5. Genetics of weed invasions

SPENCER C. H. BARRETT

Abstract

Understanding the genetics of colonization is important not only to evolutionary studies and population biology, but also to agriculture and conservation. Basic features of weediness and successful worldwide colonists are briefly reviewed with emphasis on genetic processes. Based on a detailed review of breeding system and genetic variation patterns in *Echinochloa* (barnyard grass) and *Eichhornia* (water hyacinth), two major aquatic weeds, strong evidence is found for the effects of founder events as well as strong selective pressures during colonization. Information on the genetic structure, reproductive biology, and evolutionary dynamics in the past and present would be helpful in devising effective methods of biological control. For example, there is indirect evidence for greater success in the biological control of asexually reproducing weeds. This is clearly a largely unexplored area in population biology.

Introduction

While weeds have a long history of association with man and his crops, the scientific study of their biology is little more than a century old. The numerical abundance of weeds in areas of human settlement, their detrimental effects on crop yields and the rapidity with which populations appear and disappear have stimulated naturalists, botanists and agricultural scientists to investigate the success of weed invasions in terms of ecological and historical factors, the morphological and physiological pre-adaptations of weeds, and more recently in the context of chemical control methods (Gray 1879; Zinger 1909; Harper 1960; Salisbury 1961; Crafts and Robbins 1962; Baker and Stebbins 1965; King 1966; Muzik 1970; Baker 1974; Holm *et al.* 1977). The changing approaches to the study of weed biology reflects an increased knowledge of their distribution and ecology as well as the growth of ideas in various biological sub-disciplines. In the past decade the development of population biology as a vigorous field of inquiry has resulted in the frequent use of weed groups as experimental systems for studies on a variety of topics including demography (Mack and Pyke 1983; Burdon *et al.* 1983), life history theory (Law *et al.* 1977), the significance of genetic polymorphism

and phenotypic plasticity to colonizing ability (Moran *et al.* 1981; Martins and Jain 1978) and mating system evolution (Clegg *et al.* 1985; Barrett and Shore 1987).

Studies of the population biology of weeds frequently involves a synthesis of information on the ecology, physiology, and genetics of populations as attempts are made to understand the development of colonizing ability in the context of both community interactions and evolution change. While population studies of weeds have enriched our understanding of many aspects of plant systematics, ecology and evolution, in general they have had relatively little impact on applied research on weeds where the primary objective is usually the eradication of populations. This situation, which has been discussed in detail by Sagar (1968), is partly reinforced by the institutional divisions that occur between biology and agriculture in most universities, particularly in N. America. Researchers in the two fields often work in isolation, affiliated with different departments and with only limited opportunities for interaction.

A considerable amount of the botanical work conducted on weeds that is relevant to applied research has been concerned with identification problems in taxonomically difficult weed groups (Warburg 1960; McNeill 1976; Barrett and Strother 1978), studies of the factors that influence the dormancy and germination characteristics of populations (Roberts 1964; Popay and Roberts 1970; Barrett and Wilson 1983) or the magnitude of weed competition on crop yields (Bleasdale 1966; Firbank and Watkinson 1986). Until recently there has been relatively little work on the genetics of weed populations, aside from early investigations of race formation which were largely undertaken within a biosystematic framework.

In this chapter I review the information currently available about the genetic characteristics of weed populations and in particular focus on some of the ecological and genetic consequences of long distance colonizing episodes that are a feature of many cosmopolitan weed species. I hope to show that basic information on the levels and organization of genetic diversity in weed populations is of value to applied biologists concerned with weed control. Since plant reproductive systems are of prime importance in determining the amounts of genetic variation in populations, I shall also discuss how studies of the reproductive biology of weed populations can have implications for the type of control practices employed to eradicate weed populations. Before I review these examples, which come from our own studies of *Eichhornia* (Water Hyacinth) and *Echinochloa* (Barnyard grass). I briefly discuss some of the prevailing ideas about the ecological and genetic attributes of successful weed species and what is known about the patterns of genetic variation in populations.

General features of weeds

Weediness has evolved many times among angiosperm families and weed

species can be found occupying a variety of different types of disturbed environments. As a consequence, a broad range of colonizing strategies are employed by weed species. Since weed invasions occur on very different scales, from range extensions and local habitat shifts to intercontinental migration, it has been suggested by Brown and Marshall (1981) that the selection pressures acting on weed populations will vary with species and event such that each case is unique. Despite this obvious complexity, many attempts either through floristic surveys (Stebbins 1965; Price and Jain 1981; Newsome and Noble 1986) or by comparative studies of related taxa (Baker 1965; Jain 1969; Barrett and Wilson 1981) have been made to identify shared attributes that are commonly found in successful weed species (Baker 1974; Brown and Marshall 1981; Barrett and Richardson 1986).

Some general features of weeds that are relevant to their genetics and evolution are summarized in Table 1. Of course many cases can be found where a particular weed species possesses traits not normally associated with high colonizing ability (e.g. Heiser 1965; Barrett 1978). Where this occurs it is often valuable to examine whether possession of such traits constrains weediness in any way, and if not, what other attributes contribute towards colonizing success. What usually emerges is that a suite of co-adapted traits are involved in determining weediness and it is the coordinated response and joint evolution of these traits that determine the particular fates of individual biological invasions. Quantitative genetic analysis of these character syndromes in conjunction with demographic and life history studies of natural and artificially established colonies may offer the most promise in untangling those features of weeds that are critical to colonizing success (also see Vrijenhock 1990, for an excellent review of asexuality in colonizing species).

Patterns of genetic variation in weeds

The earliest studies of variation in weed species were largely directed towards describing the patterns of ecotypical differentiation among populations in relation to easily measured environmental factors. In widespread species, marked inter-population genetic differentiation can be regarded as the rule and individual populations usually display distinctive morphological and ecological properties. The amount of variation is associated with adaptation to the local environment as opposed to genetic drift has rarely been investigated although reciprocal sowing and transplant studies can be useful in this regard. Applied biologists should be aware that race formation in weeds is both ubiquitous and rapid although the high phenotypic plasticity of many weed species can complicate attempts to assess the nature of genetic differentiation based strictly on field observations. By growing samples collected from different sites under uniform garden or glasshouse conditions, the magnitude of population differentiation can be assessed directly. When studies of this type are undertaken it is usually apparent that a considerable amount of both morphological and ecological variety is subsumed within the

Table 1. Some ecological and genetical features of weeds (modified from Baker 1965 and Brown and Marshall 1981).

1. Well developed dormancy mechanisms with germination requirements fulfilled in many environments.
2. Rapid growth, development and reproductive maturation.
3. High phenotypic plasticity often with the ability to reproduce as long as growing conditions permit.
4. Unspecialized pollination mechanisms involving self-pollination, wind-pollination or generalist insects.
5. Uniparental reproductive systems involving selfing, apomixis, or clonal propagation.
6. High reproductive capacities through seed or vegetative propagules.
7. Mechanisms for the short- and long-distance dispersal of weed.
8. Polyploidy with attendant fixed heterozygosity.
9. Genetically depauperate populations with strong multilocus associations that originate from a limited number of colonizing genotypes.
10. Substantial interpopulation differentiation owing to founder effects, drift and variable environments.

latin binomial. As a general rule statements about the ecological characteristics of weed species A or B based on studies of single populations should be treated with caution! Further discussion of the factors influencing race formation in weeds can be found in Baker (1974) and Barrett (1982, 1983).

Detailed studies of the patterns of genetic variation *within* weed populations are more recent and are largely in their infancy. Work of this type is important from both the pure and applied standpoints since the amount, kinds and organization of genetic diversity in populations will largely determine their capacity to respond to the local selection pressures imposed by the physical and biotic environment. Understanding the selection response of weed populations to specific agricultural practices might be particularly useful since it is possible that the crop environment could be manipulated to take advantage of the nature of genetic variation for important life history traits.

For example, the recent trend to shorten the growing period of many rice varieties in California may eventually lead to a loss of the rice mimic *Echinochloa phyllopogon* from fields as a result of the limited amounts of genetic variation in populations of the weed for maturation time (Barrett 1983). Seeds of the rice mimic are frequently harvested with those of cultivated rice at harvest and redistributed in contaminated rice seed the following year. Unfortunately there has been relatively little work on the quantitative genetics of agricultural weeds nor on the evolutionary responses of weed populations to agronomic practices. In some ways this is surprising since in comparison with plant populations from uncultivated land, agricultural weeds inhabit a relatively uniform environment in which the selective pressures are often easily identified and closely controlled. Furthermore weeds are abundant, possess rapid life cycles and are easily grown and

measured. As such they provide an excellent source of experimental material for the evolutionary geneticist.

The highly developed dispersal mechanisms and vagile life styles of most weeds have important consequences for the genetic structure of populations. In many cases the invasion of new territory is associated with frequent genetic bottlenecks, small population sizes, inbreeding and strong directional selection (Barrett and Husband 1989). These influences can result in rapid selection responses and an erosion of genetic variation in populations. Studies of electrophoretic variation in weed populations have revealed a large number of cases in which populations contain very low levels of genetic polymorphism or are completely uniform at isozyme loci. A variety of other factors can counteract these influences; these include the multiple introduction of genotypes from geographically separated and hence genetically differentiated source populations, outbreeding, introgressive hybridization with related taxa, and the rapid expansion of populations after founding. Table 2 lists some of the major factors influencing the levels of genetic variation in weed populations and the topic is covered well in several recent reviews (e.g., Brown and Marshall 1981; Clegg and Brown 1983; Jain 1983; Barrett and Richardson 1986; and Barrett and Shore 1988).

