

Crop Mimicry in Weeds¹

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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

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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; Hamerton, 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