

Weed Management in Agroecosystems: Ecological Approaches

Editors

Miguel A. Altieri

Associate Professor
College of Natural Resources
Division of Biological Control
University of California, Berkeley
Albany, California

Matt Liebman

Assistant Professor
Department of Plant and Soil Science
University of Maine
Orono, Maine



CRC Press, Inc.
Boca Raton, Florida

Chapter 5

GENETICS AND EVOLUTION OF AGRICULTURAL WEEDS

Spencer C. H. Barrett

TABLE OF CONTENTS

I.	Introduction.....	58
II.	Weed Strategies.....	58
III.	Genetic Variation.....	60
IV.	Evolution Under Cultivation.....	62
V.	Barnyardgrasses.....	64
	A. Variation Patterns and Histories of Introduction.....	64
	B. Ecological Differentiation.....	66
	C. Genetic Variation in Californian Populations.....	67
VI.	Future Crop/Weed Associations.....	70
VII.	Conclusions.....	71
	Acknowledgments.....	71
	References.....	71

I. INTRODUCTION

Most weed species originated as pioneers of the early stages of secondary succession and possess attributes that enable them to colonize and rapidly regenerate in open, disturbed environments.^{1,2} A feature of many forms of natural disturbance is that the open patches that appear are transient and unpredictable in both space and time. This heterogeneity constrains colonizing potential and restricts the number of plant species able to take advantage of disturbed conditions. Today, as a result of modern agriculture, disturbance occurs on a large scale, with vast areas of relative environmental homogeneity and a high level of predictability associated with land use patterns. One of the major goals of modern crop husbandry is to minimize the heterogeneity of the physical and biotic components of the agroecosystems to produce uniform growing conditions. The modern crop environment, therefore, presents a new set of challenges for weed populations, the most serious of which is the farmer's determination to eradicate them by whatever means available.

There is evidence that weed populations have responded to these challenges by developing races adapted to the crop environment.³⁻⁷ This diversification of weed strategies cautions against generalizations about the ideal attributes of invading species, since many agricultural races of ruderal weeds possess specialized traits that prevent them from colonizing most disturbed habitats. Instead of exhibiting broad ecological tolerance, many agricultural weeds are specialized in their habitat requirements to the extent that in some cases they are unable to survive in the absence of the crop with which they have evolved.⁷ Unfortunately, there has been relatively little experimental work on the population biology and evolution of agricultural weeds, particularly with respect to the occurrence of genetic differentiation resulting from the selection pressures imposed by standard agricultural practices such as cultivation methods, fertilizer regimes, irrigation, herbicides, crop characteristics (e.g., variety, phenology, and density), and harvesting methods. This is unfortunate since these features of modern crop husbandry largely determine the environment with which weed populations interact and undoubtedly influence the genetic structure, life histories, and evolutionary dynamics of populations.

This chapter is divided into two parts. In the first, recent literature on the ecological genetics and evolution of agricultural weeds is reviewed; the second provides a brief summary of some of our own recent comparative work on weedy taxa of barnyardgrass (*Echinochloa* Beauv.). An attempt is made throughout to highlight deficiencies in our knowledge of weed ecology and genetics and to suggest lines of inquiry that could profitably be followed. Although much of the work that I review was not designed with weed control in mind, I shall attempt to comment on the applied implications of the findings where appropriate.

II. WEED STRATEGIES

Weeds have originated from diverse taxonomic families, occupy a broad range of disturbed environments, and as a result display a wide variety of colonizing strategies. Since colonization can occur on very different scales from local range extension to intercontinental migration, it has been suggested that the evolutionary forces acting on colonizing species vary with species and event such that each case is unique.⁸ Notwithstanding this complexity, ecologists and evolutionists have sought to identify the shared attributes found in successful weed species.^{2,6,8} Two contrasting suites of traits frequently occur, depending on whether the weeds in question are annual or perennial. The former usually exhibit rapid growth and development to reproductive maturity, rely entirely on seed reproduction, and are predominantly self-fertilizing. In contrast, many perennial weeds regenerate by clonal propagation, take longer to reach reproductive maturity, and are often outcrossing. The almost ubiquitous co-occurrence of both annual and perennial weed associations in most major crops indicates that there is no optimal solution to the problem of invading agricultural land.

Table 1
 ECOLOGICAL CHARACTERISTICS OF HABITATS OF RUDERAL AND
 ARABLE LAND

Feature	Ruderal	Cultivated field
Disturbance	Variable intensity, often unpredictable	Frequent, highly predictable in space and time
Moisture supply and soil fertility	Heterogeneous, resulting in a wide range of plant performance	Homogeneous, resulting from regular plowing, irrigation, and inputs of fertilizer
Plant cover	Open areas and a patchy distribution of plants owing to environmental heterogeneity and asynchronous seasonal phenologies	Synchronized phenology with rapid closure of stand
Biotic complexity	Variable, dependent on pattern of disturbance and successional status	Monoculture of genetically uniform crop variety, with restricted number of pests, diseases, and weeds

During the past 2 decades, population biologists have largely considered colonizing ability within the theoretical frameworks of *r*- and *K*-selection and other life history theories.⁹⁻¹¹ Rapid development to reproduction, high-phenotypic plasticity, large reproductive effort, and well-developed dispersal mechanisms have all been identified as important traits for colonization and regeneration in disturbed environments. While there is still active debate on the application of various life history models to specific groups of organisms, there seems to be general agreement that weeds represent classic examples of *r*-strategists. Grime^{12,13} has developed a general theory of strategies for plants that takes into account their distinctive features. He distinguishes three primary groupings, termed the ruderal, competitive, and stress-tolerant strategies. According to this view, the ruderal strategy (essentially similar to the *r*-strategy of MacArthur and Wilson¹⁰) has evolved primarily in open, productive habitats that are exposed to repeated and severe disturbance. Although the majority of agricultural weeds fall into this category, it is worth examining traits that distinguish them from typical ruderal species since they are likely to have arisen from the specific demands imposed by the crop environment. Some of the ecological features of arable land that are likely to shape the life histories and genetics of weed populations are given in Table 1.

The restricted distributions of many agricultural races of weeds (agroecotypes), particularly those associated with specific crops, suggests that their life history strategies have become modified by selection pressures that are absent from areas experiencing other forms of disturbance. Many satellite weeds of crops, such as crop mimics, are so intimately linked to their crop models that they are unable to survive outside the crop environment or even in a different cropping system. Here a specialized weed strategy has evolved in which the weed is largely dependent on the crop and its environment for survival. This behavior reflects the fact that during the process of adaptation to the crop environment, weeds have evolved a syndrome of 'crop-like' traits that have low survival value away from agricultural land.

Crop varieties themselves generally have only weak colonizing ability and rarely persist for more than a few generations in the absence of repeated sowing and conscious cultural practices that favor their growth. Similarly, the traits commonly found in crop mimics — such as weak dormancy; upright, determinate growth; flowering and fruiting synchronized with the crop; reduced shattering; and low dispersability of seeds — are likely to reduce their relative fitness in habitats away from the crop environment. Further discussion of crop mimics, their character syndromes, distribution, and evolution can be found in the literature.^{6,7,14-17}

III. GENETIC VARIATION

The amount and organization of genetic variation within weed populations largely determine their capacity to respond to the selection pressures imposed by the local physical and biotic environment. Colonizing species are of particular interest for studies in population genetics since in many cases the invasion of new territory is accompanied by genetic bottlenecks, inbreeding, and strong directional selection. These influences can result in rapid selective responses and erosion of the genetic variability of populations. In contrast, multiple introduction of genetic material from source populations, outbreeding, introgressive hybridization with related taxa, and rapid population expansion all aid in either maintaining or increasing genetic diversity.^{1,18-20}

Since allelic variation at unlinked loci is distributed independently in populations of outbreeding organisms, in theory all possible combinations of alleles should be found. In practice, however, forces such as population bottlenecks and inbreeding, which are particularly evident during the early stages of the invasion process, lead to strong linkage disequilibrium among loci and the production of a limited number of multilocus associations within populations.²¹

Agricultural weeds are likely to be especially susceptible to the processes that lead to loss of genetic variation in populations and the development of multilocus associations. Introduction of a crop weed into a region often results from contamination of seed lots with weed seeds. The intercontinental migration of agricultural weeds frequently occurs in this manner.⁵ Often few propagules are introduced, and where long distances are involved the likelihood of recurrent invasion is low. As a result, only a small proportion of the genetic variation present in the source region may be introduced to the alien range. Genetic bottlenecks of this type are particularly evident in agricultural weeds, since many are annuals that reproduce primarily by self-fertilization. Selfing leads to an overall reduction in heterozygosity, and populations of selfers often tend to be genetically uniform but highly differentiated from one another.^{22,23} If a long-distance colonizing episode involves genetic material from a single source population, loss of allelic variation and founder effects will be evident. As a result, highly differentiated homozygous population systems can develop in the introduced region. Although polygenic mutation can subsequently generate considerable heritable genetic variation for quantitative traits even in selfing species,^{24,25} the strong directional selection that may be associated with specific agronomic practices, such as those involved with weed control, may rapidly erode this variation.

