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THE ORIGIN OF WEEDINESS

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ABSTRACT.—Weediness is the ability of an organism to adapt to a man-disturbed environment. The origin of weediness for any particular taxon has its source in the genetic variability available to the taxon and the plasticity of its expression. Weeds originate by selection for plasticity which directly mimics a crop ecologically and or morphologically. The variability that forms the basis of this selection originates from introgressive hybridization among colonizing species and hybridizations between a crop and its wild relatives.

Crops, weeds, colonizers, and wild taxa form a progression in descending order of their ability to survive in man-disturbed habitats. Weedy plants are adapted to selection regimes as established by man's activity, and cannot compete successfully with wild plants in their stable environments (de Wet, 1968). Disruption of habitats can be brought about by both natural and man-made forces. The mere presence of man results in disruption. Since the beginnings of agriculture, man's activities have accounted for ever greater and more rapid disturbances. The objective of this paper is the discussion of the origin of the genetic systems responsible for weediness, and the plasticity of their expression.

PHENOTYPIC PLASTICITY IN WEEDS

Although an important adaptive characteristic in all plants, phenotypic plasticity is exploited to a greater extent by weeds. Phenotypic plasticity is the ability of the same genotype to produce different phenotypes under various environmental regimes. It is also the ability of different genotypes to appear as one phenotype. Bradshaw (1965) discussed the evolutionary significance of plasticity in plants with regard to various selection regimes. Disruptive selection, which results from recurrent fluctuations of the environment in space and time is commonly encountered by weeds and non-weeds. Bradshaw indicated that annual weeds such as *Chenopodium album* and *Poa annua* were more plastic under disruptive selection than their nearest perennial relative. Annuals have evolved a more plastic form than perennials of the same genus. Agriculture gives rise to disruptive selection on a tremendous scale, and plasticity that mimics the crop is of great adaptive advantage.

Stebbins (1950) indicated that in the weed species *Camelina sativa* two forms exist. One form is very plastic, found in various agricultural fields, and has a normally branching growth pattern. When this form is found in flax fields, it appears taller and less branched. This is perhaps related to the density at which the flax is planted. In areas where flax is cultivated on a more extensive scale, *C. sativa* var. *linicola* appears. It is less plastic and has a genetically based form which mimics flax. Selection in this has been for plasticity and for genetically fixed mimicry. The amount of plasticity will vary between populations of the same taxon as is the case for *Capsella bursa-pastoris* (Bradshaw, 1965).

Directional selection demands that one environmental factor be met if the plant is to survive. Any ecological factor that does not vary in a particular habitat enough to establish a disruptive selection, can be the causal factor in directional selection. Bradshaw (1965) discussed Turreson's data that demonstrated plasticity in *Atriplex latifolium, A. patulatum* and *Chenopodium album.* Under intense light these plants had a prostrate growth form, while under normal light the plants grew upright. The overall impact of plasticity is to allow the individual plant to survive stress which prevents its contribution to the gene pool from being lost. There is no available data that contrasts plasticity in weeds and nonweeds. A majority of taxa cited for their plasticity however, are weeds. Since the amount of plasticity varies among populations of a species, direct specific level comparisons would be meaningless.

Jain (1969) compared two weed taxa, *Avena fatua* and *A. barbata* in the amount of genetic and environmentally induced variation. *Avena fatua* and *A. barbata* are both predominantly inbreeding taxa, having less than three percent outcrossing. Genetic based polymorphism was high in *A. fatua* and low in *A. barbata,* whereas for overall pehnotypic plasticity the reverse was true. *Avena barbata* had greater overall phenotypic variability. Both species are introduced weeds from the Mediterranean area, both are polyploids, but their weediness originates from variability of different sources.

Baker (1965) indicated that many weed taxa exploit plasticity to a great degree by occupying widely divergent habitats and niches. He suggested that several of these taxa originate through hybridization as evidenced by their triploid and pentaploid chromosome numbers. Baker hypothesized that these hybrids have a genetype that allows for great plasticity. This "all purpose" genotype is fixed by vegetative propagation or apomictic forms of reproduction as is the case for *Oxalis corymbosa, Polypodium dispersum* and *Taraxacum officinale.* In *Taraxacum* sexual diploid races native to central Europe hybridize and form triploid apomictic forms. Adaptive types were able to spread beyond their geographical ranges to western and northern Europe as well as to North America (Stebbins, 1971). Solbrig and Vuilleumier (1970) reported that these introduced taxa formed very phenotypically variable populations in the United States as judged by exhibited isoenzyme polymorphisms.

