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GENETIC VARIATION IN WEEDS

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Evolution by natural selection depends on the presence of heritable variation in populations. Fisher (1) demonstrated that there is a precise relationship between genetic variation and the maximum possible rate of natural selection. Hence the rate of increase in fitness of a population is equal to its genetic variance in fitness at that time. Therefore, it is of some importance in evolutionary studies to determine the amount and nature of genetic variation present in natural populations of organisms. In fact, the study of genetic variation has become a major preoccupation of evolutionary biologists in recent years (2–4).

Weedy plant species are suitable organisms for genetic and evolutionary studies because they are usually abundant, grow rapidly, and produce large numbers of offspring (5). As a result, some information on the genetic structure and levels of variation in populations of weed species is now available. The objective of this chapter is to review the existing literature concerned with genetic variation in weeds and to discuss some of the factors that determine the genetic structure of populations of colonizing plants. An attempt is made to relate this information to the methods employed in biological weed control.

WEED CHARACTERISTICS

There are many different definitions of what constitutes a weed (6–8). For the purpose of this discussion, I shall use the botanical definition of Baker

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(9) that a plant is a weed, "if in any specified geographic area, its populations grow entirely or predominantly in situations markedly disturbed by man, without being deliberately cultivated." I shall also refer to particular weed species as ruderals, which occur primarily on waste ground and along roadsides, and agrestals, which are found principally as weeds of agroecosystems. These latter categories are not mutually exclusive since many weeds can occur in either situation. Aquatic weeds comprise a third class of weeds that is usually restricted to canals, drainage ditches, reservoirs, and other forms of water impoundment.

Although weed species have evolved independently in many diverse taxonomic groups, they frequently share similar sets of adaptations or life history traits. It is worthwhile to consider some of these attributes since they strongly influence the genetic properties of weeds and hence their evolutionary potential. Baker (5,9) has compiled a list of "ideal" weed characteristics. Some common features of weed species are presented in Table 1. Not all weeds exhibit these traits, and many nonweeds possess some of these characteristics. Nevertheless, it is useful to keep these features of the life history of weeds in mind when analyzing individual cases of colonizing success and in comparative studies of related weed and nonweed groups (5, 9-11).

In a review of the biological characteristics of the world's 18 most serious weeds, Brown and Marshall (12) identified four common features: (1) reproduction either by self-fertilization or clonal propagation with a high reproductive capacity; (2) extensive continental distribution and hence adaptation to a wide range of environments; (3) ecotype formation; and (4) polyploidy. These characteristics all have important genetic implications and are useful in formulating a general theory for the population biology and evolution of weeds.

SELECTION PRESSURES ON WEEDS

Many weed species have survived and evolved over many centuries of environmental change (13). This is particularly notable in Eurasia, where there is a long history of large-scale disturbances through agriculture and deforestation. Many of the most widespread and successful weeds in North America are Eurasian in origin and have been introduced to the New World in historic times (14,15). One of the reasons for the success of these aliens over native North American species may be related to their longer association with agriculture. This longer association provides time

TABLE 1. Some Common Features of Weeds

1. Dormancy and asynchronous germination
2. Rapid development
3. Phenotypic plasticity
4. Clonal, apomictic, or autogamous reproduction
5. High reproductive capacity
6. Small, easily dispersed seeds
7. Ecological race formation
8. Polyploidy

for the evolution of characteristics that are favored under disturbance (16).

Improvements in agricultural techniques result in altered selection pressures on weed populations. These forces are often of a general nature affecting entire weed floras. The introduction of new crops, as well as alterations in fertilizer treatments, times of sowing, herbicide usage, and crop spacing will influence most weed species in some manner. For example, the development of continuous flooding techniques in Californian rice fields has altered the composition of the weed flora by reducing infestations of weed taxa such as *Ammannia coccinea*, *Echinochloa crus-galli* var. *crus-galli*, and *Leptochloa fascicularis*, which are unable to establish in deep water (17). In some cases the selective forces are highly specific, as with the use of biological control methods intended to reduce populations of particular weed species (18). Responses to these selection pressures vary. Some species are unable to adapt and are replaced by other weed taxa. In California *E. crus-galli* var. *oryzicola*, a large seeded variety of barnyardgrass that is capable of establishing in deep water, has now replaced *E. crus-galli* var. *crus-galli* as the most serious weed of rice in the state (17,19). Alternatively, if the appropriate genetic variation is available, populations may respond by evolving new adapted forms, as has occurred in several weed species subjected to regular applications of S-triazine herbicides (discussed later in this chapter). The important point is that natural selection is an ongoing process in today's agroecosystems and weed adaptation will depend on the strength of the selective forces applied by the agriculturalist as well as the genetic composition of weed populations. At this time, attempts to predict the outcome of these interactions is a difficult task because of our general ignorance of the adaptive value of most forms of genetic variation (20).

THE NATURE OF VARIATION

PHENOTYPIC PLASTICITY

Populations of weeds often exhibit striking variation in size and expression of morphologic characters. Much of this variability is a consequence of phenotypic plasticity: the ability of individual genotypes to alter their growth and development in response to changes in environmental factors. Several authors (9,12, 21–23) have discussed the ecological importance of phenotype plasticity and its adaptive significance to weed populations.

