Crop Mimicry in Weeds[1]

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The selective forces imposed by agricultural practices have resulted in the evolution of agricultural races of weeds or agroecotypes. Some agroecotypes are intimately associated with a specific crop. Such associations can involve a system of mimicry, whereby the weed resembles the crop at specific stages during its life history and, as a result of mistaken identity, evades eradication. Mimetic forms of weeds are most likely to be selected by handweeding of seedlings or by harvesting and seed cleaning procedures. A striking example of morphological and phenological resemblance is found in the cultivated rice mimic, Echinochloa crus-galli *var.* oryzicola, *a native of Asian rice fields but now widely distributed in rice-growing areas of the world. Comparative studies of the growth, development and patterns of phenotypic variation of cultivated rice,* E. crus-galli *var.* oryzicola *and* E. crus-galli *var.* crus-galli *demonstrate that the crop mimic is more similar to rice in many attributes than it is to its close relative. It is proposed that intense handweeding practices in Asia constitute the main selective force favoring the evolution of rice mimicry in* E. crus-galli *var.* oryzicola.

The clearance of natural vegetation and creation of open, disturbed sites have been major activities associated with the development of human civilization. Prior to sedentary agriculture, forest clearing occurred on a relatively small scale in association with shifting cultivation and village settlement. Plant species of natural communities with well developed powers of dispersal, high reproductive capacity and short life cycles soon established in the open areas created by man and in doing so became man's first weeds (Anderson, 1952). These early weeds were pioneers of secondary succession and possessed a set of adaptations which enabled them to proliferate in disturbed conditions (Bunting, 1960). Today a much broader spectrum of "adaptive strategies" exists in weed species as a result of the development of varied agricultural systems and the creation of a wide array of weed niches.

The arable field provides a different environment for weed populations than habitats of open, derelict land. Weed communities found within the crop frequently differ in species diversity and life history from those found at the periphery of fields. Conditions of the field are closely controlled by the farmer and are usually less complex, with disturbance, in the form of ploughing, cultivation and herbicide applications, frequent and highly predictable (Snaydon, 1980). One of the major objectives of modern monocultures is to minimize the heterogeneity of the physical and biological components of the environment in an effort to produce a uniform set of growing conditions.

The selective forces imposed by agricultural practices have resulted in the diversification of adaptive strategies of weed populations. Agricultural races of

weeds or agroecotypes have developed in weeds originally found in open, disturbed sites (Sinskaia, 1931; Gregor, 1938; King, 1966). Some weed species closely associated with a particular crop (see below) were domesticated while others became members of crop-weed complexes united by gene exchange (Harlan, 1970; Doggett and Majisu, 1968; Pickersgill, 1981). The high degree of specialization which has developed in agroecotypes of weeds often restricts their distribution to particular crops grown under specific cultural conditions. These satellite weeds of crops represent a contrast to pioneering weeds of broad ecological tolerance.

Of particular interest to the evolutionist are cases in which weed populations develop a close resemblance to some phase of the life history of a crop and as a result of mistaken identity evade eradication. This phenomenon, known as crop mimicry, is poorly documented and most of the pertinent literature is anecdotal. In this review, I will discuss race formation in agricultural weeds and examine the evidence for crop mimicry. A comparison of the life histories of varieties of barnyard grass (*Echinochloa crus-galli* [L.] Beauv.) will then be made to enable a characterization of the adaptive strategy of the rice mimic *E. crus-galli* (L.) Beauv. var. *oryzicola* (Vasing) Ohwi.

SELECTIVE FORCES IN AGRICULTURE

Progressive changes in systems of crop husbandry continually modify the selective forces acting on weed populations. Changes in the composition of weed communities associated with peasant agriculture were probably gradual because of the conservatism of the peasant farmer and the relatively slow rate of weed migration compared to the present. Nevertheless, agricultural weeds, particularly in tropical regions, have probably been influenced to some extent by artificial selection through cultivation practices, handweeding, threshing and winnowing. These effects are more likely to occur where intensive agriculture has a long history rather than in regions where shifting cultivation predominates.

During the last century the strength and nature of the selection pressures exerted on weed populations by farming practices have altered greatly. The more important contemporary influences include the introduction of mechanization and chemical herbicides, the development of new crops and crop varieties, and the increase in size and structure of land holdings. In recent years many weeds have undergone spectacular range extensions (Sculthorpe, 1967; Baker, 1972) whereas others that were formerly widespread have all but disappeared. In Europe, improved threshing and seed-cleaning procedures, changes in soil fertility, and the introduction of new crops, have resulted in the decline of species such as *Adonis annua, Agrostemma githago, Artemisia vulgaris, Bromus secalinus* and *Chrysanthemum segetum* from arable fields (Godwin, 1960; Salisbury, 1961; Hammerton, 1968). In California, changes in irrigation techniques in rice fields have altered the species composition of the weed flora (Barrett and Seaman, 1980), and a vigilant seed certification programme has eliminated the wild rice *Oryza sativa* var. *rufipogon* from cultivated rice stocks (Bellue, 1932).

Chemical selection by herbicides is currently one of the most important influences on the composition of crop weed floras. With the exception of some tropical areas, herbicides are used routinely in most forms of crop production and their

continued use can result in striking changes in the spectrum of weeds infesting a crop. In the United States, annual grasses have increased in abundance in maize whereas in soybeans broad-leaved weeds have replaced grasses as the most serious weeds in some states. In plantation crops in tropical regions herbicide usage has led to a preponderance of perennial species. Further discussion of the impact of herbicides on weed communities can be found in Hanson (1962), Bachthaler (1969), Fryer and Chancellor (1970), and Parker (1977). With the increasing range of chemical compounds available, shifts in the life form of weeds following repeated usage of a single herbicide will be less frequent, but alterations in the genetic structure of weed populations seem likely (see below).

RACE FORMATION

If selection imposed by agricultural practices continues for any length of time and appropriate genetic variation occurs, locally adapted races of weeds will arise (King, 1966; Barrett, 1982). Some of the earliest observations of the evolution of agroecotypes involve the selection of dwarf forms of *Aethusa cynapium* and *Torilis japonica* in cereal crops following the introduction of the reaper (Salisbury, 1961). Genecological studies of managed grasslands subject to varying grazing intensities have revealed the presence of races of numerous grass species with different growth forms, and genetic changes in pastures are well documented (Gregor and Sansome, 1927; Stapledon, 1928; Snaydon, 1978). The regular mowing of lawns and bowling greens can result in the evolution of dwarf and prostrate races of common weeds (Nelson, 1965; Warwick and Briggs, 1978a,b, 1980). In most cases these forms have limited colonizing potential and are restricted in distribution to the types of managed environment in which they arose.

Where regular use of fertilizers occurs it seems likely that weed races adapted to high fertility regimes will develop. Studies of the managed Park Grass Plot at Rothamsted Experiment Station in England have demonstrated the rapidity with which edaphic races of the grass *Anthoxanthum odoratum* have evolved in response to contrasting fertilizer treatments (Snaydon, 1970; Snaydon and Davies, 1972). Although ecotypes of common agricultural weeds have been shown to differ in their nutritional requirements (Ramakrishnan and Jain, 1965; Ramakrishnan, 1968; Ramakrishnan and Gupta, 1973), in most cases it is not known whether these differences evolved as a result of their association with particular agricultural systems.

There is some evidence that weed populations which are continuously associated with a specific agricultural system may evolve phenological patterns which optimise survival within the most favourable growing period. This process has apparently occurred in teosinte (*Zea mexicana*), a weed of maize. In Mazatlan, Mexico, fields are planted to maize in one year and are fallowed and grazed the following year. Populations of *Z. mexicana* exhibit a germination inhibitor which prevents germination during fallow years and hence predation of the plants by grazing animals. The weed population is, therefore, in phase with alternate year planting of maize. This adaptation appears to have been developed in recent times since the management practice began in the 1920s. No other populations of *Z. mexicana* with this type of dormancy pattern have been observed (Wilkes, 1977).

In annual crops the period favourable for vegetative growth and reproduction

is often of short duration, and selection for rapid development and precocious reproduction in weed races may become particularly important where short-season crop varieties are used. In the rice fields of Malaysia, annual races of the normally perennial *Monochoria vaginalis* occur. Precocious reproduction, following a short juvenile period, in these forms enables populations to escape the drying period at rice harvest and thus to survive from season to season (Steenis, 1957). Precocity seems to be particularly well developed in aquatic plants from seasonally inundated habitats. In Californian rice fields, populations of *Sagittaria montevidensis* flower 25–35 days after flooding and enough seeds mature before herbicides destroy most plants (Barrett and Seaman, 1980). It seems probable that herbicides exert strong enough selective forces to modify the growth patterns of weeds resulting in "avoidance strategies" whereby individuals escape the destructive impacts of the spray. Avoidance strategies could take the form of precocious reproduction, or delayed germination in cases where herbicides are applied at the seedling stage. More information is required on the effects of herbicides on the life history parameters of weed populations.