HYBRIDIZATION OF COLONIZING SPECIES

Interspecific hybridization is the crossing of different adaptive gene complexes. The immediate effect of this is to increase greatly the amount of variability in the gene pool. Competition from better adapted parents generally precludes the existence of hybrids in the parental niche. Successful hybrids are more often found in non-parental niches. Disturbed opened areas are habitats available for newly created adaptive gene complexes. Hybridization is prevented between most taxa by pre and postzygotic mechanisms (Stebbins, 1966).

Colonizing species are those that are the first to enter a newly created habitat. They differ from true weeds in that they are not as successful in competing for permanently man-disturbed habitats. Species that are normally isolated geographically can be brought together by the expansion of their geographical ranges into areas disturbed by man. This phenomena occurred between *Bothriochloa grahamii* from the Ganges area of India and *B. ischaemum* from Eurasia. Introgressive hybridization between these two colonizing taxa created a series of highly variable weedy population in the Northwest of India (Harlan, 1963a; 1963b).

Accidental plant introductions is another means by which geographically isolated taxa can become sympatric. Several genera are represented in the United States weed flora by very diverse introductions. *Chenopodium* is represented by taxa from tropical America, Australia, Europe, Eurasia, and several native species. Other weed genera with diverse origins include: *Allium, Polygonum, Cardaria, Convolulus, Setaria, Amaranthus* etc.

When colonizing species are isolated because of hybrid sterility, hybridization followed by polyploidy can often act to restore fertility. The reasons for this are two-fold. Genetically determined pairing of chromosomes has been demonstrated in several amphiploid taxa. When these major genes are present polyploid taxa behave cytogenetically as diploids. This is best demonstrated with wheat, a hexaploid that forms twenty-one bivalents (Riley and Law, 1965). If the hybridization occurs between a tetraploid and a diploid or between two tetraploids, a common genome i.e. one that is shared between the two hybridizing taxa can act as a buffer allowing for introgression. Tetraploid by diploid hybridizations can form triploid F_1's that are partially fertile (Lewis, 1967). Triploids can serve as bridges between tetraploid genetic receivers and diploid doners. Vardi (1971) demonstrated that introgression can occur between tetraploid and diploid species and that by the third backcross generation there is a marked increase in tetraploid-like individuals and greater stability in meiosis in comparison to the original F_1.

Stebbins (1970) discussed the distribution of polyploidy in weeds and concluded that they do not contain significantly higher number of polyploids when compared to the nonweedy flora. Of 118 introduced weed genera 44 were diploid, 36 contained both diploid and polyploid taxa in both native and introduced areas and 28 genera had only polyploid taxa in the introduced area. Stebbins reported that in genera with both diploid and polyploid species the polyploid is more likely to be weedy.

Polyploidy when measured by chromosome number alone can be misleading. In *Lolium,* known inbreeding weedy taxa had 35 percent more nuclear DNA than non-weedy outbreeding taxa. The DNA was found to proportional to chromosome volume and dry nuclear mass (Rees and Jones, 1967). All *Lolium* species appear as diploids (2n=14), but DNA content would suggest that in the weedy inbreeding taxa duplication of some aspects of the genome has occurred. Polyploid taxa are often capable of absorbing genetic information from several related species and using this to expand their geographical and ecological ranges. Species with these abilities are termed compilospecies. Since these are aggressive species they are often weedy or have weedy races. *Bothriochloa intermedia* (de Wet and Harlan, 1966), *Achillea millefolium* (Ehrendorfer, 1959), and *Aegilops umbellulata* (Pazy and Zohary, 1965) are examples of comilospecies.