Reproductive systems

The methods by which a species reproduces can play a major role in determining the levels and pattern of genetic variation in populations. In perennial weeds the emphasis on clonal propagation and the frequency of sexual reproduction and seedling recruitment can have a profound influence on the genetic diversity of populations. In species where reproduction is principally

Table 2. Some factors that influence the level of genetic variation in weed populations (After Barrett 1981).

Factor	Influence
Founder effect	Number 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
Matin system	Level of inbreeding
Hybridization	Opportunities for gene exchange with related taxa
Environmental heterogeneity	Spatial and temporal variation of habitat

by seed, the mating system, the frequency of cross- and self-fertilization, controls the character of genetic transmission and the levels of heterozygosity in a population. Surveys of genetic variation among species with contrasting mating systems provide evidence of the importance of this component of the genetic system in regulating the level of genetic diversity within populations. In general outbreeding species display higher levels of genetic polymorphism, allelic variation and heterozygosity than predominantly selfing species (Brown 1979; Hamrick *et al.* 1979). However, since the mating system can be influenced by a range of environmental and demographic factors (Loveless and Hamrick 1984) and in addition can itself exhibit genetic variation, a wide frequency of outcrossing levels can be displayed by different populations of the same species (Schemske and Lande 1985). Accordingly, levels of genetic variation can also vary dramatically among different populations of a single species (Rick *et al.* 1979; Schoen 1982; Glover and Barrett 1987).

Most weed species are capable of some form of uniparental reproduction either through selfing, apomixis or clonal propagation (Baker 1965; Brown and Burdon 1987) and shifts in mating systems towards increased selfing are often associated with the colonization of unoccupied territory (Baker 1955; Lloyd 1980). Nevertheless, this pattern is not always found and in several studies (reviewed by Brown and Marshall 1981) increased outcrossing rates and heterozygosity have been found in colonizing populations in comparison with populations from presumed source regions. The diversity of reproductive systems that can be found both within and between plant species as well as the importance of local ecological factors in influencing the nature of reproduction should caution us against extrapolation of a species' reproductive behavior from one area to another based on studies from only a limited portion of its range. The following case studies of two weed groups will clearly illustrate this point.

Case studies of weed groups

The use of the comparative approach in studies of related taxa of colonizing species, originally pioneered during the 1960's by J. L. Harper (reviewed in Harper 1977) and Baker (1965), has provided valuable information on those ecological attributes that are likely to influence colonizing success. In recent years comparative studies have been extended to include experimental demographic studies of natural populations of a variety of weed species with contrasting life history characteristics and genetic systems (e.g. Sarukhan 1974; Solbrig and Simpson 1974; Jain and Martins 1979; Warwick 1980; Law 1981). These detailed studies have largely concerned ecological processes operating in one or a limited number of sites in close proximity to one another. Comparative ecological studies of populations from different portions of the range of widely-distributed weed species have been less frequently conducted because of the logistical difficulties inherent in such

work. In contrast genetic studies of geographically separate populations of cosmopolitan species are more easily undertaken since much of the experimental work is conducted at one location on plant material collected from different parts of the range. Valuable information on both the regional and geographical patterns of genetic diversity in wide ranging weed species has been obtained by using this approach (e.g. Clegg and Allard 1972; Kahler *et al.* 1980; Giles 1983; Bosbach and Hurka 1981; Lyman and Ellstrand 1984; Warwick *et al.* 1987). The next step in studies of the genetic structure of weed populations will be investigations of the temporal patterns of micro-evolutionary change within populations. To date there are few chronological studies of the flux of genotypes or phenotypes in weed populations through time (Burdon *et al.* 1983), despite the relevance of such an approach to the process of natural selection.

Our own work on the ecological genetics of weeds began with a careful consideration of which weed groups could be most profitably studied from both the biological and applied viewpoints. It was decided to investigate two groups of weeds of wide distribution and major economic importance but which displayed contrasting colonizing strategies. The two chosen were the free-floating aquatic weed *Eichhornia crassipes* (Water Hyacinth) and members of the *Echinochloa crus-galli* complex (Barnyard Grass), weeds of a broad range of crops. Perusal of the literature in the mid-seventies when the work began indicated that remarkably little was known of the ecological genetics of either species despite the fact that both are among the world's most noxious weeds (Table 3) and are excellent experimental organisms, being easily grown and widely available. The remainder of this chapter summarizes work on these two groups of weeds and their close relatives.

The water hyacinth genus (Eichhornia)

Eichhornia is perhaps the classic example of where a single species (*E. crassipes*) in a genus has become a serious weed whereas the remaining taxa shown only a limited tendency to become aggressive. All members of *Eichhornia* have widespread distributions in their native range, a feature of many aquatic plants. However, none have shown the dramatic world-wide spread of *E. crassipes*, despite the fact that several of the species (*E. azurea*, *E. paniculata*) have been used as pond ornamentals in various parts of the world and presumably have had opportunities to escape.

Comparisons of the genetic systems of *Eichhornia* species are largely uninformative in accounting for the difference in behavior between *E. crassipes* and its relatives (Table 4). Although predominant self-fertilization has evolved on a number of occasions in the genus, in association with the breakdown of trimorphic incompatibility (Barrett 1985a), the selfing species have shown no tendency to become aggressive weeds, despite the increased colonizing potential selfing might be expected to convey. While *E. crassipes*

Table 3. A ranked list of the world's worst 10 weeds of crops (after Brown and Marshall 1981 based on information in Holm *et al.* 1977).

Species	Distribution		Habit[a]	Pollination	Ployploid	Reproductive capacity
	Countries	Crops				
1. *Cyperus rotundus*	92	52	Per	Cross	*	tubers: 40 tons/ha
2. *Cynodon dactylon*	80	40	Per	Cross	*	stolons
3. *Echinochloa crus-galli*	61	36	Ann	Self	*	40,000 seeds/plant
4. *Echinochloa colonum*	60	35	Ann	Self	*	1,000 seeds/plant
5. *Eleusine indica*	60	46	Ann	Self?	*	135,000 seeds/plant
6. *Sorghum halepense*	53	30	Per	Cross	*	rhizomes: 33 tons/ha
7. *Imperata cylindrica*	73	35	Per	Cross?	?	rhizomes: 4.5×10^6 shoots/ha
8. *Eichhornia crassipes crassipes*	>65	waterways	Per	Cross[b]	*	stolons: 0.04 ha/ plant/season
9. *Portulaca oleracea*	81	45	Ann	Self	*	10,000 seeds/plant
10. *Chenopodium album*	47	40	Ann	Self	*	0.5×10^6 seeds/plant

[a] Per = perennial; Ann = annuasl.
[b] But see Table 4.

Table 4. Genetic systems and weediness in *eichhornia* species (modified from Barrett **and** Richardson 1986).

Taxon	Ploidy	Major breeding system*	Asexual reproduction	Distribution	Weed Status
E. paniculata	2×	tristylous	none	N. Brazil, Jamaica & Cuba	occasional in rice fields
E. paradoxa	2×	s. homostylous	none	neotropics; rare, disjunct	no reports
E. meyeri	2×	s. homostylous	none	Paraguay & Argentina, rare	no reports
E. azurea	4×	tristylous	moderate	neotropics; widespread	local problem
E. crassipes	4×	tristylous	highly developed	worldwide	noxious aquatic weed
E. heterosperma	4×	s. homostylous	moderate	netoropics; local	no reports
E. diversifolia	4×	s. homostylous	moderate	neotropics; widespread	occasional in rice fields
E. natans	—	s. homostylous	moderate	Africa; widespread	occasional in rice fields

* Tristylous species are largely outcrossing; semi-homostylous species are predominantly selfing. In each of the three tristylous species semi-homostylous races occur. The clonal structure of *E. crassipes* populations results in considerable inbreeding as a result of geitonogamy. For further details see Barrett 1977, 1979, 1985a.

is polyploid, so are several other species in the genus that exhibit no weedy tendencies.

Water Hyacinth's invasive powers are principally the result of its free-floating life form and prolific powers of asexual reproduction by stolons. No other member of the genus possesses the clonal architecture and free-floating habit which are adaptations to the periodic water-level fluctuations and temporary habitats that are a feature of Water Hyacinth's native Amazonian habitats. These observations of the genus *Eichhornia* support Stebbins' (1965) view that "no particular type of mating system or chromosomal condition is either necessary or generally favorable for pre-adapting a group of species to evolve in the direction of weediness. A hereditary predisposition toward weediness or the ability to colonize areas disturbed by human interference must reside in certain morphological and physiological characteristics of the plants concerned". In *E. crassipes* these are easily identified.