The transient nature of many weed populations, particularly those subject to eradication by herbicides, can prevent the build-up of large, stable population systems capable of maintaining large stores of genetic variation. However, where weed species have a long history in a particular region, local genetic differentiation can occur, resulting in the ecological diversification of weed races.⁶ Changes in cropping systems, fallow periods, and rotation, as well as the occurrence of a diversity of weed niches associated with open habitats (ditch banks, hedgerows, roadsides, etc.) are all likely to aid in maintaining genetic diversity in weed species by providing opportunities for cycles of differentiation and hybridization among locally adapted populations. In contrast, the creation of uniform monocultures with only limited areas of uncultivated land, as well as standardized weed control methods, are likely to select for genetic uniformity in weed populations.

During the past decade electrophoretic studies of isozyme variation in weed species have provided valuable information on the mating systems and genetic structure of populations. A wide range of patterns of genetic diversity has been revealed, ranging from species in which populations are genetically uniform²⁶ to populations that contain extremely high levels of genetic variation.²⁷ These differences not only distinguish species with contrasting life histories but can also be found among populations of a single species.²⁸ As a group, however,

Table 2
 ISOZYME VARIATION IN FIVE WEEDS OF CORN AND SOYABEAN FROM S.
 ONTARIO, CANADA³⁰

	<i>Abutilon theophrasti</i>	<i>Panicum miliaceum</i>	<i>Setaria faberi</i>	<i>Sorghum halepense</i>	<i>Datura stramonium</i>
Chromosome no.	2n = 42	2n = 36	2n = 36	2n = 40	2n = 24
No. of populations	39	38	8	13	9
No. of enzymes	16	11	14	14	12
No. of loci	27	19	24	21	22
No. (%) of loci monomorphic	25 (93%)	18 (95%)	21 (88%)	18 (86%)	22 (100%)
No. (%) of loci polymorphic	2 (7%)	1 (5%)	3 (14%)	3 (14%)	0
No. (%) of duplica- ted loci with en- zyme multiplicity	14 (52%)	8 (42%)	13 (54%)	3 (14%)	2 (9%)
No. of multilocus phenotypes	4	2	9	10	1

weeds tend to be less variable than other groups of plants,²⁹ and a significant number of studies have reported species in which populations are depauperate in isozyme variability.^{8,18,20} A recent survey by Warwick³⁰ of isozyme variation in five weed species of agricultural land in Canada clearly illustrates this point. *Abutilon theophrasti* Medic., *Datura stramonium* L., *Panicum miliaceum* L., *Setaria faberi* Herrm., and *Sorghum halepense* (L.) Pers. have invaded maize and soyabean fields in the corn-belt region of the U.S. During the past 15 to 30 years they have extended their ranges northward into southern Ontario in association with the expansion of maize and soyabean production. Four of the five species are polyploid and each is a self-pollinating annual. The electrophoretic survey of populations of the five species revealed a striking lack of genetic polymorphism at isozyme loci, with each population usually composed of one or, more rarely, several multilocus genotypes (Table 2). In the polyploid species, 'fixed heterozygosity' was apparent for up to half of the enzyme loci screened. It has been suggested that this type of genetic variation, involving different alleles at homoeologous loci, may increase biochemical versatility and enable individuals of polyploid weed species to extend the range of environments that they can successfully colonize.^{31,32} The role of polyploidy in colonizing plant species has been considered by Ehrendorfer,⁸ Brown and Marshall,²⁰ Levin,³³ and Barrett and Richardson.³⁴

Although populations of many weeds that are primarily self-fertilizing often contain a limited number of multilocus isozyme genotypes, this does not necessarily imply that populations are entirely devoid of genetic variation at other gene loci. Where studies of quantitative characters (e.g., time to flowering, plant height, and seed production) have been conducted in weed species with little isozyme variation, considerable inter- and intrapopulation genetic variation for life history traits has been revealed.³⁵⁻³⁹ Lewontin⁴⁰ and Brown and Burdon⁴¹ review different aspects of the complex problem of the relationships between isozyme variation and quantitative characters. It appears from the limited data available for plant species that the mating system strongly influences the relationship. Price et al.⁴² have argued that enzyme loci may provide more information about other genes in selfers than in outcrossers. This should be expected, given the cohesive nature of the genome in selfers; isozymes are likely to be useful neutral markers to index variation.⁴¹

There is limited evidence suggesting that when populations of weeds become associated with agriculture, by the invasion of cultivated fields, the amounts and patterns of genetic variation change in comparison with nearby wild or ruderal populations. In some cases it has been suggested that such effects are the direct result of the selective influence of herbicide

applications.⁴³⁻⁴⁸ In California, Price and Kahler⁴⁷ report that populations of *Avena fatua* L. collected from fields under cultivation for wheat and barley had lower polymorphic indices for several isozyme loci in comparison with adjacent populations that occupied noncultivated ruderal sites. The cultivated populations also differed from nearby sites for a range of quantitative traits. Plants from cultivated fields had larger flag leaves, and were later flowering and taller. It has been suggested that these differences may be associated with the evolution of agricultural races of *A. fatua* in California.¹⁰⁶ The difficulties of establishing whether evolutionary changes are occurring in weed populations in response to cultivation pressures are considered below.

IV. EVOLUTION UNDER CULTIVATION

To provide a convincing demonstration of the evolutionary response of weed populations to agronomic practices, it is necessary to have genetic information from the populations prior to the commencement of the treatment and at various intervals after the onset of cultivation. For evolution to occur, there must be changes in the genetic structure of populations accompanied by an increased fitness of the selected individuals. Studies of the demographic genetics of plant populations are in their infancy⁴⁹ and as yet there has been little detailed monitoring of either the population genetics or the demography of weed infestations. Reciprocal transplant experiments are useful for demonstrating that the agricultural race is better adapted (as judged by survivorship and fertility measures) to its own site than are populations of the weed from nonagricultural situations. Poor performance of the agricultural weed in other habitats might also provide evidence of its specialized requirements. It is surprising that while transplant experiments have been used extensively by plant biologists for over 2 centuries,⁵⁰ there have been relatively few studies in relation to agricultural weeds.

Much of the evidence for evolutionary change in weed populations associated with agriculture is circumstantial, albeit perfectly reasonable. The older literature documents many examples of agroecotypes in which cultivation practices are assumed to have exerted selection pressures on various plant traits, resulting in closer adaptation to the crop environment. In many cases, with improved technologies the weeds have disappeared. Detailed studies of the satellite weeds of cultivated flax (*Linum usitatissimum* L.) in Poland by Kornas^{51,52} have demonstrated how this can occur. Before 1950, a group of weeds closely connected with flax culture known as 'linicolous plants' were consistently associated with primitive agricultural practices in the isolated Gorce mountain range of the Polish Western Carpathians. The dispersal biology of these species (*Camelina alyssum* [Mill.] Thell., *Cuscuta epilinum* Weihe, *Lolium remotum* Schrank, and *Spergula maxima* Weihe.) involved anthropochory with seeds retained within the fruits and the fruits harvested along with the linseed crop each year. However, introduction of improved seed cleaning and a seed certification scheme for linseed during the period 1950 to 1960 resulted in the almost complete extinction of this assemblage of specialized agricultural weeds. Similar disappearances of linicolous weeds, associated with improved seed cleaning practices, have also been documented in a number of other European countries.^{53,54}

Unfortunately, the extinction of these associations prevents detailed modern experimental studies of the ecology and evolution of these complex relationships. Even when crop mimics still persist within the crop, the selection pressures hypothesized to have resulted in mimicry may not be operating. This is the case in the rice mimics *Echinochloa phyllopogon* (Stapf) Koss. and *E. oryzoides* (Ard.) Fritsch in California where handweeding, the presumed selective agent responsible for vegetative mimicry, is no longer practiced.⁷

By using common garden techniques, several workers have revealed an association between habitat and generation time in a number of species of annual weeds, e.g., *Capsella*

bursa-pastoris (L.) Medic.,⁵⁵ *Avena fatua*,⁵⁶ (but see Price and Kahler⁵⁷ for the reverse pattern), *Arabidopsis thaliana* (L.) Heyn.,^{57,58} *Rumex crispus* L.,^{59,60} and *Senecio vulgaris* L.⁶¹ In each case, populations originating from intensively cultivated areas flowered earlier and reached reproductive maturity more rapidly than populations collected from sites away from arable land. The differences in life history are genetically based and suggest that in some of the species continuous cultivation may have resulted in the evolution of reproductive precocity as a strategy to avoid weed control measures. In these examples, transplants would be useful to evaluate whether or not individuals with delayed flowering are selected against, either by cultivation practices or possibly through competition with associated cultivated species.

