Wild Sunflower Germplasm: A Perspective on Characteristics of Use to Sunflower Breeders in Developing Countries.

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Genes or genetic factors that determine the heritable characters of plants differ from one plant to another within a species, with greater differences among species. The continual recombining of genes that occurs as a result of sexual reproduction and occasional mutations that result in new genes or the modification of existing genes, creates unique characteristics that enable plants to grow and survive in different environments. The magnitude of the range of genes that constitute the germplasm of a given population of plants is described by the term genetic diversity. The transient evolutionary history of *Helianthus* (sunflower) has sequentially coupled natural selection pressures (natural introgression, geographic isolation) with artificial selection (disruptive selection with ethnological isolation) for early domestication and subsequent modernization of genotypes adapted to cultivation.

Development of cultivated sunflower from wild species had resulted in individual plants being selected over many years by early agriculturists on the basis of reproductive potential, adaptation, and the preferences of those involved with seed production. Domestication of the crop thus resulted in fewer gene combinations or less genetic diversity than the species as a whole. This has produced a crop with a narrow genetic base, which could benefit from utilization of wild relatives of the cultivated crop. The future competitiveness of the sunflower industry in developing countries will rely on the development of new technologies and novel methods to enhance and escalate utilization of wild (unadapted) sunflower germplasm.

Germplasm Collection :

The United States Department of Agriculture, Agricultural Research Service (USDA-ARS) established a wild sunflower species collection at Bushland, Texas, in 1976. It was moved to the USDA-ARS North Central Regional Plant Introduction Station, Iowa State University, Ames, Iowa in 1985. The present collection contains 2152 accessions of wild sunflowers. Of these, 1442 are annual, while 710 are perennial. About 1,000 of the annual accessions are the common wide-ranging annual species *H. annuus*. Small quantities (generally 100 seeds) of wild species germplasm are distributed free of charge for bona fide research or educational purposes.

Genetic Diversity :

Genetic diversity in the genus *Helianthus* is reflected by habitat diversity among the species. Dry sandy soils are inhabited by annual species such as *H. anomalus*, *H. deserticola*, *H. neglectus*, and *H. niveus* subsp. *tephrodes*, while annual *H. agrestis* and *H. paradoxus*, and perennial *H. angustifolius*, *H. nuttallii* and *H. tuberosus* inhabit very moist habitats. Wild species are distributed from deep woods (*H. decapetalus*) to prairies (*H. pauciflorus* subsp. *subrhomboideus*) to deserts (*H. anomalus*). The diverse habitats which wild sunflower species inhabit are reflections of genetic variability among populations. One annual species, *H. paradoxus*, inhabits moist, heavy saline soils, while another, *H. exilis*, occupies dry serpentine soils. Both are potential sources of genes for transferring salt tolerance into cultivated sunflower.

It is important to learn as much as possible about the distribution and variability of wild sunflower species. This knowledge will be useful in the future when specific characteristics are sought for improving cultivated sunflower. Based on geographic location and immediate environment, selection of potential species for a particular character will become easier, more accurate, and efficient.

Genetic Resource Utilization :

Wild *Helianthus* species constitute the genetic stock from which cultivated sunflower originated. They have contributed useful characteristics for sunflower improvement (Thompson et al., 1981; Seiler, 1992; Seiler and Rieseberg, 1997). The genus *Helianthus* contains 50 species and 19 subspecies, with 14 annual and 36 perennial species (Heiser et al., 1969; Schilling and Heiser, 1981). All species are native to North America. Species are adapted to a wide diversity of habitats and possess considerable variability for most economic and agronomic characteristics, insect and disease resistance and seed quality factors (Thompson et al., 1981; Rogers et al., 1982; Seiler, 1992; Seiler and Rieseberg, 1997). The use of the wild species in breeding programs for developing countries has the potential for markedly improving commercial sunflower production. This is particularly important when production is expanding into new areas, subjecting the crop to intensified disease and insect problems and extremes in environmental conditions. Hence, there is a need for greater genetic diversity providing additional sources of resistance and tolerance to pests and improvement of seed quality in the sunflower crop.

Cytoplasmic Male Sterility :

Cytoplasmic male sterility (CMS) is a maternally inherited trait preventing plants from producing normal pollen. It is used to generate F_1 hybrids in sunflower. Sunflower is now the second largest hybrid crop in the world. Use of a single cytoplasm derived from wild *H. petiolaris* has narrowed the genetic base of cultivated sunflower. Development of the CMS hybrid system has facilitated the use of wild sunflower species in breeding programs by allowing the hybridization of genetically distant species and the subsequent incorporation of specific characteristics for the improvement of cultivated sunflower. Several research programs generating alloplasmic combinations have identified 62 new sources of male sterile

cytoplasms, 40 annual and 12 perennial (Serieys, 1999). Related fertility restoration genes are needed to utilize these cytoplasms, but in some cytoplasms they have not yet been found.