Although herbicides alter the composition and ecological interactions of weed communities, there have been relatively few cases of the evolution of genetic resistance to herbicides. Harper (1956) and Gressel and Segel (1978) have examined some of the reasons why weeds are less likely to develop resistance to biocides than animal populations. Selection for increased resistance might be anticipated in circumstances where a specific herbicide has been repeatedly used during an extended period. Holliday and Putwain (1980) examined 46 populations of the annual weed *Senecio vulgaris* from fruit farms in England which had been subjected to application of the herbicide simazine. They demonstrated significant interpopulation variation in herbicide susceptibility and a positive linear relationship between the percentage survival of populations following application of the herbicide, and the number of consecutive years of use. Their results strongly suggest that natural selection for simazine resistance had developed in *Senecio vulgaris*.

Most cases where herbicide resistance in weeds has developed involve the S-triazine herbicides, atrazine and simazine (Holliday and Putwain, 1974, 1977; Bandeen and McLaren, 1976; Radosevich, 1977; Maltais and Bouchard, 1978; Warwick et al., 1979). The genetics of resistance to S-triazines has been investigated in *Brassica campestris* (Souza Machado et al., 1977), *Chenopodium album* (Warwick and Black, 1980), and *Senecio vulgaris* (K. R. Scott unpubl. data, cited in Holliday and Putwain, 1980). In each species the resistance mechanism appears to be inherited through the female parent. This has important implications in relation to the establishment of the resistance gene(s) in weed populations since gene flow via pollen cannot influence its rate of spread once the mutation arises. The discovery that S-triazine resistance is maternally inherited, possibly through the cytoplasm, is of interest since the site of the tolerance mechanism seems to occur within the chloroplasts of resistant plants.

The tempo of race formation in agricultural weeds will be strongly influenced by the amount and nature of genetic variation stored within weed populations. Compared with some other plant life forms, populations of weed species frequently exhibit reduced levels of genetic diversity (Levin, 1975; Crawford and Wilson, 1977, 1979; Moran and Marshall, 1978; Hamrick et al., 1979; Whalen,

1979; Brown and Marshall, 1981). Low variation within weed populations may result from genetic bottlenecks associated with repeated episodes of colonization, small population size, founder effects, extensive cloning, inbreeding and the relative homogeneity of many agricultural habitats (Barrett, 1982). Substantial stores of genetic variation have been revealed in weeds such as wild oats and wild barley which often form large populations and occupy complex environments that vary greatly both spatially and temporally (Jain, 1969; Allard et al., 1978; Brown et al., 1978; Nevo et al., 1979). Unfortunately most of the detailed electrophoretic analysis of genetic variation in weed populations has involved ruderal species and as yet there is little information on weeds restricted to arable crops.

CROP MIMICRY

Agricultural operations are usually designed to promote the growth and yield of the crop but, despite the efforts of the farmer, they usually encourage the development of specialized weeds. The more closely a weed species resembles the crop in habit, phenology and ecological requirements, the more difficult it is to control without causing damage to the crop (Bunting, 1960; Hammerton, 1968; McNeill, 1976; Parker, 1977; Harlan, 1981). Some crop-weed associations are so intimate that their interaction with man has led to the evolution of mimetic forms of weeds. These often resemble the crop in morphology and behaviour and thereby avoid eradication. Unfortunately, there are virtually no experimental studies of this type of coevolutionary phenomenon in weeds and most reports in the literature merely document the form of resemblance between crop and weed.

Although mimicry has been extensively studied for over a century, there still exists considerable debate over the concept and the various forms which mimicry can take (Wickler, 1968; Vane-Wright, 1976). Mimetic systems are widespread in animals and are particularly well documented among the insects. In plants the subject has received less attention although reports of mimicry can be found scattered throughout the literature on the natural history of various plant groups. Harper (1977) has suggested that botanists have been reluctant to accept animals as important selective agents and that this may account for the paucity of detailed studies of mimicry in plants.

Recently Wiens (1978) has reviewed much of the literature on plant mimicry as well as attempting a classification of mimetic phenomena. Following Wiens and as a prelude to this discussion of weed mimicry, the following terms central to the concept are defined: *the model*—the object (animate or inanimate) or function which is being imitated; *the mimic*—the imitating organism; *the operator*—the organism that is unable to discriminate effectively between the model and the mimic. According to Wiens (1978), any purported case of mimicry should involve these 3 elements. This presents problems of definition in the case of seed mimicry in weeds (see below) because in a strict sense there is no interorganismal sensory discrimination in the interaction. The selective agents or operators are mechanical devices designed and operated by man. On the basis of this essentially semantic difficulty, Wiens (1978) excluded cases of seed mimicry in weeds from his treatment of the subject. In contrast, the earlier reviews of mimicry by Wickler (1968) and Vane-Wright (1976) accepted that crops such as rye (*Secale*) and oats (*Avena*) have evolved from weed forms during the cultivation of wheat (*Triticum*) by an essentially mimetic process involving resemblance of the fruits or caryopses of

crop and weed (see below). Perhaps of more importance than these problems of definition is the fact that a critical analysis of mimetic phenomena in weeds is made difficult because in most cases the selective forces responsible for resemblances between model and mimic are no longer in operation. Much of our discussion must therefore rely on inferences drawn from contemporary field observations.

For the purpose of this review it is convenient to distinguish 2 major forms of crop mimicry in weeds that correspond to the main period in the life cycle of the crop where resemblance and hence deception occurs. In "vegetative mimics" the close similarity in appearance occurs during the seedling and vegetative growth periods. The presumed selective force is manual weed control practices by hand, hoe or any other implement directly operated by man. Here man can be viewed as a type of predator, and interorganismal sensory discrimination is clearly involved. In "seed mimics" the resemblance occurs between the seeds of the crop and weed and involves similarities in weight, density, as well as appearance. A third type of "mimicry" has been suggested where races of weeds have evolved a similar reaction spectrum to herbicides as the crop in which they grow (Harlan, 1981). This type of resemblance is similar in some ways to the development of mimicry due to handweeding. However, an intimate relationship among the 3 elements of a mimicry system (model, mimic and operator) is not required for the evolution of herbicide resistance to occur since changes in the weed populations could in theory be brought about in the absence of the model. For these reasons it is probably best to treat examples of herbicide resistance simply as cases of chemical selection.

Vegetative mimicry

The practice of removing weeds from crops is presumably as old as the history of agriculture itself. Handweeding is most likely to be carried out where cultivated plots are small, labour is abundant and crops are grown in rows. Where fields are large and seed is broadcast, handweeding may be expected to be less intense because of the effort required and the damage which would result from weeding activities in the stand. In either circumstance, weeding is most likely to be practised during the early stages of crop growth and weed seedlings that resemble those of the crop are the most likely to be overlooked. Most cases of vegetative mimicry involve the Gramineae and this probably reflects the superficial similarity among seedlings of members of the family.

A common weed of maize fields of Central America and Mexico is teosinte (*Zea mexicana*). It is fully interfertile with its congener maize (*Zea mays*) and hybridization occurs frequently under field conditions. Great variation occurs among teosinte populations ranging from forms adapted to persistence in natural vegetation to those found exclusively in maize fields. Wilkes (1967, 1977) has made detailed studies of teosinte in the region and has described mimetic forms of the weed in the Valley of Mexico. The process of mimicry is enhanced by gene exchange from crop to weed. Where maize varieties with red plant colour, hairy leaf sheaths and wide leaves are grown, the teosinte populations have developed these characters. As a result teosinte plants are virtually indistinguishable from maize during the vegetative condition and thus plants growing along the

rows escape weeding. During the flowering period teosinte can be distinguished from maize because of the difference between the 2 species in inflorescence architecture, and plants are cut from the rows. However, the cut plants are fed to cattle which ingest any seeds of teosinte that are mature. Cattle manure is used to fertilize the following crop and seeds of teosinte are returned to the field during seed-bed preparation. These cultural practices ensure the survival of teosinte and historical evidence indicates that the weed has existed as a mimic of maize since the Spanish Conquest (Wilkes, 1977).

Elsewhere among New World crops gene flow from crop to weed has been reported in the grain chenopods and grain amaranths (Sauer, 1967; Heiser and Nelson, 1974; Wilson and Heiser, 1979). In some populations of weed races of *Chenopodium berlandieri* and *C. hircinum,* domesticated characters including terminal and compact inflorescences, nonshattering habit, large fruits and a lack of seed dormancy occur. These traits enable the weeds to survive in the crop environment and characters that lead to phenotypic similarity enhance the ability of the weeds to escape handweeding.