In *Achillea* diploid species are isolated from each other genetically. This isolation allows for greater differentiation and morphological divergence. Tetraploid and hexaploid *Achillea* species have access to this wide variation. These polyploid complexes are characterized by hybridization with diploids followed by backcrossing to the polyploid parent which allows for the absorption of the genetic information from the diploids. Some of these polyploid taxa introgressively hybridize with each other to such an extent that they might be considered conspecific. The weed *Achillea millefolium* is composed of tetraploid and hexaploid races and throughout its range it can exchange genetic information with diploid, tetraploid and hexaploid relatives. Weediness in this taxon is attributable to variation created by intogression among colonizing taxa and wild taxa.

Hybridization among diploid species of *Aegilops* gave rise to amphidiploids. These tetraploid taxa are colonizers and have introgressively hybridized to form mixed populations which are aggressive weeds in disturbed areas and roadsides. All of the tetraploids share a common pivotal genome from *A. umbellulata.* The other portions of their genomes came from one of seven other species. The hybrid plants created by tetraploid X diploid crossings are low in fertility. Seed set in these plants is due primarily to pollen from open pollinating parental (diploid) taxa. Progeny of these plants regain fertility in one or two generations. Pazy and Zohary (1965) and Feldman (1965) presented cytogenetic hybridization, and field analyses data to support this. Three of the species they investigated in Turkey, Greece and Israel are also introduced grasses in the U.S. flora. The question arises whether this same phenomenon is occurring in the United States.

WILD-WEED-CROP COMPLEXES

Weeds are associated with man's diverse endeavors. Many weeds have originated from the same complexes that spawned crops. This is not surprising since the same adaptations required of many crops make good weedy attributes as well. These characteristics all involve adaptations to disturbed habitats. Most annual (if not all) crops have weed forms that are recognized as conspecific, subspecific, or as a closely related species. These include: *Phleum pratense* (Timothy), *Cynodon dactylon* (Bermuda grass), *Pennisetum clandestinum* (Kikuyu grass), *Lotus corniculatus* (bird's foot treefoil), *Daucus carrota* (Carrot), *Pastinaces sativa* (parsnip), *Cannabis sativa* (Marihuana), *Oryza sativa* (rice), *Ricinis cummunis* (castor bean), *Coix lacryma-jobi* (Job's tears), *Echinochloa crusgalli* (barnyard millet), *Helianthus annum* (sunflower), *Chicorium intybus* (chickory), *Avena sativa* (oats, once a weed in Emmer fields), *Sorghum halepense* (Johnson grass), and *Rhaphinus sativa* (radish). This list is by no means complete but serves to illustrate the diversity of genera in which this occurs. Harlan (1965) lists other weed races of cultivated plants. The question that these data begs is how much genetic change is required to complete the transition from weed to crop or from crop to weed and what is the qualatative nature of this change?

Weediness has also originated by introgression of wild and crop taxa. *Glycine gracilis* is a weedy member of the soybean group of *Glycine.* Its putative origin is the hybridization of *G. ussuriensis* with cultivated *G. max* (Hymowitz, 1970). *Solanum sparsipilum* is a weed member of the potato genus and originated through hybridization of the crop (*S. tuberosum*) with one of three wild taxa as discussed by Ungent (1970). Weed sorghums have evolved as hybridization products of cultivated *Sorghum bicolor* and wild taxa (de Wet et al, 1970). *Rhaphinus raphinestrum* (Panetos and Baker, 1967), a weed, has by introgression with *R. sativa* created a weedy race of *R. sativa. Latuca serriola* (weed lettuce) possibly owes its weediness to genes of *L. sativa* (Lindquist, 1960). A new weed recently noticed in Illinois called "bigweed" or "jolly green giant" might have originated from introgression between *Setaria viridis* and *S. italica* (millet). This possibility is currently being investigated at the Crop Evolution Laboratory.

Nearly every crop has associated with it a weedy and a wild relative. Gene exchange in any combination among weed, wild and crop taxa can create weediness. Few of the wild and weed taxa related to crops have been investigated in any detail and therefore the origins of our most important crops and weeds remain obscure.

Acknowledgments

The author thanks Dr. J.M.J. de Wet of the Crop Evolution Laboratory, Department of Agronomy, University of Illinois for reading the manuscript and for his advice.

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Manuscript received September 27, 1971.