T1988PLE02

THE GENUS HELIANTHUS AS A SOURCE OF GENETIC VARIABILITY FOR CULTIVATED SUNFLOWER

Gerald J. Seiler, USDA, Agricultural Research Service, Conservation and Production Research Laboratory, P.O. Drawer 10, Bushland, TX 79012.

SUMMARY

The genus Helianthus, besides constituting the basic genetic stock from which cultivated sunflower originated, continues to contribute specific characteristics for cultivated sunflower improvement. Much potential genetic variability still remains to be exploited. This paper discusses the genetic diversity available in the genus relative to the following subject areas: taxonomy and classification; germplasm exploration and collection; interspecific hybridization; cytoplasmic male sterility; diseases; insects; physiology; oil and seed quality; and agronomic characteristics. The continued need for additional genes to improve cultivated sunflower emphasizes the necessity to collect, maintain, and enhance the genetic diversity of the wild Helianthus germplasm for utilization in the future for the improvement of cultivated sunflower.

INTRODUCTION

According to the theory of evolution, the many genes or genetic factors that contribute to the heritable characters of germplasm of plants may differ somewhat from one plant to another within a given species; further differences occur among species. The continual reordering of genes in new combinations that occurs as a result of sexual reproduction and occasional mutations that result in new genes or the modification of existing genes creates differences among characters 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. When crops were developed from the wild species, individual plants were selected over many years by early agriculturalists on the basis of reproductive potential under cultivation, adaptation, and the preferences of those involved with seed production. Each primitive variety of a crop, thus, produced a smaller number of gene combinations or less genetic diversity than the species as a whole.

Wild Helianthus germplasm, besides constituting the basic genetic stock from which cultivated sunflower originated, continues to contribute specific characteristics for sunflower improvement (Thompson et al., 1981). The genus Helianthus contains 49 species and 19 subspecies, with 12 annual and 37 perennial species (Heiser et al., 1969; Schilling and Heiser, 1981). All species are native to the Western Hemisphere and 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 (Rogers et al., 1982). Therefore, the use of the germplasm in breeding programs has the potential for markedly improving commercial hybrid sunflower production (Thompson et al., 1981; Dorrell and Whalen, 1978; Laferriere, 1986). This is especially important today because the expanded production of sunflower worldwide is subjecting the crop to intensified sunflower disease and insect problems and extreme environmental conditions. Hence, there is a need for greater genetic variability, additional sources of resistance to

disease and insects, and seed quality characteristics among modern sunflower hybrids.

A broader genetic base for sunflower hybrids is not only needed for the problems mentioned above but also from a genetics and breeding point of view. The present cultivated sunflower is based on an extremely narrow genetic base, mainly the cytoplasmic male sterile cytoplasm derived from the wild species H. petiolaris (Leclercq, 1969). This extremely narrow genetic base has left the cultivated sunflower crop extremely vulnerable to an impending disaster such as was seen with the southern corn leaf blight epidemic of 1970 (Tatum, 1971). The wild species of sunflower offer a broad genetic base and considerable genetic variability for improvement of the cultivated sunflower. Genetic variability in the cultivated sunflower may be increased by crossing it with the numerous wild Helianthus species.

This paper will discuss the genetic diversity available in the genus Helianthus relative to the following subject crops: taxonomy and classification; germplasm exploration and collection; interspecific hybridization; cytoplasmic male sterility; diseases; insects; physiology; oil and seed quality; and agronomic traits.

TAXONOMY AND CLASSIFICATION

Classification of the genus Helianthus has attracted the attention of many botanists for more than two centuries. Linnaeus (1753) originally described nine species of the genus and added another two species in subsequent years. During the 18th and 19th centuries, more than 200 species of the genus Helianthus were described by various authors. In the early 20th century, Watson (1929) attempted to monograph the genus Helianthus. He named 108 species, including some 40 newly described taxon. In addition, the monograph contained a supplementary list of 25 species of Helianthus without special descriptions and a list of 41 additional species which were excluded. Watson's keys are virtually unusable. With few exceptions, he failed to place the species in any order to show relationships, acknowledge the existence of hybrids, or give distribution maps. On the other hand, his botanical descriptions were good, and he brought together some widely scattered taxonomic literature and called attention to a number of taxonomic problems in the genus.

In a more recent publication, Heiser et al. (1969) described 66 species of Helianthus, of which 48 are distributed in North America and 18 in South America. Heiser et al. (1969) recognized 12 annual species and 36 perennial species in three sections and seven series. Recently, Robinson (1979) transferred 20 perennial species of the South American Helianthus to the genus Helianthopsis. The treatment of the genus Helianthus by Anashchenko (1974, 1979) is a radical departure from all previous ones. He recognized only one annual species, H. annuus (with three subspecies) and only nine perennial species (with 13 subspecies). Schilling and Heiser (1981) proposed an infrageneric classification of Helianthus using phenetic, cladistic, and biosystematic procedures. Forty-nine species of Helianthus were placed in four sections and six series by Schilling and Heiser (1981) (Table 1).

As we see from the above discussion, species of Helianthus have been variously defined. Part of this confusion may have arisen from the complexity of the many interspecific hybrids in the genus and the different ploidy levels of several species which make it difficult for taxonomists to define "pure" species. While hybridization makes identifying and classifying species of the genus difficult, this genetic diversity is all important as a potential source of genes for the improvement of cultivated sunflower.

GERMPLASM EXPLORATION AND COLLECTION

Explorations to locate and collect wild sunflower species represent one of the more difficult and challenging phases in the process of conserving genetic diversity in the genus Helianthus (Seiler, 1988). Helianthus is one of the few crop genera with wild relatives (species) that are native to North America and, more specifically, to the Southwestern United States. Having the wild progenitors of sunflower within the boundaries of the United States has facilitated exploration to collect germplasm of wild sunflower species.

The important benefit of using the wild species of sunflower to increase genetic diversity in cultivated sunflower was recognized by early plant breeders. Explorations were undertaken by Drs. Murray Kinman and Aurelio Luciano in Texas and Oklahoma in 1963 in search of a source for rust resistance. Another exploration for sources of rust resistance and a survey for rust races in the North Central Great Plains was undertaken by myself in 1972 under the direction of Drs. Dave Zimmer and Gary Fick. During the 1970's, Dr. Ben Beard of USDA-ARS, Davis, California, collected wild sunflower throughout the Southwestern United States. These early collections formed the nucleus of the USDA's wild species sunflower collection from the mid-1960's to the early 1970's.

The USDA-ARS established a wild sunflower species collection at Bushland, Texas, in 1976 under the direction of Dr. Tommy Thompson. The objective of the program was to establish a wild sunflower germplasm collection with as many accessions of the known wild species as possible and practical. The decision to create a permanent wild species collection greatly increased the number of plant explorations for wild sunflower species populations. During 1976, Drs. Tommy Thompson and Charlie Rogers collected wild species in Texas and New Mexico. In 1977, they collected sunflower in the West, Southwest, and Southeast United States. In 1979, several explorations were made throughout the United States when the USDA-ARS served as a host to a delegation from the U.S.S.R. collecting sunflower germplasm. In 1980, Dr. Luka Cuk of Novi Sad, Yugoslavia, and I collected in the Southern United States (i.e., North Carolina, west to California). In 1984, an exploration was undertaken in south Texas. The Eastern and Northeastern United States were explored in 1985 by Drs. Bill Roath, Dragan Skoric (Novi Sad, Yugoslavia), and myself (Seiler, 1987a). In 1987, an exploration was undertaken to the Pacific Northwest by Jeff Pomeroy, Radovan Marinkovic (Novi Sad, Yugoslavia), and myself. The Food and Agriculture Organization of the United Nations (FAO) and International Board for Plant Genetic Resource (IBPGR), European Cooperative Program for Genetic Resources (ECP/GR) has participated in several of the more recent explorations in the United States.

Researchers have travelled the equivalent of several times around the world in search of wild sunflower species. The germplasm collection contains germplasm from some populations of all the known species but does not contain, in most cases, an adequate number of populations of several species to have a good cross-section of the genetic diversity available. Explorations are planned for the Midwest United States (Wisconsin, Michigan, Illinois, Indiana, and Ohio) in 1989 and the Great Plains (North Dakota, South Dakota, Nebraska, Kansas, and parts of Oklahoma, New Mexico, Colorado, and Wyoming) in 1990. Southern Canada is proposed for collection in 1991. Plans are to collect in Mexico in 1992, particularly in the Baja and Sonora regions.

Through the collection efforts of many researchers, an excellent wild sunflower germplasm collection has been assembled. Seeds or rootstocks of all known species and subspecies of wild sunflower have been collected. The entire collection now contains over 2,000 accession numbers (Seiler, 1988). The active collection contains approximately 1,000 annual and 500 perennial accessions. Since 1976, 4,200 accessions of wild sunflower have been distributed to 30 different countries from the germplasm collection at Bushland, Texas (Seiler, 1984a). The wild species that have been distributed have become the basis for several wild species collections distributed throughout the world (IBPGR, 1985). Most notable is the collection at the Institute of Field and Vegetable Crops, Novi Sad, Yugoslavia (IBPGR, 1984), which contains 39 of the 50 wild sunflower species.

There is little doubt that additional populations of several species should be collected to increase the genetic diversity available from the wild sunflower germplasm collection. One thing to keep in mind is the amount of time and effort needed to maintain the populations for future use. Almost 70% of the wild species are perennial, and a substantial effort is required to maintain these population accessions. The price to collect and maintain germplasm is high; but once the germplasm is collected, it is priceless!

GERMPLASM COLLECTION

Genetic diversity in the genus Helianthus is reflected by habitat diversity among the species (Table 2). Dry, sandy soils are inhabited by such species as H. anomalus, H. deserticola, H. neglectus, and H. niveus ssp. niveus, while very moist soils are inhabited by H. angustifolius, H. agrestis, H. californicus, H. giganteus, H. nuttallii ssp. nuttallii, and H. tuberosus. Wild sunflower species are distributed from deep woods (H. decapetalus) to those species which occupy the prairies (H. rigidus ssp. subrhomboideus, H. maximiliani, and H. grosseserratus). Some species inhabit moist, heavy, and very saline soils. One annual species, H. paradoxus, has a high tolerance for salt and has great potential as a source of genes for salt tolerance in cultivated sunflower (Seiler et al., 1981; Chandler and Jan, 1984).

The diverse habitats occupied by species of wild sunflower are reflections of the genetic variability present in the various populations within the species. Knowledge of a particular habitat and adaptations of the species occurring there can often better help identify potential sources of genes for a desired trait. The recent release of six Plasmopara halstedii

(downy mildew) resistant (Race 4) lines illustrated this point (J. F. Miller, personal communication). The lines released were two from wild H. annuus, three from wild H. praecox ssp. runyonii, and one from H. argophyllus. The interesting thing about these germplasm releases is that all the species populations occurred within 20 to 30 km of Corpus Christi, Texas, which is located on the Texas coast of the Gulf of Mexico. This area is favorable for the natural occurrence of downy mildew, and it appears that at least some local populations of the wild species have developed a tolerance for the disease. Jan and Chandler (1985) studied the transfer of Erysiphe cichoracearum (powdery mildew) resistance from Helianthus debilis ssp. debilis. The original wild population came from the Atlantic coastal area (Hutchinson Island) of Florida. Again, this habitat should be ideal for the natural occurrence of the disease; and a source of resistance was found in the wild species from that area.

To improve cultivated sunflower, it is important to learn as much as possible about the distribution and variation of wild sunflower species. This knowledge will be useful in the future when specific characteristics are sought. Based on where a species occurs and its immediate environment, selection of potential species for a particular characteristic may become easier and more accurate.

INTERSPECIFIC HYBRIDIZATION

Much success has been achieved in recent years in hybridizing different species of plants by using newer breeding techniques. The genus Helianthus offers a prime example of the potential that these methods hold for plant breeders and serves to illustrate the importance of the preservation of wild germplasm as a source of genetic variability for breeding materials for the future (Laferriere, 1986). The use of wild species in sunflower breeding programs is frequently obstructed by incompatability, genetic distance, and increased chromosome numbers and aberrations in tetra- and hexaploid species. Many of the species hybridize readily with one another in nature and in cultivation (Heiser et al., 1969; Heiser, 1976). Helianthus annuus crosses most easily with other diploid annuals and less easily with the polyploid-perennial species (Georgieva-Todorova, 1984, 1985). When making diploid interspecific hybrids, there remains an open question whether we eliminate a genome or genomes which carry chromosomes with resistance genes. There is insufficient knowledge of genetic structure in the species of the genus Helianthus; thus, it is advisable to screen wild species for disease resistance and study their chromosomal structure and genomic structure simultaneously (Skoric, 1987).

Anashchenko (1982) reported that there appear to be three primary genomes in Helianthus, all of which have the basic chromosome number x = 17. According to Anashchenko (1982), genome A is native to the Southern Appalachians and characteristic of most of the North American perennial sunflowers; genome B is native to the Rocky Mountains and characterized by annual sunflowers; and genome C is also native to the Rockies and characterized by western perennial species, H. ciliaris and H. pumilus. Some of the polyploid species contain various combinations of these three basic genomes. There also is some evidence that even the three primary genomes may themselves be the result of some very ancient polyploidy

(Heiser and Smith, 1955; Jackson and Murray, 1983). Among the annual sunflower, H. debilis appears to have the chromosomal configuration most nearly resembling the ancestral condition. Helianthus annuus and H. neglectus are the most highly differentiated (Chandler et al., 1986).