The exemplary demographic studies conducted by Law on *Poa annua* L.⁶²⁻⁶⁴ indicate the range of genetically based life history variation that can occur both within and between populations of a weed occupying sites with contrasting degrees of plant cover. In this work, plants sampled from open, disturbed environments (opportunist populations) were short lived, with rapid development to reproduction and high-seed output in the first year of life. Those sampled from pastures were longer lived, with longer prereproductive periods and a much greater seed output during the second year of life. These data are consistent with the theories of r- and K-selection,¹⁰ which predict differences in life history due to density-independent and density-dependent regulation of population numbers. However, Law et al.⁶² point out that this conclusion does not exclude the possibility that other unknown environmental variables (e.g., grazing pressure) influence the selection of these divergent life histories.

Agricultural practices may also influence natural selection on seed and seedling traits, particularly the degree of dormancy and pattern of germination in weed populations. Studies of dormancy in *Avena fatua* by Naylor and colleagues^{65,66} are of interest in this regard. A study of seed dormancy in populations of *A. fatua* originating from three sites with contrasting land-use patterns revealed striking genetic differences among the sites in dormancy and germination behavior. At the two sites in which little or no cultivation, summer fallowing, or herbicides had been used, dormancy was weakly developed, compared with a site in which periodic summer fallowing and regular herbicide sprays had been administered. While the specific causes of the differentiation in dormancy among sites are uncertain, Naylor and Jana⁶⁵ suggest that weed control practices may constitute a selection pressure in favor of genotypes with well-developed dormancy. Further studies of germination behavior in *A. fatua* populations exposed to different types of cultivation practices would be valuable to assess these ideas. It is worth noting that strong dormancy may not always be adaptive for weed populations inhabiting intensively cultivated land as appears to be the case among barnyardgrass taxa that mimic cultivated rice.^{7,67} In these species, weak dormancy and germination synchronized with that of the rice crop may be critical for survival under the intensely competitive conditions of the rice stand.

To provide evidence of evolutionary change in weed populations, it is necessary to demonstrate that phenotypic responses to agricultural practices have a genetic basis. Studies of the influence of herbicides on the evolution and population dynamics of the annual weed *Senecio vulgaris* by Putwain and co-workers⁶⁸⁻⁷⁰ illustrate the complex nature of responses that weed populations may exhibit in the face of intense chemical selection. These studies are of interest because they provide evidence that both evolutionary and ecological changes can occur.

Holliday and Putwain⁶⁹ examined 46 populations of *S. vulgaris* from fruit farms in England that had been subjected to applications of the herbicide simazine for varying lengths of time. They demonstrated significant interpopulation variation in herbicide susceptibility and a positive linear relationship between the percentage survival of plants in populations following controlled application of herbicide, and the number of consecutive years of use (Figure 1). Although genetic analysis of broad sense heritability of simazine susceptibility was low in

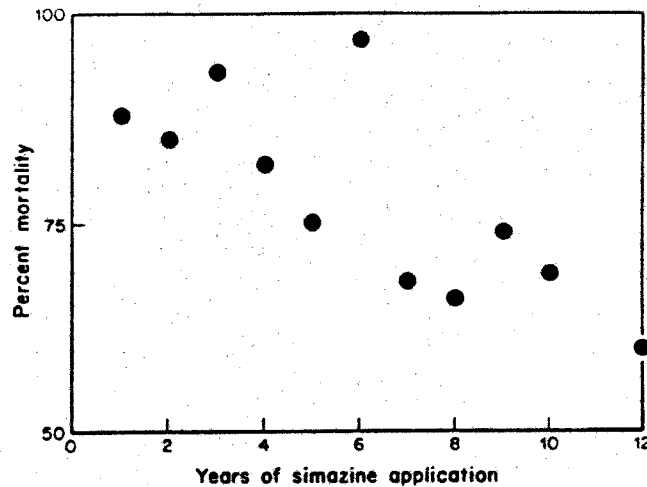


FIGURE 1. Relationship between susceptibility to simazine in *Senecio vulgaris* and the number of consecutive years of simazine application. The relationship is statistically significant: $y = 87.14 - 1.895x$ ($p < 0.01$). (From Holliday, R. J. and Putwain, P. D., *J. Appl. Ecol.*, 17, 779, 1980. With permission.)

comparison with other species examined,^{71,72} apparently sufficient genetic variation occurs for some response to selection. Data from the 46 fruit farms suggest that this is more likely to occur if the same herbicide is applied continuously for an extended period of time.

A different kind of response was revealed in a comparative study⁷⁰ of the population dynamics of *S. vulgaris* in two blackcurrant plantations, one in which simazine had been applied each spring for 10 years and the other in which no herbicides had been used: Demographic studies conducted over a 2-year period showed that the two populations displayed different phenological patterns. In the untreated site, seedlings of *S. vulgaris* appeared mainly in April and May and dispersed most of their seeds during the summer months. Seedlings emerging during the summer failed to survive, owing to heavy competition from other species that colonized the untreated area. In contrast, the simazine-treated population of *S. vulgaris* switched completely to a winter annual life cycle, thus avoiding the phytotoxic effects of the herbicide. The change in phenology could be achieved by natural selection for delayed germination; however, this does not appear to be the cause in *S. vulgaris*, since it was demonstrated that populations possess little heritable variation for innate dormancy. Instead, the shift in phenology apparently results from differences between the two blackcurrant plantations in the seasonal availability of suitable microsites for germination with a hazard-free period for seedling establishment in late summer at the simazine-treated site. These studies demonstrate that without detailed demographic and genetic studies, careful interpretation of suspected cases of evolutionary change in weed populations is required.

V. BARNYARDGRASSES

Among the world's most noxious weeds of agriculture are members of the cosmopolitan genus *Echinochloa* (barnyardgrass). The genus contains approximately 50 species⁷³ 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, barnyardgrasses often rapidly colonize and become serious weed problems. The most widespread and economically important member of the genus is the annual *E. crus-galli* (L.) Beauv., which ranges from 50°N to 40°S latitude

and is reported as a weed in 36 different crops in 61 countries.^{74,75} Other weeds of agriculture include *E. colona* (L.) Link, *E. crus-pavonis* (H.B.K.) Schult, *E. oryzoides*, *E. phyllopogon*, *E. pyramidalis* (Lam.) Hitchc. et Chase, *E. stagnina* (Retz.) Beauv., and *E. microstachya* (Wieg.) Rydb. It is commonplace to find 3 to 6 species of *Echinochloa* occurring in a region as weeds of agriculture and often the assemblage is composed of both native and alien species. The most striking patterns of variation are evident in regions of the world in which cultivated rice is grown. The variation has been frequently noted in the rice weed literature by agronomists and weed control experts who have experienced difficulty in identifying taxa of barnyardgrasses.^{73,76}

The co-occurrence of closely related species that constitute different weed problems provides an opportunity to assess the historical, ecological, and genetic factors that account for variation in colonizing success. Our own work has involved comparative studies of the ecological genetics of several *Echinochloa* spp. that have invaded the rice agroecosystems of California and Australia. Historical links between the two regions, examined in detail by McIntyre and Barrett,⁷⁷ suggest that several barnyardgrasses now present in Australian rice fields were introduced to the continent with imported rice seed stocks from California. Comparative studies of populations from the two regions are being used to substantiate this proposal as well as to provide insights into the process of genetic differentiation following intercontinental dispersal.