In Africa, mimetic weeds of pearl millet (*Pennisetum americanum* subsp. *americanum*) and sorghum (*Sorghum bicolor*) have apparently evolved by similar processes involving gene exchange from crop to weed (Harlan et al., 1973; Brunken et al., 1977; Harlan, 1981). Both millets are grown under "primitive" agricultural conditions over a wide area of Africa, and considerable variation exists in the cultivated and weed races as a result of geographical differentiation and hybridization. Striking patterns of parallel variation between crop and weed occur in many parts of the range of the 2 complexes. In Ethiopia, where varieties of sorghum with loose, open panicles are cultivated, the weed forms exhibit similar inflorescences. Similarly, where cultivars with dense inflorescences are grown, the weed sorghums infesting these varieties exhibit dense inflorescences (de Wet et al., 1976; Harlan, 1981). In pearl millet, weed forms with long inflorescences and elongated terminal bristles are only found in cultivars that share these features (Brunken et al., 1977). Although these resemblances noted by Harlan and co-workers involve reproductive characters, it seems probable that vegetative similarities also exist and seedlings of crop and weed may be mistaken for one another. Concordant geographical patterns of resemblance between model and mimic are characteristic of many mimicry systems and are particularly well documented in several neotropical butterfly complexes (Turner, 1971), but in most cases the similarities in phenotypic expression do not result from gene flow.

The major feature distinguishing the mimetic weed millets and their crop models concerns their respective seed-dispersal mechanisms. Infructescences of the weed forms exhibit a shattering habit and most seed is returned to the soil although, because of the synchronous flowering patterns of crop and weed, some seed from late-flowering inflorescences may be harvested and resown with the crop. In sorghum at least 2 systems of the inheritance of shattering are reported (Ayyangar et al., 1936; Karper and Quinby, 1947); one involves a single recessive gene (sh_1) and the other a pair of complementary dominant genes (Sh_2Sh_3). In pearl millet, 3 recessive genes with additive effects control the degree of shattering (Bilquez and Lecomte, 1969). Although mimetic forms can disperse their seeds, they rapidly disappear from cultivated fields once they are abandoned and colonized by

other weed species (Brunken et al., 1977). The inability to survive without man's aid is a common feature of crop mimics, a characteristic which they share with their models.

In many regions of the world, wild rices are serious weed problems in cultivated rice fields (Grist, 1953; Purseglove, 1972; Parker and Dean, 1976). Both hand-weeding and herbicide control are made difficult by the similarity between crop and weed in morphology, growth, behaviour and physiology. During the 1970s large areas of mechanised rice cultivation in Swaziland were abandoned largely due to infestations of the native wild rice *Oryza punctata*. The wild rice was first recognized in rice fields in the mid-1950s and its subsequent multiplication and spread were very rapid. Due to the similarities between crop and weed, the extent of the weed problem was not appreciated until populations were too large to control effectively. Early diagnosis of potential weed problems becomes a difficult task where the weed's presence is more or less cryptic.

Several wild rices are interfertile with cultivated rice (*Oryza sativa*) and hybrid swarms between crop and weed frequently occur in rice fields. In these circumstances mimetic forms of wild rice can develop and are difficult to remove from the crop. In an effort to overcome the problem of distinguishing between wild and cultivated forms of rice in the seed bed, plant breeders in India developed purple-leaved, cultivated strains of rice which could be easily separated from the green-leaved, wild forms. Unfortunately shortly after their introduction, crossing between crop and weed followed by artificial selection by handweeding resulted in the establishment of purple-leaved strains of the weed (Dave, 1943; Harlan et al., 1973; Parker and Dean, 1976).

The transfer of characters from the cultivated strains of rice to wild forms is fostered by the breeding structure of rice populations. The cultivars are predominantly self-fertilizing whereas wild forms are outcrossed to varying degrees (Oka and Chang, 1959). Since individuals in the wild rice populations are usually at a relatively low density in comparison to the crop, they are likely to be cross-fertilized by pollen originating from cultivated plants, assuming that flowering periods are roughly synchronous. Gene exchange from cultivated strains of rice to *Oryza perennis* (*O. rufipogon*) has been studied extensively by workers from the National Institute of Genetics in Japan (Oka and Chang, 1959, 1961; Morishima et al., 1961, 1963; Chu and Oka, 1970). Where rice fields are prepared in swampy areas containing wild populations of *O. perennis,* complex patterns of variation resulting from introgressive hybridization frequently arise. Oka and Chang (1959) found that a population of wild rice occurring in rice fields of the Central Province of India displayed several domesticated characters including weak dormancy, synchronous germination, reduced shattering ability and delayed flowering. Nearby populations in a swamp were uncontaminated by domesticated traits and populations occupying sites with intermediate levels of human disturbance exhibited combinations of wild and domesticated features. These workers suggest that the syndrome of cultivated characters present in the weed populations originated by hybridization and are maintained by "cultivation pressure" associated with the cultural practices of rice growing. If one of these pressures is handweeding, which seems likely, then the close resemblance between crop and weed may be viewed as a mimetic phenomenon enhanced by unidirectional gene exchange.

Weeds which become closely associated with a specific crop may develop growth forms which resemble those of the cultivar. In annual crops grown in dense stands, the phenotypic similarities frequently involve an erect, slender habit, reduced branching, and delayed reproduction in the weed. The evolution of races with these traits in *Camelina sativa* var. *linicola* in flax (Sinskaia and Beztuzheva, 1931) and *Brassica nigra* var. *pseudocampestris* in rape (Sinskaia, 1928) probably has little to do with a system of vegetative mimicry since the fields in which these crops are grown are large and handweeding is not practised to any great extent (Wickler, 1968). The tall, erect growth habits of the weed are likely to be selected by the dense, competitive conditions which prevail within the crop canopy. Baker (1974) has described a similar situation in *Picris echioides* where erect annual forms are weeds of wheat fields in England whereas perennial decumbent forms are found in exposed coastal habitats. As Sinskaia (1931) first emphasized, "phytosociological factors" can act as important selective influences on plant evolution resulting in biotic race formation. Such effects are likely to be particularly pronounced in "satellite weeds" where neighbour effects are highly predictable both spatially and temporally.

The remaining reports of mimicry involving vegetative resemblances between crop and weed are difficult to evaluate. Although it seems likely that mimetic races of oats, rye and barley (Schwanitz, 1966; Wickler, 1968; Harlan et al., 1973; Ladizinsky, 1975) have evolved in association with cereal growing, little detailed information on the selection pressures involved in the interactions are available. The curious report of phenotypic mimicry in wild oats infesting a barley and wheat nursery (H. V. Harlan, 1929; J. R. Harlan, 1975, 1981) appears to involve no genetic differentiation in the weed population and is, therefore, not a case of mimicry in the strict sense. Similar effects involving weed seedlings that "mimic" the species with which they are grown are reported by Kalachevska (1929). The close resemblance between the male plants of *Datisca cannabina* and *Cannabis sativa* is interpreted by Small (1975) as the result of convergent evolution although the selective forces involved are not known. The 2 species are native to the New and Old World respectively and occur in different types of habitat.

Seed mimicry

Some weed seeds are inadvertently harvested with the crop despite the shattering habit of the majority of weed species. Various methods have been devised which attempt to remove weed seeds from those of the crop. The most ancient and widely used technique is winnowing. Here the heavier, threshed grain is separated from the lighter chaff and weed seeds by wind or a forced current of air. Weed seeds that possess similar winnowing characteristics to those of the crop are more likely to escape removal from the grain. Thus the farmer, through winnowing, exerts a strong selective force on the shape, size and weight of weed seeds and there is good evidence that some species have evolved races which are crop seed mimics.

A classic example of seed mimicry involves *Camelina sativa,* an annual weed of flax in Eurasia. Mimetic races of the weed have been extensively studied by Zinger (1909), Tedin (1925) and Sinskaia and Beztuzheva (1931), and more recently reviewed by Stebbins (1950). In parts of Russia where flax is intensively grown, a specialized race, *C. sativa* var. *linicola,* that is restricted to flax fields,

occurs. Populations of this race flower at the same time as the crop and because of the nondehiscent habit of fruits are harvested with the flax. The winnowing properties of the seed so closely resemble those of flax seed that the two tend not to be separated and are resown the following season. Crossing experiments by Tedin (1925) indicate that the genetic basis of the seed characters influencing mimicry is polygenic.

In common with some of the vegetative mimics discussed above, parallel patterns of geographical variation in model and mimic occur in the flax *Camelina sativa* system. These patterns involve a range of traits including vegetative period, growth habit, branching pattern, number of leaves, thickness of stem, flowering time, and fruit and seed characters. Particularly interesting is the evolution of shattering forms of *C. sativa* subsp. *crepitans* in association with the ancient flax cultivar *Linum crepitans* in southern Russia. The flax has dehiscent seed capsules and is harvested before maturity so that the seeds, which are used for oil, are not lost. If the capsules of *Camelina* were not dehiscent, the seeds would not become mixed with those of flax, and hence the association would break down. Several other "satellite" weeds also infest flax fields. They include *Agrostemma linicola, Cuscuta epilinum, Eruca vesicaria, Lepidium sativum, Lolium remotum, Polygonum lapathifolium, Silene gallica, S. cretica, S. linicola, Sinapsis alba* and *Spergula arvensis* (Stebbins, 1950; Schwanitz, 1966; Small, unpubl.). Some of these species resemble flax in habit and seed characters but to what extent the similarities are the product of mimetic processes is unclear.

