The Origin of Weediness in Plants[1]

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Organisms become weedy when they start to compete with man for the habitat he is creating for himself, and true weeds when they become adapted to the permanently disturbed man-made habitat. Although tool-making and fire-using hominids have been disturbing habitats at least since Middle Pleistocene, the evolutionary history of weeds dates back only some 10,000 years to the time when man first learned how to cultivate the soil. Primitive agriculture made possible settled communities, resulted in the first major population explosion, and it was not many millennia before the land was being disturbed on a continental scale. Almost unlimited disturbed habitats became available for exploitation by colonizer species, and selection soon must have sorted out those phenotypes that withstood continuous disturbances. The recent origins of weeds make them excellent subjects for phylogenetic studies. Some general characteristics of weediness will be discussed with special reference to those grasses being studied in our laboratories.

Origin of Weeds

Species vary considerably in degree of weediness. At the one extreme are truly wild populations confined to stable habitats. At the other extreme are crop plants, adapted strictly to habitats created for them by man. In between are complexes that range from essentially wild, through aggressive colonizers, to weeds. Truly wild species are successful only in their own stable habitats. Weeds will not survive when competing with wild species for these habitats. Even in disturbed habitats weeds will eventually be replaced by the invading colonizers if left to fend for themselves. But only weeds can survive in habitats that are continuously being disturbed by man. Particularly in plants, but also in insects and higher animals, the exact boundaries between colonizer, weed, and domesticated taxa are often poorly defined. Bermuda grass *(Cynodon dactylon)* is an introduced weed or cultigen in the New World and Australia, while in the Old World, cultivated, weed and truly wild races are known. Similarly, cattle known today strictly as a domesticated animal over most of the world are represented in India by an obnoxious weed, the holy Brahman cow. Even the well-known *Drosophila melanogaster* includes races that range from wild, through weedy, to the domesticated laboratory fruit fly.

Natural selection must have played a major role in the origin of wild colonizers. Glaciation, erosion, landslides and fire have been creating disturbed habitats for exploitation ever since the origin of a land flora. However, the natural distribution ranges of the more successful colonizers are almost exactly the areas occupied by the known earliest centers of agriculture. Many present day weeds are natives of the Mediterranean region, the Middle-East, the highlands of tropical America and to a lesser degree Southeast Asia.

The majority of urban and agricultural weeds originated from wild colonizers (Fig. 1). Disturbing the habitat during the last 10,000 years brought numerous previously isolated colonizers together, and introgression between them probably account for the weediness of most species. Harlan (1963b) indicated that extensive agriculture in northeastern India and Pakistan brought the Eurasian colonizer *Bothriochloa ischaemum*

[1]Supported in part by grants GB-3192 and GB-4644 from the National Science Foundation.

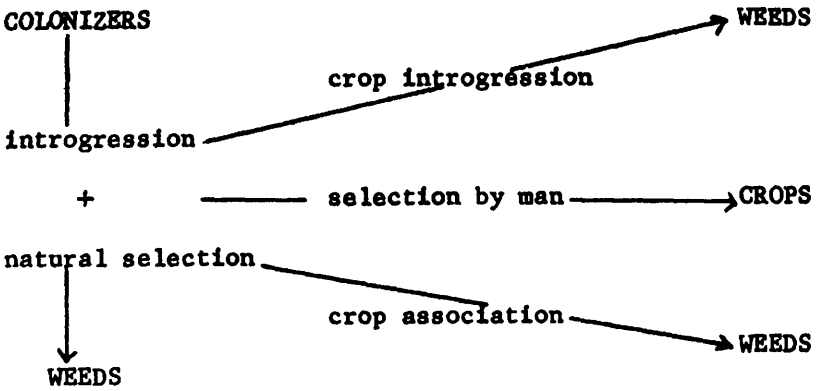

Figure 1. Relationships between wild species, and their weed and crop relatives.

into contact with *B. grahamii*, a colonizer from the Gangetic plains. Introgression between them produced an obnoxious weed-complex that is now widely distributed in northwestern India. Introgression, even between only moderately successful colonizers, may produce weeds. In southern Africa, *Bothriochloa radicans* forms part of the climax grassland vegetation, and *B. intermedia* is commonly encountered along water courses and other habitats that are only sporadically disturbed. Hybridization between these two species together with an increase in chromosome number gave rise to *B. insculpta*, one of the most successful roadside weeds in many parts of subtropical Africa (de Wet and Higgins, 1963).

From among wild colonizers man probably selected at least some of his first crops. Most major cultigens have closely allied wild colonizers with which they introgress to form wild-weed-crop complexes. There are weed sunflowers, weed sugarcanes, weed sorghum, weed wheat, weed barley, weed rice and many more. In some complexes, continuous introgression between the colonizers and cultivated forms has completely masked the original wild forms, and only weed-crop complexes remain, while others are characterized by very distinct cultivar, weed and colonizer races (Harlan, 1966).