By growing plants of *Echinochloa crus-galli* var. *crus-galli* from a single population under stressed and fertilized conditions, it is possible to produce plants which vary by as much as 8537 times in above-ground biomass and 9410 times in seed fecundity (Table 2). This type of environmentally induced variation presumably enables genotypes of barnyardgrass to survive and reproduce in the heterogeneous and unpredictable environments associated with seasonally flooded land.

Many strictly aquatic weeds also exhibit striking phenotypic plasticity. In a single colony, plants of *Eichhornia crassipes* (waterhyacinth) may differ markedly in size, leaf shape, and petiole swelling. Such diverse phenotypes, which result from different light and nutrient conditions, have been treated as ecotypes (24) or confused with related species such as

TABLE 2.   Phenotypic Plasticity in ECHINOCHLOA CRUS-GALLI var. CRUS-GALLI (Barnyardgrass)[a]

Character Measured $(n = 10)$[b]	Fertilized Treatment	Density-Stress Treatment
Above-ground biomass (g)	219.4	0.0257
Time to flowering (days)	54.1	95.0
Tiller production	17.6	1.0
Seed production	17,880.0	1.9
Harvest index (%)	13.4	10.4

Source: Ref. 11 and unpublished data.

[a]Seed was collected from a population at the periphery of a rice field in California. Plants in the fertilized treatment (NPK) were grown singly in 31,860-cm³ pots; plants in the density-stress treatment were grown at a starting density of 100 plants per 88-cm³ pot. Both treatments were set up during May–September 1978 under glasshouse conditions.

[b]Average values.

Eichhornia azurea (examination of major herbarium collections of waterhyacinth confirms this point). In fact, the contrasting forms may often be members of the same clone. Thus the great morphologic variation observed in weed populations under field conditions may not necessarily reflect a high level of genetic diversity.

In California the two annual wild oats *Avena barbata* and *A. fatua* exhibit contrasting patterns of phenotypic and genetic variability. *Avena barbata* is less variable genetically than *A. fatua* but exhibits greater overall phenotypic variation in natural populations. It appears that *A. barbata* relies less on genetic diversity and more on phenotypic plasticity than does *A. fatua* in adapting to heterogeneous environments (23,25,26).

GENETIC DIFFERENTIATION

Variation in weed species also results from genetic differentiation, both within and between populations. The extent of intraspecific variation varies widely among species. In some groups the variability is treated taxonomically by the formal naming of subspecies or varieties. More often the variants are simply recognized as ecotypes or ecological races. Race formation has been described in many common weeds; see Baker (5,9) and Holm et al. (27) for specific examples. Discussions of the systematic and evolutionary implications of intraspecific variation in plant populations are available in Davis and Heywood (28) and Heslop-Harrison (29). As might be anticipated, the evolution of genetic differentiation in weed species is favored if populations can persist in an area long enough to enable adaptation to the local environment.

THE MEASUREMENT OF VARIATION

Several measures can be used to quantify the levels of genetic variation in a species. Genetic diversity resides both within and between individuals, populations, and regions. Marshall and Brown (30) recognized two major classes of measurement: (1) measures based on genetic variance in quantitative traits such as plant height, time to flowering, and total biomass and (2) measures of allelic diversity at loci governing qualitative characters. These are usually genetic polymorphisms for observable morphologic and biochemical characters.

Measures of genetic diversity based on quantitative characters involve the collection of progenies from individual genotypes from the field. Random sampling of seed parents both within and among populations is usually employed. Families of 5–20 genotypes are grown from each

parent in replicated experiments under uniform conditions and measured for a range of vegetative and reproductive parameters. Statistical comparisons are made of the partitioning of phenotypic variance in metrical characters both within and among families and populations. These techniques have been used extensively by population biologists interested in measuring genetic variation in colonizing species (10,25,31–35), as well as by plant breeders analyzing the components of yield (36). However, estimates of variation in quantitative characters are merely indirect measures of genetic diversity since they reflect only that portion of the genetic variability that is expressed phenotypically. The amount of variability actually observed will depend on the character being measured as well as the genetic background and environmental conditions in which it is expressed (30).

Application of the techniques of gel electrophoresis to population genetic studies during the past 15 years has enabled a more direct assessment of the levels of genetic variation in plant and animal populations. The degree of genic variation in a species can be estimated if allelic variants of single genes representing a random sample of the total genome can be detected (37). Electrophoretic techniques permit the detection of allelic variants at enzyme loci. Since most enzymes are the products of individual genes, it is possible, to a first approximation, to equate enzyme variation with variation in genes. Variant and invariant gene loci can be identified and a random sample of genes surveyed. Reviews of electrophoretic techniques and their application to the measurement of genetic variation include those of Lewontin (20), Ayala (38), and Brown (39).