Commercial crops of lentils (*Lens esculenta*) in central Europe are often infested with a form of *Vicia sativa* with seeds that are similar in appearance to those of lentil. Seeds of *Vicia sativa* are normally round whereas lentil seeds are flattened and lenticular in shape. A number of explanations have been proposed to account for the flat-seeded race of *V. sativa*. Bleier (1929) proposed that the form was a product of hybridization between lentils and vetch whereas Dmitriev (1952) considered the form of *V. sativa* a case of the "conversion of one species to another by cultivation pressure"! However, Rowlands' (1959) genetic studies demonstrated that the flat-seeded condition is due to a single recessive mutation with the round-seeded form dominant. It seems most likely therefore, as Vavilov (1949) suggested, that once the mutation became established in weed populations of vetch, "unconscious selection by the sorting machine" during seed-cleaning procedures favoured its spread with lentils.

A similar example which also results from a simple genetic change involves the parasite *Cuscuta epilinum* (Wickler, 1968). The species often grows as a creeper around flax plants but its seeds can normally be separated from those of the crop because they are smaller in size. However, a mutant form with double seeds has become established in some areas of Europe as a weed and is now unintentionally sown along with the crop. In the Near East small-seeded forms of *Cephalaria syriaca*, with similar winnowing characteristics to wheat, have a long history as contaminants of wheat seed (Hillman, 1981; D. Zohary, pers. com.). Although seed-cleaning equipment is much improved today, seed mimicry can still arise. Recently the balloonvine (*Cardiospermum halicacabum*) has developed into a serious weed problem in soybean fields in the southern United States. The seeds resemble those of the crop and escape seed cleaning procedures (Johnston et al., 1979). Further discussion of the close association between crops

and weeds owing to resemblances in seed characters can be found in Hitrovo (1912), Welch (1954), King (1966), Harlan et al. (1973) and Harlan (1981).

RICE MIMICRY IN BARNYARD GRASS

With the exception of the wild rices discussed above, members of the barnyard grass complex (*Echinochloa crus-galli* [L.] Beauv.) are the most noxious weeds of cultivated rice. Certain forms are vegetative mimics of rice and are restricted to the rice field habitat. Unlike other cases of vegetative mimicry, the close phenotypic resemblance between crop and weed is not aided by gene exchange since the 2 genera are phylogenetically distinct. The remainder of this paper will examine the general features of the rice-mimicry syndrome of *E. crus-galli* in the context of life cycle studies.

Barnyard grasses are self-pollinating, annual, C_4 grasses of seasonally-wet habitats and are native to Eurasia. The complex is exceedingly variable in morphology, growth form and ecological preference. Varieties of *E. crus-galli* are reported as weeds in over 60 countries and 36 different crops, principally in a latitudinal zone from 50°N to 40°S (Holm et al., 1977; Barrett and Wilson, 1981). Variation is particularly complex in several rice-growing regions with a number of taxa and numerous distinct biotypes occurring in sympatry (Yabuno, 1961, 1966; Chirila and Melachrinos, 1976; Smith et al., 1977; Michael, 1973; Barrett and Seaman, 1980). The variation almost certainly arises from multiple introductions of barnyard grass seed as contaminants of imported rice stock followed by close inbreeding. Lack of any comprehensive taxonomic treatment of the group complicates identification problems and the various forms are frequently given different names in different regions (Michael, 1973). Here I follow the nomenclature and taxonomic concepts of Gould et al. (1974). In their treatment of *Echinochloa* in the United States, widespread weedy forms with small seeds are recognized as *E. crus-galli* (L.) Beauv. var. *crus-galli* and large-seeded crop mimic forms of rice fields are treated as *E. crus-galli* (L.) Beauv. var. *oryzicola* (Vasing) Ohwi.

Phenetic similarity to rice

Although *Echinochloa* and *Oryza* are in different tribes of the Gramineae, plants in the vegetative condition of both genera are superficially similar in appearance. As a consequence, it is not uncommon for seedlings of barnyard grass to be accidentally introduced to rice fields during transplanting operations (Holm et al., 1977). Seedlings of *E. crus-galli* var. *oryzicola* so closely resemble those of cultivated rice that it seems probable that they are rice mimics (Fig. 1). The similarity between the 2 taxa was first recognized by Vasinger-Alektrova (1931) and presumably influenced the naming of this taxon, whether treated at the varietal or specific level (*E. oryzoides, E. oryzicola*).

Echinochloa crus-galli var. *oryzicola* is native to Asia but has been introduced to rice-growing regions of Australia, California, and Europe. Several different rice mimics are reported from among the barnyard grass varieties of Japan (Yabuno, 1961, 1966). These include 2 forms of *E. crus-galli* var. *oryzicola*, both of which are common in lowland flooded rice fields, mimetic forms of *E. crus-galli* vars. *caudata* and *formosensis*, and a mimic of upland (nonflooded) rice. Ehara and Abe (1950) observed that individuals of barnyard grass in Japanese rice fields
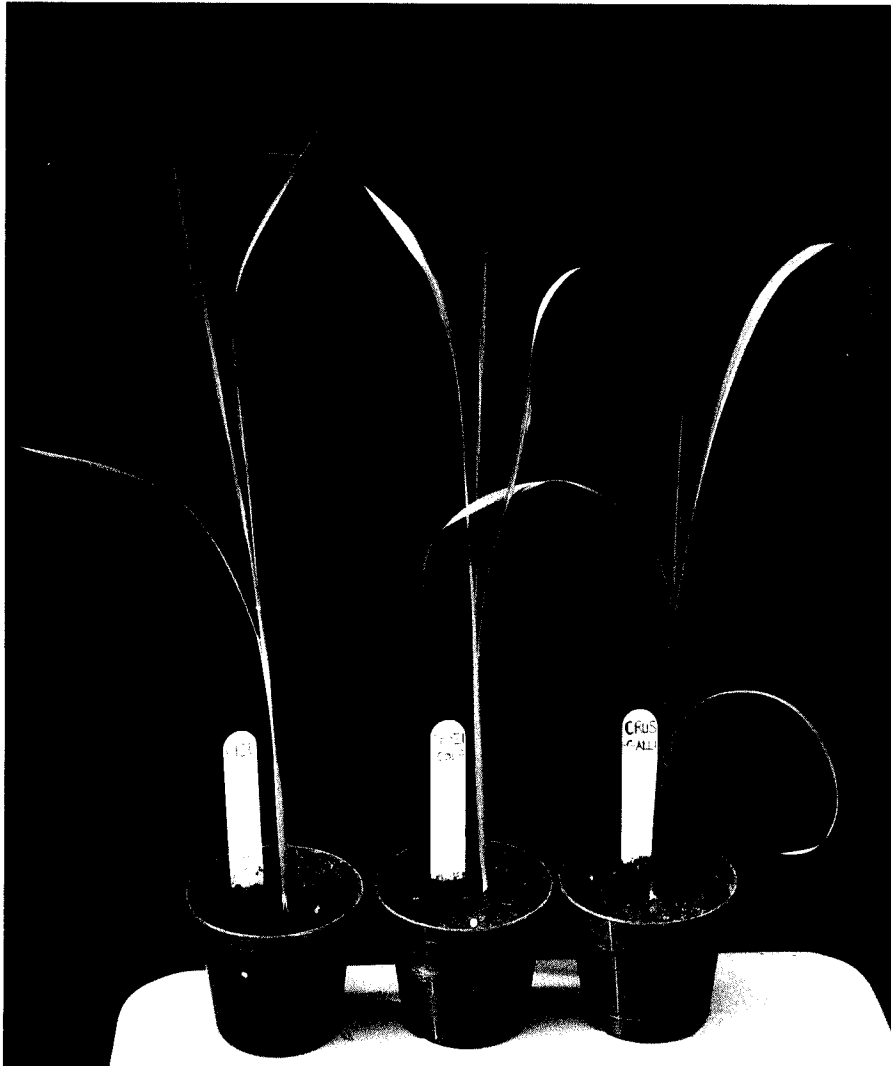
Fig. 1. Three-week-old seedlings of, from left to right, cultivated rice (*Oryza sativa*), *Echinochloa crus-galli* var. *oryzicola* (4x) and *Echinochloa crus-galli* var. *crus-galli*. Note the close phenotypic resemblance of rice and its mimic and the presence of a ligule in rice.

that most resembled the rice plant in morphology were less likely to be removed from the crop by handweeding. Hence, as in the cases described above, weed control practices may provide a potent selective force favouring the evolution of rice mimicry. These processes are most likely to occur in the intensive small scale farming which typifies rice culture in the Orient. Today handweeding is still practised throughout Asia and it is possible that mimetic forms of barnyard grass are evolving in association with changes in farming techniques and the introduction of new rice varieties with different phenotypes.