Controlled interspecific hybridization of Helianthus has been conducted for many years. The main interest of the Soviet breeders was to obtain resistance to pests and diseases (Whalen, 1978). Attempts at using interspecific hybridization in sunflower breeding dates back to 1916, when the Soviet scientist Sazyperow first used hybrids between H. annuus and H. argophyllus in an attempt to develop cultivated H. annuus with rust resistance (Cockerell, 1929). The early interest in interspecific hybridization of Helianthus species in North America was more theoretical and morphological. Leclercq (1969) reported cytoplasmic male sterility (CMS) in backcross progeny of the hybrid H. petiolaris x H. annuus. Today, there is renewed interest in many countries in interspecific hybridization for insect and disease resistance and to find additional sources of CMS and fertility restoration.

Many successful interspecific crosses among the wild species of Helianthus have been reviewed by Whalen (1978). The primary objective of many of these crosses was to obtain taxonomic information for evolutionary studies, not for obtaining information about agronomic potential. Nonetheless, interspecific hybridization between species has been used to facilitate the use of wild species for agronomic purposes. Whalen (1976) used wild H. annuus as an "intermediate" parent or "bridge" to produce the hybrids with both H. giganteus and H. maximiliani. Direct hybridization between the cultivar 'Krasnodarets' and H. giganteus produced a single, highly sterile hybrid. Repeated pollinations with or without embryo culture failed to give backcross progeny. Pollinating both H. giganteus and H. maximiliani with wild H. annuus, however, produced three and four hybrids, respectively. These hybrids subsequently gave small quantities of seed when pollinated with Krasnodarets pollen. Continued backcrossing with commercial cultivars has yielded apparent cytoplasmic male sterile segregants from both the H. giganteus and H. maximiliani cytoplasms (Whalen, 1980; Whalen and Dedio, 1980).

Other aids in interspecific hybridization are irradiation of pollen (Tsvetkova, 1974), temperature shock (Pustovoit, 1969; Vinitskaya, 1973), and grafting (Pustovoit, 1969). These methods usually involved hybridization between H. tuberosus and H. annuus. Whalen (1978) has hybridized H. annuus with H. tuberosus, H. rigidus, and their punitive hybrid, H. x laetiflorus. Initial F_1 hybrids were among the crosses readily obtained. Backcross seed was obtained with difficulty by repeated pollinations with H. annuus pollen.

Use of conventional crossing methods has been sufficient to produce interspecific hybrids between cultivated sunflower and some of the wild species, especially the diploid annuals. However, several of the wild species, especially the diploid perennials, remain untapped as useable germplasm for agronomic purposes because they have not been hybridized with cultivated sunflower. Abortion of the hybrid embryo is one mechanism that prevents hybridization of these perennials (Chandler and Beard, 1978). The classical solution to this problem in other crops has been the use of embryo culture, i.e. excising the embryo before it aborts, and

placing it on nutrient media to grow in vitro into a seedling capable of supporting itself. Whalen (1976) had limited success with embryo culture of interspecific sunflower hybrids.

In embryo culture, embryos are removed 3 to 7 days after pollination and placed on a solid nutrient medium until they became 2 to 6 mm in diameter. Then, they are transferred to a vial containing a liquid medium. Chandler and Beard (1983) successfully made 53 interspecific Helianthus combinations using the embryo culture system. Twenty-one of these combinations had not previously produced progeny using conventional methods; these combinations consisted of 13 annual x annual species, one perennial x perennial (H. gracilentis x H. maximiliani, three perennial x annual, and four annual x perennial combinations. All hybrids among annual species had a higher percentage of normally stained pollen than did the perennial x annual hybrids. The perennial x annual hybrid involving H. angustifolius x H. annuus was completely sterile. The lack of fertilization in some of the attempted crosses presents a serious barrier to hybridization, but such infertility could possibly be overcome by using different population accessions within a particular species. Variation in pollen staining of various populations of wild Helianthus has been previously reported (Seiler, 1984c).

Another problem reported in conventional interspecific hybridization is dormancy of hybrid seed. Well developed, supposedly viable hybrid seed from some crosses have been obtained that would not germinate (Heiser et al., 1969). This dormancy is strongest in the annual desert species, e.g. H. anomalus, H. deserticola, and H. niveus spp. tephrodes, which are potential germplasm sources of drought tolerance (Chandler and Jan, 1985). In interspecific combination, embryo culture may sometimes avoid the embryo dormancy barrier. Embryo culture also may be useful in certain programs by increasing the number of generations per year. Embryos resulting from some crosses between annual species and cultivated sunflower develop quite quickly. Thus, in less than a year, four successive hybridization and backcross generations from a cross between H. petiolaris and the cultivated sunflower may be obtained (Chandler and Beard, 1983). Shortened generation times might also help in breeding projects where only a few plants are needed per generation, such as transferring fertile inbred line characteristics into sterile cytoplasm or backcrossing a desirable gene into an inbred line.

Utilization of many species of wild Helianthus is limited by poor crossability and the high degree of F_1 sterility in interspecific hybrids. Doubling the chromosome number of one or both parents has improved interspecific crossability in some crops (Dewey, 1980). Chromosome doubling of interspecific hybrids generally is effective in improving fertility when sterility is associated with meiotic abnormalities in sunflower (Jan et al., 1983). Chromosome doubling by applying colchicine to apical meristems of young seedlings has been demonstrated in cultivated sunflower (Dhesi and Saini, 1973; Gupta and Roy, 1979; Downes and Marshall, 1983). Also, chromosome doubling of diploid perennial species and their interspecific hybrids has been reported by Heiser and Smith (1964) and Jackson and Murray (1983). Chromosome doubling of cultivated x wild diploid interspecific hybrids was reported by Jan et al. (1983) and Jan and Chandler (1988).

Jan and Chandler (1988) reported that plants at the true two-leaf stage submerged for 5 hours in a 0.15% colchicine solution at pH = 5.4 and 2% DMSO (dimethyl sulfoxide) provided a 32% success rate of chromosome doubling. Chromosome doubling of heads was verified by pollen stainability (Alexander, 1969), pollen grain size, and size of disk florets. Size of pollen was the best criterion for discriminating between doubled and nondoubled chromosome number of plants because pollen grains from tetraploid heads were substantially larger than those from diploids. There were no obvious general morphological characteristics associated with chromosome doubling except the relative size of disk florets, pollen stainability, and pollen size (Jan and Chandler, 1988).

The doubling of chromosomes by using colchicine was evaluated for an interspecific hybrid of the cultivated line H. annuus (P21) x H. bolanderi by Jan and Chandler (1988). They found the stainability of pollen from diploid heads was 5%, while the stainability of pollen from the tetraploid heads was 70%. Chromosome doubling did not change the self-incompatibility of the hybrids; they were still highly self-incompatible. Chromosome doubling increased sib-pollination seed set. Sib-pollinated seeds were obtained on treated plants at an average of 4.5 seeds/head, while the derived tetraploid (4x) plants averaged 61.8 seeds/head. Crosses of amphiploid heads involving the diploids HA89 or P21 resulted in even greater seed set: 13.3, 3.0, 45.8, and 38.8 seeds/head for 4x x P21, 4x x HA89, P21 x 4x, and HA89 x 4x, respectively. These amphiploid seeds may provide material for further backcrossing between wild and cultivated types when parental hybrid plants do not set seed in the backcross generation. Since nondoubled heads had very low pollen stainability, the doubled pollen grains and ovules must have had an advantage in forming viable zygotes. The use of chromosome doubling may be even more dramatic for the more difficult interspecific hybrids with near-zero pollen viability.

Meiotic chromosome pairing and pollen stainability of amphiploids and 2x hybrids with P21 and H. bolanderi also were studied by Jan and Chandler (1988). Helianthus bolanderi used in the study may have differed from P21 by seven reciprocal translocations. The 2n = 68 amphiploids had 49.8 chiasma per pollen mother cell (PMC), about double the 24.0 frequency of the diploid hybrid. On the other hand, the amphiploid had a much higher frequency of multivalents (1.8%) than that of the diploid hybrid (1.1%). The meiotic chromosome arrangements and separation were comparable in amphiploids and 2x hybrids. Over 98% of the amphiploid pollen grains were large, and 69% of the grains were stainable. These traits provided evidence that the negative effect of F_1 translocation heterozygosity on fertility was overcome by preferential pairing among identical chromosomes as a result of chromosome doubling. The increased pollen stainability of the amphiploids corresponded with their increased backcross seed set. The use of chromosome doubling to increase fertility of interspecific hybrids, its consequences on chromosome constitutions of backcross progenies, and its practical value in interspecific gene transfer needs further clarification, but chromosome doubling appears to be a potentially useful technique for overcoming low fertility in F_1 interspecific hybrids.

CYTOPLASMIC MALE STERILITY

Cytoplasmic male sterility (CMS) is a maternally inherited trait preventing plants from producing normal pollen. CMS is used as a tool to generate F_1 hybrid seed in maize, rice, sorghum, and sunflower. Alloplasmic male sterility (arising from interspecific or intergeneric crosses) is thought to be due to incompatibility between the nucleus and the cytoplasm.

Another use for interspecific hybridization is in the creation of male sterile parents for hybrids, which has revolutionized the sunflower industry by making possible the production of high-quality hybrid sunflower. Leclercq (1969) reported CMS in the progeny of a cross between H. petiolaris and cultivated sunflower, where subsequent crosses with fertile cultivated sunflower produced progenies that also were sterile, thus providing a stable CMS in sunflower. Kinman (1970) obtained the CMS source of Leclercq and discovered genetic fertility-restoring genes in lines that were also derived from wild species. Leclercq (1971), Enns et al. (1970), Vranceanu and Stonescu (1971; 1978), and Fick et al. (1974) also subsequently reported fertility-restoring genes. Thus, the two factors necessary for the cytoplasmic-nuclear system of hybrid seed production were discovered and distributed among sunflower breeding programs in the world. The first hybrids produced by this system were made available for commercial production in the United States in 1972; and by 1976, over 80% of the sunflower production area in the United States was attributed to these hybrids (Miller, 1987).

Development of the CMS hybrid system has greatly facilitated the use of wild sunflower species in breeding programs by allowing distant crosses to be made and incorporation of specific characteristics to improve cultivated sunflower. Since the cultivated sunflower hybrids are presently based on one cytoplasm (French), they are extremely vulnerable to an impending disasters due to their limited genetic diversity.

Several researchers continue to look for new sources of male sterility. Vranceanu and Stonescu (1973) obtained new lines of CMS from sources of H. petiolaris. They subsequently also found two restorer genes among the cultivated varieties. Kuban 1-70 and VIR-126M CMS sources originating from a cross of H. lenticularis (wild H. annuus) with cultivated sunflower were discovered by Anashchenko in 1974 (Mileyeva and Anashchenko, 1976; Anashchenko, 1977) . Whalen and Dedio (1980) released CMG-1, CMG-2, and CMG-3 as potential CMS sources which were open-pollinated composites of partial interspecific substitution of the nucleus of cultivated sunflower into cytoplasms of the annual species H. petiolaris and the perennial species H. giganteus and H. maximiliani. Leclercq (1983) reported an additional new CMS source from H. petiolaris. Heiser (1982; 1985) developed Indiana-1 CMS by crossing a single male sterile plant of H. annuus ssp. lenticularis with cultivated sunflower. Vranceanu et al. (1986) described a new CMS source Fundulea-1 from an open-pollinated wild H. annuus ssp. texanus population. Serieys (1987) reported new sources of CMS from four different populations of H. annuus, one from H. bolanderi, and one from H. petiolaris ssp. fallax.

Completely sterile progeny have been recorded in different backcross generations of the CMS sources CMG-1, CMG-2, and CMG-3 with certain sunflower inbreds; but the expression of male sterility varies greatly, even within a single progeny. While most plants showed almost normally developed anthers, frequently there were plants with vestigal anthers lacking pollen (Vranceanu et al., 1986). Wolf and Miller (1985) showed that the pollen fertility restoration pattern for each cytoplasm source (CMG-1, CMG-2, and CMG-3) was different and that different gene actions were observed for pollen fertility restoration. In the 'Heiser' cytoplasm, completely sterile plants were sometimes found; and in other cases, different ratios of partially fertile plants were noted, especially in BC_1 and BC_2 generations (Gedge, 1985; Vranceanu et al., 1986). Serieys (1987) reported an unstable CMS from H. niveus ssp. canescens; and he speculated that the instability was due to segregating progenies, likely due to unfixed female plants with complementary restoration systems in unsteady cytoplasms.

Fertility restoration can often be a problem in the development of new CMS. The gene in the parent with CMS often is termed a fertility factor gene rather than a restoration gene. Partial restoration of fertility has been observed in many parents with CMS, indicating the presence of modifying genes that often are greatly influenced by the environment, which makes their inheritance difficult to determine (Miller, 1987).

The classical method for differentiating cytoplasm sources has been the reaction for the restoration of male fertility by various inbred lines crossed with a suspected source of CMS (Leclercq, 1983, 1984). Other methods for distinguishing between CMS sources are becoming available. With the advent of molecular techniques permitting direct examination of cytoplasmic genomes, cytoplasms can now be further differentiated (Leroy et al., 1985). Two cytoplasms with indistinguishable inbred line reactions from given restorer genes can be distinguished if their cytoplasmic genomes exhibit restriction site heterogeneity. Evidence suggests that mitochondria are carriers of genetic determinants conditioning CMS in plants. Since 1976, it has been possible to clearly distinguish fertile from sterile cytoplasms in different plant species using restriction endonucleases and types of low molecular weight mitochondrial DNA (mtDNA) molecules which they bear (Levings and Frings, 1976). It also is possible to characterize each cytoplasm for some species by studying native mtDNA (Leroy, 1985). Brown et al. (1986) studied variation in mtDNAs, chloroplast DNAs (ctDNAs) and double-stranded RNAs (dsRNAs) of Canadian sunflower lines (CM400 and CMS CM400) carrying fertile and male sterility conferring cytoplasms, which are two chromosomally isogenic lines differing only in cytogenes. A circular 1.45-kilobase (kbp) plasmid DNA was found in mitochondria of the fertile line that was absent in the male-sterile line. Restriction enzyme analysis of mtDNAs of fertile and male-sterile cytoplasms with Bamh I Ecor I, and Hind III revealed no fragment mobility differences between them other than those which could be ascribed to the 1.45-kbp circle. Similar restriction analysis of ctDNA showed no difference between fertile and male-sterile cytoplasms. The dsRNA molecules (3.3 and 1.5 kbp) were the only dsRNAs common to CM400 and CMS CM400 with no consistent difference separating them. The specific association of the 1.45-kbp plasmid with fertile cytoplasm without variation in ctDNA and dsRNA suggests involvement of mtDNA in sunflower CMS (Brown et al., 1986).