Our studies of barnyardgrasses have addressed the following general questions:

1. How many biological (and taxonomic) species are present in Californian and Australian rice fields and what patterns of phenotypic variation are characteristic of each taxon?
2. What ecological attributes (seed biology, life history variation) are responsible for the habitat preferences and differences in colonizing ability among species?
3. What levels and patterns of genetic variation are associated with generalist (*E. crus-galli*) vs. specialist (*E. oryzoides*, *E. phyllopogon*) weed strategies?

To answer these questions, we have employed a range of experimental approaches that include controlled environment studies, measures of quantitative genetic variation under uniform glasshouse conditions, and electrophoretic analysis of isozyme variation. Where possible, we have worked with seed families from randomly sampled individual maternal parents from natural populations. Below is a brief overview of our results to date.

A. Variation Patterns and Histories of Introduction

The patterns of phenotypic variation in barnyardgrass populations in Californian and Australian rice fields are highly complex as a result of morphological polymorphism, well-developed phenotypic plasticity, predominant self-fertilization and, in alien taxa, the multiple introduction of genetic material. Plate 1* illustrates the range of variation that can occur at a single site. This variation has been a source of considerable confusion to weed control specialists who have not been able to identify which barnyardgrasses pose the most serious threat in terms of yield reduction. In some cases (e.g., California) all variation has been treated as *E. crus-galli*, when in reality several distinct species with contrasting ecologies are involved. Despite this complexity, cytological and electrophoretic studies clearly indicate that the variation can be organized into a number of separate intersterile assemblages, each of which deserves specific status. In California, four taxa are commonly found in and around rice fields. These are the aliens *E. crus-galli*, *E. oryzoides*, *E. phyllopogon* (*E. crus-galli* [L.] Beauv. var. *oryzicola* [Vasing] Ohwi), and the native *E. microstachya* (*E. muricata* [P. Beauv.] Fern. var. *microstachya* Wiegand). Two additional alien species, *E. colona* and

* Plate 1 appears after page 72.

Table 3
DISTRIBUTION AND HISTORY OF INTRODUCTION OF
BARNYARDGRASSES TO CALIFORNIA (U.S.) AND NEW SOUTH
WALES (AUSTRALIA)

Taxon (ploidy), origin	California	New South Wales
<i>E. crus-galli</i> (6×) Eurasia	Widespread weed introduced mid-19th century	Widespread weed introduced late-19th century
<i>E. oryzoides</i> (6×) Asia	Restricted to Californian rice fields; earliest records 1912—1915	Restricted to N.S.W. rice fields; earliest record 1938
<i>E. phyllopogon</i> (4×) Asia	Restricted to Californian rice fields; earliest records 1912—1915	Absent
<i>E. microstachya</i> (4×) N. America	Widespread in river banks, ditches, wasteground	Largely restricted to rice-growing areas; earliest record 1938

E. crus-pavonis, are occasionally encountered.⁷ In Australia four alien species are widespread (*E. crus-galli*, *E. oryzoides*, *E. microstachya*, and *E. colona*) and two other species (*E. crus-pavonis* and *E. inundata* Michael and Vickery) have been reported rarely.⁷⁷ The distribution and history of introduction to the two regions of the major barnyardgrasses are presented in Table 3. Two points are worth highlighting. First, in both countries *E. crus-galli* is the most abundant and widespread species. Its arrival predates the introduction of rice culture, which took place in 1912 to 1915 in California⁷⁸ and in 1926 in New South Wales (N.S.W.), Australia.⁷⁷ Second, the earliest herbarium records of *E. oryzoides* and *E. phyllopogon* in California and *E. oryzoides* and *E. microstachya* in N.S.W. are from rice research stations (Biggs and Leeton, respectively), indicating that their introductions to the two regions were most likely associated with the importation of contaminated rice seed stocks. Given the seriousness of barnyardgrasses as weeds of rice, it is worth emphasizing the importance of rigorous seed certification schemes to prevent the accidental introduction of 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 source populations should be encouraged. Barrett and Seaman⁷⁸ documented that in California, the following alien taxa were first collected from in and around rice fields at the Biggs rice experiment station in Butte County: *Cyperus difformis* L., *Dopatrium junceum* (Roxb.) Ham., *Echinochloa oryzoides*, *E. phyllopogon*, *Monochoria vaginalis* (Burm. f) Presl., *Ottelia alismoides* (L.) Pers., *Rotala indica* (Willd.) Koehne, and *Bacopa repens* (Swartz) Wettst. Several of these species are among the world's most cosmopolitan weeds of rice.

B. Ecological Differentiation

The four barnyardgrasses in Table 3 can be divided into two 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 wide range of seasonally inundated habitats both agricultural and ruderal. In contrast, *Echinochloa oryzoides* and *E. phyllopogon* are large-seeded, less-fecund specialists that mimic cultivated rice and are largely restricted to flooded rice fields.

In California the development of 'permanent flooding' techniques, in which water is maintained on fields to a depth of 8 to 20 cm for the duration of rice growth, has largely eliminated the two small-seeded barnyardgrasses from within rice fields. However, large populations, particularly of *E. crus-galli*, do infest rice levees and ditches surrounding fields. Experimental studies⁸⁷ on the establishment of barnyardgrasses at different water levels demonstrate the inability of small-seeded types to emerge through deep water (Table 4). This behavior is unlikely to be associated with different capacities for anaerobic germination

Table 4
ESTABLISHMENT OF THREE SPECIES OF
BARNYARDGRASS AND CULTIVATED RICE FROM
VARIOUS WATER DEPTHS

Treatment	Number of individuals reaching reproductive maturity			
	<i>E. crus-galli</i>	<i>E. oryzoides</i>	<i>E. phyllopogon</i>	Rice
Saturated soil	42.6	74.3	34.3	78.2
9.0 cm	0.7	41.9	27.7	95.1
18.0 cm	0.1	33.1	21.9	89.2

Note: Experimental method: One hundred seeds of each barnyardgrass were incorporated into the top 2 cm of soil in plastic boxes. The soil was then flooded and rice was sown at field density (131 seeds per box). Each treatment was replicated $\times 10$ and the boxes were randomized on a glass house bench.

since barnyardgrasses are capable of germination and early growth in an oxygen-free environment.⁷⁹ The difference is more likely the result of differences in seed size. Limited storage reserves in small-seeded taxa must restrict seedling growth in deep water.⁶⁷

The introduction of continuous flooding in Californian rice fields may have indirectly encouraged the spread of the two large-seeded species by severely reducing densities of their congeneric competitors. Today in California *E. oryzoides* is among the most economically important weeds of rice, and *E. phyllopogon*, although less of a problem, is widely distributed throughout the rice-growing areas of the state. Despite the fact that in rice fields both species form immense populations composed of thousands of individuals, few plants are found outside the rice agroecosystem. As mentioned previously, this niche restriction is a common feature of satellite weeds of crops. The factors restricting the spread of the two species are discussed by Barrett and Wilson.^{67,80}

In Australia, continuous deep-water flooding is not employed in many areas, and *E. crus-galli* and *E. microstachya* are found commonly throughout the rice crop, with *E. crus-galli* usually predominating. Populations of *E. oryzoides* in N.S.W. are not as large or as numerous as they are in California. This may be partly historical since the species was introduced to N.S.W. more recently, but may also reflect two ecological factors: (1) the presence in rice fields of the aggressive *E. crus-galli* and (2) the different cultural practices employed in rice production in N.S.W. In contrast to *E. crus-galli*, *E. oryzoides* does not exhibit strong seed dormancy,⁶⁷ thus the practices of crop rotation and fallowing that are customary in N.S.W. are likely to rapidly exhaust the soil seed bank. An additional factor that may be important in reducing the rate of expansion of *E. oryzoides* in Australia concerns the patchy distribution of rice fields, which may constrain the dispersal of the large-seeded *E. oryzoides*.⁷⁷ Continuous rice monoculture and the large contiguous areas used for rice growing in California have doubtless favored the rapid expansion of *E. oryzoides* over the past 50 years.

