. Although *Salicornia* is largely inbreeding through the production of cleistogamous flowers, this characteristic alone is unlikely to account for the extensive regional monomorphism of each species. Wolff and Jefferies (1987a) suggested that the electrophoretically uniform populations observed in northeastern North America may have arisen by

a severe genetic bottleneck associated with the destruction of coastal habitats following glacial advance during the Pleistocene. They also speculated that the highly specialized salt marsh environment, with its high predictability and low biotic diversity, may account, in part, for the paucity of isozyme variation. The idea that open habitats with restricted biotic diversity select for low genetic polymorphism is discussed further below.

Although populations of predominantly selfing species, such as *Salicornia*, are often genetically uniform at isozyme loci, this does not necessarily imply that they are devoid of variation at other gene loci. In studies of quantitative life history traits, considerable inter- and intrapopulation genetic variation has been revealed in colonizing species with little isozyme variation, (Moran and Marshall, 1978; Moran et al., 1981; Giles, 1983; Warwick and Black, 1986.; Warwick et al., 1987b; S. C. H. Barrett and A. H. D. Brown, unpublished data). The difficulties of comparing patterns of genetic variation at isozyme loci and quantitative traits have been reviewed by Lewontin (1984), Price et al. (1984), Brown and Burdon (1987) and are discussed further in the chapter by Hamrick (this volume).

Environmental Factors

Whereas historical factors and the specific life history and reproductive characteristics of colonizers play important roles in determining the patterns of genetic diversity within and among populations, the nature of the physical and biotic environment that a colonist occupies will ultimately determine the maintenance and adaptive significance of this variation. Environmental factors that potentially affect the relative fitness of genotypes include physical factors such as temperature, moisture, and soil type; and biotic factors such as interspecific competitors, pests, and diseases.

It has been suggested that the open early-successional habitats in which most colonizing species appear are primarily influenced by physical factors and tend to be relatively homogeneous environments. In contrast, in later successional stages biotic complexity results in a high degree of environmental heterogeneity (Hamrick et al., 1979). Theoretical studies predict a positive relationship between the levels of genetic variation in populations and the degree of environmental heterogeneity (Levins, 1968; Antonovics, 1971; Hedrick et al., 1976). Isozyme surveys of species classified by successional stage indicate that species inhabiting early successional stages exhibit significantly lower levels of genetic diversity and more pronounced interpopulation differentiation than those from mature climax communities (Hamrick et al., 1979; Loveless and Hamrick, 1984; see the chapter by Hamrick in this volume). Although these patterns are consistent with theoretical expectations, the problem of intercorrelation among life history traits and successional stage makes it exceedingly difficult to resolve fully the direction of causality between environmental factors and genetic variation.

One way to reduce some of the difficulties of interpretation posed by large surveys encompassing species of diverse phylogenetic histories is to examine population genetic structure in closely related taxa. Although this approach controls many variables, it still may not clearly distinguish between the relative importance of the different factors governing genetic variation.

An example of an attempt to examine the relationship between environmental heterogeneity and genetic variation in colonizing species involves a comparative study of isozyme variation in Californian populations of the annual, selfing, hexaploid barnyard grasses *Echinochloa crus-galli* and *E. oryzoides* (S. C. H. Barrett and A. H. D. Brown, unpublished data). The former can be viewed as a generalist weed; it is cosmopolitan in distribution and invades a wide range of disturbed environments (Maun and Barrett, 1986). In contrast, *E. oryzoides* is a highly specialized rice mimic that has invaded most of the world's rice-growing regions as a seed contaminant of imported rice stocks; it is largely confined in distribution to flooded rice fields (Barrett, 1983). Like most annual monocultures, the Californian rice agroecosystem is deliberately made uniform by the grower and is highly predictable in space and time. In contrast, ruderal habitats such as paths, ditches, and open waste ground are more complex both in terms of physical and biotic diversity. As a result of the differences in environmental heterogeneity that occur between agricultural and ruderal habitats, it was predicted that populations of the two species would display different amounts of genetic diversity within populations (Barrett, 1982).