Leroy et al. (1985) reported that mitochondria from male-fertile HA89 cytoplasm contain a low molecular weight (LMW) mtDNA molecule of 1.45 kbp in addition to the major mtDNA. On the contrary, mitochondria from male-sterile cytoplasm contain no LMW molecules. Treatment with DNAse, RNAse, and nuclear SI show that the LMW mtDNA molecule consists of a supercoiled circular DNA. The mtDNAs from sterile and fertile cytoplasms also were studied using restriction endonuclear digestions (Sal I, Xho I, Bgl I). Electrophoresis of resulting fragments revealed several differences between sterile and fertile cytoplasms. It must be emphasized that the sterile cytoplasm came from H. petiolaris, while the fertile cytoplasm came from H. annuus. The observed differences in mtDNA could have been due to their origins and might not, in fact, have a causal relationship with the CMS trait. Nevertheless, presence of LMW mtDNA molecules in the fertile cytoplasm constitutes a rapid and efficient marker to differentiate fertile and sterile cytoplasms of HA89.

Heyraud et al. (1987) described the structural arrangement of chloroplast DNA (cpDNA) in sunflower as an initial step in analyzing cytoplasmic variability in Helianthus. They found that circular DNA contains an inverted repeat structure with two copies (23 kbp each) separated by a large (86 kbp) and a small (20 kbp) single copy with the exception of an inversion of a 23.5 kbp segment in the large single copy region. Analyses of the Bamh I restriction fragment patterns suggest that structural variations are present in Helianthus. While H. occidentalis ssp. plantagineus presents a Bamh I restriction pattern identical with H. annuus, other species (H. grosseserratus, H. decapetalus, H. giganteus, and H. maximiliani) gave the same Bamh I patterns as H. tuberosus. Clones of this variable region, as well as others under investigation, will be used to prepare a molecular phylogeny of cytoplasms of Helianthus (Heyraud et al., 1987). Clones also should allow molecular discrimination of various cytoplasms within species or subspecies, some of which are already known by their nucleo-cytoplasmic behaviors.

Crouzillat et al. (1987) characterized mtDNA of CMS in a series of sunflower lines and in some populations of wild Helianthus species to establish molecular analysis of sunflower CMS's. They analyzed the following different cytoplasms: French (H. petiolaris), unknown (H. argophyllus?), Indiana (H. annuus ssp. lenticularis), Bolanderi (H. bolanderi), Petiolaris (H. petiolaris), Fallax (H. petiolaris ssp. fallax), and Kuban (H. annuus ssp. lenticularis). A circular supercoiled 1.45 kbp plasmid DNA, previously reported in mitochondria of fertile H. annuus, was not detected in mitochondria of an isogenic French CMS line containing H. petiolaris in the presence of an H. annuus nuclear background (Leroy et al., 1985). Fertility restoration by nuclear genes had no effect on the absence of the plasmid (Brown et al., 1986). There is no apparent relationship between mitochondrial plasmid DNA and CMS in Helianthus species (Crouzillat et al., 1987). On the contrary, each Helianthus CMS and male-fertility strain can be characterized by digestion fragment patterns (Sal I and Bgl I). It must be emphasized that male-sterile cytoplasms originate from different species of wild Helianthus (H. annuus ssp. lenticularis, H. petiolaris, and H. bolanderi). Male-fertile cytoplasm is found in cultivated sunflower which has undergone quite a long period of selection. Differences in mtDNA patterns could be due to these different origins and may not, in fact, have any causal relationship with the CMS trait. Analyses of mtDNA

from wild Helianthus strains indicated a relation between some CMS and the strain from which they were maternally derived; for example, Indiana cytoplasm and H. annuus ssp. lenticularis and French cytoplasm and H. petiolaris ssp. fallax. The fact that these wild strains, apparently containing CMS cytoplasms, show normal male-fertile phenotypes suggests that they also must contain nuclear restorer genes. Thus, the CMS phenotype does not appear to alter the physical map of mitochondria of a sunflower species, and the evolution of the mitochondrial DNA structure appears to be independent of the nuclear environment.

Future improvements of cultivated sunflower through the hybridization with new sources of CMS and through introgression of characters of agricultural interest (resistance to frost, drought, natural predators) from wild species of Helianthus into sunflower lines will require extensive knowledge of the genetic properties of the species. Although an infrageneric classification of Helianthus already has been proposed using complementary methods of biosystematics, uncertainties about the phylogenetic relationships of some species remain unresolved, preventing their rigorous classification. In addition, genetic diversity within species, particularly those used for the production of CMS for hybrids, is an important factor for obtaining diverse CMS.

PHYSIOLOGY

A wide variety of agronomic traits, e.g. resistance to environmental stress, has been examined among wild Helianthus species for possible use in improving the hardiness and productivity of cultivated sunflower. During plant evolution, mechanisms enabling plants to survive stress have been selected, not all of which fully maintain the plant's productive process (Turner, 1979). For plants living in natural ecosystems, survival of environmental stress is probably more important than high grain (seed) productivity, whereas in agricultural systems, maximization of productivity is of paramount importance (Turner, 1981). It is conceivable, therefore, that during selection by plant breeders for high seed productivity, some drought resistance characteristics have been inadvertently lost and that current breeding programs to improve drought resistance in cultivated sunflower may benefit from an infusion of germplasm from wild sunflower species.

Variations in stomatal aperture can markedly affect the transpiration rate and net photosynthesis in plants through their negative regulation of CO_2 exchange. Stomatal response has been suggested as a potentially useful trait to consider in developing crop plants with improved water-use efficiency (DeMichele and Sharpe, 1974). Preliminary evaluation of 19 perennial and one annual species of wild sunflower for leaf diffusive resistance, transpiration, and stomatal densities under irrigation was reported by Seiler (1983a). All perennial species except H. pumilus had higher diffusive resistance, transpiration, and stomatal density than wild H. annuus. Diffusive resistances of the adaxial surface of leaves were lower than those of the abaxial surface. In general, transpiration was higher from the adaxial surface than the abaxial surface. Stomatal densities varied by sides of the leaves. In all perennial species, stomatal densities were higher on the abaxial surface than the adaxial surface. Stomatal densities on the adaxial surface varied from a low of $16/mm^2$ in H. resinosus to a high of $127/mm^2$ in H. strumosus. Stomata

on the abaxial surface varied from a low of 110/mm^2 in H. resinosus to a high of 153/mm^2 in H. decapetalus. However, in wild H. annuus, there were more stomata on the adaxial (198/mm^2) than the abaxial surface (155/mm^2). A similar arrangement of stomata has been reported for some commercial sunflower lines (Blanchet and Gelfi, 1980). The evidence presented by Seiler (1983a) indicated that variability for the transpiration and diffusive resistance exists among the wild species and that some of these, by virtue of their high diffusive resistance and low transpiration, have potential for developing sunflower plants with improved water-use efficiencies.

Limited information is available on wild sunflower physiology and their responses to water deficits. Sobrado and Turner (1983a) compared tissue water relation characteristics and biomass productivity of two cultivars of H. annuus and two wild species (H. nuttallii and H. petiolaris) under field conditions. Water deficits induced a major reduction in leaf area development and dry matter accumulation in all species. Water deficits also induced a significant decrease in the osmotic potential at full turgor and a decrease in turgid weight to dry weight ratio in the cultivated lines and not the wild species.

Sobrado and Turner (1983b) compared water relations and stomatal responses of cultivated sunflower with one species of wild sunflower (H. petiolaris) under conditions in which the rate of drying could be controlled and manipulated. They concluded that cultivated H. annuus and H. petiolaris differ in their ability to osmotically adjust to water deficits. However, in other respects, the two species behave similarly in their responses to water deficits. They also demonstrated a strong correlation between osmotic potential at full or zero turgor and the turgid to dry weight ratio. They suggested that changes in cell size may play a role in osmotic adjustment and drought resistance in sunflower.

Leaf expansion as affected by plant water availability in wild H. petiolaris ssp. fallax and cultivated H. annuus was reported by Sobrado and Rawson (1984). The stress imposed was sufficient to curtail leaf growth so that plants in the dry treatment had only 60% of the leaf area of irrigated plants at the onset of rewatering. Both species were affected by stress to the same relative extent, though their leaf areas at this stage differed seven-fold. Both genotypes also recovered to the same degree in the long term, finally having leaf areas and gross dry matter distribution patterns which were indistinguishable from plants which were irrigated throughout the experiment. However, water stress resulted in different leaf area distribution patterns. Helianthus annuus produced larger leaves at the top of its single stem, which compensated for the reduced area in lower leaves, whereas H. petiolaris compensated for lost leaf area in the leaves on its branches. Leaf expansion rates were affected earlier in the stress cycle than leaf conductance in H. annuus but not in H. petiolaris. The data indicated that leaf expansion is sensitive to water deficits in both H. annuus and H. petiolaris. There is evidence, however, that the wild species is marginally less sensitive than the cultivated one but that the cultivated species may have the propensity for a longer period of compensation after stress relief.

Morizet et al. (1984) evaluated an interspecific hybrid between cultivated H. annuus and H. argophyllus for drought tolerance. They measured

photosynthetic and water relations of two groups of plants; the first were hybrid plants most similar to H. argophyllus and the second with individuals most similar to H. annuus. Plants of the H. argophyllus type wilted more rapidly and at higher leaf water potentials than plants of the H. annuus type. Under similar environmental and edaphic conditions, H. argophyllus types generally had lower leaf water potential than H. annuus. In addition, photosynthetic activity of H. argophyllus was slightly higher for a given leaf water potential. However, no difference was detected between the two groups for transpiration or stomatal resistance.

The effects of water deficits on photosynthesis, plant growth, and carbon allocation in the wild sunflower H. petiolaris and in the cultivated sunflower H. annuus grown under controlled conditions were reported by Sobrado and Turner (1986). Water deficits reduced the rate of net photosynthesis and dry weight of leaves, stems, roots, and reproductive parts in both species. The decrease in growth induced by water deficits was a consequence of a reduction in both leaf area production and net photosynthesis. During mild water stress, carbon allocation to stems decreased, while it increased to the reproductive organs. When plants were severely stressed and then rewatered, the proportion of carbon allocated to leaves increased when compared to unstressed plants. The ability to change the allocation pattern following an environmental cue (in this case, a moderate water deficit) contributes to the ability of the species to persist in a heterogeneous environment. The presence of a plastic response (i.e. with allocation patterns due to environmental factors) is an important adaptive characteristic in arid regions.

Blanchet and Gelfi (1980) tested 10 southwestern species of Helianthus for various aspects of drought tolerance. They examined stomatal resistance, leaf water potential, photosynthetic activity, leaf structure, and number of stomata. They recommended H. argophyllus as the most likely source of drought resistance because its pubescent leaves reflect sunlight and reduce water loss and it exhibits low transpirational rates. It was also low in stomatal resistance, especially at high temperatures; and it has a powerful taproot and hybridizes easily with H. annuus. Helianthus niveus ssp. canescens was their second choice. Helianthus anomalus, an endemic diploid annual native to northern Arizona and southern Utah, has also been recommended as a source of genes for drought resistance (Nabhan and Reichhardt, 1983).

Emitted thermal radiation, a measure of the canopy temperature, is related to plant water status (Blum, 1984). Plant canopy temperature, as an indicator of crop water stress under irrigation and rainfed conditions, was studied in interspecific hybrids of H. petiolaris, H. argophyllus, H. anomalus, H. praecox, H. annuus, and H. exilis (Seiler, 1986a). Preliminary results indicate genotypic differences exist for canopy temperature minus air temperature ($T_c - T_a$) but were influenced by the soil water status. The $T_c - T_a$ difference was greater for irrigated than for rainfed plots. Under irrigation, canopy temperatures of cultivated hybrids averaged 0.8°C lower than the canopy temperatures of interspecific hybrids, indicating that cultivated hybrids had a higher transpiration rate than interspecific hybrids. Under dryland conditions, canopy temperatures of cultivated hybrids were higher than canopy temperatures of the interspecific hybrids, indicating that the cultivated

hybrids are more sensitive to water stress. Preliminary results indicate that there appear to be differences in $T_c - T_a$ between genotypes of cultivated and interspecific hybrids and that this should be used in combination with physiological measurements such as leaf water potential and stomatal resistance to better define water stress.

Leaf water potential characteristics integrate an array of water stress avoidance and tolerance mechanisms. Examination of plant turgor response is especially appealing because maintenance of turgor integrates both water supply and water loss mechanisms of the plant. Leaf water potential, osmotic potential, and turgor pressure of 28 wild perennial and one annual cultivated hybrid '894' were evaluated under full irrigation (Seiler, 1987b). Leaf water potentials in about half of the perennial species were significantly different than the cultivated hybrid at the flowering stage. In general, leaf water potential of perennials was higher until flowering, then decreased. Osmotic potentials in eighteen of the wild perennial species also was significantly different than the cultivated hybrid at the flowering stage. Wild perennial species appeared to be adjusting osmotically under full irrigation, with a general decrease as the species matured. Nine of the 28 perennial species had negative leaf turgor pressure at the flowering stage and were unable to osmotically adjust to maintain a positive turgor pressure, even under irrigation. Considerable variability for leaf water relation characteristics among the wild perennial species has been observed. Future studies will be needed to delineate the physiological reactions of the perennial species as they undergo water deficits.

