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SUNFLOWER BREEDING FOR RESISTANCE TO ABIOTIC STRESSES

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SUMMARY

Due to a specific structure of its main organs (root, stem, leaves, head), sunflower can be successfully grown on marginal soils and in semi-arid conditions and it is more resistant to abiotic stresses than other field crops. In sunflower breeding for resistance to abiotic stresses, the greatest progress has been made in selection for drought resistance. Breeders use over 30 different parameters in sunflower screening for drought resistance, with physiological ones being the predominant type. Best breeding results have been achieved using the phenomenon of stay-green, with the added bonus that this method incorporates into the cultivated sunflower not only drought resistance but resistance to *Macrophomina* and *Phomopsis* as well. The diversity of the wild *Helianthus* species offers great possibilities for increasing the genetic resistance of the cultivated sunflower towards abiotic stresses. In using wild sunflower species in sunflower breeding for drought resistance and resistance to salinity, best results have so far been achieved with *H. argophyllus* and *H. paradoxus*, respectively. In addition to the use of wild *Helianthus* species, sunflower breeding for abiotic stress resistance should also make more use of molecular breeding techniques. More progress has been made in sunflower breeding for heat resistance than in that for cold resistance. Specific breeding programs dealing with sunflower resistance to mineral deficiency and mineral toxicity have yet to be established. Sunflower breeders worldwide should commit to a greater use of wild *Helianthus* species in breeding for resistance to abiotic stresses.

Key words: sunflower, breeding, resistance, abiotic stresses, wild species, genus *Helianthus*

INTRODUCTION

Abiotic stresses not only determine the geographic and regional distribution of crops but also dictate if a potentially arable piece of land can actually be used for cultivation. According to an estimate, 24.2% of the world's geographic area is potentially arable. However, only 10.6% of the geographic area is under actual cultivation,

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while the rest is not available for cultivation due to one or more abiotic stresses (Singh, 2000). According to the same author, drought is the main abiotic factor, as it affects 26% of the arable area. Mineral toxicities/deficiencies are second in importance, while frost stands third. Drought is the most limiting of all abiotic stresses and it affects well over one third of the soils worldwide. Plants that manage to survive the effects of drought stress show a decrease in fertility, yield and product quality (Monti, 1986).

Sunflower is grown in a number of countries on so-called marginal soils, often in semi-arid conditions where almost every year an abiotic stress of one kind or another is present acting as a limiting factor on crop production. However, of all field crops, sunflower is best able to withstand stress conditions, primarily on account of the structure of its organs (Škorić *et al.*, 1988).

Fick and Miller (1997) reported that sunflower is considered moderately resistant to drought and is often grown in hot, semi-arid climatic regions. Breeding for resistance to drought and high temperatures is an important objective in many sunflower programs.

Drought is the main cause not only of differences between mean yield and potential yield but also of yield variations from year to year and therefore of yield instability (Monti, 1986).

Merrien and Champolivier (1996) conducted a three-year study of eight French hybrids for their response to drought using several parameters (leaf area index and duration, water status in the plant, photosynthesis/transpiration, water use efficiency, harvest index, *etc.*) and found there were no differences among the hybrids with regard to drought. The best hybrid under no limitation in water availability remained the best under dry conditions as well.

Using the results of our own studies and those of other authors, the present paper discusses the progress that has so far been made in sunflower breeding for resistance to abiotic stresses and indicates possible future directions in this area of sunflower research.

Achievements and future directions of sunflower breeding for resistance to drought

An abundant literature exists on the three adaptative mechanisms (escape, avoidance, tolerance) of plants to drought and on their genetic bases and genetic variability. Several selection indexes and methods have been found and utilized in breeding programs. In spite of all these efforts, breeding for drought stress remains a difficult task because of the scarce knowledge of the physiological mechanisms of drought resistance, their genetic backgrounds, and appropriate screening techniques (Monti, 1986).

According to Singh (2000), drought seems to be rather difficult to define and more difficult to quantify. For example, the common criteria used in the various definitions are: precipitation, air temperature, relative humidity, evaporation from free water surface, transpiration from plants, wind, airflow, soil moisture and plant conditions. A working definition of drought may be "the inadequacy of water availability, including precipitation and soil moisture storage capacity, in quantity and distribution during the life cycle of a crop to restrict expression of its full genetic yield potential".