Not all allelic variants are detected by electrophoresis; consequently, the amount of genetic variation is underestimated (20,40). However, at present there is no evidence to indicate that there is a bias in the detection of variability associated with particular ecological or taxonomic groups. Hence the underestimate of allelic variability is probably not a major problem in comparative studies (4).

The basic data obtained from electrophoretic surveys of enzyme and protein variation consist of the genotypic or allelic frequencies at each locus sampled within a population. Four measures of intrapopulation variation are commonly calculated: the mean number of alleles per locus (A); the percentage of loci that are polymorphic (P); a polymorphic index equivalent to the heterozygote frequency under Hardy-Weinberg equilibrium (PI); and the mean heterozygosity per individual (H).

Since the first application of electrophoretic techniques to population biology, over 100 different plant species have been assayed for levels of genetic variation including some 20–30 weed species. Several reviews of

the plant data are available. Gottlieb (41) and Brown (39) discussed the relationship between the mating systems of populations and genetic variation, and Gottlieb (42) examined the biochemical consequences of the speciation process. Hamrick (43) and Hamrick et al. (4), while summarizing data from electrophoretic surveys of 113 plant taxa, examined the relationship between life history parameters and levels of genetic variation. Much of the following discussion utilizes data from these reviews.

FACTORS THAT INFLUENCE GENETIC VARIATION

Many factors determine the genetic structure and levels of variation present in a population at a given time. These include the factors that regulate recombination, such as chromosome number, frequency of crossing over, sterility and fertility barriers, mating system, pollination system, dispersal system, and the life history strategy of the species. In addition, various historical and ecological factors such as founder effect, genetic drift, and the degree of environmental heterogeneity can also play a major role. It is an extremely difficult task to determine the extent to which these factors are acting separately or in concert to affect variability. Nevertheless, some patterns are emerging from comparative studies of closely related species as well as from general surveys. This review focuses on those factors that are most relevant to the population genetics of colonizing species and for which data are available (Table 3).

TABLE 3. Some Factors That Influence the Levels of Genetic Variation
in Weed Populations

Factor	Influences
Founder effect	Numbers and types of immigrants
Genetic drift	Frequency of genetic bottlenecks during colonizing episodes
Population age and size	Stability of habitat and life history features of species
Degree of sexuality	Importance of cloning and frequency of sexual reproduction
Mating system	Level of inbreeding
Hybridization	Opportunities for gene exchange with related taxa
Environmental heterogeneity	Spatial and temporal variation of habitat

HISTORICAL FACTORS

In many regions of the world and in many crops, the weed flora is composed primarily of alien or introduced species (14,44,45), although exceptions do occur (17). Successful colonization of new territory by introduced species will depend on the degree of preadaptation to the new environment, the number of immigrant propagules that arrive, and the availability of suitable habitats. In many cases of continental migration, only a part of the genetic variation present in a species will be transferred to the new area of occupation. Consequently, populations of alien weeds, particularly those that originate from a single or limited number of introductions, may contain low genetic variation as a result of such "founder effects" (46).

Founder effects combined with an absence or restriction of sexual reproduction can result in striking cases of genetic uniformity. The dioecious aquatic weeds *Elodea canadensis* in Europe (47) and *Myriophyllum brasiliense* in California (14) serve as examples. In the absence of male flowers in the areas of introduction of both species, plants can reproduce only by clonal propagation. Nevertheless, considerable range extensions have been achieved as in the case of *E. canadensis*, which has become a serious weed problem throughout the inland waterways of Europe. It is possible that many widespread aquatic weeds, such as *Salvinia molesta* (48,49), *Hydrilla verticillata* (50), and *Eichhornia crassipes* (51–53), which reproduce predominantly by clonal means, are represented by relatively few genotypes in parts of their alien ranges.

Not all populations of alien weeds exhibit low variation in comparison with source populations. Brown and Marshall (12) found no differences in the average levels of genetic diversity (measured electrophoretically) between native and introduced populations of *Bromus mollis*, respectively, in England and Australia. In fact, the Australian populations exhibited higher levels of heterozygosity than did those from England. Clearly, founder effects may or may not be important in influencing the levels of genetic variation in weed species. Much will depend on the amount of variability in the source population, the extent of immigration, and the reproductive system of the colonist.

REPRODUCTIVE SYSTEMS

Higher plants exhibit a great diversity of reproductive systems (for reviews, see Refs. 54–56). From the standpoint of their influence on genetic diversity, two extremes can be identified. Populations of some species that often reproduce primarily by cloning, such as the bracken

fern *Pteridium aquilinum* and the grasses *Festuca rubra* and *Holcus mollis*, can consist of one or a few clones covering large areas (57). At the other extreme are completely sexual, obligate outbreeders with populations containing large amounts of genetic diversity. Among this group are the long-lived tree species, some of which display the highest levels of genetic variation recorded for any living organism (43). For the purpose of this discussion, four modal classes of reproductive system are treated. They are connected by many intermediate conditions.