Research into the physiological mechanisms and characteristics which allow the wild species to survive in their natural environments is just beginning. Characterization of drought is very complex and interrelated with many factors, and selection of characteristics for breeding for increased yield (productivity) becomes more difficult.

DISEASES

Cultivated sunflower lacks genes for acceptable levels of resistance for the majority of sunflower diseases. Diseases are still a limiting factor to high productivity in the majority of sunflower growing countries. Genetic variability of cultivated sunflower may be increased by crossing it with the numerous wild Helianthus species as sources of genes are identified from the wild species.

According to Putt and Sackston (1963), Puccinia helianthi was the first disease to be genetically controlled by resistance genes R_1 and R_2 incorporated from wild annual H. annuus from Renner, Texas. Wild Helianthus species H. annuus and H. petiolaris contain a vast reservoir of rust resistance genes that can broaden the rust protection base of domestic cultivars (Hennessy and Sackston, 1972; Zimmer and Rehder, 1976). Resistance to Races 1 and 3 of rust was found in H. praecox ssp. runyonii, H. praecox ssp. hirtus, H. argophyllus, and 18 wild H. annuus populations (Thompson et al., 1978). Rust resistance appears to be common in wild sunflowers (Fick et al., 1974). Wild annual Helianthus provides a sanctuary for the rust fungus in the absence of susceptible cultivars (Zimmer and Hoes, 1978). Studies on wild annual sunflowers suggest that many races of rust occur, with their number being limited

only by the number of differentials used. Rust can be controlled effectively on sunflower for long periods by using specific genes for resistance, especially since a free breeding rust population exists on wild sunflowers. Puccinia helianthi is confined to the genus Helianthus, where it occurs on more than 35 annual and perennial species (Arthur and Cummins, 1962; Hennessy and Sackston, 1972; Zimmer and Rehder, 1976; Zimmer and Fick, 1974). Wild populations of annual sunflower contain some rust resistant plants (Hennessy and Sackston, 1972; Zimmer and Rehder, 1976); but completely resistant or totally susceptible populations rarely are found.

Resistance to downy mildew in cultivated sunflower is conditioned by PL genes, PL_1, PL_2, PL_3, PL_4, and PL_5 (Vranceanu et al., 1981; Zimmer and Kinman, 1972; Vear and Leclercq, 1971; Vear, 1974; Fick and Auwarter, 1982; Miller and Gulya, 1987). Wild Helianthus has served as a source of downy mildew resistant genes. Helianthus praecox ssp. runyonii, H. praecox ssp. hirtus, H. argophyllus, and 18 wild H. annuus entries are resistant to Race 2 of downy mildew (Thompson et al., 1978). Further testing has shown that these species also are resistant to Races 3 and 4 (Jerry Miller, personal communication). The resistance in some of the species may be due to the PL_2 gene. Some of the resistant species were collected in Texas, where the PL_2 resistant materials were originally found (Zimmer and Kinman, 1972). Downy mildew resistance to Red River Race 2 is most common among five perennial species (H. tuberosus, H. rigidus, H. grosseserratus, H. maximiliani, and H. nuttallii), while the annual species were very susceptible (Fick et al., 1974).

The "group immunity" cultivars developed by Pustovoit et al. (1976) from interspecific crosses of H. annuus and H. tuberosus are resistant to downy mildew in Europe, but the identify of resistance genes was unknown. Two hybrids were derived from this material and released as 'Progress' and 'Novinka' (Pustovoit et al., 1976). Recently, Miller and Gulya (1987) showed that these two open-pollinated cultivars had the PL_5 gene imparting resistance to Races 2 and 3 of downy mildew.

Verticillium dahliae (Verticillium wilt) is an important wilt disease in sunflower. Resistance to Verticillium wilt is widespread in wild sunflower (Hoes et al., 1973). Helianthus annuus collected from Manitoba, Saskatchewan, and North Dakota generally are less resistant to V. dahliae than those collected from more southern latitudes (i.e., Colorado and Kansas). Helianthus petiolaris generally is more resistant than H. annuus. Populations of H. annuus from the Central and Southern Great Plains, coinciding with the hypothetical center of origin of H. annuus and H. petiolaris, appear to have relatively higher levels of resistance to V. dahliae (Hoes et al., 1973). Putt (1964) discovered a source of genetic resistance to Verticillium alboatrum in line CM144, which is derived from an interspecific hybrid. Pustovoit et al. (1976) reported that H. tomentosus is resistant to Verticillium dahliae.

Alternaria helianthi (Alternaria leaf spot) has been reported from sunflower in both the United States and other parts of the world (Sackston, 1981). Morris et al. (1983) tested 21 annual and 37 perennial taxa of Helianthus for resistance to Alternaria helianthi under greenhouse conditions. Only three perennial species (H. hirsutus, H. rigidus ssp. subrhomboideus, and H. tuberosus) were moderately resistant. All

21 annual species tested were very susceptible. Helianthus tuberosus and H. hirsutus show high levels of resistance to Alternaria in Yugoslavia field tests (Dragan Skoric, personal communication). Although some potential sources of resistance to this disease have been identified, it remains to be determined whether the resistance genes can be transferred to cultivated lines with high combining ability.

Erysiphe cichoracearum (powdery mildew) is a widely distributed pathogen of cultivated sunflower in warmer regions of the world (Zimmer and Hoes, 1978). Saliman et al. (1982) found annual species H. debilis ssp. silvestris, H. praecox ssp. praecox, and H. bolanderi and 14 perennial species that were tolerant to powdery mildew in both field and greenhouse tests. Some populations of the perennial species H. grosseserratus and H. maximiliani were resistant, but others were not. These results indicate that several populations of a species may need to be tested to detect genes for resistance in a species. Jan and Chandler (1985) identified a source of resistance to powdery mildew in the wild H. debilis ssp. debilis, which they later transferred to cultivated sunflower. Resistance was incompletely dominant in the F_1 and backcross progenies. This source of disease resistance may enable the production of resistant hybrid cultivars suitable for warm, humid climates.

Rhizopus head rot (Rhizopus spp.) has become an important disease of sunflower in the United States (Rogers et al., 1978). Only four of the 32 native Helianthus species (H. divaricatus, H. hirsutus, H. x laetiflorus, and H. resinosus) evaluated for resistance using the insertion- innoculation method were moderately resistant to R. arrhizus and R. oryzae (Yang et al., 1980). These four species may be good sources of Rhizopus resistance in hybrids; however, interspecific crossing will be required to determine the genes conditioning the resistance (Yang, 1981).

Orbanche cumana (broomrape) is a seed producing root parasite of cultivated sunflower in several countries (Cubero, 1986). Most sources of genetic resistance to this disease were derived from wild H. tuberosus. Pustovoit et al. (1976) have developed several varieties based on H. tuberosus which are resistant to several races of broomrape. Broomrape can be an important disease in some of the drier areas, such as Turkey.

Diaporthe/Phomopsis helianthi (stem canker) is one of the most widely distributed diseases of cultivated sunflower (Skoric, 1985). This disease is now prevalent in Yugoslavia, Romania, Hungary, Brazil, Argentina, and Australia (Mihaljcevic et al., 1980; Skoric, 1985). Skoric (1982) reported a high degree of susceptibility to stem canker in all hybrids and in most varieties. Cuk (1982) reported that a certain number of wild sunflower species were free of Diaporthe/Phomopsis helianthi, and he assumed that these species were potential sources of resistance to the pathogen. Four lines tolerant to stem canker were identified (two based on H. tuberosus, one on H. annuus, and one on H. argophyllus) (Skoric, 1985). Other wild species that are potential sources of resistance are H. debilis and H. rigidus (Cuk, 1982). Hybrids based on the H. tuberosus and H. argophyllus species have been developed and have a high field-tolerance to stem canker (Skoric, 1985). Resistance to stem canker is positively correlated with resistance to Macrophomina phaseoli, Phoma oleracea var. helianthi-tuberosi, and drought (Skoric, 1985). It remains

to be determined whether these resistances are controlled by linked genes.

Sclerotinia sclerotiorum is a major pathogen of sunflower that causes roots, stems, and flower heads to rot or wilt (Zimmer and Hoes, 1978). The pathogen causes root rot and wilt in wild H. annuus (Edmunds, 1964) and crown rot of H. tuberosus (Bisby, 1924). Genetic resistance to Sclerotinia is badly needed in North America (Orellana, 1975) and in Europe. Thompson et al. (1978) found that most of several hundred accessions of wild Helianthus from the United States and Canada were highly susceptible (> 90% infected plants), but some were moderately resistant (70-79% infected) to Sclerotinia under greenhouse conditions. Thompson et al. (1978) felt that annual species (especially H. annuus) may be the best source of resistance; however, Skoric (1987) found the wild annual species to be more sensitive to the Sclerotinia root rot than the wild perennials. Resistance to S. sclerotiorum head rot has been previously reported in some species of wild Helianthus (e.g. H. tuberosus and H. rigidus) and interspecific hybrids (Pustovoit and Gubin, 1974; Pustovoit et al., 1976). A high degree of resistance was not, however, found in accessions of H. tuberosus and H. rigidus evaluated by Thompson et al. (1978). Serieys (1987) reported that stem rot resistance was greater in the wild perennial species H. resinosus and H. rigidus than the in annual species.

The Sclerotinia disease complex appears to be very complicated. Looking to the wild sunflowers for resistance to this disease has not been very successful, and the prospect of finding a single dominant gene for resistance does not look too promising at the moment. Interspecific hybrids tested for Sclerotinia root rot indicate that it is possible to select genotypes with increased tolerance, especially if selection is started in early generations of selfing (Skoric, 1987). One other possibility is that not enough populations of the species that have shown some degree of tolerance have been evaluated.

INSECTS

One problem with incorporating pest resistance into crop plants is that the pests represent living, evolving populations; that makes the plant breeder's job a never-ending battle. New pests can arise from seemingly innocuous species, or old pests can mutate into virulent new biotypes capable of decimating cultivars that once were resistant.

Wild species of Helianthus are also attacked by many species of pests in their natural environments, pests which might also mutate into biotypes which could attack the domesticated sunflower. Such a transition in pest status of a species from scattered wild populations to domesticated monocultures would greatly enhance the immediate biological fitness of the pest species, causing great increases in pest population density.

Intraspecific differences, both within wild H. annuus and other Helianthus species, need to be recognized because not all plants of a species exhibit identical levels of resistance to a given pest. It is important to consider more than one accession of a species in determining whether resistance genes are obtainable from that species. Differences in

expression of resistance may even be seen within genotypes grown in the field and in the greenhouse.

Until recently, very little attention was given to developing insect-resistant sunflower. Exceptions include the report by Pustovoit (1966) of the Soviet Union on apparent resistance to the aphid Brachycaudus helichrysi (Kaltenbach) in cultivated varieties based on H. mollis, H. tomentosus, and H. macrophyllus and resistance to the larva of the "European sunflower moth" Homoeosoma nebulellum (Schiff.) from H. tuberosus var. purpurens. Also, in the United States, Kinman (1966) and Teetes et al. (1971) reported tentative resistance and/or differing degrees of susceptibility to larvae of the sunflower moth H. electellum (Hulst) in H. petiolaris and among commercial varieties. Thompson and Rogers (1977) and Rogers and Thompson (1978a) reported on the potential use and evaluation of Helianthus as a source of resistance to insect pests.

Because wild sunflowers are native to the United States, their associated insect herbivores and their entomophages coevolved in natural communities that often exist in noncultivated fields of sunflower. The long association of wild sunflower and insects in the United States has resulted in hundreds of species of insects that frequent the plants (Cockerell, 1914; Robertson, 1922; and Satterthwait, 1946). Fortunately, most species of insects associated with sunflower are either innocuous or benefactors of the plants, and relationships range from obligatory to purely causal and nonessential (McGregor, 1976). However, pest problems on sunflower have been more acute in the United States than elsewhere due to natural coevolutionary associations of sunflower with its natural herbivores. Species of insects that are recognized as pests of cultivated sunflower in the United States have been summarized by Walker (1936), Beckam and Tippins (1972), Phillips et al. (1973), and Schulz (1978).

Several species of Lepidoptera use sunflower as a host and attack cultivated sunflower (Rogers, 1988). Historically, the sunflower moth has been and continues to be the most damaging insect pest of cultivated sunflower in the United States. Wild species of sunflower have served as sources for moth-resistant germplasm lines (Rogers et al., 1984). These germplasms were based on H. tuberosus and H. petiolaris. The three released germplasms have a phytomelanin layer which becomes extremely dense after its deposition in the pericarp, making the achenes with this characteristic more resistant to mechanical puncture by larvae at an earlier stage of development (Stafford et al., 1984). The hardened pericarp is thought to protect achenes from damage by younger sunflower moth larvae. All species of Helianthus have phytomelanin in pericarps, although the characteristic does not appear to be present in all populations of a species (Seiler et al., 1984).

Wild sunflower species may also offer a natural defense for control of economically important insect pests. Recently, it has been found that sesquiterpene lactones extracted from glandular trichomes on the apex of anthers of H. maximiliani caused a high acute mortality of H. electellum larvae in laboratory bioassays (Gershenzon et al., 1985; Rossiter et al., 1986; Rogers et al., 1987). Chemical extracts from H. annuus florets contain diterpenoid acids that produce a chronic lengthening of larval

stadia but not a high mortality (Waiss et al., 1977; Rossiter et al., 1986).