At each of 10 rice field sites in the Central Valley of California, open-pollinated families of the two species were collected. Populations of *E. crus-galli* were sampled from the mosaic of disturbed

habitats around the edges of rice fields, whereas those of *E. oryzoides* were obtained from the flooded interior of rice fields. Both species were relatively low in genetic diversity with virtually no heterozygosity at polymorphic loci and a high degree of genetic differentiation among populations. This finding is consistent with data from other annual colonizing species that are primarily self-fertilizing. At most of the sites that were sampled, populations of the generalist *E. crus-galli* were more variable both in terms of the proportion of isozyme loci that were polymorphic and the number of alleles present within populations (Table 5.5). Differences in genetic polymorphism for loci controlling the enzyme alcohol dehydrogenase (*Adh*) were particularly striking in the two species (Figure 5.3). In *E. crus-galli*, 12 homozygous multilocus genotypes were evident in the sample as a result of polymorphism at one to three loci. Populations contained different numbers of *Adh* genotypes, ranging from one to six. In contrast, all but one population of *E. oryzoides* contained the same multilocus *Adh* genotype. The exceptional population was fixed for a variant allele at a single locus.

Table 5.5. *Comparison of genetic variation in Californian rice-field populations of the generalist weed* Echinochloa crus-galli *and the specialist, crop mimic,* Echinochloa oryzoides *based on 31 and 32 isozyme loci, respectively*

	Echinochloa crus-galli			*Echinochloa oryzoides*		
Site	Number of polymorphic loci	Number of alleles at polymorphic loci	Diversity	Number of polymorphic loci	Number of alleles at polymorphic loci	Diversity
A	8	26	1.899	2	4	0.569
B	6	14	2.788	1	2	0.391
D	8	18	2.543	3	6	0.375
E	7	15	1.992	2	4	0.356
F	3	7	1.647	2	4	0.615
G	7	16	1.854	2	4	0.605
H	3	7	0.816	3	6	0.996
I	9	18	2.327	2	4	0.250
J	3	6	0.800	2	4	0.836
K	3	14	2.077	1	2	0.231
L	6	12	0.897	2	4	0.977
Mean	5.7	13.0	1.785	2.0	4.0	0.564

What factors might account for the striking differences in the amounts and kinds of enzyme polymorphism in Californian populations of the two barnyard grass species? Although the data are in accord with the suggestion that differences in environmental heterogeneity may play a role, this is difficult to prove in selfing species with little recombination. The difference in levels of enzyme polymorphism in *E. crus-galli* and *E. oryzoides* may result from their differing histories of introduction into California. Multiple introductions from a wide geographical range are likely to occur in a generalist weed such as *E. crus-galli*. In contrast, a relatively small number of contaminated rice seed lots, probably from Asia (Barrett and Seaman, 1980), may have been responsible for the introduction of *E. oryzoides*. If this is true the contrasting patterns may simply reflect the joint action of repeated founder effects, finite population size, and genetic drift.

Few studies of colonizing species have attempted to relate the degree of heterozygosity at isozyme loci to habitat disturbance. Bosbach and Hurka (1981), in a survey of 17 loci in 81 European populations of the annual *Capsella bursa-pastoris*, reported higher levels of heterozygosity in populations that were judged to be in more disturbed sites. However, several problems are apparent in the study, including small sample sizes, lack of statistical analysis, and questionable genetic interpretation of isozyme data (see their Table 1). The authors suggest that high levels of disturbance result in periodic germination of genetically diverse seeds from the seed bank. In less disturbed sites they suggest that strong biotic selection pressures imposed by "successional stress" operate on individuals and lead to populations with less genetic diversity. This interpretation contrasts with the suggestion that increased levels of biotic complexity, mediated through competitors and pest and disease