Therefore, under conditions of drought, water stress develops in the plants as the demand exceeds water supply; this may occur due to atmospheric or soil conditions; and is reflected in a gradient of water potentials developed between the soil/soil-root interface and the leaf, the transpiring organ. Thus, moisture stress may be defined as the inability of plants to meet the evapotranspirational demand. Moisture stress is likely to develop to a different rate in different plant organs along this gradient (Blum, 1988).

At any stage of plant development, a soil moisture deficit will have a negative impact on sunflower yield, but the severity of drought effect depends on the developmental stage sunflower plants are in at the time. Greatest yield reductions resulting from drought occur at flowering up until seed maturation. Drought effects on sunflower seed quality are at their highest after flowering (Robelin, 1967), *i.e.*, at the X phase of organogenesis (seed formation stage). Drought at this stage causes seed oil percentage to decrease by 7-8%. At budding, drought has increased effect on seed embryo number and hence yield itself. According to Šitalov (1969), sunflower susceptibility to soil moisture deficit is at its highest at organogenesis stages VI through IX, *i.e.*, from the start of stamen formation to the start of fertilization. A drought occurring at this stage significantly reduces pollen functionality and vitality.

Drought resistance may be defined as mechanism(s) causing minimum loss of yield in a drought environment relative to the maximum yield in a constraint-free, *i.e.*, optimal environment for the crop. However, it does not exist as a unique heritable plant attribute. The various mechanisms by which a crop can minimize yield loss due to drought are grouped into the following three categories:

- 1-drought escape,
- 2-dehydration avoidance and
- 3-dehydration tolerance (Singh, 2000).

Drought escape describes the situation where an otherwise drought-susceptible variety performs well in a drought environment simply by avoiding the period of drought. Early maturity is an important vehicle for drought escape, suitable for environments subjected to late-season drought stress (Singh, 2000).

In the case of sunflower, Merrien and Champolivier (1996) argued, it appears that the escape from water deficit (*i.e.*, sowing date, earliness, *etc.*) could provide yield benefits higher than those coming from the genetic effect (more than 1 t/ha, versus 0.1 to 0.2 t/ha for the genetic gain). Similar findings were reported by Fick and Miller (1997), who have concluded that one approach in breeding for drought resistance is to develop high-yielding cultivars that flower and mature before soil water conditions become limiting.

Early sunflower hybrids generally have lower leaf area index, lower total evapotranspiration and lower yield potential than later ones. According to Škorić (1989), early sunflower hybrids are most often susceptible to *Macrophomina*, so in cases when there is an early occurrence of drought such hybrids may become affected, thus nullifying any positive effect early maturity may bring.

Dehydration avoidance is the ability of a plant "to retain a relatively higher level of 'hydration' under conditions of soil or atmospheric water stress." Therefore, the various physiological, biochemical and metabolic processes, involved in plant growth and yield production, are not being internally exposed to stress, but they are protected from water stress (Blum, 1988). The common measure of dehydration avoidance is the tissue water status as expressed by water or turgor potential under conditions of water stress. This can be achieved either by reducing transpiration (such plants are often called water savers) or increased water uptake (such plants are often termed as water spenders). Wild species are readily classifiable as 'water savers' and 'water spenders', but crop plants ordinarily exhibit a combination of both features, probably as a result of selection by man.

It has been established that some genotypes respond differently to drought depending on the stage of development they are in. Tissue and cell dehydration resulting from drought disrupts a series of physiological and biochemical processes.

Soil drought limits plant water uptake and consumption. The rate of transpiration decreases dramatically and the plant becomes overheated at high air temperatures as a result. The plant protects itself against the loss of water by increasing the water retention capacity of its cells. Drought usually increases the plant respiration rate, while prolonged droughts reduce the energy efficiency of plant respiration (Žolkevič, 1968). Photosynthesis diminishes even when water deficit is small.

Drought not only reduces the rate of photosynthesis but also directs photosynthetic metabolism towards increased formation of low molecular weight compounds such as alanine, hexoses, malic acid, *etc.* (Turčevskij, 1964). When the drought ends, sunflower plants are capable of again having a high rate of photosynthesis, thus compensating for the negative effects of water deficiency.