A. *Geographical distribution of style morphs*

In many parts of the adventive range of Water Hyacinth, it is represented by

a limited number of asexually reproducing clones and extensive areas of genetic uniformity prevail as a result of the rampant clonal multiplication of water-dispersed vegetative fragments. Water Hyacinth exhibits the rare genetic polymorphism tristyly (Barrett 1977) and observations of the geographical patterns of style morph distribution are a guide to the history of colonization, the occurrence of sexual reproduction, and the extent of genetic uniformity in an area. In the native Amazon Basin, Mato Grosso and parts of Argentina, all three style morphs occur although individual populations are often monomorphic. In the adventive range only two morphs are found, and the mid-styled morph predominates in most regions. This uneven distribution of style morphs is the result of founder effects and prolific clonal propagation (Fig. 1). Absence of the short-styled morph of *E. crassipes* from the introduced range is probably the result of chance. Short-styled genotypes were apparently not among the initial introductions to North and Central America and the Old World. As a result of the genetic basis of tristyly (two loci S, M, with two alleles at each locus and S epistatic to M), the short-styled morph cannot arise by segregation from crosses or selfs of long- and mid-styled morphs. Thus a separate introduction of this morph would be necessary for colonization of the alien range. This has not occurred.

The unusual pattern of style morph distribution in *E. crassipes* has led to several misconceptions about the reproductive biology of the species. Studies restricted to the alien range led to the conclusion that the short-styled morph was missing from the species and that the true breeding system was in fact
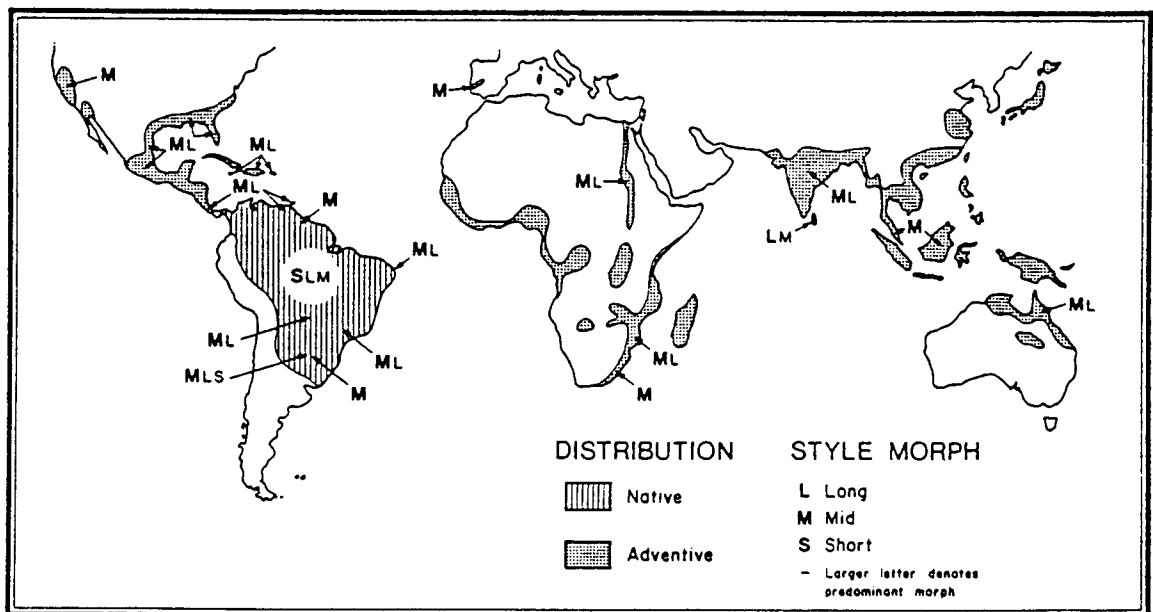

Fig. 1. The geogrpahical distribution of style morphs in *Ecihhornia crassipes*. After Barrett (1977) and Barrett and Forno (1982).

distyly (Faegri and van der Pijl 1971; Mulcahy 1975). In addition, because the species is heterostylous it has been repeatedly stated in the literature that individual clones are self-incompatible and that the absence of sexual reproduction in populations was because of their monomorphic structure (e.g. Baker 1965; Richards 1986). The apparent sterility of clones has led to the assumption that the destruction of vegetative colonies by herbicides or desiccation would largely eradicate the weed problem. However, while most heterostylous taxa are strongly self-incompatible, *E. crassipes* is an exception, with high levels of self-fertility a feature of most clones (Fig. 2). Our own field studies indicate that populations composed of a single style morph usually produce abundant seed, although seed germination and seedling establishment are usually restricted in many artificial water bodies (such as canals or reservoirs) owing to the absence of suitable safe sites for germination and establishment (Barrett 1985b).

Current management techniques employed for aquatic weed control in various parts of the world (e.g. "drawdowns" in Southeastern U.S.A.) involve the removal of water from infested lakes and reservoirs during certain periods of the year. This can result in the drying out and death of vegetative fragments. However, since large quantities of seed are also produced in most populations, these practices can provide an opportunity for seed germination and the establishment of seedlings, particularly if rains occur following the drying-out period. Interestingly, these weed management practices mimic the natural water level fluctuations that are a feature of Amazonian habitats to which the Water Hyacinth's sexual reproductive cycle is adapted. Weed control practices that enhance sexual reproduction can favor the build-up of genetic diversity in Water Hyacinth populations.

An indication of the successful occurrence of sexual reproduction in Water Hyacinth can be seen from observations of the patterns of style morph distribution in particular regions. Where water level fluctuations characterize an area, either as a result of seasonal climates (e.g. parts of India, Queensland)
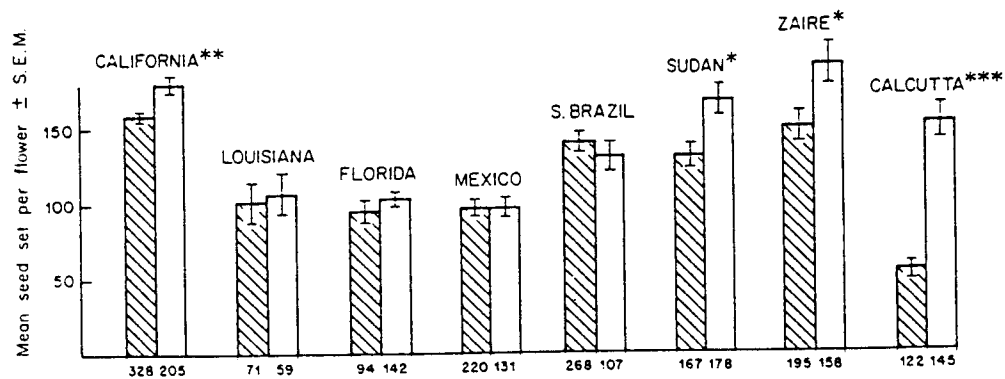

Fig. 2. Seed roduction following controlled self- and cross-pollinations of *Eichhornia crasspies* clones. All cross-polllinations involved a single clone from Costa Rica. Sample sizes are the number of flowers pollinated; *P < 0.025, **P < 0l01, *** P < 0.001. After Barrett (1981a).

or management techniques (S.E. U.S.A.) the long-styled morph is frequently found at low frequency in mid-styled populations. This morph arises through segregation as a result of self- and geitnogamous pollinations of mid-styled clones heterozygous at the *M* locus (*ssMm*). In California, where only the mid-styled morph occurs, clones are heterozygous at the *M* locus, and seed is produced in most populations. But the absence of suitable safe sites for seedling establishment prevent segregation of long-styled plants (Barrett 1980b).

Electrophoretic surveys of clonal diversity in different parts of the native and adventive range of Water Hyacinth would be valuable to establish whether the patterns evident for style length loci reflect the overall levels of genetic diversity in populations. We have used this approach in the related diploid *Eichhornia paniculata* which exhibits a remarkably similar pattern of style morph distribution associated with its migration from lowland South America to the Caribbean region.

In contrast to *E. crassipes*, reproduction and dispersal in *E. paniculata* is primarily by seed and its Caribbean distribution (Cuba and Jamaica) pre-dates human introduction suggesting natural spread to the region. Surveys of style morph distribution in populations of *E. paniculata* from N.E. Brazil indicate that the majority are tristylous although dimorphic (L, M) and monomorphic (M) populations occur. However, on Jamaica the short-styled morph is absent and monomorphic populations (M) predominate with dimorphic populations (L, M) occurring rarely (Barrett 1985a). Thus in both *Eichhornia* species the short-styled morph is largely restricted in its distribution to N. Brazil while throughout the remainder of the range the mid-styled morph predominates with the long-styled morph occurring less often. In both species these changes in population structure from trimorphism to monomorphism are associated with colonization of new territory and the breakdown of tristyly to homostyly (Barrett 1979, 1985b).

B. *Genetic variation in continental and island populations*

Investigations of the mating systems and genetic structure of *E. paniculata* populations from N.E. Brazil and Jamaica indicate the importance of founder effects and increased levels of self-fertilization on genetic diversity. A survey of 21 allozyme loci in 11 populations revealed that Jamaican populations were genetically depauperate in comparison with those from Brazil (Table 5). Outcrossing rates (t) were significantly correlated with the number of poly-morphic loci, and mean observed heterozygosity of populations (Barrett and Husband 1990). This demonstrates the important influence of the mating system on levels of genetic variation in populations (Fig. 3).