Asexual Reproduction

Clonal Propagation. Many perennial weeds are capable of clonal or vegetative propagation in addition to reproduction by seed. Methods include propagation by surface stolons and runners, underground rhizomes, tubers, offset buds, corms and bulbs, adventitious buds on cut stems or fallen leaves, and vegetative propagules arising within a flower or inflorescence (vivipary). In every case, genotype duplication occurs and limited genetic diversity may result with extensive cloning and restricted sexual reproduction. In certain weedy forms of *Oxalis pes-caprae* (9) and *Euphorbia cyparissias* (58,59), all reproduction and spread are by clonal methods because of the genetic sterility of populations.

Genetic monotony probably occurs in parts of the adventive range of the waterhyacinth, which is capable of prolific clonal growth through stolon formation. Although seeds are produced in most populations, they frequently fail to produce plants because of the absence of suitable environmental conditions for germination and seedling establishment (52,53). Evidence to support this view comes from genetic studies and observations of the reproductive biology of populations. Waterhyacinth exhibits the rare genetic polymorphism, tristyly (51). Populations of tristylous species usually contain three genetic forms or morphs that differ from one another in style and stamen lengths. In the Amazon Basin the native range of waterhyacinth, long-, mid-, and short-styled forms occur, whereas in many parts of the adventive range of the species only mid-styled forms occur. This suggests that limited genetic diversity was introduced from the native range.

In California, only the mid-styled form of waterhyacinth occurs. However, open-pollinated seeds from a population at Stockton, California, when grown to flowering under glasshouse conditions segregated long- and mid-styled plants. Absence of the long-styled morph under field conditions in conjunction with observations of an absence of seedlings at the site strongly support the view that cloning is the only method by which the population reproduces (53).

A quite different situation is evident in Florida and Louisiana, where the drainage of water ("drawdown") from infested water bodies is often used for control of certain aquatic weeds. This technique favors sexual reproduction and the buildup of genetic diversity in waterhyacinth populations by providing suitable conditions for seed germination and seedling establishment. The water level fluctuations that occur during the drainage and refilling of water bodies parallel the natural flooding regimes of Amazonian habitats to which waterhyacinth is highly adapted. A range of genotypes, including long-styled and heterozygous and homozygous mid-styled forms as well as flower color variants, occur in the southeastern United States (see Refs. 51, 52, and Barrett, unpublished data). Although some of these forms may have arisen from separate introductions from the Neotropics, it is clear that weed control practices that enhance sexual reproduction favor the buildup of genetic diversity in the region.

If clonal species persist in a suitable habitat for a long period of time, considerable levels of genetic diversity can develop (60–62). This is aided by the fact that clonal species are frequently outbreeders. Nevertheless, it seems likely that in many clonally propagated weeds of agricultural land, periodic habitat destruction will reduce opportunities for the development of high genetic diversity, particularly if sexual reproduction is infrequent.

Apomixis.   Apomixis is the production of viable seeds without fertilization. There are several types of apomictic reproduction, and the embryologic details are complex and may vary in every case (63). The usual result of apomixis is the formation of seeds that are genotypically identical to the maternal parent. Apomixis is widespread in higher plants and is frequent among perennial, polyploid species, including many weeds such as *Chondrilla juncea* (64), *Cortaderia jubata* (65), *Eupatorium adenophorum* (9), *Hypericum perforatum* (59), and *Taraxacum officinale* (66).

In some plant groups apomixis replaces sexual reproduction altogether (obligate apomixis), whereas in others, some seeds are formed by the sexual process and the remainder are produced asexually (facultative apomixis). In apomictic species, population variation is split into a series of homogeneous groupings, each differing from one another in minor features. Facultative apomixis provides enormous breeding and evolutionary potential, enabling both genetic recombination and the replication of successful genotypes (67).

Unfortunately, there have been few detailed studies of genetic variation in apomictic species. Solbrig and Simpson (68) demonstrated the presence of a minimum of four electrophoretically distinct genotypes of

Taraxacum officinale (common dandelion) among 300 plants sampled from three adjacent but contrasting habitats in Michigan. Two of these genotypes were common but differed in their relative abundance at the sites. Detailed uniform garden and transplant studies provided strong evidence that the two biotypes possessed contrasting suites of life history traits and were differentially adapted to their respective habitats (68,69). It is not known whether the adaptive differentiation evolved at the site or resulted from introduction of preadapted weed forms.

Usberti and Jain (70) compared allozyme variation at eight gene loci in six populations of the facultative apomict *Panicum maximum*, a roadside weed in many parts of the tropics (71). Three populations were sexual, and the remainder reproduced by a mixture of sexual and apomictic reproduction. The entirely sexual populations exhibited consistently higher genetic variation within populations with $P = 100.0, 50.0$; $A = 2.69, 1.92$; and $PI = 0.377, 0.139$ (refer to the section on measurement of variation), for the sexual and asexual populations, respectively. However, the asexual populations displayed a considerable degree of genetic heterogeneity among the populations sampled.

More information is required on the genetic structure of populations of apomictic weeds, and it is premature to attempt generalizations. Of crucial importance is the amount of genetic recombination that occurs within populations. The balance between sexual and asexual reproduction has a genetic basis in some apomictic species but can also be influenced by environmental factors (63,67,72).