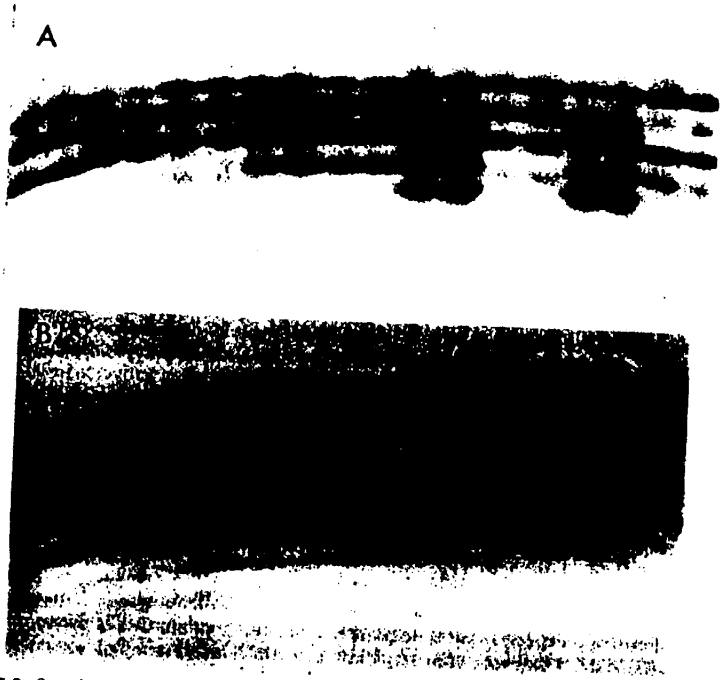

Fig. 5.3. Starch gel of Californian rice-field populations of hexaploid *Echinochloa crus-galli* (A) and *Echinochloa oryzoides* (B) assayed for alcohol dehydrogenase (ADH) activity. ADH is dimeric with three polymorphic loci readily visible in *E. crus-galli* and four predominantly monomorphic loci in *E. oryzoides*. A single variant genotype is visible in *E. oryzoides* and results from polymorphism at a single locus. All genotypes illustrated are multiple homozygotes as a result of the predominantly selfed mating system of the two barnyard grass species.

pressure, will place a selective premium on genetic variation (Levin, 1975; Clarke 1976; Burdon, 1985). Because few genetic studies of plant populations have examined temporal changes in diversity associated with successional change, it is difficult at present to evaluate the importance of biotic selection pressures in regulating patterns of genetic variation.

POLYPLOIDY AND COLONIZING ABILITY

Is there an association between polyploidy and colonizing ability, and if so, how are they causally related? Can enhanced colonizing ability be attributed to the polyploid condition, and how might polyploidy bring this about? These questions have often been posed (e.g., Baker, 1965; Stebbins, 1965; Ehrendorfer, 1965; Mulligan, 1965; Brown and Marshall, 1981; Barrett and Richardson, 1986), but the answers remain unclear. The most recent evidence for such an association was noted by Brown and Marshall (1981) and Clegg and Brown (1983); all 18 of the world's worst weeds (Holm et al., 1977) are polyploid.

An approach employed in the search for an association between polyploidy and colonizing ability has been the use of survey data. Heiser (1950), Stebbins (1965), and Mulligan (1965) demonstrate the absence of correlation between weediness and polyploidy in the weed floras of Indiana, California, and Canada, respectively. However, attributes associated with polyploidy complicate

attempts to examine such correlations. For example, Müntzing (1936) demonstrated that polyploidy is less frequent among annuals than perennials within the same genera of herbs. Heiser (1950) showed that in the weed flora of Indiana low levels of polyploidy are correlated with a high frequency of the annual habit, and Gustafsson (1948) also pointed out that weed floras composed chiefly of annuals have a lower percentage of polyploid species.