C. Genetic Variation in Californian Populations

Both historical factors, associated with the manner of introduction and differences in life history, are likely to influence the levels and patterns of genetic variation within and between populations of barnyardgrass species. An electrophoretic survey of isozyme variation among populations of the generalist *E. crus-galli* and the two rice weed specialists, *E. oryzoides* and *E. phyllopogon*, from in and around rice fields in the Central Valley of California revealed contrasting patterns in the three taxa.¹⁰⁵ All three taxa were relatively low in genetic polymorphism with virtually no heterozygosity at polymorphic loci and a high degree of

Table 5
**ISOZYME VARIATION IN RICE FIELD
 POPULATIONS OF THREE SPECIES OF
 BARNYARDGRASS FROM CALIFORNIA¹⁰⁵**

	Total variation			Population average		
	CG	O	P	CG	O	P
Populations	11	12	12	11	12	12
Total loci surveyed	31	32	25	31	32	25
Polymorphic loci	16	5	7	5.7	2.0	1.25
Polymorphic alleles (PA)	41	10	15	13.0	4.0	2.50
PA per polymorphic loci	2.56	2.0	2.14	2.28	2.0	2.0
Diversity	2.68	1.19	1.84	1.79	0.60	0.36

Note: CG = *Echinochloa crus-galli*, O = *E. oryzoides*, and P = *E. phyllopogon*

Table 6
**PROPORTION OF ISOZYME VARIATION
 AMONG POPULATIONS IN THREE SPECIES
 OF BARNYARDGRASS FROM
 CALIFORNIAN RICE FIELDS¹⁰⁵**

	<i>E. crus-galli</i>	<i>E. oryzoides</i>	<i>E. phyllopogon</i>
Loci	0.644	0.600	0.821
Alleles	0.432	0.300	0.450
Diversity	0.332	0.496	0.804

genetic differentiation among populations. This finding is expected in highly self-fertilizing species in which populations usually display marked interpopulation genetic differentiation. Of the three taxa, *E. crus-galli* maintains significantly more genetic variation in populations than the other two species by each of the criteria that were employed (Table 5). *Echinochloa oryzoides* appears to be a genetically depauperate, although not entirely uniform, form of *E. crus-galli*. While similar at the population level, *E. phyllopogon* shows more total diversity in California than *E. oryzoides*; in addition it exhibits a greater degree of genetic differentiation among populations than the other species (Table 6). Comparisons of isozyme variation in Australian populations of *E. crus-galli* and *E. oryzoides* indicated similar patterns, except that *E. oryzoides* was highly depauperate with all populations except one composed of the same multilocus isozyme genotype. The exceptional population was fixed for a variant allele at a locus coding for the enzyme *Pgm*.

The contrast in patterns of genetic variation at loci controlling the enzyme alcohol dehydrogenase (*Adh*) were particularly interesting in the three California barnyardgrass taxa. In *E. crus-galli*, a total of 12 homozygous multilocus genotypes was evident as a result of polymorphism at one to three loci. All populations in California contained at least one of the genotypes, with some containing up to six. All populations of *E. oryzoides* except one contained the same multilocus genotype. Plate 2* illustrates zymograms for *E. crus-galli* and *E. oryzoides*. In *E. phyllopogon* there was no genetic variation at *Adh* loci. The almost complete absence of *Adh* variation in populations of the specialist rice weeds may reflect

* Plate 2 appears after page 72.

Table 7
 QUANTITATIVE VARIATION IN BARNYARDGRASS
 POPULATIONS FROM CALIFORNIAN RICE
 FIELDS¹⁰⁵

Traits	No. populations with significant between- family (genetic) variation			Mean coefficient of variation (%) among populations		
	CG	O	P	CG	O	P
N (populations)	9	10	10	9	10	10
Days to flowering	7	9	7	13.6	6.5	5.4
Inflorescence height	8	3	4	19.2	10.7	15.1
Flag leaf length	6	2	1	23.7	13.8	16.0
Mature plant height	8	6	2	16.8	9.9	12.1
Total biomass	6	3	3	31.4	19.3	25.1

Note: CG = *Echinochloa crus-galli*, O = *E. oryzoides*, and P = *E. phyllopogon*; traits measured on two plants from each of 15 families per population grown under uniform glasshouse conditions.

selection for an 'optimum' *Adh* genotype adapted to the relatively uniform conditions of flooded rice fields. In contrast, polymorphism at *Adh* genes in *E. crus-galli* may be maintained by the heterogeneous nature of the disturbed wetland environments it occupies.

Elsewhere, studies of allelic variation at *Adh* loci in the annual weed *Bromus mollis* have revealed differences among isozyme variants in germination and growth under anaerobic conditions.⁸¹ There is considerable evidence that *Adh* enzymes function to enable plants to tolerate the anaerobic conditions associated with flooded environments.⁸² In the case of *Echinochloa* it would be of interest to survey populations of the three species from other rice-growing regions, particularly in their native Asia, to observe if the patterns observed in California are maintained and whether the two rice field specialists exhibit the same *Adh* genotypes throughout their ranges. Our survey of Australian populations revealed that *E. crus-galli* was polymorphic for *Adh* genes, whereas *E. oryzoides* was genetically uniform and fixed for the predominant Californian genotype.

The low levels of recombination in selfing species and our overall ignorance of the functional significance of most isozyme variation restrict meaningful interpretation of the ecological significance of measurements of most genetic variation based on isozymes. On the other hand, analysis of quantitative variation in life history traits may be helpful for two reasons. First, it provides an opportunity to assess genetic variation for ecological traits that are likely to have direct adaptive value. Second, the patterns of variation may enable predictions of the likely selective response of weed populations to changes in agronomic practices.

Measurements of quantitative variation in California populations of the three barnyardgrass species were in overall agreement with the results obtained from the isozyme survey. Populations of the generalist *E. crus-galli* were more variable for a range of quantitative traits than populations of either of the two rice field specialists, as judged by the number of populations with statistically significant between-family variation or the average coefficient of variation for individual traits (Table 7). Despite frequent colonizing episodes and a high level of self-fertilization in barnyardgrasses, populations are capable of maintaining moderate levels of quantitative genetic variation. This variation may result from occasional hybridization events between different biotypes as well as polygenic mutation at loci governing quantitative traits. The observed variation suggests that populations of *E. crus-galli* in California would be most responsive to altered selection pressures, and it is possible that

the low genetic variation in the two rice field specialists limits their ecological amplitude and contributes toward habitat restriction.

VI. FUTURE CROP/WEED ASSOCIATIONS

Many of the specialized agroecotypes that originated under 'primitive' agricultural conditions have either become extinct or are disappearing from cultivated land as a result of improved agronomic practices. In their place new associations of weeds more suited to modern crop husbandry are developing. Anticipating new weed problems is difficult because it requires knowledge of the changes likely to take place in crop systems and agricultural technology. For developing countries this is less of a problem since, if current trends continue, the changes are likely to parallel those that have already occurred in the developed world where larger farm sizes, greater mechanization, and extensive herbicide usage prevail. Parker⁸³ has reviewed some of the likely future weed problems in tropical countries as a result of these changes.

Two distinct problems likely to worsen due to herbicide use are the increased development of herbicide tolerance in weed populations and the difficulty of eradicating weed races (or close relatives) of crop species. An extensive literature exists on both topics and I will only briefly summarize the major problems here.

Where herbicides are used extensively, interspecific selection is the most obvious outcome, resulting in dramatic changes in the relative frequency of species according to the types of chemical applied.^{84,85} These fluctuations in species abundance do not involve evolutionary changes since there are no alterations in the genetic structure of weed populations. Although the evolution of herbicide tolerance is not a widespread phenomenon in weed populations (for possible reasons see Harper⁸⁶ and Gressel and Segel⁸⁷), an increasing number of cases are coming to light,⁸⁸ particularly in response to the use of the S-triazine herbicides (atrazine and simazine).

Of future interest is the extent to which plant populations that have not been exposed to chemical methods of weed control possess genetic variability for herbicide tolerance. A study of populations of three species (*Avena barbata* Brot., *A. fatua*, and *Clarkia williamsonii* [Dur. and Hilg.] Lewis and Lewis) that had not previously been exposed to herbicides revealed levels of herbicide tolerance considerably higher than would be expected on the basis of mutation alone.⁸⁹ The authors suggest that selection favoring genes that confer herbicide tolerance may occur in natural populations and that polymorphism at 'herbicide response' loci in previously unexposed populations may be associated with traits such as stomatal size, cuticular thickness, and various physiological characteristics. Their results suggest that the potential for developing tolerance to herbicides may be more extensive than was previously thought. Increased dosage rates and the use of herbicides in combination may be the growers' response to combat the development of herbicide-tolerant populations.