Sexual Reproduction

Inbreeders. Colonization of unoccupied sites is an important feature of the life history of weeds. Therefore, it is perhaps not surprising that most are capable of self-fertilization and hence autogamous seed production. Autogamy ensures the production of seeds irrespective of the proximity of mates (73), the high genetic fidelity of progeny (74), and the maintenance of adaptive gene combinations (39,75). Many of the most successful and widespread weeds, including *Ammannia coccinea, Avena fatua, Chenopodium album, Echinochloa crus-galli, Erodium cicutarium, Hordeum murinum, Lactuca serriola, Monochoria vaginalis, Oxalis corniculata, Portulaca oleracea, Rottboellia exaltata,* and *Rumex crispus,* are primarily self-fertilizing (5,12,17,31).

Two major viewpoints on the genetic structure of self-fertilizing species have developed during the past three decades. Darlington and Mather (76) and Stebbins (74) argued that populations of inbreeders are likely to be composed of one or a few highly fit homozygotes and thus near

uniform populations. On the other hand, in a review of the genetics of inbreeding populations, Allard et al. (77) concluded that although inbreeding should theoretically lead to homozygosis and a greater chance of selection among homozygotes (free variability), this may or may not be realized in natural populations of autogamous plants. After reviewing data on the population structure of several widespread self-pollinating weeds, Allard (31) and Kannenberg and Allard (33) concluded that local populations could be composed of a very large number of different genotypes and that most individuals were heterozygous to some extent.

Today it is recognized that these viewpoints represent opposite ends of a spectrum of conditions found in inbreeding species (78). Furthermore, as Jain (78,79) has emphasized, it is also possible to find these extremes among populations of a single species. For example, populations of *Avena barbata* from California are largely monomorphic for morphologic and allozyme markers throughout much of the Central Valley, the Sierra Nevada foothills, and southern California. In contrast, in the adjacent coastal range, populations are polymorphic to a varying degree with highly variable populations occurring in the vicinity of the San Francisco Bay area (26,79). Hypotheses to account for these differences in the patterns of genetic variation include founder effect, small differences in outcrossing rates among populations, and perhaps introgressive hybridization with the cultivated oat *A. sativa* (79). Related studies in California on *A. fatua* have demonstrated substantial stores of genetic variation within populations such that no two individuals appear to be genetically similar (25,26,32).

In contrast, several recent surveys of enzyme variation in widespread inbreeding weed species have demonstrated almost no detectable genetic variation. The cattails *Typha latifolia* and *T. domingensis* are emergent perennial aquatics that are native and widespread throughout North America. Although they constitute important components of marshland vegetation, they are also common weeds of irrigation canals, drainage ditches, and cultivated rice fields (17). Mashburn et al. (80) sampled 74 populations of *T. latifolia* and 52 populations of *T. domingensis* from the southeastern United States. They found no variation in electrophoretic assays involving 10 enzyme systems. The study was recently extended to include more than 500 *Typha* stands from a broad geographic range in North America with similar findings. Sharitz and co-workers (80) suggest that the apparent lack of intraspecific allozyme variability in *Typha* may be associated with several factors, including extensive inbreeding in the species, genetic drift, and undetected variability at regulatory loci (80,81). The work is of particular interest because of earlier reports of ecotype formation in North American populations of *Typha* (82).

In Australia, Moran and Marshall (83) surveyed the degree of genetic polymorphism at 13 enzyme loci in 12 populations of the cocklebur (Noogoora burr) *Xanthium strumarium*. The species is a predominantly inbreeding, monoecious annual of worldwide distribution, reported as a weed in 11 crops from 28 countries (27). The species is highly polymorphic and has been divided into eight races on the basis of fruit morphology (84). Four of these races are naturalized in Australia, and all were included in Moran and Marshall's study. This study found very little variation within each of the four races, although they were genetically differentiated from one another. Within three of the races all individuals assayed were homozygous for the same alleles at all gene loci. Hence the races in Australia may be represented by a single genotype at these loci (83). It is not known whether founder effects are responsible for the allozyme uniformity of *X. strumarium* in Australia. Surveys of populations from the native New World range may resolve this question.

In a broad electrophoretic survey of 10 taxa in the New World *Solanum* section *Androceras*, Whalen (85) found that the eight annual weeds in the group displayed significantly lower levels of genetic variation than did the two perennial nonweeds. Of the 19 populations of the weed taxa included in the survey, most were genetically monomorphic at the seven gene loci assayed. Additional evidence of low levels of allozyme variation within and in some cases among populations of weed species come from the studies of Levin (86) on *Oenothera biennis*, Rick et al. (87) on *Lycopersicon pimpinellifolium*, Crawford and Wilson (88,89) on *Chenopodium* spp., and Moran on *Xanthium spinosum* and Marshall and Weiss on *Emex spinosa* (both unpublished, cited in Ref. 12).

In summary, although populations of inbreeding weeds can contain significant amounts of genetic variation, it appears that in a significant number of cases populations are markedly depauperate in allozyme variation when compared to nonweed species. This pattern could arise from genetic bottlenecks associated with colonization and as a result of habitual inbreeding. As is discussed later, some of these findings may have important implications for biological control.