Interspecific Hybridization :

Much success has been achieved in recent years in hybridizing different species of plants. By using newer breeding techniques, the genus *Helianthus* affords a prime example of the potential that these methods hold for plant breeders and illustrates the importance of the preservation of wild germplasm as a source of genetic diversity for the future (Laferriere, 1986). Incompatibility, genetic distance, and chromosome numbers and aberrations in tetraand hexaploid species frequently obstruct the use of the wild species. The genus *Helianthus* contains 14 annual diploid species, 26 perennial diploid species, three perennial tetraploid species, and seven perennial hexaploid species.

The poor crossability and frequent F_1 sterility in interspecific hybrids limit the usefulness of many wild *Helianthus* species. Abortion of the hybrid embryo is one mechanism that prevents interspecific hybridization. An embryo rescue technique has facilitated the success of several interspecific crosses (Chandler and Beard, 1983). Sterility associated with meiotic abnormalities of F_1 s can be decreased by doubling chromosomes using colchicine (Jan et al., 1983). The low fertility associated with some interspecific crosses presents a serious impediment to hybridization, but such infertility sometimes can be overcome by using different populations of species for crossing. Some populations of a species have variable pollen staining indicating differences in pollen fertility (Seiler, 1984, Atlagic, 1990, Rieseberg et al., 1995). Another problem observed in interspecific crosses is achene dormancy. A very useful technique using achene scarification and a low level of growth hormone (GA₃) has increased germination to 70% in interspecific crosses, as well as in wild species populations, especially perennial species (Chandler and Jan, 1985).

Pathogens :

Wild sunflower species have been one of the few sources of resistance genes for many of the common pathogens of cultivated sunflower. *Helianthus annuus, H. petiolaris, and H. praecox* are the major sources of genes for Verticillium wilt (*Verticillium dahliae*) resistance (Hoes et al., 1973). These species plus *H. argophyllus* are also the major sources of resistance genes for downy mildew (*Plasmopara halstedii*) and rust (*Puccinia helianthi*) in cultivated sunflower. Resistance genes for these pathogens occur frequently in the wild annual species (Tan et al, 1992; Quresh et al., 1993). Resistance to broomrape (*Orobanche cernua*) has been observed in most of the wild perennial species (Fernandez-Martinez et al., 2000) and annual *H. anomalus*. Early reports of broomrape resistance were from the former Soviet Union where they developed cultivars 'Progress' and 'Novinka' using the 'Group Immunity' breeding approach (Pustovoit and Gubin, 1974). Phoma black stem (*Phoma macdonaldii*) resistance has been reported in several perennial species, *H. decapetalus, H. eggertii, H. hirsutus, H. resinosus* and *H. tuberosus* (Skoric, 1985). Phomopsis stem canker (*Phomopsis helianthi*) resistance has been found in perennials *H. maximiliani, H. pauciflorus, H. hirsutus, H. resinosus, H. mollis,* and *H. tuberosus* (Skoric, 1985; Dozet, 1990). Alternaria leaf spot

(Alternaria helianthi) resistance was observed in perennials H. hirsutus, H. pauciflorus, and H. tuberosus (Morris et al., 1983). Rhizopus head rot (Rhizopus arrhizus) resistance was observed in perennials H. divaricatus, H. hirsutus, H. resinosus, and H. x laetiflorus (Yang et al., 1980). Powdery mildew (Erysiphe cichoracearum) resistance was observed in annuals H. debilis subsp. debilis, H. bolanderi, and H. praecox (Saliman et al., 1982; Jan and Chandler, 1985). Sclerotinia (Sclerotinia sclerotiorum) head rot tolerance was observed in perennials H. resinosus, H. tuberosus, H. decapetalus, H. grosseserratus, H. nuttallii, and H. pauciflorus (Pustovoit and Gubin, 1974, Mondolot-Cosson and Andary, 1994). Sclerotinia root rot tolerance was observed in perennials H. mollis, H. nuttallii, H. resinosus, and H. tuberosus (Skoric, 1987). Sclerotinia midstalk rot tolerance was observed in annual H. praecox, and perennials H. pauciflorus, H. giganteus, H. maximiliani, H. resinosus, and H. tuberosus (Skoric, 1987).