The low levels of allozyme polymorphism on Jamaica probably result from a restricted number of long-distance dispersal events to the island (Husband and Barrett 1991). Since self-pollinating variants of the mid-styled

Table 5. Summary of genetic differences between Brazilian and Jamaican populations of eichornia paniculata based on a survey of 21 isozyme loci (after Glover and Barrett 1987).

Parameter	Symbol	Brazil	Jamaica
% loci polymorphic per pop.	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 pops.	H_s	0.091	0.027
Gene diversity between pops.	G_{st}	0.40	0.57
Inter- to intra-pop. ratio	R_{st}	0.81	1.7
Av. genetic distance	$\bar{d}0.085$	0.049	

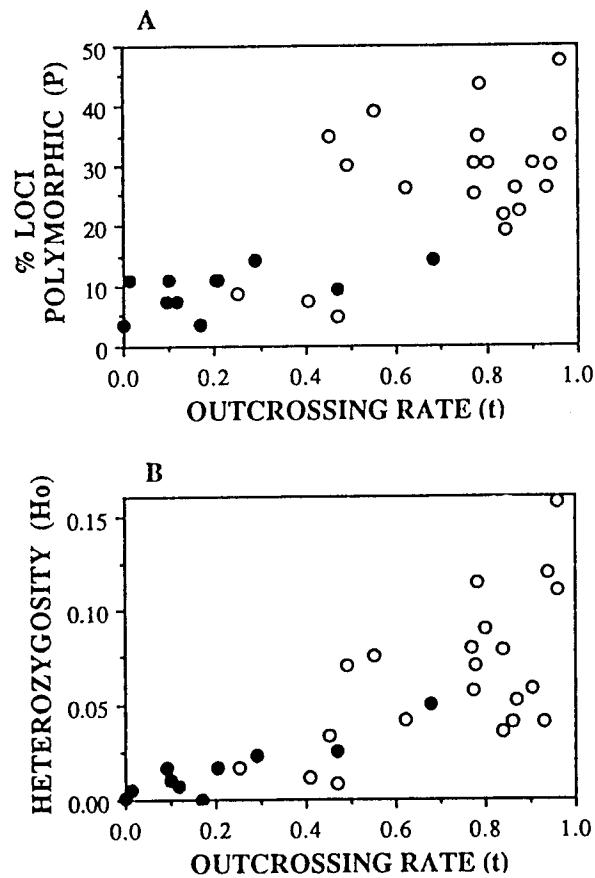Brazil N = 6 populations, Jamaica N = 5 populations

Fig. 3. The relationship between outcrossing rate (t) and the proportion of loci polymorphic (P), mean number of alleles per locus (K) and mean observed heterozygosity (Ho) in populations of *Eichhornia paniculata* from N.E. Brazil and Jamaica. Two additional self-pollinating monomorphic (M) populations from Jamaica were invariant at the 21 isozyme loci that were surveyed precluding estimates of t. After Glover and Barrett (1987).

morph predominate on Jamaica it seems likely that they were favored following establishment after long-distance dispersal. The primarily selfing mode of these variants in conjunction with genetic drift may have resulted in further losses of genetic variation during colonization. Differences in the mating system of *E. paniculata* populations in the two regions probably also account for differences in the partitioning of genetic variation within and among populations. Although populations within both regions are highly differentiated from one another, in N.E. Brazil populations contain more variation than is distributed among them, while in Jamaica the reverse pattern exists (Table 5).

Although the data for both style morph and allozyme loci indicate that Jamaican populations are relatively uniform with respect to genetic variation, it does not follow that they are entirely devoid of variation at other gene loci. A study of quantitative variation in several life history traits conducted in five Jamaican populations demonstrated significant between family variation for most traits within each population (S.C.H. Barrett, unpubl. data). Two of the populations included in the study were fixed for selfing variants of the mid-styled morph and contained no allozyme variation at the 21 loci surveyed. This disparity is in accord with several other studies that have compared variation in isozymes and quantitative traits and have found considerable variation in life history traits in species uniform with respect to electro-phoretically detectable enzyme variation (Moran *et al.* 1981; Giles 1983). Further discussion of the complex relationships between isozyme polymor-phisms and variation in quantitative traits can be found in Price *et al.* (1984), Lewontin (1984) and Brown and Burdon (1987). The latter authors suggest that because of the cohesive nature of the genome in selfers and apomicts, allozymes are likely to serve as useful neutral markers to index variation, without necessarily being causative agents.

Barnyard grasses (Echinochloa spp.)

Among the world's most noxious weeds of agriculture are members of the cosmopolitan genus *Echinochloa* (Barnyard Grass). The genus contains approximately 50 species of annual or perennial C_4 grasses that inhabit marshes, lake margins, riverbanks and other seasonally inundated habitats. Where man provides disturbed open environments with an assured moisture supply, such as with irrigated arable land, Barnyard Grasses often rapidly colonize and become serious weed problems. The most widespread and economically important member of the genus is the annual *E. crus-galli* which ranges from 50 °N to 40 °S latitude and is reported as a weed in 36 different crops in 61 countries (Holm *et al.* 1977; Maun and Barrett 1986). Other weeds of agriculture include *E. colona*, *E. crus-pavonis*, *E. oryzoides*, *E. phyllopogon* and *E. microstachya*. Superficial similarities between taxa in gross morphology, combined with their highly plastic nature, often results in

difficulties of identification for weed control specialists. This problem is particularly striking where cultivated rice is grown and it is commonplace to find 3—6 species of *Echinochloa* as weeds of rice in a particular region (Michael 1983).

Our research on this group has involved comparative studies of the ecological genetics of *Echinochloa* spp. that have invaded the rice agroeco-systems of California and New South Wales, Australia. Historical links between the two regions suggest that several barnyard grasses now present in Australian rice fields were introduced to the continent with imported rice seed stocks from California (McIntyre and Barrett 1986). Studies of the patterns of genetic variation in populations from the two regions have been used to substantiate this proposal as well as to provide insights into the pro-cesses of genetic differentiation following intercontinental dispersal (Barrett and Husband 1989).

The correct identification of taxa is a critical first step in any comparative study of the population biology of a group of closely related weeds. Thus at the outset we focussed our attention on unravelling the complex patterns of phenotypic variation in the two regions to determine how many taxonomic (and biological) species were present in each. The multiple introduction of genetic material in alien taxa, predominant self-fertilization, a high degree of phenotypic plasticity and considerable genetically-based morphological poly-morphism all contribute to the identification problems in *Echinochloa*. In California all variation has been treated as *E. crus-galli* when in reality several distinct species with contrasting ecologies and which pose different threats to yield reduction occur. Cytological and electrophoretic studies indicated that in California the variation can be organized into 4 separate intersterile assemblages each of which deserves specific rank. In Australia three of these taxa (*E. crus-galli*, *E. oryzoides*, *E. microstachya*) occur. The distribution and history of introduction to the two regions of the Barnyard Grasses studied are presented in (Table 6). Two important points are worth noting. First in both areas *E. crus-galli* is by far the most abundant and widespread species although the introduction of permanent deep water cul-ture in Californian rice fields has reduced population densities dramatically so that it no longer poses such a serious threat to crop yields (Barrett and Wilson 1983). In both countries the arrival of *E. crus-galli* predates the commencement of commercial rice production, which took place during the period 1912—15 in California (Barrett and Seaman 1980) and in the year 1926 in New South Wales (McIntyre and Barrett 1986).

The second point is that the earliest herbarium records of *E. oryzoides* and *E. phyllopogon* in California and *E. oryzoides* and *E. microstachya* in N. S. Wales are from rice experiment stations at Biggs and Leeton, respec-tively. This indicates that their introductions to both regions were most likely associated with the importation of contaminated rice seed stocks. Two lessons can be drawn from these observations. Clearly rigorous seed certifi-cation schemes need to be maintained to prevent the accidental introduction

of noxious weeds from one region to another. In addition, the fact that alien taxa are often collected for the first time in a country in the vicinity of research stations suggests that the early identification and elimination of potentially weedy populations should be encouraged soon after a species is introduced by chance or design.

The four species of Barnyard Grass in Table 6 can be divided into two broad ecological groups on the basis of their geographical distributions, habitat preferences and colonizing ability. *Echinochloa crus-galli* and *E. microstachya* are small seeded, highly fecund generalists capable of colonizing a broad spectrum of wet disturbed land both agricultural and ruderal (Barrett and Wilson 1981). The two species are very similar in overall appearance to the extent that flora writers rarely distinguish the two species and specimens of *E. microstachya* are usually filed as *E. crus-galli* in most herbaria. In contrast, *E. oryzoides* and *E. phyllopogon* are satellite weeds of rice with large seeds and lower fecundity (Barrett 1983). Despite their abundance in rice fields, populations rarely occur outside the rice agroecosystem and thus they can be viewed as obligate rice weed specialists. Figure 4 illustrates the differences in distribution of *E. crus-galli* and *E. oryzoides* in California.