Outcrossers. Outcrossing mechanisms such as self-incompatibility and dioecism restrict colonizing ability since population establishment requires the introduction of at least two compatible individuals to a site (73,74). Few widespread weeds exhibit such mechanisms, although exceptions include *Rumex* spp. and *Silene alba*, which are dioecious (54), and *Helianthus annuus* and *Turnera ulmifolia*, which possess self-incompatibility systems (90,91). Nevertheless, many self-compatible weeds are outbred to some extent, thus enhancing the buildup of genetic variation in populations.

There are relatively few studies of the levels of genetic variation in fully outbreeding weeds because of the general scarcity of such weeds. Among these, assays of enzyme polymorphisms in *Helianthus annuus* and *Lolium* spp. (cited in Ref. 4) have demonstrated substantial amounts of genetic variation both within and among populations. Also, surveys of a large number of nonweed species (4,39,41) indicate that the overall levels of genetic variation in outbreeding species are significantly higher than those of inbreeders (Table 4).

HYBRIDIZATION AND POLYPLOIDY

The migration of weeds into unoccupied territory can provide opportunities for hybridization with related taxa. In some cases one of the hybridizing species may be native to the area, as in the case of hybridization between the native *Silene dioica* and the introduced weed *S. alba* in Great Britain (92). Alternatively, several species may be sympatric in the alien range and produce hybrids, as in *Tragopogon* spp. in western North America (see following paragraphs and Ref. 93). In either case hybridization and the establishment of hybrid progeny may be favored because of the disturbed, open nature of many weed habitats. The products of

TABLE 4.   Levels of Electrophoretically Detectable Genetic Variation in Plants from Different Stages of Succession and with Varying Patterns of Mating

Plants from Different Stages of Succession and with Varying Mating Systems	Number of Species (N)	Mean No. of Loci	Percentage of Loci Polymorphic (P)	Number of Alleles per Locus (A)	Polymorphic Index[a] (PI)
Stages of Succession					
Weedy and early	54	12.5	29.7	1.6	0.116
Middle	49	9.7	37.9	1.6	0.137
Late	10	12.0	62.8	2.1	0.271
Mating System					
Selfed	33	14.2	17.9	1.3	0.058
Mixed	42	8.6	14.2	1.8	0.181
Outcrossed	36	11.3	51.1	1.9	0.185

Source: After Hamrick et al. (4). Reproduced, with permission, from the *Annual Review of Ecology and Systematics*, Vol. 10, copyright 1979 by Annual Reviews, Inc.

[a]$P < .01$ following ANOVA.

hybridization vary and can include (1) new more vigorous genotypes, as in *Carduus nutans* and *C. acanthoides* in Canada (94) and *Emex spinosa* and *E. australis* in Australia (95); (2) sterile, but vegetatively vigorous types such as *Salvinia molesta* (48,49); (3) hybrid swarms as in *Raphanus sativus* and *R. raphanistrum* (96) and *Helianthus* spp. (90,97,98) in California; and (4) formation of new species, such as *Spartina anglica* (99,100), *Galeopsis tetrahit* (101), and *Lamium moluccellifolium* (102) in Europe. Usually the resultant hybrid populations contain substantially more genetic variability than do those of their progenitors.

Several examples serve to illustrate the point. *Helianthus annuus* (common sunflower) is a widespread annual weed of ruderal habitats that is native to parts of North America. It is unusual among annual weeds in exhibiting several features not normally associated with colonizing ability. These features are self-incompatibility, a relatively low reproductive capacity, and weakly developed seed dispersal and dormancy mechanisms. However, the species is highly variable both morphologically and physiologically, and Heiser (90) has suggested that this variation may be the key to its success as a weed. Heiser's detailed studies of annual *Helianthus* spp. (90,103,104) suggest that the great variability of *H. annuus* has resulted from frequent hybridization with related species during its westward migration in association with humans. Enrichment of the gene pool of *H. annuus* may have enabled colonization of a broad range of habitats. *Helianthus annuus* may be considered a compilospecies, that is, "a genetically aggressive species, plundering related species of their heredities" (105). Much of the variability in other weed complexes may arise from similar processes, although it may often be difficult to distinguish the effects of introgressive hybridization from simple ecotypic differentiation (98,106).

Hybridization can set the stage for polyploid formation and the evolution of new species. This has occurred among biennial *Tragopogon* spp. (salsify or goat's beard), which are common ruderal weeds in North America and native to the Old World. The three diploid species, *T. dubius*, *T. porrifolius*, and *T. pratensis*, are frequently found together and sterile F_1 hybrids are formed (93). As a result of the natural doubling of the chromosomes of F_1 hybrids, two tetraploid species, *T. mirus* and *T. miscellus*, were formed during this century in populations from Washington and Idaho. Using morphologic and karyologic evidence, Ownbey (93) was able to document the parentage of these new weeds, which are the only unambiguous examples of the recent natural origin of allotetraploid plant species.