Breeding systems impose constraints on whether or not polyploidy will evolve in populations and confound simple correlative analysis. It has been frequently argued (e.g., Grant, 1971; Stebbins, 1971) that there is a greater likelihood of the establishment of polyploidy in selfing species. This is because self-fertilization of a polyploid variant would result in fertile polyploid progeny whereas in an outcrossing species backcrossing to diploids would result in sterile progeny. In many groups of related annual and biennial species, the selfing species contain allopolyploids whereas the outcrossers are strictly diploid (Grant, 1971). The kind of polyploidy also varies with breeding system (Stebbins, 1957). Generally, allopolyploid species tend to be selfing whereas autopolyploids are outcrossing (Stebbins, 1957; Bingham, 1980). It is clear that if survey data are used to draw inferences concerning the causal relationship between colonizing success and polyploidy, careful statistical approaches that control for several variables must be undertaken.

Stebbins (1965) has cautioned against the use of survey data and suggests that a more fruitful approach is intense investigation within taxonomic groups containing diploids and related polyploids. He suggests that whereas colonizing ability does not require polyploidy, where diploids and related polyploids both occur, the polyploids have a greater likelihood of becoming weeds. A correlation between weediness (or colonizing ability) and polyploidy is apparent in many groups, e.g., *Knautia* spp. (Ehrendorfer, 1965), *Claytonia perfoliata*, *Amsinckia* spp. (Stebbins, 1965), *Ageratum* spp. (Baker, 1965), *Deschampsia cespitosa* (Rothera and Davy, 1986), and *Eichhornia* (Barrett, 1988b). However, in other cases, there is a correlation between diploidy and weediness, or diploids and polyploids may be equally weedy. For example, diploids appear to be better weeds than polyploids in the *Eupatorium microstemon* species aggregate (Baker, 1965, 1967), and in *Oxalis pes-caprae* weediness has clearly preceded the occurrence of pentaploidy since diploids and tetraploids are more successful as weeds in the native South African range than the sterile pentaploid (Ornduff, 1987). Historical factors have probably led to the introduction of only the pentaploid to other parts of the world where it is now a noxious, widespread weed. Grant (1967) found no apparent relationship between chromosome number and geographic distribution of weedy species of the genus *Amaranthus*. Further, he found no association between polyploidy and weediness in the genus *Celosia* (Amaranthaceae) and concluded that polyploidy does not appear to be a cause of weediness. Thus, although there appears to be some association between polyploidy and colonizing success in many groups, it is by no means a universal association.

The intercorrelation of several factors makes it difficult to sort out what attributes are under a selective premium in colonizing plants. Is polyploidy, breeding system, habit, or some other factor critical, or is it an interaction of two or more of these attributes? Perhaps in addition to survey data and comparative studies, a population biology approach to addressing these questions is required, much as Stebbins (1976, 1985) has undertaken for species of *Erharta*, *Stipa*, *Elymus*, and *Phalaris*. Long-term demographic studies of natural and synthesized polyploids (both auto- and allopolyploids) and their diploid progenitors under a wide range of natural field conditions are most likely to provide the experimental data necessary to resolve these issues. Unfortunately, such studies require a major research commitment of both time and effort.

Release of Variation in Colonizing Polyploid Populations

Emphasis on the causal connection between polyploidy and colonizing ability has focused on the greater biochemical diversity of polyploids potentially providing individuals increased homeostasis and therefore the capacity to respond to new environmental challenges upon colonization (reviewed by Levin, 1983). Here we consider whether the polyploid condition might, in addition, provide enhanced levels of genetic variation upon which selection can act allowing adaptation to novel environments.

In colonizing species it is important to know whether the potential for evolutionary response is

possible in founding populations. Autopolyploids can maintain large stores of variability that can be released through segregation and recombination with polysomic inheritance. Polysomic inheritance has a conservative effect on genetic variation and reduces the stochastic loss of variation (Haldane, 1930; Mayo, 1971). This may be important in colonizers that experience repeated bottlenecks in population size. In allopolyploids, particularly those that are primarily inbreeding, considerable biochemical diversity may be tied up within individuals as "fixed heterozygosity" (e.g., Roose and Gottlieb, 1976). However, it is not clear whether this potential source of variation can be released. In theory, mechanisms such as gene silencing, intergenomic recombination, and the regulatory divergence of duplicate loci could alter variation, but the extent to which these processes occur in allopolyploid plant populations is unknown.