Insects:

Wild sunflowers are native to North America where their associated insect herbivores and entomophages co-evolved in natural communities. This provides the opportunity to search for insect resistance genes in the diverse wild species. Sunflower moth (*Homoeosoma electellum*) tolerance was observed in annual *H. petiolaris*, and perennials *H. maximiliani*, *H. ciliaris*, *H. strumosus*, and *H. tuberosus* (Rogers et al., 1984). Stem weevil (*Cylindrocopturus adspersus*) tolerance was found in perennials *H. grosseserratus*, *H. hirsutus*, *H. maximiliani*, *H. pauciflorus*, *H. salicifolius*, and *H. tuberosus* (Rogers and Seiler, 1985). Sunflower beetle (*Zygogramma exclamationis*) tolerance was observed in annuals *H. agrestis* and *H. praecox*, and perennials *H. grosseserratus*, *H. salicifolius*, and *H. tuberosus* (Rogers and Seiler, 1985). Sunflower beetle (*Anternationis*) tolerance was observed in annuals *H. agrestis* and *H. praecox*, and perennials *H. grosseserratus*, *H. salicifolius*, and *H. tuberosus* (Rogers and Seiler, 1985). Sunflower beetle (*Anternationis*) tolerance was observed in annuals *H. agrestis* and *H. praecox*, and perennials *H. grosseserratus*, *H. pauciflorus*, *H. salicifolius*, and *H. tuberosus* (Rogers and Thompson, 1978 and 1980).

Oil, Oil Quality, and Protein :

Variability for oil concentration exists in the wild species. While oil concentration is lower in the wild species than cultivated sunflower, backcrossing to cultivated lines quickly raises the oil concentration to an acceptable level. Annual *H. niveus* subsp. *canescens* had the highest concentration of 402 g kg⁻¹ followed by *H. anomalus* with 379 g kg⁻¹, *H. petiolaris* with 377 g kg⁻¹, and *H. deserticola* with 343 g kg⁻¹. Perennial *H. salicifolius* had a concentration of 370 g kg⁻¹ (Seiler, 1985). Cultivated sunflower generally contains 450 to 470 g kg⁻¹. Reduced concentrations of saturated palmitic and stearic fatty acids have been observed in a population of wild *H. annuus*, which had a combined palmitic and stearic acid concentration of 58 g kg⁻¹ (Seiler, 1998). This is 50 % lower than in oil of cultivated sunflower. A combined palmitic and stearic acid concentration of 65 g kg⁻¹ was observed in a wild perennial species, *H. giganteus* (Seiler, 1998). Whole seed protein concentrations in the annual species were highest in *H. porteri* with 305 g kg⁻¹, followed by *H. paradoxus* with 227 g kg⁻¹. Perennial *H. nuttallii* had 348 g kg⁻¹, followed by 315 g kg⁻¹ for *H. silphioides*, and 284 g kg⁻¹ for *H. maximiliani*.

Salt and Drought Tolerance :

Several species of *Helianthus* are native to salt-impacted habitats. Interspecific germplasm derived from *H. paradoxus* has been identified with high salt tolerance withstanding salt concentrations up to EC 24.7 dSm⁻¹. It appears that one major gene controls salt tolerance, although a modifier gene may also be present, possibly recessive in control. Mechanisms enabling plants to survive stress have been selected during plant evolution, and not all maintain fully the plant's productivity process (Turner, 1979). In natural ecosystems, a plants ability to survive environmental stress is probably more important than high seed (grain) productivity. During the process of selecting plants for high seed yield, breeders may inadvertently lose some drought survival mechanisms common in wild species and may benefit from the infusion of germplasm from the wild species and selection to enhance drought tolerance in cultivated sunflower.

Stomatal responses have been suggested as potentially useful traits to consider in developing plants with improved water-use efficiency. Evaluation of 19 perennial and one annual wild sunflower species indicated that perennial species had higher diffusive resistance, transpiration, and stomatal densities than annual species (Seiler, 1983). In all perennial species, stomatal densities were higher on the bottom surface than the top surface, similar to cultivated sunflower, while it was opposite in the annual species. Blanchet and Gelfi (1980) evaluated stomatal resistance, leaf-water potential, photosynthetic activity, leaf structure, and number of stomata. They concluded that *H. argophyllus* is the most likely source of drought tolerance because its pubescent leaves reflect sunlight, reduce water loss, and exhibit low transpiration rates. *Helianthus niveus* subsp. *canescens* was their second choice.

Herbicide Tolerance :

A wild population of annual *H. annuus* from a soybean field in Kansas that had been repeatedly treated with imazethapyr for seven consecutive years developed resistance to the imidazolinone and sulfonylurea herbicides (Al-Khatib et al., 1998). Resistance to imazethapyr and imazamox herbicides has great potential for producers in all regions of the world for controlling several broad-leaf weeds. Genetic stocks IMISUN-1 (oil maintainer), IMISUN-2 (oil restorer), and IMISUN-3 (confection maintainer) have been developed and released (Al-Khatib and Miller, 2000). In addition, the two herbicides may control broomrape in areas of the world where this parasitic weed attacks sunflower (Alonso et al., 1998).

Conclusions :

The genus *Helianthus*, besides constituting the basic genetic stock from which cultivated sunflower originated, continues to contribute specific characteristics for cultivated sunflower improvement. However, there is a continued need to collect, maintain, evaluate and enhance wild *Helianthus* germplasm for future utilization in cultivated sunflower. The genetic diversity of the wild species can make a significant contribution to sunflower in developing countries by providing genes for resistance (tolerance) to pests and environmental stresses, allowing the crop to become and remain economically viable.

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