A. *Genetic variation in generalist and specialist weeds*

The contrasts in distribution and ecological amplitude between the two *Echinochloa* groups raise the issue as to whether different patterns of genetic variation are associated with the generalist and specialist weed strategies. To examine this question a comparative study of the levels of genetic variation for isozyme loci and quantitative traits was undertaken in California an

Table 6. Distribution and history of introduction of barnyard grasses to California (U.S.A.) and New South Wales (Australia).

| Taxon origin	Ploidy	California	New South Wales
E. crus-galli Eurasia	(6×)	Widespread weed (introduced mid-19th Century)	Widespread weed (introduced late-19th Century)
E. oryzoides Asia	(6×)	Restricted to Californian rice fields earliest records 1912—15	Restricted to N.S.W. rice fields (earliest record 1938)
E. phyllopogon	(4×)	Restricted to Californian rice fields earliest records 1912—15	Absent
E. microstachya N. America	(4×)	Widespread in riverbanks, ditches, wasteground	Largely restricted to rice-growing areas (earliest record 1938)
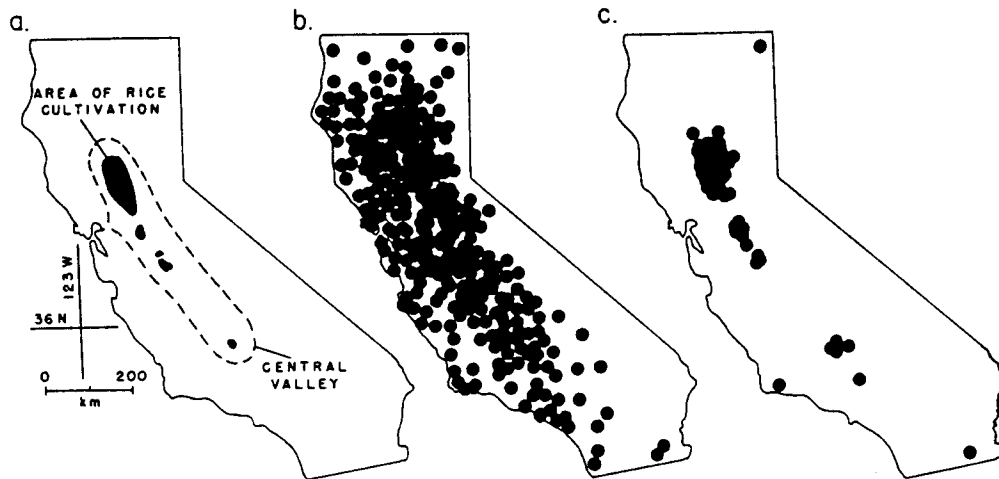
Fig. 4. The distribution of the generalist weed *Echinochloa crus-galli* and the specilaist rice weed *Echinochloa oryzoides* in relation to the areas of rice cultivation in California.

Australian populations of the two hexaploid species *E. crus-galli* and *E. oryzoides* (S. C. H. Barrett and A. H. D. Brown unpubl. data). In the Central Valley of California at each of 10 rice field sites, open pollinated families were collected of the two species. Populations of *E. oryzoides* were sampled from the flooded interior of rice fields whereas those of *E. crus-galli* were obtained from the mosaic of wet disturbed habitats around the edges of rice fields. Starch gel electrophoresis was then employed to assess the magnitude of enzyme polymorphism within and among populations of the two species.

Results of the study indicated that 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 expected in highly self-fertilizing species and has often been found in isozyme surveys of self-pollinating weeds (Brown and Marshall 1981; Brown and Burdon 1983, 1987). At virtually all sites sampled, populations of the generalist *E. crus-galli* were more variable at isozyme loci both in terms of the proportion of genes that displayed polymorphism and the number of alleles present within populations (Table 7).

Of particular interest were the differences in genetic polymorphism for loci controlling the enzyme alcohol dehydrogenase (*Adh*) in the two Barnyard Grass species. In *E. crus-galli*, a total of 12 homozygous multilocus genotypes were evident as a result of polymorphism at 1-3 loci. All populations in California contained at least one of the genotypes, with some composed of up to six, and most were characterized by different combinations of *Adh* genotypes. In contrast all populations of *E. oryzoides* except one, contained the same multilocus genotype. The exceptional population was fixed for a variant allele at a single locus. In a parallel survey of the other rice field specialist, *E. phyllopogon*, no variation was detected at *Adh* genes.

The almost complete absence of *Adh* variation in populations of the two

Table 7. Comparison of isozyme variation in Californian ricefields populations of *echinochla crus-galli* and *echinochloa oryzoides*. S. C. H. Barrett and A. H. D. Brown, unpublished data.

Site	echinochla crus-galli (n = 31 loci)			echinochloa oryzoides (n = 32 loci)		
	No. of polymorphic loci	No. of alleles at polymorphic loci	Diversity	No. of polymorphic loci	No. 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	8	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

specialist rice weeds may reflect selection of an "optimum" *Adh* genotype adapted to the relatively uniform conditions of flooded rice fields. In contrast, polymorphism at *Adh* genes in the generalist *E. crus-galli* may be maintained by the heterogeneous nature of the disturbed wetland habitats it occupies. Unfortunately, although there is considerable evidence that *Adh* enzymes function to enable plants to tolerate the anaerobic conditions associated with flooded environments the low levels of recombination in selfing species and strong linkage disequilibrium complicate attempts to determine the adaptive significance of variation at individual isozyme loci (Lewontin 1974). Surveys of *Adh* variation in other parts of the range of these Barnyard Grass species would, however, be valuable to establish whether the patterns observed in California occur elsewhere.

Studies of quantitative variation in life history traits in California populations of the two Barnyard Grass species were largely in accord with data obtained from isozymes. Populations of *E. crus-galli* contained significantly more between family variation than *E. oryzoides* for most traits that were examined. Particularly striking were the differences between the two species with respect to the time taken to flower from germination. Populations of *E. oryzoides* displayed strong synchrony in flowering time and a relatively small amount of inter-population genetic differentiation in comparison with *E. crus-galli*.

Historical factors in the form of founder effects and frequent genetic bottlenecks have undoubtedly played a major role in determining both the

levels and pattern of genetic variation in populations of the two *Echinochloa* species in California. Since agricultural weeds often initially enter a new region as crop seed contaminants, multiple introductions of genetic material would be expected in a generalist weed such as *E. crus-galli* which is associated with a range of different crop plants. In addition, its longer residency in the state would also provide more opportunities for this process to occur. In contrast the low overall levels of genetic variation in *E. oryzoides* may simply reflect a limited number of introductions of seed in contaminated rice stocks. In both species occasional outcrossing among different biotypes may enable some mixing of genetic variation although frequent colonizing episodes and the transient nature of many agricultural habitats are likely to retard the build up of genetic diversity in populations and the development of locally adapted races.

B. *Genetic bottlenecks associated with continental invasions*

The success of commercial rice production in California's Sacramento Valley provided the impetus to develop rice growing in the Murrumbidgee Irrigation Areas of N.S.W. (Australia) after observations of the similarities in soils and climate between the two regions. The first successful rice crop in Australia was sown in 1922 using imported Californian rice varieties (McIntyre and Barrett 1986). As mentioned earlier, among the earliest records in Australia of the rice weed specialist *E. oryzoides* and the N. American *E. microstachya* are from in and around rice fields at Leeton Rice Experiment Station (Table 6). This points to California as the most likely source area for the Australian invasion of the two Barnyard Grass species. Historical hypotheses such as this which involve tracing the origin of weed invasions can be assessed by the use of isozymes as genetic markers, as long as sufficient polymorphism occurs in the species under study. Isozymes can also be used to examine whether intercontinental dispersal events such as those proposed for the two Barnyard Grass species are associated with significant bottlenecks causing a reduction in genetic variation in the introduced area.

An isozyme survey of 10 rice field populations of *E. oryzoides* from N.S.W. indicated that all populations were genetically uniform at the 32 loci that were screened. The only variation observed involved a single population that was fixed for a variant allele at a locus coding for the enzyme *Pgm*. The Australian sample represents a highly limited extract of the genetic variation present in California, a pattern consistent with the historical information. A comparison of quantitative variation in California and Australian populations further indicates that populations from the two regions are for the most part indistinguishable from one another (Fig. 5). This suggests that relatively little genetic differentiation has occurred in response to local conditions following the species introduction to Australia. Two factors are likely to be important in this regard. First, the ecological conditions present in rice fields in the two
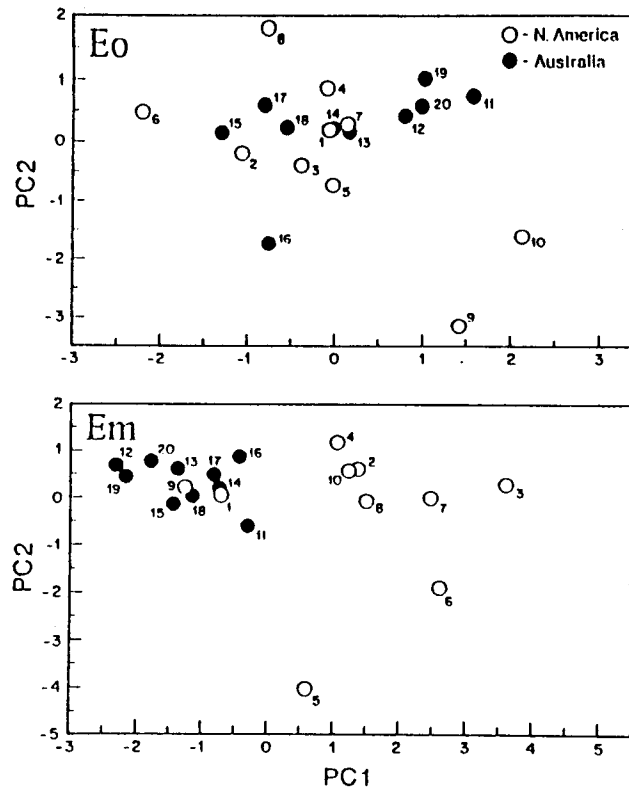
Fig. 5. Principal components analysis of quantitative variation in twelve life history traits in populations of Echinochloa oryzoides (Eo) and Echinochloa microstachya (Em) from N. America (open circles, 1—10) and Australia (closed circles, 11—20). The twenty populations of each species were grown under uniform glasshouse conditions. Note the absence of differentiation between populations from the two regions in E. oryzoides and in E. microstachya the occurrence of two N. American populations (1, 9) that cluster with the Austrlaian sample. The two populatiosna re from N. California (S. C. H. Barrett and A. H. D. Brown unpubl. data).