That allopolyploids can undergo adaptive evolution is best exemplified by studies of island colonization and evolutionary divergence in Hawaiian *Bidens* (Helenurm and Ganders, 1985). Allohexaploid *Bidens* species on different Hawaiian islands exhibit dramatic morphological and ecological differentiation but show little isozyme divergence or intersterility. The possible role of released homoeologous genetic variation in the divergence of these allopolyploids is not known. However, if homoeologous genetic variation has been released, it has not altered the expression of isozyme variation but instead has been important in generating variability in characters of morphological and ecological significance.

Genetic Variation in Polyploid Colonizers

The levels of genetic variation have been assessed in a number of allopolyploid colonizing species using gel electrophoresis. These include *Chenopodium* ssp. (Wilson and Heiser, 1979; Wilson, 1981; Al Mouemar and Gasquez, 1983); *Avena* spp. (e.g., Jain and Singh, 1979; Kahler et al., 1980); *Hordeum jubatum* (Babbel and Wain, 1977); *Oryza* spp. (Second, 1982); and *Echinochloa* spp. (S. C. H. Barrett and A. H. D. Brown, unpublished data). The recently derived allotetraploids *Tragopogon mirus* and *T. miscellus* exhibit 43% and 33% duplicate loci with "fixed heterozygosity", respectively (Roose and Gottlieb, 1976). Much of the genetic diversity within allopolyploid *Tragopogon* spp. is intergenomic; very little intragenomic diversity occurs (Brown and Marshall, 1981). Using isozyme markers, Rieseberg and Warner (1987) recently documented hybridization between *T. mirus* and *T. miscellus*. Although the evolutionary significance of this hybridization is unclear, its occurrence demonstrates that levels of genetic variation can potentially increase through hybridization among related polyploids of independent origin. Intersterility among the progenitors of allopolyploid species usually precludes gene exchange at the diploid level.

Populations of an older allopolyploid, *Bromus mollis*, display more intragenomic diversity than occurs in *Tragopogon* spp., 22.2% versus 2.7%, respectively (Brown and Marshall, 1981). This demonstrates that allopolyploidy does not preclude the maintenance of intragenomic variability, and this variation may provide the basis for evolutionary response during colonization. Warwick (1989) estimated the percentage of duplicate loci exhibiting "fixed heterozygosity" in four polyploid weed species (Table 5.4). The values range from 14% for *Sorghum halpense* to 54% for *Setaria faberi*. Little intragenomic variation occurs in populations of these species. Thus, allopolyploids may maintain high levels of heterozygosity, resulting from genetic differences between each of their component genomes despite being uniform intragenomically, or they may benefit from both sources of genetic diversity. Weedy allopolyploid populations may possess an enhanced capacity to respond to new selection pressures upon colonization, if they can liberate the potential variation that is tied up intergenomically. In addition, it is possible that the "fixed heterozygous" condition is of direct adaptive value under colonizing situations.

Studies of isozyme variation in autopolyploids in general are few (Soltis and Rieseberg, 1986) and studies of colonizing or weedy autopolyploids are even rarer. Perhaps this is because most colonizers are selfing and autopolyploidy is almost always found in outcrossing species (Stebbins, 1957; Bingham, 1980). Isozyme studies of weedy autopolyploids have been carried out in *Haplopappus spinulosus* (Hauber, 1986) and *Turnera ulmifolia* (Shore, 1986; J. S. Shore and S. C. H. Barrett, unpublished data). Studies of isozyme variation in nonweedy autopolyploids include *Veronica peregrina* (Keeler, 1978); *Medicago* spp. (Quiros, 1982); *Solanum tuberosum* (Martinez-

Zapater and Oliver, 1984); *Galax urceolata* (Epes and Soltis, 1984); *Coreopsis grandiflora* var. *longipes* (Crawford and Smith, 1987); *Heuchera grossulariifolia* (Wolf et al., 1987); *H. micrantha* (Ness et al., 1986), and *Tolmiea menziesii* (Soltis and Rieseberg, 1986).