To illustrate the degree of phenetic similarity between rice and *E. crus-galli*

var. *oryzicola* (4*x* race) during the vegetative phase, a comparison of the 2 taxa and *E. crus-galli* var. *crus-galli* was made under uniform glasshouse conditions. A total of 15 morphological and growth characters was recorded during the first 30 days of growth. All characters were quantitative and included measurements made at regular intervals of plant height, leaf length, leaf width, leaf angle, leaf number and culm width. Two multivariate methods were used to assess the degree of morphological resemblance among 34 plants of each of the 3 taxa. In both the principal components analysis and the canonical discriminant functions analysis, similar clustering patterns are revealed. Cultivated rice and the rice mimic occupy similar overall positions in multivariate space with *E. crus-galli* var. *crus-galli* separated by a considerable distance from the other 2 taxa (Fig. 2a,b). Although model and mimic exhibit similar patterns of resemblance, there are significant differences between the group means in the discriminant functions analysis (Fig. 2b).

Several qualitative characters also separate the 3 taxa, the most prominent of which involves the degree of anthocyanin pigmentation of the plant body. The culm and leaf bases of rice and *E. crus-galli* var. *oryzicola* are usually dark green whereas in *E. crus-galli* var. *crus-galli* these structures range from pink to deep red. The reddish appearance of seedlings of *E. crus-galli* var. *crus-galli* which develops within 14 days from germination makes them readily apparent in young rice stands and this trait would be strongly selected against by handweeding. Another prominent seedling character that serves to distinguish *E. crus-galli* var. *crus-galli* from rice and its mimic is the wide, white midrib of its leaves. The midrib is much reduced in size in *E. crus-galli* var. *oryzicola* and because of its upright, narrower leaves (see below), it is less noticeable. Since most species of *Echinochloa* exhibit anthocyanin pigmentation and possess leaves with white midribs it seems reasonable to assume that they are present in the ancestors of *E. crus-galli* var. *oryzicola* and have been selected against during the shift to the rice-field habitat.

The major distinguishing feature between seedlings of rice and *E. crus-galli* var. *oryzicola* is the presence of a ligule in rice. This structure is absent from all species of *Echinochloa* and may have been lost early in the evolution of the genus. Obviously severe developmental constraints prevent its re-emergence in association with the mimicry syndrome, restricting opportunities for finer adaptation between model and mimic. The absence of a ligule in the rice mimic enables discrimination under field conditions but whether or not the experienced handweeder has learned to recognize this difference is not known.

One of the most striking similarities between rice and *E. crus-galli* var. *oryzicola* is the upright habit of both tillers and leaves. Nonmimetic barnyard grasses possess lax, drooping leaves and frequently exhibit a decumbent growth form. As mentioned above, erect-plant architecture is probably an adaptation to life in dense crop stands and optimizes light capture by older leaves at lower levels in the canopy. Rice breeders have recognized the importance of erect-plant architecture in retarding light attenuation in crop canopies (Monsi et al., 1973) and most rice varieties exhibit narrow, upright leaves.

The erectness of the leaves of *E. crus-galli* var. *oryzicola* compared to those of *E. crus-galli* var. *crus-galli* is the result of anatomical differences between the taxa. Although the number of vascular bundles is similar in the 2 varieties, the
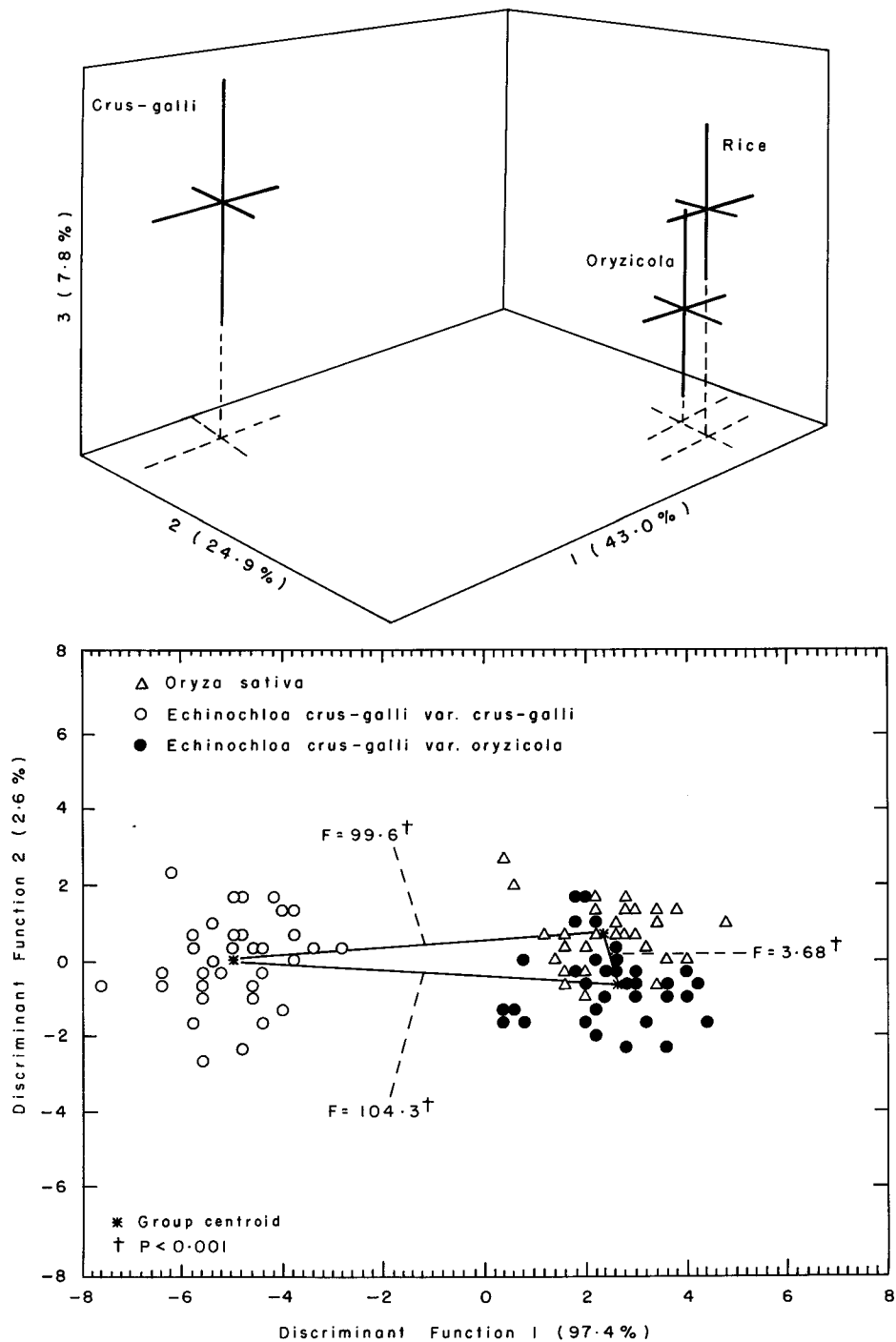
Fig. 2. Multivariate analysis of phenetic similarity in seedlings of cultivated rice, *Echinochloa crus-galli* var. *oryzicola* (4x) and *Echinochloa crus-galli* var. *crus-galli*: (a) Ordination of average values with 95% confidence limits of a principal-components analysis of 15 quantitative characters. (b) Canonical discriminant functions analysis of 9 quantitative characters with F values for comparisons of group centroids.

smaller intercostal distance between the bundles of *E. crus-galli* var. *oryzicola* results in a higher density of supporting tissue along the length of the leaf. Since the leaves of the mimic are narrower, there is less tissue to support and they are maintained in an upright position. The angle at which the leaves depart from the culm is in part determined by the size and structure of the pulvinus that is larger, with more sclerenchyma, in the mimic compared with its close relative. This may control the difference in the amount of inrolling of the adaxial surface of the leaf between the 2 taxa. In the mimic the leaves are markedly inrolled giving a narrow, rice-like appearance whereas in *E. crus-galli* var. *crus-galli* this condition is less pronounced.

Life history studies

Although mimetic forms of barnyard grass originated under "primitive" agricultural systems in Asia, they are at present among the most serious weeds of mechanized rice culture. In California, *E. crus-galli* var. *oryzicola* has replaced *E. crus-galli* var. *crus-galli* as the major weed problem in rice fields. Barrett and Wilson (1983) discuss the probable cause of the change, which involves alteration in the flooding regime of rice fields (and see below). Two distinct races of *E. crus-galli* var. *oryzicola* were introduced to California as rice seed contaminants during the beginnings of rice culture in the state in 1912–1915 (Barrett and Seaman, 1980). In California, the 2 races behave as distinct biological species and differ in chromosome number, morphology, flowering time and distribution. They are considered separate species by some European workers (Table 1).