In an effort to verify the parentage of the new *Tragopogon* species and to compare the patterns of electrophoretic variation in the diploids and

tetraploids, Roose and Gottlieb (107) analyzed variability in 13 enzyme systems coded by a minimum of 21 gene loci. The study confirmed the proposed phylogeny of Ownbey (93) and revealed striking differences in the patterns of genetic variation among the five species. Populations of the three diploids were monomorphic, or nearly so, for different alleles at about 40% of their genes. Only six of the 292 individuals sampled were heterozygous at a single gene. In contrast, the tetraploids exhibited a fixed heterozygous multienzyme, phenotype specified, respectively, by 43% (*T. mirus*) and 33% (*T. miscellus*) of the 21 duplicated genes examined. With few exceptions, heterozygosity was displayed by all tetraploid individuals. Roose and Gottlieb (107) suggested that substantial levels of fixed heterozygosity and the resultant enzyme multiplicity may contribute to the wide ecological amplitude of polyploid species. It is noteworthy that since its origin *T. miscellus* has become a common weed in the vicinity of Spokane, Washington.

Nearly all the world's most serious weeds are polyploids (12). Presumably, the hybrid origin of many polyploids and the resultant high levels of fixed heterozygosity confers greater tolerance to environmental heterogeneity (107,108). In addition to the intergenomic diversity per homoeologous set of genes, there is evidence that polyploids may be more variable intragenomically than diploids (12). Thus among weedy groups it is probable that taxa with high chromosome numbers produce a variety of recombinant progeny and maintain a greater degree of genetic variation in populations than do their related diploid species.

ENVIRONMENTAL HETEROGENEITY

Although the genetic system and in particular the pattern of mating may strongly influence the genetic composition of offspring, the selective exigencies of the environment ultimately mold the genetic structure of populations. Theoretical studies (109,110) and limited empirical evidence (111,112), suggest a positive relationship between the levels of genetic variation in populations and the degree of environmental heterogeneity. Apart from the problem of measuring and comparing environmental heterogeneity among habitats, it is often difficult to determine the direction of causality. Do heterogeneous environments select for genetic diversity, or are populations with high genetic variation fitter in variable environments?

In the survey of Hamrick et al. (4), taxa from weedy (disturbed) and early successional habitats were significantly less variable than those from the middle and climax stages of succession (Table 4). Because of their simple structure and relatively low biotic diversity, weed habitats are

generally considered less heterogeneous than most other vegetation types (4,113). Considering just weed habitats and assuming that a relationship does exist between genetic variation and environmental heterogeneity, we may make several predictions. First, populations of agrestals should in general exhibit lower genetic variation than those of ruderals or range-land weeds. This follows from differences between the habitats occupied by these weed groups. Agroecosystems, particularly those involving monocultures of annual crops, are deliberately made uniform by the agriculturalist and can be highly predictable in time and space. In contrast, ruderal habitats tend to be more complex, and in grassland habitats considerable biotic and edaphic diversity may occur. Whereas weeds of crops may be surrounded by a single genetic strain, ruderal and pasture weeds may interact with a variety of neighbors. Second, we may expect that specialized crop weeds such as crop mimics that are restricted to a particular crop (e.g., *Echinochloa crus-galli* var. *oryzicola* in rice) may be less variable than agrestals capable of infesting a wide range of different crops (e.g., *E. crus-galli* var. *crus-galli*, *Cynodon dactylon*, and *Cyperus rotundus*). Unfortunately, most electrophoretic studies of genetic variation in weeds have so far dealt with widespread ruderal species. Surveys of genetic variation in agricultural weeds are also required.

IMPLICATIONS FOR BIOLOGICAL CONTROL

Diseases and insects exert strong selective pressures on the genetic systems and evolution of plant populations (113,114). The greatest forces are exerted on long-lived, relatively stable communities, especially tropical climax communities. The weakest pathogen and herbivore pressures ostensibly occur in transient, weedy communities of the temperate regions. Levin (113) has suggested that this pattern is a function of host predictability. In a North American survey, annual plants (mostly weeds) were found to have fewer pathogens per unit area or vegetational zone than did perennial herbs, shrubs, or trees (113). Nevertheless, weeds are invariably attacked by diseases and insects, and there has been a growing recognition over the past two decades that plant pathogens have a potential for the control of weeds (116–118).

An important issue concerns the likelihood of weeds evolving disease resistance after release of a pathogen into an area or during repeated applications of a microbial herbicide. Because of our general ignorance of the processes of coevolution in natural communities, it is difficult to make precise predictions of the outcome of such weed-pathogen interactions. Much will depend on the levels and nature of genetic variation in both the

host and the pathogen. Two possibilities could arise. In the first case, resistance genes may be absent from the gene pool of the weed in the introduced region. Whether resistance would arise and how long this might take are matters of speculation. Nelson (119) has suggested that in natural communities the evolution of *de novo* resistance to a "new" parasite is probably accomplished by a simple genetic change at a single locus resulting in "race-specific" resistance. Subsequent coevolution would result in the ultimate accumulation of many resistance and fitness genes in the host and pathogen, and the establishment of a host-pathogen genetic equilibrium (120). Alternatively, resistance genes may already be present in the gene pool of the weed as a result of previous coevolutionary interactions with the pathogen in other regions of the world. It is uncertain whether such genes would be maintained in the absence of the specific plant pathogen. It is possible that they would be lost either because there is some cost associated with their maintenance or through random mutations. Leonard and Czochor (115) have recently reviewed much of the theoretical work concerned with the population genetics and evolution of host-pathogen interactions, but more empirical studies are required before firm conclusions can be reached (see also Chapter 7).