The curculionids, as a group, have been the most economically damaging insect pests of cultivated sunflower in the Central and Northern Great Plains states of the United States. Weevil larvae attack every part of the plant and often inflict severe tissue destruction and yield loss before their presence is evident. A stem weevil, Cylindrocopturus adspersus (Le Conte), has been a particularly troublesome pest of cultivated sunflower whenever the crop is grown west of the Mississippi River (Phillips et al., 1973; Rogers et al., 1983). Twenty-four species of Helianthus (11 annual and 13 perennial) have significant levels of resistance to C. adspersus female oviposition and/or larval development (Rogers and Seiler, 1985). Hence, the use of host resistance through germplasm derived from wild sunflower species holds considerable promise as an enduring, efficient management strategy for stem weevil control in cultivated sunflower.

The carrot beetle, Bothynus gibbosus (De Geer), is a widely distributed pest of several crops in the United States (Hayes, 1917). It is a potential pest of sunflower grown on sandy soils in the United States. Helianthus petiolaris is among the preferred natural hosts of carrot beetle (Rogers, 1974). No effective control strategies, either cultural or chemical, are presently available. When grown in an infested field at Munday, Texas, severe root damage occurred in H. annuus, H. argophyllus, and H. maximiliani, while the roots of H. hirsutus, H. tuberosus, and H. mollis showed no evidence of injury by the carrot beetle (Rogers and Howell, 1973). Laboratory and greenhouse studies showed that about one-half of the wild Helianthus species are resistant to carrot beetle injury (Rogers et al., 1980; Rogers and Thompson, 1978b). Carrot beetles feeding on the roots of H. arizonensis, H. atrorubens, H. occidentalis ssp. plantagineus, and H. porteri suffered a high acute mortality in no-choice feeding tests (Rogers et al., 1980).

The sunflower beetle, Zygogramma exclamationis (L.), has long been recognized as an important defoliator of sunflower in the Northern Plains of the United States (Criddle, 1922) but not a serious pest in the Southern Plains (Rogers, 1977). In laboratory studies, about one-half of the wild sunflower species exhibited resistance to feeding and/or reproduction by sunflower beetle (Rogers and Thompson, 1978c, 1980). Antibiosis against both larvae and adult beetles was strongly expressed, particularly by the perennial Helianthus species. It appears that incorporation of germplasm from Helianthus species in sunflower has merit as a management strategy for sunflower beetle and other coleopterous pests.

Several other insect species attack cultivated sunflower but are of no great economic concern. Aphids, Masonaphis masoni (Knowlton), and leafhoppers, Empoasca abrupta (Delong.), are sometimes abundant on sunflower. Laboratory and greenhouse studies showed that several species of Helianthus that are cross-compatible with cultivated sunflower are resistant to attack by the aphid and the western potato leafhopper (Rogers and Thompson, 1978d, 1979; Rogers, 1981).

Host resistance in cultivars via incorporation of germplasm from wild Helianthus offers a tremendous potential for long-lasting, economical management of several insect pests of cultivated sunflower. Also, for the short term, it appears that if more were known about the bionomics of pests on the native Helianthus hosts, much could be learned about ecologically sound strategies which could be developed for management of insects on cultivated sunflower (Rogers, 1988).

OIL AND SEED QUALITY

Wild sunflower species possess considerable variability for most economic and agronomic characteristics and seed quality factors (Thompson et al., 1981). Seed oil content of most wild species has been reported (Seiler, 1985a; Thompson et al., 1978; Thompson et al., 1981; Fick et al., 1976; Dorrell and Whalen, 1978). All wild Helianthus accessions that were evaluated had lower (< 41%) oil content than cultivated sunflower (Thompson et al., 1981). Helianthus niveus ssp. canescens has the highest oil content (40.2%) among the wild species, followed by H. niveus ssp. tephrodes (37.4%), H. petiolaris ssp. petiolaris (37.4%), H. petiolaris ssp. fallax (37.7%), and 37% for H. salicifolius (Thompson et al., 1981). Seiler (1985a) reported oil content of 37.9% in H. anomalus and 34.3% in H. deserticola. Oil content of several native populations of H. annuus averaged 22.3 to 30.3% (Seiler, 1983b; Thompson et al., 1981; Fick et al., 1976).

Environmental factors, especially temperature during the period of seed development and maturation, affect both the content and composition of oil in maturing cultivated sunflower seed. The effects of temperature on oil content, however, are variable (Robertson et al., 1979; Canvin, 1965; Harris et al., 1978; Unger and Thompson, 1982). Average oil content of wild H. annuus does not vary significantly when native populations are grown in a uniform environment (Seiler, 1982, 1983b, 1984b, 1986b). Average oil content of H. annuus varies from 23.8% to 25.5%, very close to the average for native populations. Seeds from seven of 22 perennial species grown at a common location had significantly different seed oil content than seed from the original populations (Seiler, 1985b). Very little information is available about effects of environmental factors on oil contents in perennial species. In perennial species, oil content may be under more rigid genetic control or less influenced by environmental factors than in the annuals, at least in the populations evaluated thus far. Path-coefficient analyses indicated that minimum temperature and total solar radiation have the greatest direct effect on seed oil content in the wild annual sunflower, though the influence is minimal (Seiler, 1986b).

Most wild species of Helianthus have been evaluated for fatty acid concentrations (Thompson et al., 1978; Thompson et al., 1981; Dorrell and Whalen, 1978; Knowles et al., 1970; Fernandez-Martinez and Knowles, 1976; Seiler, 1982, 1983b, 1984b, 1985a, 1986b). Concentrations of linoleic acid averaging over 72% have been reported in H. porteri (82.3%), H. simulans (78.0%), H. laevigatus (77.5%), H. heterophyllus (75.5%), H. smithii (75.2%), H. rigidus ssp. subrhomboides (75.1%), H. microcephalus (74.1%), H. cusickii (72.8%), H. debilis ssp. tardiflorus (77.6%), H. exilis (77.8%), H. strumosus (73.7%), and H. radula (76.6%) (Seiler, 1985a; Thompson et al., 1981). Several species had one or more

populations having linoleic acid concentrations above 72%; the range for the entire genus was from 37% in one population of H. argophyllus to 83% in H. porteri.

Oleic acid, another important fatty acid, appears to be quite variable in the wild sunflower species. Species accessions having oleic acid contents of 40% and above are: H. arizonensis (41.1%), H. hirsutus (46.8%), H. silphioides (45.7%), H. atrorubens (53.8%), H. debilis ssp. cucumerifolius (40.1%), H. praecox ssp. runyonii (41.0%), H. annuus (46.3%), H. argophyllus (47.5%), and H. resinosus (44.8%) (Thompson et al., 1981). The lowest oleic acid concentration of the wild species was reported in H. porteri (5.5%) and H. radula (9.3%) (Seiler, 1985a; Thompson et al., 1981).

Seeds of species of many accessions examined for fatty acid concentration were from plants in their original habitats and not from plants in a common location. Environmental conditions in various locations where individual accessions were collected may have influenced oleic and linoleic acid concentrations. Fatty acid concentrations of 22 perennial species (one accession each) from the original habitats were compared with these traits in seeds of respective accessions grown at a single location (Bushland, Texas) to determine environmental influences on fatty acid concentrations (Seiler, 1985a). Oleic acid concentrations were significantly different for 10 of the 22 species examined for the original vs. common environments, while linoleic acid concentrations were significantly different in five of the 22 species. Palmitic acid was not significantly affected by different environments in any species, and stearic acid was significantly affected by different environments in only H. mollis and H. occidentalis ssp. occidentalis. Undoubtedly, some of this variation was caused by differences in environments at different locations. However, the fact that different individual plants within a species accession at a single location have distinctly different levels of oleic and linoleic acids suggests that the variation may also have a genetic component (Knowles et al., 1970).

Multiple regression analysis indicated that day of year, total solar radiation, and maximum temperature significantly influenced linoleic acid in H. annuus, whereas oleic acid was influenced only by the latter two factors (Seiler, 1983b). Path-coefficient analysis indicated that minimum temperature and solar radiation had the primary influences on oleic acid concentration in wild annual sunflower and cultivated sunflower, with maximum temperature being less important (Seiler, 1986b). Linoleic acid concentration was primarily influenced (negatively) by minimum temperature and solar radiation in wild annual and cultivated sunflower, as indicated by path-coefficient analysis. The analysis also indicated that wild annual sunflower reacts similarly to cultivated sunflower to the environmental factors examined.

Interrelationships among fatty acid concentrations should also be a consideration in sunflower breeding programs. Wild annual sunflower grown at a single location showed a significant positive association between palmitic and stearic acid ($r = 0.561$) (Seiler, 1985b). This also was seen in the cultivated hybrid '894'. There is a strong negative association between oleic and linoleic acid in the wild annual sunflower ($r = -0.989$) (Seiler, 1985b). Both fatty acids showed some association with stearic

acid, so the selection for either may affect the level of stearic acid. The association of palmitic acid with linoleic and oleic acid was weak (low). Hence, breeding or selection for these acids should not affect palmitic acid. However, moderate positive association between palmitic and stearic acid indicates that selection for palmitic acid may affect the level of stearic acid and vice versa.

The wild species may have the potential of improving the chemical composition of cultivated sunflower seed (Laferriere, 1986). Protein is one factor of interest if the seeds are to be used for human or livestock consumption. Defatted kernels of H. rigidus, for example, are reported to contain 71% protein (Georgieva-Todorova and Heistova, 1975). In commercial sunflower meal, protein content is approximately 44% (dehulled) and 28% (whole seeds) (Doty, 1978). Pustovoit and Krasnokutskaya (1975) reported protein content ranging from 29 to 35% in 39 wild species of Helianthus. Seiler (1984d) reported that crude protein in whole seeds ranged from 34.7% in H. nuttallii ssp. nuttallii to 6.5% in H. pumilus. Seed crude protein was higher in all except three of the wild species (H. pumilus, H. laciniatus, and H. ciliaris) than either the wild annual (H. annuus) (18.0%) or cultivated sunflower (18.9%). In other wild Helianthus species (6 perennials and 19 annuals), whole seed crude protein varied from 13.7% in H. neglectus to 30.5% in H. porteri (Seiler, 1986c). The crude protein of whole seeds of annual species is generally lower than that of perennial species (Seiler, 1984d). Laferriere (1986) suggested that it is possible that the high protein content of seeds of wild species may be due to their smaller size. Sufficient variability exists in the wild Helianthus species to be useful in breeding programs whose objective is to increase protein concentration in the seed. In any breeding work for increased protein content, it would be necessary to maintain or improve the balance of essential amino acids. In the long run, this may be more crucial than the percentage of crude protein.

Chlorogenic acid, which is present in both hulls and meal of sunflower, is primarily responsible for the green discoloration that may develop in sunflower meal (Singleton and Kratzer, 1969). While not toxic, chlorogenic acid does make the isolation and preparation of colorless meal difficult. Breeding for an absence or lower levels of the acid could result in eliminating the need for costly extractions of the chlorogenic acid. Dorrell (1976) evaluated 42 wild H. annuus populations for chlorogenic acid and found a range from 1.5% to 2.7%, which, on the average, is somewhat lower than the cultivated types. The variability in chlorogenic acid in the wild species is encouraging, but many more species and populations will have to be evaluated.

AGRONOMIC TRAITS

A wide variety of agronomic traits has been examined among wild Helianthus species for possible use in improving the hardiness and productivity of cultivated sunflower (Laferriere, 1986). Each wild species population has the potential of contributing germplasm that is different from any other source. The wild H. annuus in different habitats frequently vary in height, anthesis date, and other characteristics; but it is not always clear whether these differences reflect genetic effects or phenotypic variations due to environments. Growing the accessions from diverse habitats in a uniform environment enables one to determine genotypic and

environmental effects of morphological and agronomic charcteristics that are potentially useful.

Over 200 populations of seven wild species grown at Fargo, North Dakota, exhibited a wide range in height and flowering time, both within and between species (Fick et al., 1974). These populations also exhibited significant differences in seedling vigor, germination, branching, seed shattering, and frost tolerance. Beard and Williams (1982) used cluster analysis technique to determine distinct groups among 177 accessions of wild H. annuus containing similar types under common environmental conditions at Davis, California. If cluster analyses are meaningful, one or two accessions in each group could be used as parental material to determine the possible germplasm potential of each population. Cluster analysis divided the 177 accessions into 10 groups containing agronomic characteristics of anthesis date, vigor rating (seedling), seed length, weight of 200 seed, oil content, and linoleic acid content. Accessions with similar flowering dates were grouped together, allowing the comparison of other agronomic characteristics. For example, two groups which flowered at the same time but had different linoleic acid concentrations indicates that fatty acid differences are due to genetic variability of accessions rather than environmental control and, therefore, potentially useful in a breeding program.

Agronomic and morphological characteristics of 90 populations of wild H. annuus were evaluated at Bushland, Texas (Seiler, 1984b). Agronomic and morphological characteristics examined were weight per 200 seeds, test weight; flowering date; flowering period; seed oil concentration; fatty acid concentrations; head and disk diameter; ray petal length, width, and number; bract length, width, and number; leaf length and width; and plant height. Considerable natural (genetic) variation existed when wild H. annuus from widely separated geographical populations were grown in a common location. Of the nine agronomic characteristics examined, variations in test weight, flowering date, flowering period, seed oil concentration, and fatty acid composition of oil indicate they are potentially useful in hybrid sunflower breeding programs. Potentially useful morphological characteristics are leaf size, which was comparable in some accessions to hybrid '894', and the short plant height of some populations for reduced height hybrids in cultivated sunflower.

Helianthus exilis is a potential genetic resource in terms of morphological and ecological features and fatty acid composition of oil (Jain et al., 1977). The serpentine sunflower (H. exilis) inhabits moist, serpentine soils of the inner coastal range in California. The potential value of H. exilis is the higher linoleic acid content in oil and germination polymorphism related to the response to red/far-red light and low temperature; that may be useful in eliminating dormancy problems.