Despite the occurrence of populations containing thousands of individuals of *E. crus-galli* var. *oryzicola* in Californian rice fields each year, as well as continued spread to uninfested rice areas, few populations are found outside the rice agroecosystem (Fig. 3). This restricted habitat preference is typical of crop mimics and the behaviour of *E. crus-galli* var. *oryzicola* contrasts broadly with that of *E. crus-galli* var. *crus-galli*. Although the 2 varieties of barnyard grass are both pernicious, world-wide weeds, they exhibit quite different adaptive strategies. *Echinochloa crus-galli* var. *crus-galli* exhibits many of the properties of a general purpose genotype(s) strategy (Baker, 1965, 1974) whereas the rice mimic can be viewed as a specialized biotic ecotype with limited ecological amplitude. Analysis of their contrasting life history traits is helpful to an understanding of the selective forces operating in their respective weed niches (Barrett and Wilson, 1981, 1983).

1) Seed and seedling phase.—A major difference between the 2 barnyard grass varieties concerns seed size and weight (Table 2). Caryopses of both *E. crus-galli* var. *oryzicola* races are on the average ×2–3 heavier than those of *E. crus-galli* var. *crus-galli*. Seed weight influences a range of ecologically important processes including dispersal, seedling establishment and competitive interactions (Harper, 1977). The heavier seeds of the rice mimics produce larger, more vigorous seedlings in comparison with *E. crus-galli* var. *crus-galli* and these can establish in flooded soils (Table 2, and see Barrett and Wilson, 1983). Most seeds of the rice mimics are shed during the harvest period of rice and local dissemination occurs in irrigation water and by mud adhering to farm machinery. Some seed is harvested with the rice crop and, if not removed during seed cleaning, provides an innoculum for further infestations.

TABLE 1. BARNYARD GRASSES IN CALIFORNIAN RICE FIELDS. [a]

Taxon (frequently used synonyms in parenthesis)	Ploidy	Origin	Rice weed status	Distribution in California	Microhabitat in rice agroecosystem
E. crus-galli (L.) Beauv. var. *crus-galli Barrett 1201*, TRT	6x	Eurasia	world wide	widespread	rice field edges, levees and shallow water areas in fields
E. crus-galli (L.) Beauv. var. *oryzi-cola* (Vasing) Ohwi	6x	Eurasia	Europe, Asia, Australia, Argentina	generally restricted to Central Valley	rice fields
a) early flowering form (*E. ory-zoides* [Ard.] Fritsch) *Barrett 1202*, TRT					
b) late flowering form (*E. phyl-lopogon*) [Stapf.] Koss) *Barrett 1203*, TRT	4x	Asia	Europe, S.E. Asia, India, Russia, China, Japan	restricted to rice-growing regions of Central Valley	rice fields
E. muricata (P. Beauv.) Fern. (*E. pungens*) *Barrett 1204*, TRT	4x	N. America	U.S. and Australia	scattered localities in Central and Northern California	rice field edges, levees and drainage ditches
E. colona (L.) Link *Barrett 1294*, TRT	6x	Asia	world wide (mostly in upland rice)	scattered localities mostly in southern California	rice field edges and levees

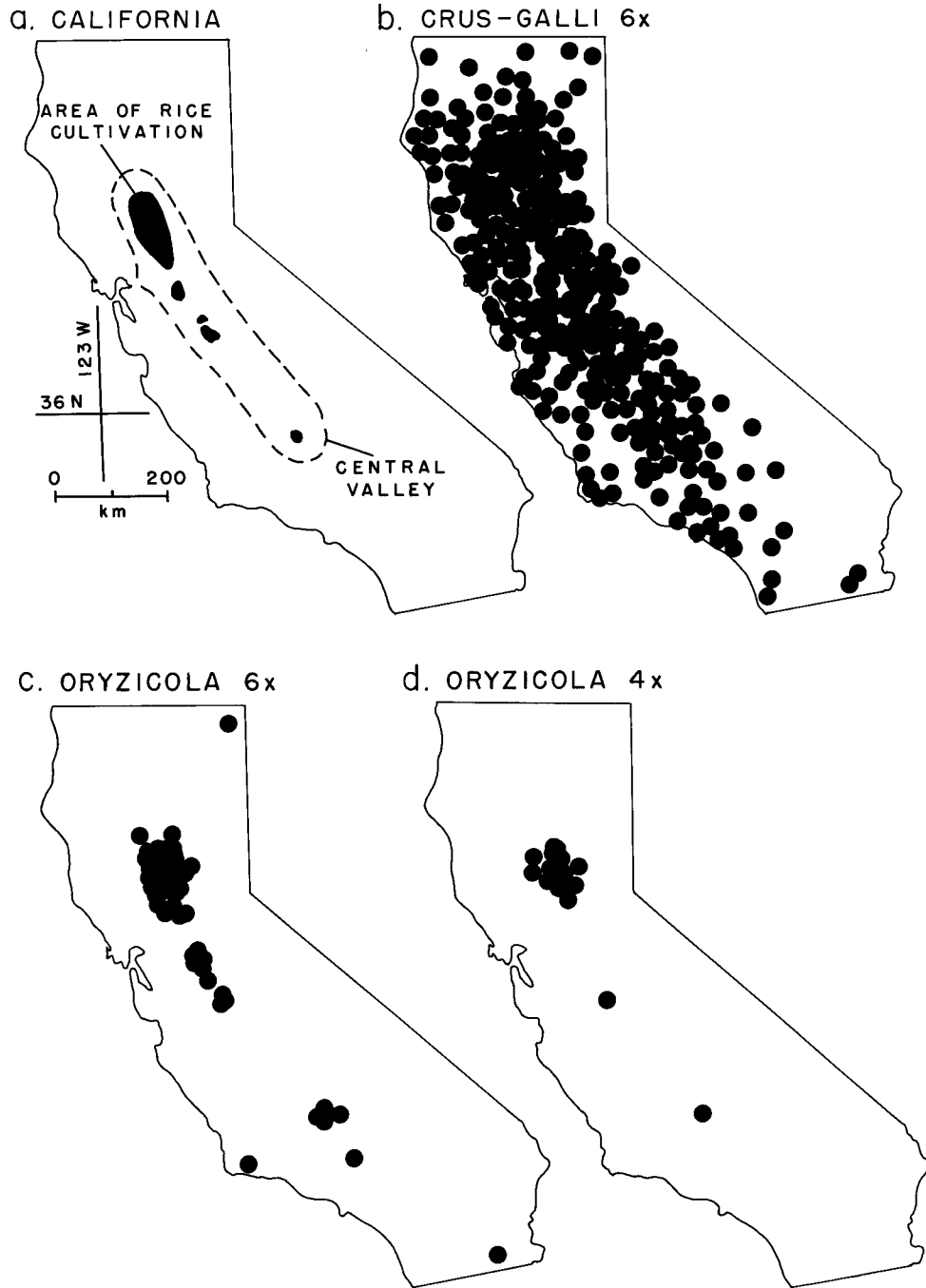[a] After Barrett and Seaman, 1980.

Fig. 3. The distribution of the major forms of barnyard grass in California (*Echinochloa crus-galli* var. *crus-galli, Echinochloa crus-galli* var. *oryzicola* (4x, 6x races) in relation to the areas of rice cultivation.

TABLE 2.   SEED AND SEEDLING PARAMETERS IN *Echinochloa crus-galli* VAR. *crus-galli* AND *E. crus-galli* VAR. *oryzicola*.[a]

Parameter	Variety crus-galli	Variety oryzicola (4x)
Seed weight (mg)[b]	1.73	4.95
Buoyancy (days for 90% of seeds to sink in water)[c]	8	4
Innate dormancy (Av. germination after 9 mo dry storage at ambient temp.)[b]	25.7	96.7
Seedling emergence from saturated soil (%)[c]		
1) 0.5 cm burial	25.0	70.0
2) 2.0 cm burial	0.0	25.0
Seedling emergence from flooded soil (%)[c]		
1) 9-cm-water depth	0.7	27.7
2) 18-cm-water depth	0.1	21.9
Seedling vigour (height in mm, 14 days from germination)[c]	62.1	126.3

[a] After Barrett and Wilson, 1983.
[b] Average based on 10 populations per variety.
[c] Average based on 1 population per variety.