Some colonizers are known to have inherited their weediness from related cultigens in recent times. Baker (1965) cited the example of *Raphanus raphanistrum* which has recently become an obnoxious weed in California after introgression with the cultivated radish. An equally striking example is Johnson grass, which is rapidly becoming one of the most common roadside weeds in parts of Texas and Oklahoma. The original *Sorghum halepense* was introduced, probably from Turkey, some time during the first half of the 19th century. Preliminary herbarium studies indicated that the original introductions were of the common Mediterranean colonizer. Morphological and cytogenetical studies strongly suggest that American Johnson grass inherited its weediness through introgression with cultivated sorghums that were introduced from Africa. Surprisingly, *S. halepense* has never become excessively weedy in its natural distribution range extending from the Mediterranean region to southern India, although sorghum has been cultivated in this range for many centuries. Introgression with cultivated sorghum is clearly obvious, particularly from Afghanistan eastward, but apparently only a particular African cultivar, probably *S. drummondii*, was able to introduce weediness into *S. halepense* to produce Johnson grass.

Some weeds have become so closely associated with cultivars, that through selective correlation they mimic particular crops in those characters that will insure survival. It was already known in biblical times that the seeds of *Lolium temulentum,* a common Old World weed in wheat fields, are almost impossible to separate from those of cultivated *Triticum* species (Harlan and de Wet, 1965).

All weeds are endowed with an amazing phenotypic plasticity. The African weed *Bothriochloa insculpta* is a tall grass under favorable conditions but along roadways some plants only a few inches high will produce seed. Similarly, in India and southeast Asia the weedy *B. pertusa* can stand continuous clippings in lawns, but will easily reach three feet in height along pathways.

Not many weeds have been studied in genetical detail. Our own observations, combined with a survey of those species discussed at a recent symposium on the genetics of colonizer species (Baker and Stebbins, 1965), revealed that weeds are widely distributed among families of higher plants, and that many insects, birds and even mammals are distinctly weedy. Plant weeds include trees and herbaceous plants that may be annual or perennial, autogamous or allogamous, diploid or polyploid, and they reproduce sexually, by means of gametophytic apomixis or vegetatively. However, all weeds have four important characteristics in common: (1) phenotypic flexibility, (2) wide environmental tolerance, (3) adaptation to man-made, permanently disturbed habitats, and (4) all weeds form part of a wild colonizer or crop complex. Zohary (1962) listed some obligate weed species, but these probably also will be found to represent part of larger complexes when they are studied in biosystematic detail.

The weed phenotype seems to originate through extensive hybridization and selection for genetic flexibility. The truly nonweedy diploids of *Dichanthium* are genetically isolated from each other and narrowly endemic. Within their stable and specialized habitats these species are often abundant, but they never successfully invade adjacent regions (Harlan, 1963a). Other diploids are phylogenetically more active, and include four sexually reproducing, mostly annual species which are often autogamous through partial cleistogamy (de Wet and Harlan, 1962). Two of the species, *D. humilius* and *D. sericeum,* are widely distributed across northern and eastern Australia, *D. setosum* extends along the eastern tableland from New South Wales to Queensland, and *D. superciliatum* is particularly common in the somewhat wetter north. These species are common colonizers of naturally disturbed habitats and are often encountered as roadside weeds. Although they are essentially isolated from each other genetically (de Wet and Singh, 1964), morphological studies suggest occasional introgression of all species with *D. sericeum.* This last mentioned species is extremely variable morphologically, has a wide environmental tolerance, and is rapidly becoming a common urban weed.

Mechanisms that are designed to increase and maintain heterozygosity must break down sterility barriers, and will not accomplish speciation. Such mechanisms contribute substantially to subspecific differentiation, and provide the genetic diversity which makes adaptation to a multitude of environmental niches within the weedy habitat possible. However, the final step in speciation is the creation of sterility barriers, a step not particularly favored at this time in maintaining a weedy genotype. Except for macromutations, sterility barriers accumulate slowly in subspecific populations. As weeds are recent in origin, most complexes are characterized by poorly differentiated isolating mechanisms.

With the present tremendous population explosion the most common habitat has become man-made, and it may not be many centuries before this will be the only habitat available. With the disappearance of stable

habitats, truly wild species will be the first to become extinct. Wild colonizers may survive as long as habitats remain that are only sporadically disturbed by man. Eventually these must also disappear and *Homo sapiens*, the ultimate of all weeds, will lord it over the domain he has created for himself, his companion weeds, his crops and domesticated animals.

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