Several wild species of Helianthus are native to salt-impacted habitats and might possess genes for salt tolerance. Chandler and Jan (1984) evaluated three wild Helianthus species for salt tolerance: H. paradoxus, H. debilis, and a H. annuus population native to salty desert areas. Helianthus debilis tolerated a salt concentration about the same as cultivated sunflower, dying at a NaCl concentration of 250 to 400 mM. The wild ecotype of H. annuus had a higher tolerance, with some plants surviving at 800 mM. Helianthus paradoxus was highly salt tolerant, with

some plants surviving at 1,300 mM. Salt tolerance was a dominant trait, with hybrids between H. paradoxus and cultivated H. annuus doing as well as the wild parent.

CONCLUSIONS

The genus Helianthus is composed of 49 species and 19 subspecies with 12 annual and 37 perennial species. These diverse species represent a considerable genetic variability which can be utilized for the improvement of cultivated sunflower. The taxonomy of Helianthus is somewhat confusing due to the complicated natural interspecific hybridization and different ploidy levels of several species. A germplasm collection of 2,000 accessions, mostly annuals, has been assembled. Interspecific hybridization has become important as a means of introducing genetic variability into the cultivated sunflowers. This has been facilitated by the use of embryo culture and chromosome doubling using colchicine to increase fertility. The wild species continue to serve as a source of CMS for cultivated sunflower. Molecular techniques of restriction endonucleases of mitochondrial DNA can be used to differentiate CMS sources. Considerable variability has been observed in the wild species for physiological characteristics of transpiration, diffusive resistance, leaf area, dry matter partitioning, and leaf water osmotic and turgor potential. The greatest impact the wild species has made on cultivated sunflower has been in the area of genes for disease resistance and, to a lesser extent, insects. A recent discovery of genes for high tolerance to the disease Diaporthe/Phomopsis helianthi is an excellent example. Considerable variability has been reported in oil content and fatty acid concentrations in the wild species as well as agronomic and morphologic traits of plant height, days to flowering, and tolerances to stress, especially salt.

The genus Helianthus, besides constituting the basic genetic stock from which cultivated sunflower originated, continues to contribute specific characteristics for cultivated sunflower improvement; and there still remains much potential to be exploited. The continued need for additional genes to improve cultivated sunflower emphasizes the necessity to collect, maintain, evaluate, and enhance wild Helianthus germplasm for future utilization for cultivated sunflower.

REFERENCES

Alexander, P. 1969. Differential staining of aborted and nonaborted pollen. Stain Technol. 44:117-122.

Anashchenko, A. V. 1974. On the taxonomy of the Genus Helianthus L. Bot. Zhurn. 59:1472-1481.

Anashchenko, A. V. 1977. Some economically useful donors in the sunflower collection. Trudy Pe Prinkladnei Botanike Genetike i Selektsii 59(3):130-136 (Leningrad).

Anashchenko, A. V. 1979. Phylogenetic relations in the genus Helianthus L. Bull. Appl. Bot. Genet., PL Breed. 64(2):146-156.

Anashchenko, A. V. 1982. Centers of genome origin and centers of the greatest diversity of Heliantahus species and forms. Vest. Skh. Nauki (Mosc) 6:47-53.

Arthur, J. C., and G. B. Cummins. 1962. Manual of the rusts in the United States and Canada. Hafner, New York. 438 pp.

Beard, B. H., and W. A. Williams. 1982. Cluster analysis of wild Helianthus annuus accessions. In Proc. 10th Int. Sunflower Conf. (Surfer's Paradise, Australia). Int. Sunflower Assoc., Toowoomba, Australia. pp. 207-209.

Beckam, C. M., and H. H. Tippins. 1972. Observations on sunflower insects. J. Econ. Entomol. 65:865-866.

Bisby, G. R. 1924. The Sclerotinia disease of sunflowers and other plants. Sci. Agric. 4:381-384.

Blanchet, R., and N. Gelfi. 1980. Physiologic vegetale-caracteres xerophytiques de quelques especes d'Helianthus susceptibles d'etre utilises pour ameliorer l-adaptation aux conditions seches du tournesol cultive (Helianthus annuus L.). C. R. Acad. S.C. Paris T. 290 Serie D. pp. 279-282.

Blum, A. 1984. Breeding crop varieties for stress environments. CRC Critical Reviews in Plant Sci. 2(3):199-238.

Brown, G. G., H. Bussey, and L. S. Desrosiers. 1986. Analysis of mitochondrial DNA, chloroplast DNA, and double-stranded RNA in fertile and cytoplasmic male-sterile sunflower (Helianthus annuus). Can. J. Genet. Cytol. 28:121-129.

Canvin, D. T. 1965. The effect of temperature on the oil content and fatty acid composition of oils from several oil seed crops. Can. J. Bot. 43:63-69.

Chandler, J. M., and B. H. Beard. 1978. Sunflower interspecific hybridization using embryo culture. In Proc. 8th Int. Sunflower Conf. (Minneapolis, Minnesota). Int. Sunflower Assoc., Toowoomba, Australia. pp. 510-515.

Chandler, J. M., and B. H. Beard. 1983. Embryo culture of Helianthus hybrids. Crop Sci. 23:1004-1007.

Chandler, J. M., and C. C. Jan. 1984. Identification of salt-tolerant germplasm sources in the Helianthus species. Agron. Abstr. p. 61. Am. Soc. Agron., Madison, Wisconsin.

Chandler, J. M., and C. C. Jan. 1985. Comparison of germination techniques for wild Helianthus seeds. Crop Sci. 25:356-358.

Chandler, J. M., C. C. Jan, and B. H. Beard. 1986. Chromosomal differentiation among the annual Helianthus species. Syst. Bot. pp. 354-371.

Cockerell, T. D. A. 1914. The entomology of Helianthus. Can. Entomol. 47:191-196.

Cockerell, T. D. A. 1929. Hybrid sunflowers. Am. Nat. 63:470-475.

Criddle, N. 1922. Beetles injurious to sunflowers in Manitoba. Can. Entomol. 54:97-99.

Crouzillat, D., P. Leroy, A. Perrault, and G. Ledoigt. 1987. Molecular analysis of the mitochondrial genome of Helianthus annuus in relation to cytoplasmic male sterility and phylogeny. Theor. Appl. Genet. 74:773-780.

Cubero, J. I. 1986. Breeding for resistance in Orobanche and Striga: A review. In S. J. Borg (ed.) Biology and Control of Orobanche. Wageningen, Netherlands. pp. 127-139.

Cuk, L. 1982. The uses of wild species in sunflower breeding. Uljarstvo 1:23-27 (Belegrade, English Summary).

DeMichele, D. W., and P. J. H. Sharpe. 1974. A porometric analysis of the anatomy and physiology of the stomata. Agric. Meteorol. 14:229-241.

Dewey, D. R. 1980. Some applications and misapplications of induced polyploidy to plant breeding. In W. Lewis (ed.) Polyploidy: Biological Relevance. Plenum Publ. Corp., New York. pp. 445-470.

Dhesi, J. S., and R. G. Saini. 1973. Cytology of induced polyploids in sunflower. The Nucleus 16:49-52.

Dorrell, D. G. 1976. Chlorogenic acid content of meal from cultivated and wild sunflowers. Crop Sci. 16:422-424.

Dorrell, D. G., and E. D. P. Whalen. 1978. Chemical and morphological characteristics of seeds of some sunflower species. Crop Sci. 18:969-971.

Doty, H. O. 1978. Future of sunflower as an economic crop in North America and the world. In J. F. Carter (ed.) Sunflower Science and Technology, Agronomy Monograph No. 19. Am. Soc. Agron., Madison, Wisconsin. pp. 457-488.

Downes, R. W., and D. R. Marshall. 1983. Colchicine-induced variants in sunflower. Euphytica 32:757-766.

Edmunds, L. K. 1964. Combined relation of plant maturity, temperature, and soil moisture to charcoal stalk rot development in grain sorghum. Phytopathol. 54:514-517.

Enns, H., D. G. Dorrell, S. A. Hoes, and W. O. Chubb. 1970. Sunflower research, a progress report. In Proc. 4th Int. Sunflower Conf. (Memphis, Tennessee). Int. Sunflower Assoc., Toowoomba, Australia. pp. 162-167.

Fernandez-Martinez, J., and P. F. Knowles. 1976. Variability in fatty acid composition of the seed oil of Helianthus species. In Proc. 7th Int. Sunflower Conf. (Krasnodar, U.S.S.R.). Int. Sunflower Assoc., Toowoomba, Australia. pp. 401-409.

Fick, G. N., and G. E. Auwarter. 1982. Resistance to a new race of sunflower downy mildew. In Proc. 10th Int. Sunflower Conf. (Surfer's Paradise, Australia). Int. Sunflower Assoc., Toowoomba, Australia. pp. 175-177.

Fick, G. N., D. E. Zimmer, J. Dominguez-Gimenez, and D. A. Rehder. 1974. Fertility restoration and variability for plant and seed characteristics in wild sunflower. In Proc. 6th Int. Sunflower Conf. (Bucharest, Romania). Int. Sunflower Assoc., Toowoomba, Australia. pp. 333-338.

Fick, G. N., D. E. Zimmer, and T. E. Thompson. 1976. Wild species of Helianthus as a source of variability in sunflower breeding. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota. pp. 4-5.

Gedge, D. L. 1985. Our experience with 'Heiser' cytoplasm. In Proc. Sunflower Research Workshop. National Sunflower Association, Bismarck, North Dakota. p. 12.

Georgieva-Todorova, J. 1984. Interspecific hybridization in the genus Helianthus L. Z. Pflanzenzucht 93:265-279.

Georgieva-Todorova, J. 1985. Hybridization between Helianthus annuus diploid equals 34 and Helianthus resinosus diploid equals 102. Genet. Sel. 18:3-11.

Georgieva-Todorova, J., and A. Hristova. 1975. Studies on several wild-growing Helianthus species. C. R. Acad. Agricole G. Dimitrov 8(4):51-55.

Gershenzon, J., M. C. Rossiter, T. J. Mabry, C. E. Rogers, M. H. Blast, and T. L. Hopkins. 1985. Insect antifeldant terpenoids in wild sunflower -- A possible source of resistance to the sunflower moth. In P. A. Hedin (ed.) Bioregulators for Pest Control. ACS Symp. Series No. 276. Am. Chem. Soc. pp. 433-466.

Gupta, S. K., and S. K. Roy. 1979. Colchiploid sunflower. Sci. and Culture 46:294-295.

Harris, H. C., J. R. McWilliam, and W. K. Mason. 1978. Influence of temperature on oil content and composition of sunflower seed. J. Agric. Res. 29:1203-1212.

Hayes, W. P. 1917. Studies on the life history of Ligyrus gibbosus. J. Econ. Entomol. 10:253-260.

Heiser, C. B. 1976. The sunflower. University of Oklahoma Press, Norman, Oklahoma.

Heiser, C. B. 1982. Registration of Indiana-1 CMS sunflower germplasm. Crop Sci. 22:1089.

Heiser, C. B. 1985. Cytoplasmic male sterility in sunflower. In Proc. 11th Int. Sunflower Conf. (Mar del Plata, Argentina). Int. Sunflower Assoc., Toowoomba, Australia. pp. 547-548.

Heiser, C. B., and D. M. Smith. 1955. New chromosome numbers in Helianthus and related genera. Proc. Ind. Acad. Sci. 64:250-253.

Heiser, C. B., and D. M. Smith. 1964. Species crosses in Helianthus: II. Polyploid species. Rhodora 66:344-358.

Heiser, C. B., D. M. Smith, S. B. Clevenger, and W. C. Martin. 1969. The North American sunflowers (Helianthus). Mem. Torrey Bot. Club 22(3):1-218.

Hennessy, C. M. R., and W. E. Sackston. 1972. Studies on sunflower rust. X. Specialization of Puccinia helianthi on wild sunflowers in Texas. Can. J. Bot. 50:1871-1877.

Heyraud, F., P. Serror, M. Kuntz, A. Steinmetz, and P. Heizmann. 1987. Physical map and gene localization on sunflower (Helianthus annuus) chloroplast DNA: Evidence for an inversion of a 23.5-kbp segment in the large single copy region. Plant Mol. Biol. 9:485-496.

Hoes, J. A., E. D. Putt, and H. Enns. 1973. Resistance to Verticillium wilt in collections of wild Helianthus in North America. Phytopathol. 63:1517-1520.

International Board for Plant Genetic Resources. 1984. Report of a working group on sunflower (first meeting). Int. Board for Plant Genetic Resources, Rome, Italy. 13 pp.

International Board for Plant Genetic Resources. 1985. Report of a working group on sunflower (second meeting). Int. Board for Plant Genetic Resources, Rome, Italy. 18 pp.

Jackson, R. C., and B. G. Murray. 1983. Colchicine induced quadrivalent formations in Helianthus: Evidence of ancient polyploidy. Theor. Appl. Genet. 64:219-222.

Jain, S. K., A. M. Olivieri, and J. Fernandez-Martinez. 1977. Serpentine sunflower Helianthus exilis as a genetic resource. Crop Sci. 17:477-497.

Jan, C. C., and J. M. Chandler. 1985. Transfer of powdery mildew resistance from Helianthus debilis Nutt. to cultivated sunflower. Crop Sci. 25:664-666.

Jan, Ç. C., and J. M. Chandler. 1988. Interspecific hybrids and amphiploids of Helianthus annuus x H. bolanderi. Crop Sci. 58 (In press).

Jan, C. C., J. M. Chandler, and B. H. Beard. 1983. A practical method of chromosome doubling in sunflower. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota. p. 12.

Kinman, M. L. 1966. Tentative resistance to the larvae of Homoeosoma electellum in Helianthus. In Proc. 2nd Int. Sunflower Conf. (Morden, Canada). Int. Sunflower Assoc., Toowoomba, Australia. pp. 72-73.