Comparisons of the dormancy and germination characteristics of Californian populations of the 2 barnyard grass varieties indicate that they differ in a manner consistent with their respective weed niches. The rice mimics exhibit weak innate dormancy that has largely decayed by 9 mo from harvest (Table 2). Seed produced during a single rice-growing season (April–September) is capable of germination the following season, provided that suitable environmental conditions prevail. Patterns of innate dormancy among *E. crus-galli* var. *crus-galli* populations are highly variable with most exhibiting strong innate dormancy. Germination synchrony is significantly greater in *E. crus-galli* var. *oryzicola* in comparison with its colonizing relative (Fig. 4). Under rice field conditions, staggered germination would be disadvantageous as seedlings emerging late in the season would suffer greatly from the shading and competitive effects of rice. Kasahara and Kinoshita (1952) and Yabuno (1966) report similar patterns of germination synchrony in Japanese populations of *E. crus-galli* var. *oryzicola* and cultivated rice.

The germination behaviour of the 2 barnyard grass varieties are in line with

TABLE 3.   LIFE HISTORY PARAMETERS OF *Echinochloa crus-galli* VAR. *crus-galli* (CG) AND *E. crus-galli* VAR. *oryzicola* (4x) (O) GROWN IN 3 SOIL VOLUMES UNDER GLASSHOUSE CONDITIONS DURING MAY–SEPTEMBER 1978.[a]

	Soil volume					
	88 cm³		360 cm³		3,180 cm³	
Parameter	CG	O	CG	O	CG	O
Time to flowering (days)	126.6[b]	153.0	69.7	143.3	54.1	115.5
Net reproductive effort (%)	10.0	0	25.8	7.4	9.2	4.6
Seed production	20.0	0	892.4	149.0	17,880	2,890
Total biomass (g)	0.54	0.46	6.7	8.0	320.8	251.8

[a] After Barrett and Wilson, 1981.
[b] Each value the mean of 10 plants.

O Echinochloa crus-galli var. crus-galli
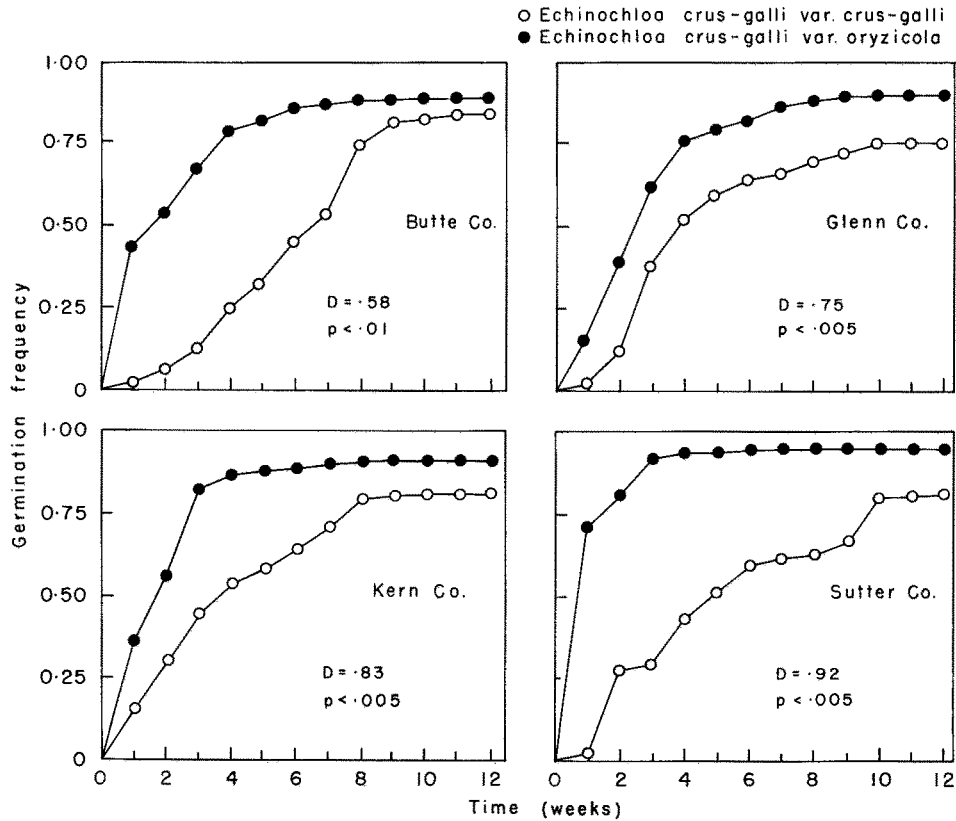● Echinochloa crus-galli var. oryzicola

Fig. 4. Germination synchrony in *Echinochloa crus-galli* var. *oryzicola* (4x) and *Echinochloa crus-galli* var. *crus-galli*. Each value is the mean of 50 replicates of 5 seeds. Seed was collected from a single rice field in each of 4 Californian counties during September 1979 and allowed to germinate in pots under uniform glasshouse conditions during the spring and summer of 1980. Cumulative % germination compared by Kolmogorov-Smirnov 2-sample tests. After Barrett and Wilson, 1983.

the theoretical predictions of Cohen (1966). He suggested that dormancy and discontinuous germination would be selectively advantageous in environments in which the risk of reproductive failure is high. Conversely in predictable habitats, where the probability of unsuccessful reproduction is low, dormancy is of less importance and synchronous germination would maximize the long-term growth rate of populations. The open, ruderal sites colonized by *E. crus-galli* var. *crus-galli* in California become progressively drier as the season proceeds and heavy mortality of seedlings commonly occurs, particularly in years with low rainfall. In contrast, the rice agroecosystem is highly predictable in space and time and moisture and nutrients are abundantly available. Many areas in California have been in continuous rice production for several decades due to low pest and disease problems, high soil fertility and the restricted range of alternate crops capable of growing on the heavy clay rice soils (Barrett and Seaman, 1980). The high predictability from year to year of the rice agroecosystem enables populations of the crop mimics to build up rapidly despite attempts at control by herbicides. The

germination pattern of *E. crus-galli* var. *oryzicola* resembles that of cultivated rice and can be viewed as part of the rice-mimicry syndrome.

Germination and establishment in the flooded conditions of rice fields present difficulties for most weed species, and as a result the floras of lowland rice are frequently composed primarily of aquatics. The depth, duration of flood, and oxygen status of water are among the most important determinants of species composition (Smith and Fox, 1973; Imam and Kosinova, 1972; Barrett and Seaman, 1980). Most higher plants require oxygen for germination and seedling growth and tolerate anaerobic conditions for only short periods before irreversible morphological and physiological damage occurs. The most well-known exception is cultivated rice which has been studied extensively because of its ability for growth under anaerobic conditions (Kordan, 1972, 1974). The rice coleoptile has been considered one of the few plant organs which can grow in anoxia (Pradet and Bomsel, 1978). However, recent studies of the physiological adaptations of barnyard grasses (Kennedy et al., 1980; Rumpho and Kennedy, 1981; VanderZee and Kennedy, 1981), demonstrate that *E. crus-galli* var. *crus-galli* and *E. crus-galli* var. *oryzicola* (4*x* race) can germinate and grow for prolonged periods in a totally oxygen-free environment. Light, darkness or oxygen concentration make little difference to germination levels with over 90% germination attained after 7 days of treatment. Although seeds of *E. crus-galli* var. *oryzicola* are one quarter the weight of rice, the seedlings produced after 7 days in nitrogen are approximately the same size (Kennedy et al., 1980).

Of particular interest is the ultrastructure of mitochondria from anaerobically-grown seedlings of the rice mimic. Mitochondrial profiles from the primary leaf are almost identical in appearance to those of seedlings grown in air (Kennedy et al., 1980; VanderZee and Kennedy, 1981). This behavior is in sharp contrast to many other species in which growth under anaerobic conditions has been investigated. Low oxygen tensions usually promote irreversible changes in the ultrastructure of mitochondria as well as alterations in their size and frequency (Oliveira, 1977; Vartapetian et al., 1978). Effects of anaerobiosis on the growth and development of seedlings of the rice mimic are largely limiting and reversible and enable seedlings to tolerate the low oxygen tensions which prevail in flooded soils.

Although both varieties of barnyard grass can germinate under anaerobic conditions, seedlings of *E. crus-galli* var. *crus-galli* are unable to establish in flooded soils (Table 2). In California, the introduction of a permanent, deep-water flooding regime has drastically reduced infestations of this variety within fields. However, seedlings of the rice mimics are capable of emerging from water depths of up to 25 cm and the new flooding regime may have indirectly favoured their spread. Variation in the capacity for establishment in deep water is probably due to the difference between the 2 barnyard grass varieties in the amount of storage reserves in their seeds.

2) Reproductive phase.—The reproductive phenology of *E. crus-galli* var. *oryzicola* populations differs depending on their geographical origin and the flowering characteristics of rice varieties with which they have coevolved. Anthesis usually coincides with that of the rice crop (Yabuno 1966). It seems reasonable to assume that the similarity in the flowering period of rice and its mimics is the product of

artificial selection. Genotypes flowering early in the rice season could be easily distinguished from rice and rogued from the crop. In addition, the similarity in maturation period of seed ensures that some seed is harvested along with the crop and resown the following season.