regions are quite similar and, secondly, the selection responses of Australian populations may be limited by a restricted amount of genetic variation present in the founding stocks.

The invasion of Australian rice fields by E. microstachya is of particular interest because it has no previous history as an agricultural weed and is limited in distribution for the most part to its native North America. The species is widespread in its native range as a ruderal weed of roadside ditches and open, naturally disturbed sites. It occurs commonly in N. California and at the present time is only occasionally found as a weed of rice. In common with E. crus-galli, the deep water conditions in California rice fields prevent successful establishment of E. microstachya and populations are largely restricted to levees and rice field edges. Prior to the introduction of permanent flooding in Californian rice fields, the species may have been a more troublesome weed problem but because of its similarity to E. crus-galli it was never recorded as such.

An isozyme survey of 20 N. American populations of *E. microstachya* revealed a high degree of inter-population genetic differentiation with each population largely composed of a unique multilocus isozyme genotype. However, the parallel survey of Australian populations collected from in and around N.S.W. rice fields revealed a markedly different pattern and one very similar to that observed in *E. oryzoides*. Of the 20 populations screened, 18 were genetically uniform and composed of the same multilocus genotype. Two variant gene loci (*Hk*, *Lap*) were evident in the remaining populations. Once again the Australian sample provides evidence for a marked genetic bottleneck associated with intercontinental migration. Of particular interest was the finding that the predominant Australian genotype could be identified from among the N. American sample of populations. The genotype occurred in a population from N. California close to Biggs Rice Experiment Station, the likely exit point for cultivated rice varieties shipped to Australia in the 1920's.

Comparisons of quantitative variation among populations from the two regions gave results that were in accord with those from the isozyme survey. A high degree of genetic differentiation was evident among the N. American sample, a result anticipated on the basis of the species wide distribution and concurrent likelihood of regional differentiation. In contrast a restricted range of variation was present among the Australian populations, a pattern indicative of a genetic bottleneck (Fig. 5). Interestingly, two populations of *E. microstachya* from N. California clustered with the Australian sample as a result of their similar life history attributes. Once again this points to N. California as the likely source region for the Australian invasion.

While the degree of genetic differentiation among Australian populations was restricted in comparison with the N. American sample, it should be noted that some local differentiation among populations was evident. In particular, there was small but significant genetic differentiation both within and between populations for the time taken to reach anthesis. This variation could have arisen since introduction to Australia as a result of the recombination and selection of polygenic mutation. Considerable amounts of quantitative genetic variation can be maintained by this process even in highly selfing species (Lande 1977). The variation may also have originated through recombination following hybridization between different founding stocks. Field studies would be required before we can conclude whether this variation reflects local adaptation to Australian conditions.

Relevance of genetic studies to weed control

The preceding case studies illustrate how in two widely distributed weed groups, founder effects and genetic bottlenecks can have an important influence on the levels of genetic diversity in a region. These processes are likely to be more pronounced in weeds than in many animal pests where it

has been argued that introduced populations maintain most of the genetic variation found in native populations (Myers and Sabath 1980). If this generalization holds up to further empirical study, it will likely reflect the prevalence of uniparental methods of reproduction in many weedy species. The occurrence of high levels of selfing, apomixis and clonal propagation can result in dramatic contrasts in population structure and levels of genetic diversity in populations occurring in different parts of the geographical range. In particular long distance migration on a continental scale is likely to be frequently associated with reduced levels of genetic diversity in newly occupied territory.

How can studies of the geographical patterns of genetic variation in weed species contribute to the development of effective weed control methods? Before we can examine this question it is important to distinguish the three main methods by which weed populations can be eradicated; i.e. biological, cultural and chemical control. Population studies are likely to have different implications for each of these methods, and to involve both direct and indirect benefits.

The conscious release of insect pests or fungal pathogens that destroy a specific weed species may be used to dramatically reduce, although not completely eradicate, populations. Of critical importance to the success of biological control programs is the likelihood of weed populations evolving resistance to pest or pathogen attack. There is some evidence that an association exists between the degree of control that has been achieved in biological control programs and the reproductive system of the target species. Asexually reproducing species appear to be more effectively controlled than those that reproduce by sexual means (Burdon and Marshall 1981). These authors suggest that successful biological control is favored by limited amounts of genetic variation in weed populations and that the reproductive system of a weed is one of the prime determinants of population genetic structure. Of course, from the viewpoint of biological control, the only genetic variation of relevance in the target weed is that which determines the differences in resistance or tolerance to control agents. Unfortunately at this time little is known about the patterns of host resistance in natural plant populations although a start has been made in examining this variation (Burdon 1985).

It is possible that if isozyme surveys of weed populations provide some index of the levels of genetic diversity in populations, they may be useful for providing a guide to the potential likelihood of the evolution of host resistance. A comparison of the patterns of genetic diversity revealed by isozyme studies in Australian populations of *Chondrilla juncea* (Burdon *et al.* 1980) and *Echium plantagineum* (Brown and Burdon 1983, 1987) is instructive in this regard. While the apomict *C. juncea* appears to be represented by only three genotypes in Australia, populations of the outbreeding *E. plantagineum* contain very high levels of genetic variation with virtually every member of the population possessing a unique genotype. The high level of polymorphism in *E. plantagineum* seems to have risen from multiple introduction of diverse

genetic material for ornamental use followed by subsequent hybridization among biotypes. These effects complicate any attempt to locate source areas within the native range for collection of potential control agents. In contrast, in *C. juncea* source regions for the three apomictic triploid clones present in Australia may be more easily located and genotype specific strains of potential biological control agents identified. In *C. juncea* there is already evidence of the presence of a genotype specific strain of the rust *Puccinia chondrillina* and this has been successfully employed for biological control in Australia (Cullen and Groves 1977; Burdon *et al.* 1981).

Information on genetic diversity may be particularly valuable for the control of clonally propagating aquatic weeds such as Water Hyacinth where only a small portion of the genetic diversity present in the native region has been introduced to the adventive range. In addition, the use of isozyme for pinpointing likely source areas of weed invasions may aid in increasing the efficiency of biological control programs by reducing the effort spent in searching for race or genotypic specific control agents in regions distant from source areas. It is noteworthy that while it has long been stressed in the biological control literature that comprehensive genetic sampling of potential control agents is necessary, the sampling of the range of genetic variation in the target weed has received much less attention. Adequate sampling of the weed is as important as that of the control agent if the aim is to ensure the best possible match between the two (Marshall *et al.*1980).

Cultural control methods encompass a broad range of agricultural practices including rotation and cultivation methods, water management, crop spacing and density, the timing of fallow periods, etc. Obviously a sound knowledge of the life history characteristics and population dynamics of problem weeds is critical in formulating cultural control methods (Crawley 1987). Mortimer (1983) has discussed at some length the importance of these approaches for understanding the mechanisms of population regulation in weeds (also see Weiner 1990). It is more difficult, however, to see how information on the genetics of weed populations can aid directly in the development of more effective cultural control methods. Nevertheless, it would seem important that weed control specialists are familiar with the range of genetic variation present in weed species and in particular are aware of the high degree of genetic differentiation that exists among weed populations for many ecologically important traits such as dormancy (Naylor and Jana 1976), development rate (Kadereit and Briggs 1985), competitive ability (Solbrig and Simpson 1977) and fecundity (Barrett and Wilson 1981). As yet we are some way from being able to predict how the introduction of particular cultural control methods will influence the genetic structure and evolution of weed populations or vice versa (Barrett 1988). However, it is clear that a prerequisite for such an approach is a sound knowledge of the quantitative genetics of life history traits in weed populations. So far there are relatively few studies on this topic, particularly of agricultural weeds.