Turnera ulmifolia is a weedy, perennial, polyploid complex native to the New World Tropics and composed of diploid, tetraploid, and hexaploid varieties (Barrett, 1978; Barrett and Shore, 1987). Although two varieties (tetraploid var. *elegans* and hexaploid var. *angustifolia*) have been introduced to the Old World where they are roadside weeds, our observations of New World populations have not revealed any association between ploidal level and degree of weediness. Diploid and tetraploid varieties in the complex are distylous, self-incompatible, and outcrossing, whereas hexaploid varieties are homostylous, self-compatible, and inbreeding. Isozyme studies indicate that tetraploids in the complex are autopolyploids whereas hexaploids display considerable "fixed heterozygosity" at isozyme loci and are allopolyploids (Figure 5.1).

We examined levels of isozyme variation in six diploid and 16 autotetraploid populations of *Turnera ulmifolia* var. *intermedia* and seven populations of autotetraploid *T. ulmifolia* var. *elegans*. Diploid populations of var. *intermedia* were collected from South and Central America, tetraploid var. *intermedia* from Puerto Rico and the Dominican Republic, and tetraploid var. *elegans* was collected from Brazil. Fourteen isozyme loci were examined. Island populations of autotetraploid var. *intermedia* show the lowest levels of genetic variation, perhaps as a result of bottlenecks associated with island colonization (Table 5.6). Autotetraploid populations of var. *elegans* from Brazil exhibit the highest levels of genetic variation for all parameters that were estimated. This suggests the occurrence of hybridization during or subsequent to the origin of this mainland variety. The high levels of observed heterozygosity in var. *elegans* likely result from the joint effects of its breeding system, tetrasomic inheritance, and high genetic diversity in the species. Bingham (1980) noted that in contrast to allopolyploidy there are no examples among crop plants of successful polysomic polyploid species which are self-pollinated. He suggested that the biochemical and physiological advantages conferred by heterozygosity are important components of autopolyploid vigor. The data for weedy *T. ulmifolia* are consistent with these observations from crop plants. Autopolyploidy is associated with self-incompatibility and outcrossing, whereas allopolyploid members of the complex self-pollinate to varying degrees.

Table 5.6. *Comparisons of genetic variation in diploid and autotetraploid varieties of* Turnera ulmifolia *(x = 5) based on a survey of 14 isozyme loci. Values are the means of populations within each variety/ploidal level*

Variety	Ploidy	N (pops)	P	A	H_S	H_O
intermedia	2x	6	44	1.5	0.11	0.10
intermedia	4x	16	20	1.2	0.04	0.07
elegans	4x	7	65	2.0	0.27	0.42

CONCLUSIONS

In the more than two decades since the publication of *The Genetics of Colonizing Species* (Baker and Stebbins, 1965) the enzyme electrophoresis revolution has provided a considerable amount of information on the population genetic structure of colonizing plants. Not surprisingly, given the variety of colonizing strategies that exists, a wide range of population genetic structures has been revealed, ranging from extensive areas of genetic uniformity in selfing, apomictic, and clonal species, to high levels of genetic diversity in outcrossing species. A recurrent theme in many colonizing species is the occurrence of marked founder effects, depauperate levels of genetic variation, pronounced interpopulation differentiation and well developed multilocus organization (Brown and Marshall, 1981). In addition, the associations between selfing, allopolyploidy, low genetic polymorphism, and high phenotypic plasticity in many agricultural weeds suggests that this combination of traits represents an adaptive strategy that has evolved independently numerous times among

angiosperm families in response to selection pressures associated with habitat disturbance and repeated colonization events.