A second aspect of herbicide tolerance that deserves more attention concerns the possibility that the development of tolerance to one herbicide automatically confers tolerance to other herbicides. This situation has recently been examined in *Avena fatua*.^{90,91} Thai et al.⁹¹ found that populations that had been exposed to the herbicide triallate were 'cross tolerant' to other herbicides (diclofop and trifluralin) with different chemical structures. How common this phenomenon is and whether cross tolerance results from a single gene or from a combination of alleles at different loci is not known.

Many crop species have close relatives that are weedy in nature, capable of hybridizing with them and are closely associated with the crop as companion weeds.⁹²⁻⁹⁴ Crop/weed complexes are in fact considered an important reservoir of genetic diversity for crop improvement.⁹⁵ However, where chemicals are used regularly, weed relatives can become serious weeds since herbicides are not capable of discriminating between the crop and the

weed, and agronomic practices that favor the crop also encourage the growth of the weed. This type of problem can be further exacerbated when weedy relatives grow in close proximity to fields in which hybrid seed crops are produced. Hybridization between crop and weed can result in contamination of hybrid seed with undesirable traits such as dormancy, premature flowering (bolting), and shattering of seed. The hybrids then persist in fields as weeds. This problem has been documented in sorghum^{96,97} and sugarbeet.^{98,99} McNeill¹⁰⁰ reviews other recent examples of weed problems caused by crop relatives and suggests that the best prospect for their control lies in attempts to ensure uncontaminated supplies of seed, coupled with crop rotation.

VII. CONCLUSIONS

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. As experimental organisms, weeds are abundant, possess rapid life cycles, and are easily grown and measured. Despite these obvious attractions as subjects for evolutionary study, population biologists, particularly in North America, have largely neglected the agricultural environment for studies of natural selection. The recent development of techniques for measuring selection in populations,¹⁰¹ combined with demographic and electrophoretic approaches, provides excellent opportunities for studying the influence of agricultural practices on the dynamics and evolution of weed populations. Information on the reproductive systems and genetic structure of weed populations may be especially helpful to workers in the field of biological control. Populations that regenerate primarily by selfing, apomixis, or clonal propagation often contain less genetic variation and as a result may be more easily controlled by biological control agents.^{18,102} Population studies can also provide useful information to the agronomist and weed control specialist since a more complete picture of the critical stages in the life cycle of weed populations can be obtained. Data on age-specific mortality and fecundity can be used to model the dynamics of weed populations and to enable predictions of changes in population size and growth.^{103,104} Finally, population studies may help to take weed biology from its current, largely descriptive state to a situation in which we can more accurately predict the influence of various agronomic practices on both weed populations and crop yields. If nothing else, collaborative studies between agriculturalists and population biologists are long overdue and may help to bridge the large gulf that exists between pure and applied biology in North America.

ACKNOWLEDGMENTS

I thank Tony Brown, Jeremy Burdon, Steven Price, and Suzanne Warwick for providing unpublished manuscripts, references, and helpful discussion; Brenda Missen for typing and editorial advice; and the Natural Sciences and Engineering Research Council of Canada for supporting my own research on the ecological genetics of weeds.

REFERENCES

1. Bunting, A. H., Some reflections on the ecology of weeds, in *The Biology of Weeds*, Harper, J. L., Ed., Blackwell Scientific, Oxford, 1960, 11.
2. Baker, H. G., Characteristics and modes of origins of weeds, in *The Genetics of Colonizing Species*, Baker, H. G. and Stebbins, G. L., Eds., Academic Press, New York, 1965, 147.
3. Sinskala, E. N., The study of species in their dynamics and interrelation with different types of vegetation. *Tr. Prikl. Bot.*, 25, 1, 1931.

4. Salisbury, E. J., *Weeds and Aliens*, Collins, London, 1961.
5. King, L. J., *Weeds of the World: Biology and Control*, Hill, London, 1966.
6. Baker, H. G., The evolution of weeds, *Annu. Rev. Ecol. Syst.*, 5, 1, 1974.
7. Barrett, S. C. H., Crop mimicry in weeds, *Econ. Bot.*, 37, 255, 1983.
8. Brown, A. H. D. and Marshall, D. R., Evolutionary changes accompanying colonization in plants, in *Proc. Int. Congr. Syst. Evol. Bio.*, Scudder, G. C. E. and Reveal, J. L., Eds., Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pa., 1981, 351.
9. Lewontin, R. C., Selection for colonizing ability, in *The Genetics of Colonizing Species*, Baker, H. G. and Stebbins, G. L., Eds., Academic Press, New York, 1965, 77.
10. MacArthur, R. H. and Wilson, E. O., *The Theory of Island Biogeography*, Princeton University Press, Princeton, N.J., 1967.
11. Stearns, S. C., The evolution of life history traits, *Annu. Rev. Ecol. Syst.*, 8, 145, 1977.
12. Grime, J. P., Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory, *Am. Nat.*, 111, 1169, 1977.
13. Grime, J. P., *Plant Strategies and Vegetation Processes*, John Wiley & Sons, New York, 1979.
14. Sinskaia, E. N. and Beztuzheva, A. A., The forms of *Camelina sativa* in connection with climate, flax and man, *Tr. Prikl. Bot.*, 25, 98, 1931.
15. Stebbins, G. L., *Variation and Evolution in Plants*, Columbia University Press, New York, 1950.
16. Wickler, W., *Mimicry in Plants and Animals*, McGraw-Hill, New York, 1968.
17. Harlan, J. R., *Crops and Man*, American Society of Agronomy, Madison, Wis., 1975.
18. Barrett, S. C. H., Genetic variation in weeds, in *Biological Control of Weeds with Plant Pathogens*, Charudattan, R. and Walker, H., Eds., John Wiley & Sons, New York, 1982, 73.
19. Jain, S. K., Genetic characteristics of populations, in *Ecological Studies: Analysis and Synthesis*, Mooney, H. A. and Godron, M., Eds., Springer-Verlag, Berlin, 1983, 240.
20. Barrett, S. C. H. and Richardson, B. J., Genetic attributes of invading species, in *Ecology of Biological Invasions: An Australian Perspective*, Groves, R. H. and Burdon, J. J., Eds., Academy of Science, Canberra, 1985, 21.
21. Brown, A. H. D., Multilocus organization of plant populations, in *Population Biology and Evolution*, Wohrman, K. and Loeschke, V., Eds., Springer-Verlag, Berlin, 1984, 159.
22. Brown, A. H. D., Enzyme polymorphism in plant populations, *Theor. Popul. Biol.*, 15, 1, 1979.
23. Loveless, M. D. and Hamrick, J. L., Ecological determinants of genetic structure in plant populations, *Annu. Rev. Ecol. Syst.*, 15, 65, 1984.
24. Lande, R., The maintenance of genetic variability by mutation in polygenic characters with linked loci, *Genet. Res.*, 26, 221, 1975.
25. Lande, R., The influence of the mating system on the maintenance of genetic variability in polygenic characters, *Genetics*, 86, 485, 1977.
26. Mashburn, S. J., Shartz, R. R., and Smith, M. H., Genetic variation among *Typha* populations of the southeastern United States, *Evolution*, 32, 681, 1978.
27. Brown, A. H. D. and Burdon, J. J., Multilocus diversity in an outbreeding weed, *Echium plantagineum* L., *Aust. J. Biol. Sci.*, 36, 503, 1983.
28. Glover, D. E. and Barrett, S. C. H., Genetic variation in continental and island populations of *Eichhornia paniculata*, 1986, *Heredity*, 59, 7, 1987.
29. Hamrick, J. L., Linhart, Y. B., and Mitton, J. B., Relationships between life history characteristics and electrophoretically detectable genetic variation in plants, *Annu. Rev. Ecol. Syst.*, 10, 173, 1979.
30. Warwick, S. I., Genetic variation in colonizing weed species, 1986, unpublished manuscript.
31. Roose, M. L. and Gottlieb, L. D., Genetic and biochemical consequences of polyploidy in *Tragopogon*, *Evolution*, 30, 818, 1976.
32. Babbel, G. R. and Wain, R. P., Genetic structure of *Hordeum jubatum*. I. Outcrossing rates and heterozygosity levels, *Can. J. Genet. Cytol.*, 19, 143, 1977.
33. Ehrendorfer, F., Polyploidy and distribution, in *Polyploidy: Biological Relevance*, Lewis, W. H., Ed., Plenum Press, New York, 1980, 45.
34. Levin, D. A., Polyploidy and novelty in flowering plants, *Am. Nat.*, 122, 1, 1983.
35. Moran, G. F. and Marshall, D. R., Allozyme uniformity within and variation between races of the colonizing species *Xanthium strumarium* L. (Noogoora Burr.), *Aust. J. Biol. Sci.*, 31, 282, 1978.
36. Moran, G. F., Marshall, D. R., and Müller, W. J., Phenotypic variation and plasticity in the colonizing species *Xanthium strumarium* L. (Noogoora Burr.), *Aust. J. Biol. Sci.*, 34, 639, 1981.
37. Giles, B. E., A comparison between quantitative and biochemical variation in the wild barley *Hordeum murinum*, *Evolution*, 38, 34, 1983.
38. Warwick, S. I., Thompson, B. K., and Black, L. D., Population variation in *Sorghum halepense*, Johnson grass, at the northern limits of its range, *Can. J. Bot.*, 62, 1781, 1984.
39. Warwick, S. I. and Black, L. D., Genecological variation in recently established populations of *Abutilon theophrasti* (velvet leaf), *Can. J. Bot.*, 64, 1632, 1986.