Kinman, M. L. 1970. New development in the USDA and State Experiment Station sunflower breeding programs. In Proc. 4th Int. Sunflower Conf. (Memphis, Tennessee). Int. Sunflower Assoc., Toowoomba, Australia. pp. 181-183.

Knowles, P. F., S. R. Temple, and F. Stolp. 1970. Variability in the fatty acid composition of sunflower seed oil. In Proc. 4th Int. Sunflower Conf. (Memphis, Tennessee). Int. Sunflower Assoc., Toowoomba, Australia. pp. 215-218.

Laferriere, J. E. 1986. Interspecific hybridization in sunflowers: An illustration of the importance of wild genetic resources in plant breeding. Outlook Agric. 15(3):104-109.

Leclercq, P. 1969. Une sterilite male cytoplasmique chez le tournesol. Ann. Amelior Plantes 19:99-106.

Leclercq, P. 1971. La sterile male cytoplasmique du tournesol. I. Premieres estudes sun la restauration de la fertilite. Ann. Amel. Plantes 21:45-54.

Leclercq, P. 1983. Estude de divers cas de sterilite male cytoplasmique chez le tournesol. Agronomie 3:185-187.

Leclercq, P. 1984. Identification de genes de restauration de fertilie sur cytoplasms sterilisants chez le tournesol. Agronomie 4:573-576.

Leroy, P. 1985. Study of the mitochondrial DNA of sunflowers: Comparison between male sterile and male fertile cytoplasms. In Proc. 11th Int. Sunflower Conf. (Mar del Plata, Argentina). Int. Sunflower Assoc., Toowoomba, Australia. pp. 553-558.

Leroy, P., S. Bazetoux, F. Quetier, J. Delbut, and A. Berville. 1985. A comparison between mitochondrial DNA of an isogenic male-sterile (S) and male-fertile (F) couple (HA89) of sunflower. Curr. Genet. 9:245-251.

Levings, C. S., and D. R. Pring. 1976. Restriction endonuclear analysis of mitochondrial DNA from normal and Texas cytoplasmic male sterile maize. Sci. 193:158-160.

Linnaeus, C. L. 1753. Species Plantarum. Holmiae. 1,200 pp.

McGregor, S. E. 1976. Insect pollination of cultivated crop plants. Agric. Handbook 496. USDA, Agricultural Research Service, Washington, DC. 411 pp.

Mihaljcevic, M., M. Petrov, M. Muntanola, and C. Vetkovic. 1980. Phomopsis sp., a new parasite of sunflower in Yugoslavia. Savremena Poljoprivreda 28:531-539.

Mileyeva, T. V., and A. V. Anashchenko. 1976. Reliable CMS and R_f source. In Proc. 7th Int. Sunflower Conf. (Krasnodar, U.S.S.R.). Int. Sunflower Assoc., Toowoomba, Australia. pp. 358-360.

Miller, J. F. 1987. Sunflower. In W. R. Fehr (ed.) Principles of Cultivar Development. II. Crop Species. Macmillan, New York. pp. 626-668.

Miller, J. F., and T. J. Gulya. 1987. Inheritance of resistance to Race 3 downy mildew in sunflower. Crop Sci. 27:210-211.

Morizet, J., P. Cruiziot, J. Chatenoud, P. Picot, and P. Leclercq. 1984. Improvement of drought resistance in sunflower by interspecific crossing with a wild species Helianthus argophyllus: Methodology and first results. Agronomie 4(6):577-585.

Morris, J. B., S. M. Yang, and L. Wilson. 1983. Reaction of Helianthus species to Alternaria helianthi. Plant Dis. 67:539-540.

Nabhan, G. B., and K. L. Reichhardt. 1983. Hopi protection of Helianthus anomalus, a rare sunflower. Southwest. Nat. 28:231-235.

Orellana, G. 1975. Photoperiod influence on susceptibility of sunflower to Sclerotinia stalk rot. Phytopathol. 65:1293-1298.

Phillips, R. L., N. M. Randolph, and G. L. Teetes. 1973. Seasonal abundance and nature of damage of insects attacking cultivated sunflowers. Texas Agric. Exp. Stn. Misc. Publ. MP-1116. Texas A&M Univ., College Station, Texas. 7 pp.

Pustovoit, G. V. 1966. Distant interspecific hybridization of sunflowers in the U.S.S.R. In Proc. 2nd Int. Sunflower Conf. (Morden, Canada). Int. Sunflower Assoc., Toowoomba, Australia. pp. 82-100.

Pustovoit, G. V. 1969. Breeding sunflower for group immunity by the method of interspecific hybridization. Agric. Biol. 4:803-812.

Pustovoit, G. V., and I. A. Gubin. 1974. Results and prospects in sunflower breeding for group immunity by using the interspecific hybridization method. In Proc. 6th Int. Sunflower Conf. (Bucharest, Romania). Int. Sunflower Assoc., Toowoomba, Australia. pp. 373-381.

Pustovoit, G. V., V. P. Ilatovsky, and E. L. Slyusar. 1976. Results and prospects of sunflower breeding for group immunity by interspecific hybridization. In Proc. 7th Int. Sunflower Conf. (Krasnodar, U.S.S.R.). Int. Sunflower Assoc., Toowoomba, Australia. pp. 193-204.

Pustovoit, G. V., and O. N. Krasnokutskaya. 1975. Protein content of sunflower meal. In Immunitet S.-Kh. rast. k. bolesnyam. vreditelyam Moskova.

Putt, E. D. 1964. Breeding behavior of resistance to leaf mottle on Verticillium in sunflower. Crop Sci. 4:177-179.

Putt, E. D., and W. E. Sackston. 1963. Studies on sunflower rust. IV. Two genes, R_1 and R_2, for resistance in the host. Can. J. Plant Sci. 43:490-496.

Robertson, C. 1922. The sunflower and its insect visitors. Ecology 3:17-21.

Robertson, J. A., W. H. Morrison, and R. L. Wilson. 1979. Effects of planting location and temperature on the oil content and fatty acid composition of sunflower seeds. USDA Agricultural Research Results. Southern Series No. 3.

Robinson, A. 1979. Studies in the HELIANTHEAES (Asteraceae). XVIII. Phytologia 44:257-259.

Rogers, C. E. 1974. Bionomics of the carrot beetle in the Texas Rolling Plains. Environ. Entomol. 3:969-974.

Rogers, C. E. 1977. Bionomics of the sunflower beetle. Environ. Entomol. 6:466-468.

Rogers, C. E. 1981. Resistance of sunflower species to the western potato leafhopper. Environ. Entomol. 10:697-700.

Rogers, C. E. 1988. Entomology of indigenous Helianthus species and cultivated sunflower. In M. K. Harris and C. E. Rogers (eds.) The Entomology of Indigenous and Naturalized Systems in Agriculture: Case History Perspective. Westview Press, Boulder, CO (In Press).

Rossiter, M. C., J. Gershenzon, and T. J. Mabry. 1986. Behavioral and growth responses of specialist herbivore Homoeosoma electellum to major terpenoid of its host, Helianthus spp. J. Chem. Ecol. 12:1505-1521.

Sackston, W. E. 1981. The sunflower crop and disease: Progress, problems, and prospects. Plant Dis. 65:643-648.

Saliman, J., S. M. Yang, and L. Wilson. 1982. Reaction of Helianthus species to Erysiphe cichoracearum. Plant Dis. 66:572-573.

Satterthwait, A. F. 1946. Sunflower seed weevils and their control. J. Econ. Entomol. 39:787-792.

Schilling, E. E., and C. B. Heiser. 1981. Infrageneric classification of Helianthus (Compositae). Taxon. 30:393-403.

Schulz, J. T. 1978. Insect pests. In J. F. Carter (ed.) Sunflower Science and Technology, Agronomy Monograph No. 19. Am. Soc. Agron., Madison, Wisconsin. pp. 169-223.

Seiler, G. J. 1982. Variation in oil and oil quality of wild annual sunflower (Helianthus annuus L.) populations in a uniform environment. In Proc. 10th Int. Sunflower Conf. (Surfer's Paradise, Australia). Int. Sunflower Assoc., Toowoomba, Australia. pp. 212-215.

Seiler, G. J. 1983a. Evaluation of wild sunflower species for potential drought tolerance. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota. p. 13.

Seiler, G. J. 1983b. Effect of genotype, flowering date, and environment on oil content and oil quality of wild sunflower seed. Crop Sci. 23:1063-1068.

Seiler, G. J. 1984a. Wild sunflower species collection and utilization in germplasm development. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota. p. 10.

Seiler, G. J. 1984b. Variation in agronomic and morphological characteristics of several populations of wild annual sunflower (Helianthus annuus L.). Helia 7:29-32.

Seiler, G. J. 1984c. Evaluation of self-compatibility and sibbing of annual and perennial sunflowers. Agron. Abstr. p. 87. Am. Soc. Agron., Madison, Wisconsin.

Seiler, G. J. 1984d. Protein and mineral concentration of selected wild sunflower species. Agron. J. 76:289-294.

Seiler, G. J. 1985a. Evaluation of seeds of sunflower species for several chemical and morphological characteristics. Crop Sci. 25:183-187.

Rogers, C. E., J. Gershenzon, H. Ohno, T. J. Mabry, R. D. Stipanovic, and G. L. Kreitner. 1987. Terpenes of wild sunflower (Helianthus): An effective mechanism against seed predation by larvae of the sunflower moth, Homoeosoma electellum (Hulst). Environ. Entomol. 16:586-592.

Rogers, C. E., and G. R. Howell. 1973. Behavior of the carrot beetle on native and treated commercial sunflower. Texas Agric. Exp. Stn. Prog. Rep. PR-3249. Texas A&M Univ., College Station, Texas. 7 pp.

Rogers, C. E., and G. J. Seiler. 1985. Sunflower (Helianthus) resistance to a stem weevil Cylindrocopturus adspersus. Environ. Entomol. 14:624-628.

Rogers, C. E., and T. E. Thompson. 1978a. Evaluation of Helianthus for resistance to insect pests. In Proc. 8th Int. Sunflower Conf. (Minneapolis, Minnesota). Int. Sunflower Assoc., Toowoomba, Australia. pp. 320-327.

Rogers, C. E., and T. E. Thompson. 1978b. Helianthus resistance to the carrot beetle. J. Econ. Entomol. 71:760-761.

Rogers, C. E., and T. E. Thompson. 1978c. Resistance in wild Helianthus to the sunflower beetle. J. Econ. Entomol. 71:622-623.

Rogers, C. E., and T. E. Thompson. 1978d. Resistance of wild Helianthus species to an aphid, Masonaphis masoni. J. Econ. Entomol. 71:221-222.

Rogers, C. E., and T. E. Thompson. 1979. Helianthus resistance to Masonaphis masoni. Southwest. Entomol. 4:321-324.

Rogers, C. E., and T. E. Thompson. 1980. Helianthus resistance to the sunflower beetle. J. Kansas Entomol. Soc. 53:727-730.

Rogers, C. E., T. E. Thompson, and G. J. Seiler. 1982. Sunflower Species of the United States. National Sunflower Assoc., Bismarck, ND. 75 pp.

Rogers, C. E., T. E. Thompson, and G. J. Seiler. 1984. Registration of three Helianthus germplasms for resistance to the sunflower moth. Crop Sci. 24:212-213.

Rogers, C. E., T. E. Thompson, and M. J. Wellik. 1980. Survival of Bothynus gibbosus on Helianthus species. J. Kansas Entomol. Soc. 53:490-494.

Rogers, C. E., T. E. Thompson, and D. E. Zimmer. 1978. Rhizopus head rot of sunflower: Etiology and severity in the Southern Plains. Plant Dis. Reptr. 62:769-771.

Rogers, C. E., P. W. Unger, T. L. Archer, and E. D. Bynum. 1983. Management of a stem weevil Cylindrocopturus adspersus in sunflower in the Southern Great Plains. J. Econ. Entomol. 76:952-956.

Seiler, G. J. 1985b. Interrelation of fatty acids in oil of wild annual sunflower (Helianthus annuus L.). In Proc. 11th Int. Sunflower Conf. (Mar del Plata, Argentina). Int. Sunflower Assoc., Toowoomba, Australia. pp. 529-534.

Seiler, G. J. 1986a. Evaluation of responses of interspecific and cultivated sunflower hybrids to water stress. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota. pp. 9-10.

Seiler, G. J. 1986b. Analysis of the relationships of environmental factors with seed oil and fatty acid concentrations of wild annual sunflower. Field Crops Res. 15:57-72.

Seiler, G. J. 1986c. Forage quality of selected wild sunflower species. Agron. J. 78:1059-1064.

Seiler, G. J. 1987a. Valuable sunflower germplasm collected in the United States. Diversity 12:12.

Seiler, G. J. 1987b. Evaluation of plant water relations of wild perennial sunflower species under irrigation. Helia (In press).

Seiler, G. J. 1988. Wild sunflower species germplasm explorations. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota (In press).

Seiler, G. J., L. Cuk, and C. E. Rogers. 1981. New and interesting distribution records for Helianthus paradoxus Heiser (Asteraceae). Southwest. Nat. 26:431-432.

Seiler, G. J., R. E. Stafford, and C. E. Rogers. 1984. Prevalence of phytomelanin in pericarps of sunflower parental lines and wild species. Crop Sci. 24:1202-1204.

Serieys, H. A. 1987. FAO subnetwork report 1984-1986. In D. Skoric (ed.) Genetic Evaluation and Use of Helianthus Wild Species and Their Use in Breeding Programs. FAO, Rome, Italy. pp. 1-23.

Singleton, V. L., and F. H. Kratzer. 1969. Toxicity and related physiological activity of phenolic substances of plant origin. J. Agric. Food. Chem. 17:497-512.