In a general review of this type it is inevitable that more questions are raised than answered. In particular, the association between polyploidy and colonizing success has stimulated vigorous discussion for many years, and, as we have seen, the problem is complex and fraught with difficulties. Nevertheless, before we conclude we cannot resist raising several additional questions and suggesting several lines of enquiry that could be profitably explored now that the mating systems and patterns of genetic variation in polyploids can be routinely assayed using electrophoretic techniques.

Isozyme studies have provided data indicating that polyploid individuals maintain high levels of biochemical diversity. Is this of direct adaptive value during colonizing episodes or is some other correlate of the polyploid condition of greater significance? Do isozymes simply provide markers of genomewide gene multiplication in polyploids, or are they of adaptive importance? Are the phenomena of phenotypic plasticity, developmental homeostasis, heterosis, and inbreeding depression in part determined by this biochemical diversity, or do they result from genetic phenomena unrelated to polyploidy? A positive relationship between heterozygosity at isozyme loci, developmental stability, growth rates, and fitness has been claimed for diploids (Mitton and Grant, 1984; see chapter by Mitton in this volume), but how do these arguments apply to allopolyploids with extensive monomorphism of individual loci but "fixed heterozygosity"? Studies of phenotypic plasticity, growth rates, and other correlates of fitness in natural and synthesized polyploids of contrasting ploidal level and heterozygosity would be valuable in assessing the relationships between biochemical diversity at the individual level and fitness. This type of work could provide more meaningful insights into the "general purpose genotype" concept in colonizing species (Baker, 1965) which, up to now, has been difficult to define or identify with any degree of precision.

The fact that allopolyploidy maintains individual heterozygosity in the face of high selfing rates in colonizing species suggests that it is the simultaneous contribution of high biochemical diversity and assured reproduction that may have led to the success of so many polyploid weeds. If allopolyploids depend on gene multiplication rather than allelic variation and outcrossing to attain heterozygosity, then the partial uncoupling of the mating system from individual heterozygosity can be viewed as the significant factor favoring colonizing ability in many polyploids.

Finally, what are the relationships between polyploidy and inbreeding depression, and how might such a relationship lead to increased colonizing success? Both theoretical and empirical studies of inbreeding depression and its converse, heterosis, have been undertaken in polyploid species (Lundquist, 1966; Busbice and Wilsie, 1966; Dewey, 1966, 1969; Bennett, 1976; Bingham, 1980; Gallais, 1984). Virtually all empirical studies have been conducted on synthetic polyploids of agronomic importance where yield has been the primary character of interest. The results have been variable, with polyploids exhibiting greater inbreeding depression than diploids in some instances and the reverse pattern occurring in others (Dewey, 1966, 1969). The relevance of these studies to natural polyploids is unclear because of the agricultural context and because levels of inbreeding depression exhibited by synthetic polyploids will be largely a function of the manner in which they are produced. Studies of inbreeding depression in natural polyploids and their diploid progenitors under field conditions are clearly required.

Lande and Schemske (1985) modelled the joint evolution of inbreeding depression and plant mating systems. Their model predicts that both autopolyploids and allopolyploids should exhibit lower equilibrium levels of inbreeding depression than diploids. If selfing is of selective importance in colonizing populations, it may arise more easily in polyploid populations, because inbreeding depression may not be of sufficient magnitude to prevent the spread of genes that confer high selfing rates. Barrett and Shore (1987) suggested that this process may explain the occurrence of self-compatible hexaploids at the margins of the geographical range of the *Turnera ulmifolia* complex. If inbreeding depression is indeed of reduced significance in polyploids (and see Hedrick, 1987), it is possible that polyploids are able to withstand marked reductions in population size and concomitant increased inbreeding, without suffering reductions in fertility due to the expression of deleterious genes. Data on mating systems, population size, and levels of inbreeding depression in related diploid and polyploid species would aid in the evaluation of these ideas.

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