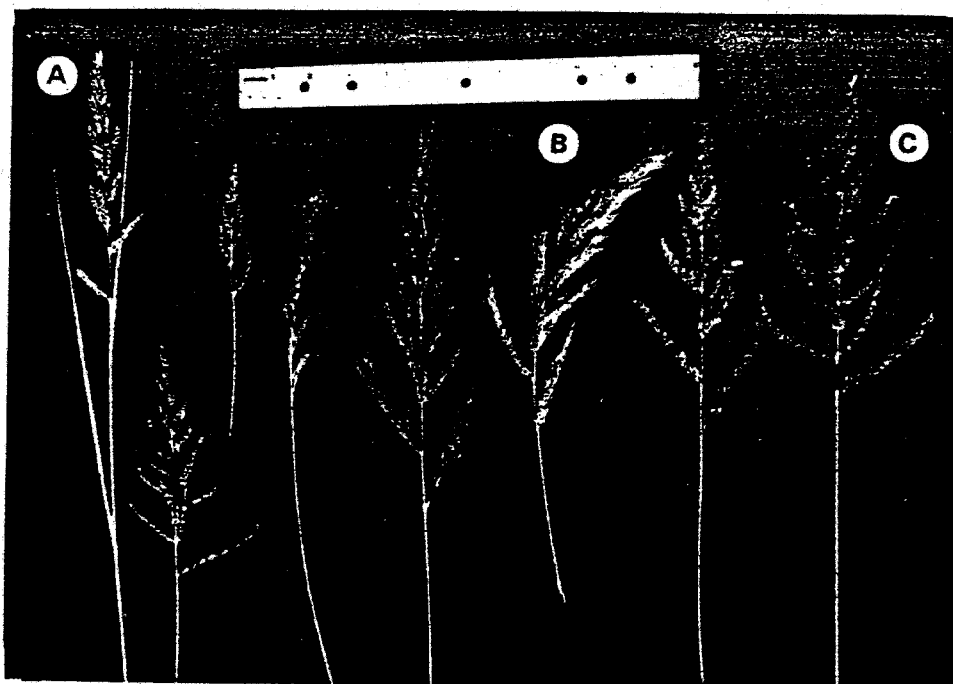
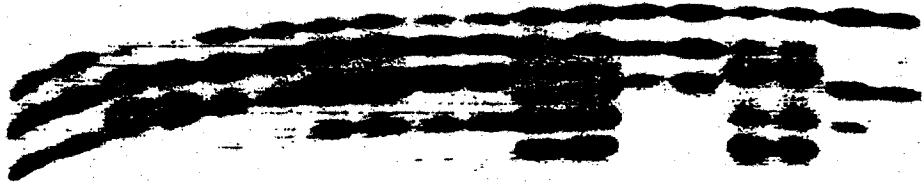


PLATE I. Inflorescences of barnyardgrasses collected in the vicinity of Biggs Rice Experiment Station, Butte County, California. (A) *Echinochloa phyllopogon*, (B) *Echinochloa oryzoides*, (C) *Echinochloa microstachya*; the remaining inflorescences are *Echinochloa crus-galli*.

40. Lewontin, R. C., Detecting population differences in quantitative characters as opposed to gene frequencies. *Am. Nat.*, 123, 115, 1984.
41. Brown, A. H. D. and Burdon, J. J., Mating systems and colonising success in plants. in *Colonization, Succession and Stability*. Gray A., Crawley, M. J., and Edwards, P. J., Eds., Blackwell Scientific, Oxford, 1987, 115.
42. Price, S. C., Shumaker, K. M., Kahler, A. L., Allard, R. W., and Hill, J. E., Estimates of population differentiation obtained from enzyme polymorphisms and quantitative characters. *J. Hered.*, 75, 141, 1984.
43. Darmency, H. and Gasquez, J., Inheritance of triazine resistance in *Poa annua*: consequences for population dynamics. *New Phytol.*, 89, 487, 1981.
44. Second, G., Origin of the genic diversity of cultivated rice (*Oryza* spp.). Study of the polymorphism scored at 40 isozyme loci. *Jpn. J. Genet.*, 57, 25, 1982.
45. Darmency, H. and Gasquez, J., Esterase polymorphism and ecotypic differentiation in *Poa annua* L.. *New Phytol.*, 95, 289, 1983.
46. Darmency, H. and Gasquez, J., Interpreting the evolution of a triazine-resistant population of *Poa annua* L.. *New Phytol.*, 95, 299, 1983.
47. Price, S. C. and Kahler, A. L., Oats (*Avena* spp.), in *Isozymes in Plant Genetics and Breeding. Part B*. Tanksley, S. D. and Orton, T. J., Eds., Elsevier Science Publishers, Amsterdam, 1983, 103.
48. Gasquez, J., Breeding system and genetic structure of a *Chenopodium album* population according to crop and herbicide rotation, in *Genetic Differentiation and Dispersal in Plants*. Jacquard, P., Heim, G., and Antonovics, J., Eds., Springer-Verlag, Berlin, 1984, 57.
49. Clegg, M. T., Kahler, A. L., and Allard, R. W., Estimation of life cycle components of selection in an experimental plant population. *Genetics*, 89, 765, 1978.
50. Langlet, O., Two hundred years of geneecology. *Taxon*, 20, 653, 1971.
51. Kornas, J., The extinction of the association *Sperguleto-Lolietum remoti* in flax cultures in the Gorce (Polish Western Carpathian Mountains). *Bull. Acad. Pol. Sci.*, 9, 37, 1961.
52. Kornas, J., Distribution and dispersal ecology of weeds in segetal plant communities in the Gorce Mountains (Polish Western Carpathians). *Acta Agrobot.*, 25, 5, 1972.
53. Tüxen, R., Grundriss einer Systematik der Nitrophilen Unkrautgesellschaften in der Eurosibirischen Region Europas. *Mitt. Flor. Soz. Arbeitsgem. Neue Folge*, 2, 193, 1950.
54. Oberdorfer, E., Süddeutsche Pflanzengesellschaften. *Pflanzensoziologie*, 10, 34, 1957.
55. Sorensen, T., Adaptation of small plants to deficient nutrition and a short growing season illustrated by cultivation experiments with *Capsella bursa-pastoris* (L.) Med.. *Bot. Tidskr.*, 51, 339, 1954.
56. Imam, A. G. and Allard, R. W., Population studies in predominantly self-pollinated species. VI. Genetic variability between and within natural populations of wild oats from differing habitats in California. *Genetics*, 51, 49, 1965.
57. Jones, M. E., The population genetics of *Arabidopsis thaliana*. I. The breeding system. *Heredity*, 27, 39, 1971.
58. Jones, M. E., The population genetics of *Arabidopsis thaliana*. II. Population structure. *Heredity*, 27, 51, 1971.
59. Akeroyd, J. R. and Briggs, D., Geneecological studies of *Rumex crispus* L. I. Garden experiments using transplanted material. *New Phytol.*, 94, 309, 1983.
60. Akeroyd, J. R. and Briggs, D., Geneecological studies of *Rumex crispus* L. II. Variation in plants grown from wild-collected seed. *New Phytol.*, 94, 325, 1983.
61. Kaderett, J. W. and Briggs, D., 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, 1985.
62. Law, R., Bradshaw, A. D., and Putwain, P. D., Life history variation in *Poa annua*. *Evolution*, 31, 233, 1977.
63. Law, R., The cost of reproduction in annual meadow grass. *Am. Nat.*, 113, 3, 1979.
64. Law, R., The dynamics of a colonizing population of *Poa annua*. *Ecology*, 62, 1267, 1981.
65. Naylor, J. M. and Jana, S., Genetic adaptation for seed dormancy in *Avena fatua*. *Can. J. Bot.*, 54, 306, 1976.
66. Naylor, J. M., Studies on the genetic control of some physiological processes in seeds. *Can. J. Bot.*, 61, 3561, 1983.
67. Barrett, S. C. H. and Wilson, B. F., Colonizing ability in the *Echinochloa crus-galli* complex (barnyard grass). II. Seed biology. *Can. J. Bot.*, 61, 556, 1983.
68. Holliday, R. J. and Putwain, P. D., Evolution of resistance to simazine in *Senecio vulgaris* L.. *Weed Res.*, 17, 291, 1977.
69. Holliday, R. J. and Putwain, P. D., Evolution of herbicide resistance in *Senecio vulgaris*: variation in susceptibility to simazine between and within populations. *J. Appl. Ecol.*, 17, 779, 1980.
70. Putwain, P. D., Scott, K. R., and Holliday, R. J., The nature of resistance to triazine herbicides; case histories of phenology and population studies. in *Herbicide Resistance in Plants*. Le Baron, H. M. and Gressel, J., Eds., John Wiley & Sons, New York, 1982, 99.