Skoric, D. 1982. Reaction of Phomopsis spp. and possibilities of sunflower breeding for resistance to the pathogen. Uljarstvo 1:15-22 (Belegrade, English Summary).

Skoric, D. 1985. Sunflower breeding for resistance to Diaporthe/Phomopsis helianthi. Helia 8:21-24.

Skoric, D. 1987. FAO subnetwork report 1984-1986. In D. Skoric (ed.) Genetic Evaluation and Use of Helianthus Wild Species and Their Use in Breeding Programs. FAO, Rome, Italy. pp. 1-17.

Sobrado, M. A., and H. M. Rawson. 1984. Leaf expansion as related to plant water availability in a wild and a cultivated sunflower. Physiol. Plant 60:561-566.

Sobrado, M. A., and N. C. Turner. 1983a. Influence of water deficits on the water relations characteristics and productivity of wild and cultivated sunflowers. Aust. J. Plant Physiol. 10:195-203.

Sobrado, M. A., and N. C. Turner. 1983b. A comparison of the water relations characteristics of Helianthus annuus and Helianthus petiolaris when subjected to water stress. Oecologia 58:309-313.

Sobrado, M. A., and N. C. Turner. 1986. Photosynthesis, dry matter accumulation, and distribution in the wild sunflower Helianthus petiolaris and the cultivated sunflower Helianthus annuus as influenced by water deficits. Oecologia 69:181-187.

Stafford, R. E., C. E. Rogers, and G. J. Seiler. 1984. Pericarp resistance to mechanical puncture in sunflower achenes. Crop Sci. 24:891-894.

Tatum, L. A. 1971. The southern corn leaf blight epidemic. Sci. 171:1113-1116.

Teetes, G. L., M. L. Kinman, and N. M. Randolph. 1971. Differences in susceptibility of certain sunflower varieties and hybrids to the sunflower moth. J. Econ. Entomol. 64:1285-1287.

Thompson, T. E., and C. E. Rogers. 1977. Wild Helianthus as a potential source of insect resistance. In Proc. Sunflower Research Workshop. National Sunflower Assoc., Bismarck, North Dakota. pp. 7-8.

Thompson, T. E., C. E. Rogers, D. C. Zimmerman, H. C. Huang, E. D. P. Whalen, and J. F. Miller. 1978. Evaluation of Helianthus species for disease resistance and oil content and quality. In Proc. 8th Int. Sunflower Conf. (Minneapolis, Minnesota). Int. Sunflower Assoc., Toowoomba, Australia. pp. 501-509.

Thompson, T. E., D. C. Zimmerman, and C. E. Rogers. 1981. Wild Helianthus as a genetic resource. Field Crops Res. 4:333-343.

Tsvetkova, F. 1974. A study of hybridization between Helianthus scaberrimus and H. annuus. Abstr. Bulg. Sci. Lit. A19(3):Abstr. 623.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. In H. Mussell and R. C. Staples (eds.) Stress Physiology in Crop Plants. Wiley-Intersceince, New York. pp. 343-372.

Turner, N. C. 1981. Designing crops for dryland Australia: Can the deserts help us? J. Aust. Inst. Agric. Sci. 47:29-34.

Unger, P. W., and T. E. Thompson. 1982. Planting date effects on sunflower head and seed development. Agron. J. 74:389-395.

Vear, F. 1974. Studies on resistance to downy mildew in sunflower (H. annuus L.). In Proc. 6th Int. Sunflower Conf. (Bucharest, Romania). Int. Sunflower Assoc., Toowoomba, Australia. pp. 297-302.

Vear, F., and P. Leclercq. 1971. Deux nouveaux genes de resistance au mildiou du tournesol. Ann. Amelior Plantes 21:251-255.

Vinitskaya, O. P. 1973. Breeding sunflower for group immunity by interspecific hybridization. Mikol. Fitopatol. 7(1):76-77.

Vranceanu, A. V., M. Iuoras, and F. M. Stoenescu. 1986. A contribution to the diversification of cytoplasmic male sterility sources in sunflower. Helia 6:21-25.

Vranceanu, A. V., N. Pirvu, and F. M. Stoenescu. 1981. New sunflower downy mildew resistance genes and their management. Helia 4:23-27.

Vranceanu, A. V., and F. M. Stoenescu. 1971. Pollen fertility restorer gene from cultivated sunflower. Euphytica 20:536-541.

Vranceanu, A. V., and F. M. Stoenescu. 1973. Restorer-gene sources for pollen fertility in sunflower. An. Inst. Cerct. Pentru. Cereale Plante Teh. Fundulea Ser. C. Amelior Genet. Fiziol. Tech. Agric. 39:253.

Vranceanu, A. V., and F. M. Stoenescu. 1978. Genes for pollen fertility restoration in sunflower. Euphytica 27:617-627.

Waiss, A. C., B. G. Chan, C. A. Elliger, V. H. Garrett, E. C. Carlson, and B. H. Beard. 1977. Larvicidal factors contributing to the host plant resistance against sunflower moth. Naturwissens 64:341.

Walker, F. H. 1936. Observations on sunflower insects in Kansas. J. Kansas Entomol. Soc. 9:16-25.

Watson, E. E. 1929. Contributions to a monograph on the genus Helianthus. Paper Michigan Acad. Sci. 9:305-475.

Whalen, E. D. P. 1976. Sterility problems in interspecific hybridization of Helianthus species. In Proc. Sunflower Workshop. National Sunflower Assoc., Bismarck, North Dakota. pp. 5-6.

Whalen, E. D. P. 1978. Cytology and interspecific hybridization. In J. F. Carter (ed.) Sunflower Science and Technology, Agronomy Monograph Number 19. Am. Soc. Agron., Madison, Wisconsin. pp. 339-369.

Whalen, E. D. P. 1980. A new source of cytoplasmic male sterility in sunflower. Euphytica 29:33-46.

Whalen, E. D. P., and W. Dedio. 1980. Registration of sunflower germplasm composite crosses CMG-1, CMG-2, and CMG-3. Crop Sci. 20:832.

Wolf, S. L., and J. F. Miller. 1985. Fertility restoration response of various sunflower cytoplasms. In Proc. 11th Int. Sunflower Conf. (Mar del Plata, Argentina). Int. Sunflower Assoc., Toowoomba, Australia. pp. 549-552.

Yang, S. M. 1981. Progress in breeding sunflower for resistance to Rhizopus head rot. Proc. EUCARPIA. Prague, Czechoslovakia. pp. 213-226.

Yang, S. M., J. B. Morris, and T. E. Thompson. 1980. Evaluation of Helianthus spp. for resistance to Rhizopus head rot. In Proc. 9th Int. Sunflower Conf (Torremolinos, Spain). Int. Sunflower Association, Toowoomba, Australia. pp. 147-151.

Zimmer, D. E., and G. N. Fick. 1974. Some diseases of sunflower in the United States -- Their occurrence, biology, and control. In Proc. 6th Int. Sunflower Conf. (Bucharest, Romania). Int. Sunflower Association, Toowoomba, Australia. pp. 673-679.

Zimmer, D. E., and J. A. Hoes. 1978. Diseases. In J. F. Carter (ed.) Sunflower Science and Technology, Agronomy Monograph Number 19. Am. Soc. Agron., Madison, Wisconsin. pp. 225-262.

Zimmer, D. E., and M. L. Kinman. 1972. Downy mildew resistance in cultivated sunflower and its inheritance. Crop Sci. 12:749-751.

Zimmer, D. E., and D. A. Rehder. 1976. Rust resistance of wild Helianthus species of the North Central United States. Phytopathol. 66:208-211.

Table 1. Infrageneric classification of Helianthus (after Schilling and Heiser, 1981).

Section	Series	Species
Helianthus	--	*H. annuus L.
		*H. anomalus Blake
		*H. argophyllus T.&G.
		*H. bolanderi Gray
		*H. debilis T.&G.
		*H. deserticola Heiser
		*H. neglectus Heiser
		*H. niveus (Benth) Brandegee
		*H. paradoxus Heiser
		*H. petiolaris Nutt.
		*H. praecox Engelm. & Gray
Agrestes	--	*H. agrestis Pollard
Ciliares	Ciliares	H. arizonensis R. Jackson
		H. ciliaris DC.
		H. laciniatus Gray
Ciliares	Pumili	H. cusickii Gray
		H. gracilentus Gray
		H. pumilus Nutt.
Divaricati	Corona-solis	H. californicus DC.
		H. decapetalus L.
		H. divaricatus L.
		H. eggertii Small
		H. giganteus L.
		H. grosseserratus Martens
		H. hirsutus Raf.
		H. maximiliani Schrader
		H. mollis Lam.
		H. nuttallii T.&G.
		H. resinosus Small
		H. salicifolius Dietr.
		H. schweinitzii T.&G.
		H. strumosus L.
		H. tuberosus L.
Divaricati	Microcephali	H. glaucophyllus Smith
		H. laevigatus T.&G.
		H. microcephalus T.&G.
		H. porteri (A. Gray) Heiser
		H. smithii Heiser
Divaricati	Atrorubentes	H. atrorubens L.
		H. occidentalis Riddell
		H. rigidus (Cass.) Desf.
		H. silphioides Nutt.

Table 1. Cont'd.

Section	Series	Species
Divaricati	Angustifolii	H. angustifolius L. H. carnosus Small H. floridanus Gray x Chapman H. heterophyllus Nutt. H. longifolius Pursh H. radula (Pursh) T.&G. H. simulans (Watson)

* Annual species; others perennial.

Table 2. Habitat data, flowering period, and survival status for Helianthus species (adopted from Rogers et al., 1982).

Species	General habitat	Annual precipitation (cm)	Flowering period	Survival status
*agrestis	damp muck	125	July-Dec.	good
angustifolius	swampy	90-175	Sept.-Oct.	excellent
*annuus	disturbed soil	25-100	July-Sept.	excellent
*anomalus	dry sand	25-50	May-Oct.	good
*argophyllus	sandy	50-100	Aug.-Oct.	excellent
arizonensis	light soils	25-50	June-Aug.	good
atrorubens	dry, open woods	114-127	Aug.-Sept.	excellent
*bolanderi	valleys, rocky soil	25-150	July-Sept.	excellent
californicus	wet, rocky	25-127	July-Oct.	excellent
carnosus	wet sand	127	June-Sept.	excellent
ciliaris	dry to damp sand	50-75	June-Oct.	excellent
cusickii	dry, rocky slopes	25-60	April-Aug.	excellent
*debilis	sandy	64-90	June-Nov.	excellent
cucumerifolius	sandy	125	Jan.-Oct.	good
debilis	sandy	75-115	April-Oct.	excellent
silvestris	sandy	125-140	May-Oct.	excellent
tardiflorus	sandy	125	March-Sept.	good
vestitus	shady woods	60-140	July-Aug.	excellent
decapetalus	sandy	12-25	May-Oct.	good
*deserticola	dry areas	75-140	July-Sept.	excellent
divaricatus	shale barrens	127	Aug.-Sept.	threatened
eggertii	sandy	127	Sept.-Oct.	excellent
floridanus	wet	50-140	Aug.-Oct.	excellent
giganteus	shady	115-152	Aug.-Sept.	excellent
glaucophyllus	dry slopes	25-50	May-Oct.	excellent
gracilentus	moist prairie	50-127	Aug.-Oct.	excellent
grosseserratus	wet sand	127-152	Aug.-Oct.	excellent
heterophyllus	dry, open	63-140	July-Oct.	excellent
hirsutus	dry slopes	25-60	June-Oct.	excellent
laciniatus	shale barrens	90-127	Aug.-Sept.	endangered
laevigatus	dry, rocky soil	127-150	Sept.-Oct.	good
longifolius	prairie	25-127	Sept.-Oct.	excellent
maximiliani	open woods	76-180	Aug.-Sept.	excellent
microcephalus	dry, open sand	90-140	July-Sept.	excellent
mollis		25-50	July-Sept.	excellent
*neglectus	sand	12-50	May-Sept.	excellent
*niveus	sand dune	< 12	All year	excellent
canescens	sand dune	< 12	Sept.-May	excellent
niveus				
tephrodes	wet	12-76	Aug.-Sept.	excellent
nuttallii	sand	50	Aug.-Sept.	excellent
nuttallii				
rydbergii				

Table 2. Cont'd.

Species	General habitat	Annual precipitation (cm)	Flowering period	Survival status
occidentalis				
occidentalis	dry sand	65-140	July-Sept.	excellent
plantagineus	dry sand	100-125	July-Sept.	excellent
*paradoxus	wet, alkaline	25	Sept.-Nov.	threatened
*petiolaris				
fallax	sand	25-80	June-Sept.	excellent
petiolaris	sand	38-127	June-Sept.	excellent
*praecox				
hirtus	sand	50	May-Oct.	good
praecox	sand	120	April-Nov.	excellent
runyonii	coastal prairie	50-100	June-Nov.	excellent
pumilus	rocky soil	25-65	July-Sept.	excellent
radula	wet sand	127-152	Sept.-Nov.	excellent
resinosus	open woods	127-178	July-Sept.	excellent
rigidus				
rigidus	prairie	63-100	Aug.-Sept.	excellent
subrhomboideus	dry prairie	38-90	July-Aug.	excellent
salicifolius	limestone soils	76-115	Aug.-Sept.	good
schweinitzii	sand	115	Aug.-Sept.	endangered
silphioides	open areas	114-140	Aug.-Sept.	excellent
simulans	wet or dry	140-150	Sept.-Oct.	excellent
smithii	shale barrens	90-127	Aug.-Sept.	threatened
strumosus	edge of woods, open areas	65-140	Aug.-Sept.	excellent
tuberosus	usually moist	50-140	Aug.-Oct.	excellent

* Annual species; others perennial.