The most effective and widespread method of weed control is through the

use of herbicides. Despite their obvious potency as selective agents, relatively little is known about the influence of herbicides on the genetic characteristics of weed populations. Genetically based shifts in ecological traits such as germination behavior, growth rate or flowering time might be anticipated as a result of the evolution of various "avoidance strategies" or, alternatively, weed populations may simply respond through phenotypic plasticity (Putwain *et al.* 1982). Studies on the levels of genetic variation for herbicide tolerance in weed populations (Price *et al.* 1983; Thai *et al.* 1985) are important since information on the potential likelihood for the evolution of tolerance is of value in the planning and assessment of herbicide programs as well as the implementation of crop rotation schemes. Despite earlier predictions to the contrary (Harper 1956; Gressel and Segel 1978), an increasing number of cases of the evolution of herbicide tolerance is coming to light, particularly in response to the use of the S-triazine herbicides (LeBaron and Gressel 1982). Integrated control strategies for aquatic weeds, reviewed by Ashton and Mitchell (1989), require further research on the ecological genetic and demographic aspects. Many theoretical and empirical advances and research needs are elegantly reviewed in Roughgarden *et al.* (1989); clearly, weed control is a closely interwoven subset of problems in the management of populations or ecosystems.

Conclusions

The input of principles and methods developed in population biology to weed control practices is likely to be gradual at first since population biology is a relatively young discipline and the interactions between fields are at present limited. Nevertheless, if weed biology is going to move from its present, largely descriptive state to a situation where it is possible to predict the influence of weeds on crop yields, and to manipulate both the ecological and genetic characteristics of weed populations through management techniques, then the approaches and methods used in population biology must be integrated into the framework of weed science (Kluge *et al.* 1986). Collaborative research studies between agriculturalists and population biologists as well as interdisciplinary programs are required to nurture the growing field of applied population biology.

Literature cited

Ashton, P. and D. S. Mitchell. 1989. Aquatic plants: Patterns and modes of invasion, attributes of invading species and assessment of control programmes. In: Drake, J. A. *et al.* (eds.) Biological Invasions: A Global Perspective. John Wiley, Chester.

Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347–349.

use of herbicides. Despite their obvious potency as selective agents, relatively little is known about the influence of herbicides on the genetic characteristics of weed populations. Genetically based shifts in ecological traits such as germination behavior, growth rate or flowering time might be anticipated as a result of the evolution of various "avoidance strategies" or, alternatively, weed populations may simply respond through phenotypic plasticity (Putwain *et al.* 1982). Studies on the levels of genetic variation for herbicide tolerance in weed populations (Price *et al.* 1983; Thai *et al.* 1985) are important since information on the potential likelihood for the evolution of tolerance is of value in the planning and assessment of herbicide programs as well as the implementation of crop rotation schemes. Despite earlier predictions to the contrary (Harper 1956; Gressel and Segel 1978), an increasing number of cases of the evolution of herbicide tolerance is coming to light, particularly in response to the use of the S-triazine herbicides (LeBaron and Gressel 1982). Integrated control strategies for aquatic weeds, reviewed by Ashton and Mitchell (1989), require further research on the ecological genetic and demographic aspects. Many theoretical and empirical advances and research needs are elegantly reviewed in Roughgarden *et al.* (1989); clearly, weed control is a closely interwoven subset of problems in the management of populations or ecosystems.

Conclusions

The input of principles and methods developed in population biology to weed control practices is likely to be gradual at first since population biology is a relatively young discipline and the interactions between fields are at present limited. Nevertheless, if weed biology is going to move from its present, largely descriptive state to a situation where it is possible to predict the influence of weeds on crop yields, and to manipulate both the ecological and genetic characteristics of weed populations through management techniques, then the approaches and methods used in population biology must be integrated into the framework of weed science (Kluge *et al.* 1986). Collaborative research studies between agriculturalists and population biologists as well as interdisciplinary programs are required to nurture the growing field of applied population biology.

Literature cited

Ashton, P. and D. S. Mitchell. 1989. Aquatic plants: Patterns and modes of invasion, attributes of invading species and assessment of control programmes. In: Drake, J. A. *et al.* (eds.) Biological Invasions: A Global Perspective. John Wiley, Chester.

Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347—349.

Brown, A. H. D., and J. J. Burdon. 1983. Multilocus diversity in an outbreeding weed, *Echium plantagineum* L. Austr. J. Biol. Sci. 36: 503—509.

——, and ——. 1987. Mating systems and colonizing success in plants, pp. 115—132. *In*: A. J. Gray, M. J. Crawley and P. J. Edwards (eds.), Colonization, Succession and Stability. British Ecological Soc. Symp. No. 26, Blackwell, Oxford.

Brown, A. H. D., and D. R. Marshall. 1981. Evolutionary changes accompanying colonization in plants, pp. 351—363. *In*: G. G. E. Scudder and J. L. Reveal (eds.), Evolution Today, Proceedings of the Second Internationl Congress of Systematic and Evolutionary Biology. Carnegie-Mellon Univ., Pittsburgh.

Burdon, J. J. 1985. Pathogens and the genetic structure of plant populations, pp. 313—326. *In* J. White (eds.), Studies on Plant Demography. Festsch. for John L. Harper. Academic Press, London.

Burdon, J. J., and D. R. Marshall. 1981. Biological control and the reproductive mode of weeds. J. Appl. Ecol. 18: 649—658.

Burdon, J. J., D. R. Marshall, and R. H. Groves. 1980. Isozyme variation in *Chondrilla juncea* L. in Australia. Aust. J. Bot. 28: 193—198.

Burdon, J. J., R. H. Groves and J. M. Cullen. 1981. The impact of biological control on the distribution and abundance of *Chondrilla juncea* in southeastern Australia. J. Appl. Ecol. 18: 957—966.

Burdon, J. J., D. R. Marshall and A. H. D. Brown. 1983. Demographic and genetic changes in populations of *Echium plantagineum*. J. Ecol. 71: 667—679.

Clegg, M. T., and R. W. Allard. 1972. Pattern of genetic differentiation in the slender wild oat species *Avena barbata*. Proc. Nat. Acad. Sci. U.S.A. 69: 1820—1824.

Clegg, M. T., and A. H. D. Brown. 1983. The founding of plant populations, pp. 216—228. *In*: C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas (eds.), Genetics and Conservation. Benjamin/Cummings, California.

Clegg, M. T., D. J. Schoen and B. K. Epperson. 1985. The interactions between phenotypic diversity and mating patterns in plant populations, pp. 287—298. *In*: J. Haeck and J. W. Woldendorp (eds.), Structure and Functioning of Plant Populations. 2. Phenotypic and Genotypic Variation in Plant Populations. North-Holland Publishing Company, Amsterdam.

Crafts, A. S. and W. W. Robbins. 1962. Weed Control, McGraw-Hill, New York.

Crawley, M. J. 1986. The population biology of invaders. Phil. Trans. R. Soc. Lond. B. 314: 711—731.

Cullen, J. M. and R. H Groves. 1977. The population biology of *Chondrilla juncea* L. in Australia. Proc. Ecol. Soc. Austr. 10: 121—134.

Faegri, K. and L. van der Pijl. 1971. The Principles of Pollination Ecology (2nd ed.) Pergamon, Oxford.

Firbank, L. G., and A. R. Watkinson. 1986. Modelling the population dynamics of an arable weed and its effect upon crop yield. J. Appl. Ecol. 23: 147—159.

Giles, B. E. 1983. A comparison between quantitative and biochemical variation in the wild barley *Hordeum murinum*. Evolution 38: 34—41.

Glover, D. E., and S. C. H. Barrett. 1987. Genetic variation in continental and island populations of *Eichhornia paniculata* (Pontederiaceae). Heredity 59: 7—17.

Gray, A. 1879. The pertinacity and predominance of weeds. Amer. J. Sci. 118: 161—167.

Gressel, J., and L. A. Segel. 1978. The paucity of plants evolving genetic resistance to herbicides: possible reasons and implications. J. Theor. Biol. 75: 349—371.

Hamrick, J. L., Y. B. Linhart, and J. B. Mitton. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Ann. Rev. Ecol. Syst. 10: 173—200.

Harper, J. L. 1956. The evolution of weeds in relation to resistance to herbicides. Proc. 3rd British Weed Control Conf. 1: 179—186.

——. 1960. Biology of Weeds. British Ecol. Soc. Symp. No. 1, Blackwell, Oxford.

——. 1977. Population Biology of Plants. Academic Press, London.

Heiser, C. B. Jr. 1965. Sunflowers, weeds and cultivated plants, pp. 391—401. *In*: H. G. Baker and G. L. Stebbins (eds.). The Genetics of Colonizing Species. Academic Press, London.

Holm, L. G., D. L. Plucknett, J. V. Pancho, and J. P. Herberber. 1977. The World's Worst Weeds: Distribution and Biology. University of Hawaii Press, Honolulu.

Husband, B. C. and S. C. H. Barrett. 1991. Colonization history and population genetic structure of *Eichlornia paniculata* in Jamaica. Heredity (in press).

Jain, S. K. 1969. Comparative ecogenetics of two *Avena* species occurring in Central California. Evol. Biol. 3: 73—118.