It is relevant at this point to consider the responses of weed populations to herbicides. Despite the extensive and repeated use of chemical control methods during the past 30 years, relatively few cases of the evolution of genetic resistance to specific herbicides have been reported, although there are numerous examples of variation in response of weed populations to herbicides (121). The only cases where genetic resistance has developed in the field as a result of herbicide treatments involve the S-triazines, atrazine and simazine. All taxa involved are temperate annuals and include *Ambrosia artemisiifolia* (122), *Amaranthus retroflexus* (123), *Brassica campestris* (124), *Capsella bursa-pastoris* (125), *Chenopodium album* (126), *Chenopodium strictum* (127), *Poa annua* (128), and *Senecio vulgaris* (129).

Gressel and Segel (130) have explored some of the possible reasons for the limited number of cases of the evolution of genetic resistance to herbicides in weed species. Several of the factors they have discussed are relevant to the microbial herbicide situation. Of particular importance are the selection pressures exerted by the control agent, the degree of phenotypic plasticity exhibited by the weed, and the dormancy and germination behavior of the weed seed reservoir. For each factor, the important consideration is the presence in the weed population of significant numbers of surviving, susceptible genotypes. In the case of the weed seed reservoir, the buffering action of the seed bank of dormant, susceptible

genotypes is likely to retard the development of resistance, particularly in weed species capable of some outcrossing.

In future microbial herbicide research it will be particularly important to determine whether weed survival results from true genetic resistance or simply from environmental factors (microclimate, application efficiency, etc.). Progeny tests of surviving individuals, followed by exposure to the plant pathogen under test, should provide an answer to this question. It is probable that in many cases an interaction of genetic and environmental factors will influence the degree of susceptibility exhibited by the host.

It has been suggested that species with reproductive systems that restrict recombination, and hence favor genetic uniformity, are more likely to succumb to disease outbreaks (57,113,131,132). In this regard, it is of interest that many of the successful cases of biological control of weeds have involved primarily asexually reproducing species (e.g., apomicts such as *Chondrilla juncea, Eupatorium adenophorum, Hypericum perforatum, Opuntia* spp., and *Rubus penetrans*). Burdon and Marshall (133) examined the degree of biological control achieved in 81 different attempts in a total of 45 weed species. They demonstrated a significant correlation between the degree of control and the predominant mode of reproduction of the target species. Asexually reproducing species were effectively controlled more often than those reproducing by sexual means (Table 5). Presumably, successful biological control is favored by limited amounts of genetic variation in weed populations. If this is true, many aquatic weeds that reproduce predominantly by clonal propagation (e.g., *Alternanthera philoxeroides, Elodea canadensis, Eichhornia crassipes, Hydrilla verticillata, Pistia stratiotes,* and *Salvinia molesta*) would seem to be excellent targets for biological control. The low levels or absence of sexual reproduction in many populations of these species would reduce the likelihood of coevolutionary responses following the introduction of a plant pathogen.

TABLE 5. Reproductive System and Average Degree of Control of Weeds Utilized in Biological Control Program

Major Reproductive Mode	Degree of Control Achieved (%)			
	None	Partial	Substantial	Complete
Asexual (n = 24 spp.)	4.2	8.1	39.0	48.7
Sexual (n = 16 spp.)	18.7	56.7	15.6	8.9

Source: Burdon and Marshall (133).

A final word of caution is required in this discussion of the relationship between genetic variation and biological control. It is quite possible that in many weed species the actual amount of genetic variation in populations will be a poor predictor of whether successful control can be achieved. What is probably more important is the nature of the genetic variation present in populations and how this will influence the rate at which host resistance may evolve under field conditions. Unfortunately, at this time little is known of the evolution and maintenance of host resistance in natural plant populations.

CONCLUSIONS

Compared with other plant life forms, populations of weed species frequently exhibit limited genetic variation. Such limited genetic variation may be the result of genetic bottlenecks associated with repeated episodes of colonization, extensive clonal propagation, inbreeding, and the relative environmental homogeneity of many agroecosystems. Nevertheless, populations of some weed species contain substantial stores of genetic variation, and interpopulation genetic differentiation is a pervasive feature of widely distributed weeds. The development of a high level of genetic diversity among weed populations is fostered by multiple seed introductions, habitat longevity, environmental heterogeneity, large population size, outbreeding, and hybridization with related taxa. Limited evidence involving biological control agents suggest that asexually reproducing weeds are more easily controlled than sexual species. This difference may be associated with the lower levels of genetic variation present in weed species with restricted recombination systems.

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