In the California rice agroecosystem, the 3 major barnyard grasses (Fig. 3) commence flowering at different times during the rice-growing season. Considerable variation exists in the time to anthesis of biotypes of *E. crus-galli* var. *crus-galli*, with the earliest flowering populations beginning anthesis in early June. The hexaploid race of *E. crus-galli* var. *oryzicola* begins flowering between mid-June–July and is followed by the tetraploid race which flowers simultaneously with rice during August. These differences were maintained when populations from 5 Californian rice-growing counties were grown under uniform glasshouse conditions indicating a strong genetic component to flowering time (Fig. 5a). Of particular interest in this experiment was the marked flowering synchrony within populations and the low interpopulation variation in time to anthesis exhibited by the tetraploid race of *E. crus-galli* var. *oryzicola*. The low variation probably results from the introduction of limited genetic material of this race to California. The most likely source of introduction was rice stocks imported from Japan to Biggs Rice Experiment Station at the commencement of rice culture in the state. Several other rice weeds native to the Far East (*Monochoria vaginalis, Rotala indica*) are restricted in North America to rice fields in the vicinity of the Rice Experiment Station at Biggs and were presumably introduced in a similar manner (Barrett and Seaman, 1980). These species also display extreme phenotypic uniformity.

The delayed flowering of *E. crus-galli* var. *oryzicola* in comparison with *E. crus-galli* var. *crus-galli* is associated with differences between the varieties in reproductive effort and seed fecundity (Table 3, Fig. 5b). The rice mimics allocate significantly less dry matter to reproductive structures and produce fewer seeds than *E. crus-galli* var. *crus-galli* when grown under a range of environmental conditions (Barrett and Wilson, 1981). As might be predicted from their contrasting ecologies the rice mimics are more sensitive to stress conditions than the generalist weed. Plants of the mimic (4x race), grown in small soil volumes, fail to mature seeds before complete senescence ensues (Table 3). Reproduction in continuously unproductive conditions has probably not been an important selective feature in the life history of the rice mimics. The rice fields to which they are adapted are undisturbed and highly productive during the growing season. This regime fulfills many of the conditions predicted by Grime (1977) to select for a competitive life-history strategy and the erect plant architecture, large vegetative biomass, delayed flowering, and heavy seeds must all contribute to the competitive ability of the mimics. An examination of the ecological basis of coexistence of the mimics with cultivated rice would be of interest. Their apparently synchronized growth patterns and phenology suggest the likelihood of strong competitive interactions. However, it is possible that some niche diversification enables the rice mimics to coexist with the crop as a minority component of stands. Assemat and Oka (1980) and Assemat et al. (1981) recently reported the results of competition studies between rice and barnyard grass in which cooperative associations at high density occurred. They suggest that the mode of niche differentiation between rice and barnyard grass differs according to the combi-
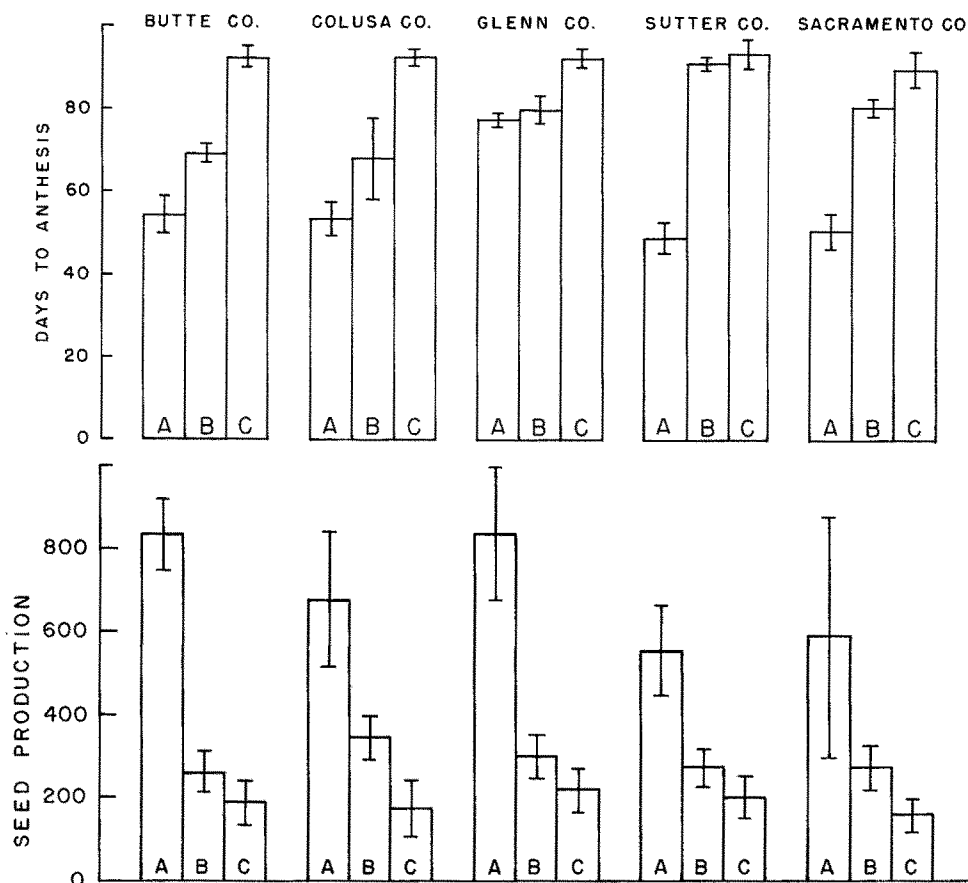
Fig. 5. Life history parameters of barnyard grasses, A. *Echinochloa crus-galli* var. *crus-galli*, B. *Echinochloa crus-galli* var. *oryzicola* (6x), C. *Echinochloa crus-galli* var. *oryzicola* (4x), from Californian rice fields. Seed of each of the 3 forms was collected from a single rice field in 5 Californian counties and grown under uniform glasshouse conditions. (a) Time to anthesis (n = 32 plants per population). (b) Seed production (n = 32 plants per population).

nation of genotypes of the 2 species which are grown together. Studies comparing the performance of populations of the mimic and rice with a long history of association with populations from different regions would be worthwhile.

The short life cycle and high seed fecundity of *E. crus-galli* var. *crus-galli* are traits commonly found in colonizing species of open, disturbed sites (Salisbury, 1961; Baker, 1965; Solbrig and Simpson, 1974). In California, *E. crus-galli* var. *crus-galli* flourishes in seasonally moist sites of the Central Valley. The failure of the rice mimics to colonize these habitats may be the result of their longer life cycle, limited dispersal potential, and weakly developed dormancy. Due to the absence of significant summer rain in this region, ruderal habitats dry out during June and July before the rice mimics have reached reproductive maturity (Barrett and Wilson, 1981). The hexaploid, earlier flowering race of *E. crus-galli* var. *oryzicola* can occasionally be found outside the rice agroecosystem as a ruderal

weed and this may reflect its ability to mature seeds before desiccation is complete. Clearly, demographic studies of artificially-established colonies of the 3 barnyard grasses would help to answer some of these questions.

Handweeding is no longer practised in Californian rice production and hence the major selective pressure responsible for the rice-mimicry syndrome in *E. crus-galli* var. *oryzicola* is no longer in operation in this region. Nevertheless the 2 races of the rice mimic have spread through much of California's rice acreage and they are also serious weeds in other regions (Table 1) where rice culture is mechanized and chemical weed control is practised. Although the mimetic syndrome no longer has adaptive significance in the context of handweeding in California, it may have aided the spread of *E. crus-galli* var. *oryzicola* races from their initial point of entry at Biggs to other rice growing areas in California. This spread has been facilitated by the distribution of contaminated rice seed harvested from seed fields thought to be weed-free. Since the mimetic forms of barnyard grass are virtually indistinguishable from rice, infestations are difficult to recognize and in the past much contaminated rice seed appears to have been certified for distribution (Bellue, 1932). Today, despite vigilant seed-purity standards in California, some barnyard grass seeds still occur in rice seed lots.

CONCLUSION

Crop mimics are the products of an intimate association among crops, weeds, and man. They represent the antithesis of the commonly held view of weeds as pioneers of open, disturbed habitats with broad ecological tolerance and high colonizing ability. Instead of a generalist adaptive strategy, crop mimics have evolved a specialized life history which is so intertwined with the crop model that in many cases the mimic is unable to survive in the absence of the crop. In cases of vegetative mimicry, the resemblance between crop and weed is usually influenced by gene exchange from crop to weed. In seed mimicry, however, hybridization is rarely involved and there may be little resemblance between the adult phenotypes of model and mimic. It seems likely that with the increased use of chemical herbicides and the development of more sophisticated seed-cleaning machinery, many crop mimics will disappear to be replaced by other specialized agroecotypes of weeds.

ACKNOWLEDGMENTS

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