——. 1983. Genetic characteristics of populations, pp. 240—256. *In*: H. A. Mooney and M. Gordon. (eds.), Ecological Studies: Analysis and Synthesis. Springer-Verlag, Berlin.

Jain, S. K., and P. S. Martins. 1979. Ecological genetics of the colonizing ability of rose clover (*Trifolium hirtum* All.). Amer. J. Bot. 66: 361—366.

Kadereit, J. W., and D. Briggs. 1985. Speed of development of radiate and non-radiate plants of *Senecio vulgaris* L. from habitats subject to different degrees of weeding pressure. New Phytol. 99: 155—169.

Kahler, A. L., and R. W. Allard, M. Krzakowa, C. F. Wehrhahn, and E. Nevo. 1980. Associations between isozyme phenotypes and environment in the slender wild oat (*Avena barbata*) in Israel. Theor. Appl. Genet. 56: 31—47.

King, L. J. 1966. Weeds of the World: Biological Control. Hill, London.

Kluge, R. L., H. G. Zimmerman, C. J. Culliers, and G. B. Harding. 1986. Integrated control of invasive alien weeds. *In*: I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar (eds.) The Ecology and Management of Biological Invasions in Southern Africa. pp. 295—303. Oxford, Cape Town.

Lande, R. 1977. The influence of the mating system on the maintenance of genetic variability in polygenic characteristics. Genetics 86: 485—498.

Law, R. 1981. The dynamics of a colonizing population of *Poa annua*. Ecology 62: 1267—1277.

Law, R., A. D. Bradshaw, and P. D. Putwain. 1977. Life history variation in *Poa annua*. Evolution 31: 233—246.

LeBaron, H. M., and J. Gressel (eds.). 1982. Herbicide Resistance in Plants. John Wiley, New York.

Lewontin, R. C. 1974. The Genetic Basis of Evolutionary Change. Columbia Univ. Press, New York.

——. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. Amer. Nat. 123: 115—124.

Lloyd, D. G. 1980. Demographic factors and mating patterns in Angiosperms, pp. 67—88. *In*: O. T. Solbrig (ed.), Demography and Evolution in Plant Populations. Blackwell, Oxford.

Loveless, M. D., and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. Ann. Rev. Ecol. Syst. 15: 65—95.

Lyman, J. C., and N. C. Ellstrand. 1984. Clonal diversity in *Taraxacum officinale* (Compositae), an apomict. Heredity 50: 1—10.

Mack, R. N. and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. J. Ecol. 71: 69—93.

Marshall, D. R., J. J. Burdon, and A. H. D. Brown. 1980. Optimal sampling strategies in the biological control of weeds. Proc. V Intern. Symp. Biol. Control of Weeds. Brisbane, pp. 103—111.

Martins, P. S. and S. K. Jain. 1978. The role of genetic variation in the colonizing ability of rose clover (*Trifolium hirtum* All.). Amer. Nat. 114: 591—595.

Maun, M. A. and S. C. H. Barrett. 1986. The biology of Canadian weeds. 74. *Echinochloa crus-galli* (L.) Beauv. Can. J. Plant Sci. 65: 739—759.

McIntyre, S., and S. C. H. Barrett. 1986. A comparison of weed communities of rice in Australia and California. Proc. Ecol. Soc. Austr. 14: 237—250.

McNeill, J. 1976. The taxonomy and evolution of weeds. Weeds Res. 16: 399—413.

Michael, P. W. 1983. Taxonomy and distribution of *Echinochloa* species with special refer-

ence to their occurrence as weeds of rice, pp. 391—306. *In* Weed Control in Rice. Proc. Conf. Int. Rice Res. Inst. Los Banos, Philippines.

Moran, G. F., D. R. Marshall, and W. J. Muller. 1981. Phenotypic variation in the colonizing species *Xanthium strumarium* L. (Noogoora Burr). Aust. J. Biol. Sci. 34: 639—648.

Mortimer, A. M. 1983. On weed demography, pp. 3—41. *In* W. W. Fletcher (ed.), Recent Advances in Weed Research. Commonwealth Agric. Bur., Farnum Royal.

Mulcahy, D. L. 1975. The reproductive biology of *Eichhornia crassipes* (Pontederiaceae). Bull. Torr. Bot. Club 102: 18—21.

Musik, T. J. 1970. Weed Biology and Control. McGraw-Hill, New York.

Myers, J. H., and M. D. Sabath. 1980. Genetic and phenotypic variability, and the success of establishment of insect introductions for the biological control of weeds, pp. 91—102. *In*: Proc. V Intern. Symp. Biol. Control of Weeds, Brisbane, Australia, CSIRO, Melbourne.

Naylor, J. M., and S. Jana. 1976. Genetic adaptation for seed dormancy in *Avena fatua*. Can. J. Bot. 54: 306—312.

Newsome, A. E., and I. R. Noble. 1986. Ecological and Physiological Characters of Invading Species, pp. 1—20. *In* R. H. Groves and J. J. Burdon (eds.). Ecology of Biological Invasions: An Australian Perspective Austr. Acad. of Sci., Canberra.

Popay, A. I., and E. H. Roberts. 1970. Factors involved in the dormancy and germination of *Capsella bursa-pastoris* (L.) Medik and *Senecio vulgaris* L.J. Ecol. 58: 103—122.

Price, S. C., J. E. Hill, and R. W. Allard. 1983. Genetic variability for herbicide reaction in plant populations. Weed Sci. 31: 652—657.

Price, S. C., K. M. Shumaker, A. L. Kahler, R. W. Allard, and J. E. Hill. 1984. Estimates of population differentiation obtained from enzyme polymorphisms and quantitative characteristics. J. Heredity 75: 141—142.

Price, S. C., and S. K. Jain. 1981. Are inbreeders better colonizers? Oecologia 49: 283—286.

Putwain, P. D., K. R. Scott, and R. J. Holliday. 1982. The nature of resistance to triazine herbicides; case histories of phenology and population studies, pp. 115—132. *In*: H. M. LeBaron and J. Gressel (eds.), Herbicide Resistance in Plants. John Wiley, New York.

Richards, A. J. 1986. Plant Breeding Systems. George Allen & Unwin, London.

Rick, C. M., J. F. Fobes, and S. D. Tanksley. 1979. Evolution of mating systems in *Lycopersicum hirsutum* as deduced from genetic variation in electrophoretic and morphological characters. Pl. Syst. Evol. 132: 279—298.

Roberts, H. A. 1964. Emergence and longevity in cultivated soil of seeds of some annual weeds. Weed Res. 4: 296—307.

Roughgarden, J., R. M. May, and S. A. Levin (eds.). 1989. Perspectives in Ecological Theory. Princeton Univ. Press, Princeton.

Sagar, G. R. 1968. Weed biology — a future? Neth. J. Agric. Sci. 16: 155—164.

Salisbury, E. J. 1961. Weeds and Aliens. Collins, London.

Sarukhan, J. 1974. Studies on plant demography in *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. II. Reproductive strategies and seed population dynamics. J. Ecol. 62: 151—177.

Schemske, D. W., and R. Lande. 1985. The evolution of self-fertilization and inbreeding depression in plants. II. Empirical observations. Evolution 39: 41—52.

Schoen, D. J. 1982. Genetic variation and the breeding system of *Gilia achilleifolia*. Evolution 36: 361—370.

Solbrig, O. T., and B. B. Simpson. 1974. Components of regulation of a population of dandelions in Michigan. J. Ecol. 62: 473—486.

——, and ——. 1977. A garden experiment on competition between biotypes of the common dandelion *Taraxacum officinale*. J. Ecol. 65: 427—430.

Stebbins, G. L. 1965. Colonizing species of native Californian flora, pp. 173—192. *In* H. G. Baker and G. L. Stebbins (eds.). The Genetics of Colonizing Species. Academic Press, London.

Thai, K. M., S. Jana, and J. M. Naylor. 1985. Variability for response to herbicides in wild oat *Avena fatua* populations. Weed Sci. 33: 829—835.

Vrijenhock, R. C. 1990. Genetic diversity and the ecology of asexual populations, pp, 175—198. *In*: K. Wohrmann and S. Jain (eds.) Population Biology. Springer-Verlag, Berlin.

Warburg, E. F. 1960. Some taxonomic problems in weedy species, pp. 43—47. *In* J. L. Harper (eds.), The Biology of Weeds. British Ecol. Soc. Symp. No. 1, Blackwell, Oxford.

Warwick, S. I. 1980. The genecology of lawn weeds. VII. The response of different growth forms of *Plantago major* L. and *Poa annua* L. to simulated trampling. New Phytol. 85: 461—469.

Warwick, S. I., B. K. Thompson and L. D. Black. 1987. Genetic variation in Canadian and European populations of colonizing weed species *Apera spica-venti*. New Phytol. 106: 301—318.

Weiner, J. 1990. Plant population ecology in agriculture, pp. 235—262. *In*: C. R. Carroll, J. H. Vandermeet, and P. M. Rosset (eds.) Agroecology. McGraw-Hill, New York.

Zinger, H. B. 1909. On species of *Camelina* and *Spergularia* occurring as weeds in sowings of flax and their origin. Trudy Bot. Muz. Imp. Akad. Nauk 6: 1—303.