(A)



(B)



PLATE 2. Zymograms of the enzyme alcohol dehydrogenase (*Adh*) in populations of A. *Echinochloa crus-galli* and B. *Echinochloa oryzoides* from Californian rice fields; the different banding patterns in *E. crus-galli* are the result of polymorphism at 1—3 loci. A different allele at 1 of 4 *Adh* loci accounts for the variant pattern in the otherwise genetically uniform *E. oryzoides*.

71. Comstock, V. E. and Anderson, R. N., An inheritance study of tolerance to atrazine in a cross of flax (*Linum usitatissimum* L.). *Crop Sci.* 8, 508, 1968.
72. Sykes, S. R., Selection for Herbicide Resistance in Cruciferous Crop Plants. Ph.D. thesis. University of Liverpool, Liverpool, England, 1980.
73. Michael, P. W., Taxonomy and distribution of *Echinochloa* species with special reference to their occurrence as weeds of rice. in *Weed Control in Rice*. Proc. Conf. Int. Rice Res. Inst., Los Baños, Phillipines, 1983. 291.
74. Holm, L. G., Plucknett, D. L., Pancho, J. V., and Herberger, J. P., *The World's Worst Weeds — Distribution and Biology*. University of Hawaii, Honolulu, 1977. 609.
75. Maun, M. A. and Barrett, S. C. H., The biology of Canadian Weeds. 74. *Echinochloa crus-galli* (L.) Beauv., *Can. J. Plant Sci.*, 65, 1985, in press.
76. Yabuno, T., Biology of *Echinochloa* species, in *Weed Control in Rice*. Proc. Conf. Int. Rice Res. Inst., Los Baños, Phillipines, 1983. 307.
77. McIntyre, S. and Barrett, S. C. H., A comparison of weed communities of rice in Australia and California. *Proc. Ecol. Soc. Aust.*, 14, 237, 1986.
78. Barrett, S. C. H. and Seaman, D. E., The weed flora of Californian ricefields, *Aquat. Bot.* 9, 351, 1980.
79. Kennedy, R. A., Barrett, S. C. H., VanderZee, D., and Rumpho, M. E., Germination and seedling growth under anaerobic conditions in *Echinochloa crus-galli* (barnyard grass). *Plant Cell Environ.*, 3, 243, 1980.
80. Barrett, S. C. H. and Wilson, B. F., Colonizing ability in the *Echinochloa crus-galli* complex (barnyard grass). I. Variation in life history. *Can. J. Bot.* 59, 1844, 1981.
81. Brown, A. H. D., Marshall, D. R., and Munday, J., Adaptedness of variants at an alcohol dehydrogenase locus in *Bromus mollis* L. (Soft Bromegrass). *Aust. J. Biol. Sci.*, 29, 289, 1976.
82. Hook, D. D. and Crawford, R. M. M., *Plant Life in Anaerobic Environments*. Ann Arbor Science Publications, Ann Arbor, Mich., 1978.
83. Parker, C., Prediction of new weed problems, especially in the developing world, in *Origins of Pest. Parasite, Disease and Weed Problems*. Cherrett, J. M. and Sagar, G. R., Eds., Blackwell Scientific, Oxford, 1976. 249.
84. Hay, J. R., The changing weed problem on the prairies, *Agric. Inst. Can. Rev.*, 24, 17, 1968.
85. Fryer, J. D. and Chancellor, R. J., Herbicides and our changing weeds, in *The Flora of a Changing Britain*. Perring, F., Ed., Bot. Soc. Br. Isles, E. W. Classey, Hampton, Middlesex, 1970. 105.
86. Harper, J. L., The evolution of weeds in relation to resistance to herbicides, *Proc. 3rd Br. Weed Control Conf.*, 1, 179, 1956.
87. Gressel, J. and Segel, L. A., The paucity of plants evolving genetic resistance to herbicides: possible reasons and implications. *J. Theor. Biol.*, 75, 349, 1978.
88. Le Baron, H. M. and Gressel, J., *Herbicide Resistance in Plants*. John Wiley & Sons, New York, 1982.
89. Price, S. C., Hill, J. E., and Allard, R. W., Genetic variability for herbicide reaction in plant populations. *Weed Sci.*, 31, 652, 1983.
90. Somody, C. N., Nalewaja, J. D., and Miller, S. D., Wild oat (*Avena fatua* and *Avena sterilis*) morphological characteristics and response to herbicides. *Weed Sci.*, 32, 353, 1984.
91. Thai, K. M., Jana, S., and Naylor, J. M., Variability for response to herbicides in wild oat (*Avena fatua*) populations. *Weed Sci.*, 33, 829, 1985.
92. Harlan, J. R., The possible role of weed races in the evolution of cultivated plants, *Euphytica*, 14, 173, 1965.
93. Doggett, H. and Majisu, B. N., Disruptive selection in crop development, *Heredity*, 23, 1, 1968.
94. Pickersgill, B., Biosystematics of crop-weed complexes, *Kulturpflanze*, 29, 377, 1981.
95. Harlan, J. R., Genetic resources in wild relatives of cultivated crops, *Crop Sci.*, 16, 329, 1976.
96. Quimby, J. R., Kramer, N. W., Stephens, J. C., Lahr, K. A., and Karper, R. E., Grain sorghum production in Texas. *Bull. Tex. Agric. Exp. Stn.*, 912, 1958.
97. Baker, H. G., Migration of weeds, in *Taxonomy, Phylogeography and Evolution*. Valentine, D. H., Ed., Academic Press, London, 1972, 327.
98. Hornsey, K. G. and Arnold, M. H., The origin of weed beet, *Ann. Appl. Biol.*, 92, 279, 1974.
99. Longdon, P. C., Sugar beet as weed, *Proc. 12th Br. Weed Control Conf.*, 1, 301, 1974.
100. McNeill, J., The taxonomy and evolution of weeds, *Weed Res.*, 16, 399, 1976.
101. Lande, R. and Arnold, S. J., The measurement of selection on correlated characters. *Evolution*, 37, 1210, 1983.
102. Burdon, J. J. and Marshall, D. R., Biological control and the reproductive mode of weeds, *J. Appl. Ecol.*, 18, 649, 1981.
103. Mortimer, A. M. and Firbank, L. G., Towards a rationale for the prediction of weed infestations and the assessment of control strategies. *Proc. 10th Int. Congr. Plant Prot.*, British Crop Protection Council, Brighton, 1983, 146.

104. **Firbank, L. G. and Watkinson, A. R.**, Modelling the population dynamics of an arable weed and its effect upon crop yield, *J. Appl. Ecol.*, 23, 147, 1986.
105. **Barrett, S. C. H. and Brown, A. H. D.**, unpublished data.
106. **Price, S. C.**, personal communication.