Tissue dehydration brings about profound changes in nitrogen metabolism (Cvetkova *et al.*, 1950). Synthetic processes are obstructed, the processes of degradation pick up speed, the toxic products of degradation accumulate, and so on. Sunflower leaves contain two and a half times more ammonia during a dry spell than under normal moisture conditions. As a result of excess ammonia, the rate of photosynthesis drops and the direction of metabolism changes as the rate of sugar formation decreases and the incorporation of carbon into amino acids and organic acids increases (Sijanova, 1964). The Krebs cycle becomes inhibited as well and changes in photosynthetic transformations occur. Intensive formation of alanine and glucose takes place, which may be regarded as an adaptive response (Neutstreva, 1968).

As sunflower plants respond to drought, the free proline content of their leaves increases, because proline, thanks to its structure, increases the water retention capacity of the cell (Gusev *et al.*, 1968).

When breeding for dehydration avoidance, it is highly important that a great deal of attention is paid to parameters such as reduced transpiration, osmotic adjustment, abscisic acid (ABA), cuticular wax, and leaf characteristics (leaf pubescence, altering the leaf angle, leaf rolling). It is also especially important to find ways to increase water uptake by creating a more powerful, deeper and well-branched root system.

A good illustration of how to gain more knowledge on the mechanism of sunflower response to drought conditions are the findings of Nicco *et al.* (1996), who studied the physiological mechanisms of adaptability to water stress. In that study, a constant water deficit (predawn leaf water potential -0.9 MPa, soil humidity 10.5%) was applied to the plants from the vegetative stage until harvest. The drought led to a decrease in leaf area and an increase in stomatal resistance to limit water consumption. Translocation rate of assimilates from leaves was reduced, but the sink effect of inflorescences was greater in stressed than in well-watered plants. Abscisic acid (ABA) accumulation in roots and leaves and higher ABA and zeatine contents in the capitulum were shown in water-stressed plants. Correlations were established between phytohormone contents and physiological responses, and ABA seems to be the main plant signal during the drought. When the pre-stressed plants recovered a normal water status, the leaves expanded again, especially if water was supplied at the beginning of the reproductive cycle. Stomatal opening size was similar to that of control plants. ABA levels in roots and leaves decreased, whereas ABA and zeatine still accumulated in inflorescence of the rewatered plants. These two hormones allowed the capitulum to keep its attractive capacity towards the photosynthate. All these responses ought to have positive repercussion on the yield (Nicco *et al.*, 1996).

Genetics of drought resistance and methods of breeding for resistance to drought

The genetics of drought resistance has not been studied as thoroughly in sunflower as in some other crop species. In sunflower, drought resistance has been estimated using a variety of parameters, such as yield stability, leaf water potential, leaf rolling, root growth, root xylem diameter, osmotic adjustment, stomatal conductance, ABA accumulation, canopy temperature, seedling establishment and growth, seedling recovery after stress, growth under stress, proline accumulation, *etc.*

Škorić (1992) reported that over 30 different parameters were used in the study of drought resistance and breeding for drought resistance in sunflower. Among these, the most frequently used ones were physiological parameters. More recently, molecular markers have proved very effective in studying the phenomenon of drought.

Sources of drought resistance

Several types of germplasm are used in sunflower breeding for drought resistance:

1. landraces;
2. cultivated hybrids and varieties;
3. wild species of the genus *Helianthus,* and
4. genetically engineered germplasm.

Use of landraces and cultivated hybrids and varieties has produced some positive results, but not to the extent that would secure stable sunflower production under drought conditions. Best results in increasing the drought resistance of cultivated sunflower have been achieved using wild species of the genus *Helianthus*. Furthermore, the potential of this particular approach has been nowhere near fully exploited yet and there are still a great many possibilities for further increase of sunflower resistance to drought using wild *Helianthus* species. Genetic engineering has not been used enough thus far, but this is expected to change in the near future.

According to Balding *et al.* (1996), their studies indicated that reasonable selection progress could be expected for relative water content and carbon exchange rate (especially when applied under drought conditions) as selection criteria to segregating populations coming from parental materials consisting of the wild species *Helianthus argophyllus* and a cultivated inbred line. The absence of detectable, non-additive, genetic effects for these physiological traits suggests that selection might be practised as early as the F_2 generation on the basis of performance of individual plants and that the effectiveness of the selection could be significantly improved by choosing the extreme values of the population. The results obtained from the correlated responses of the other traits allow some considerations on the use of physiological traits for the selection of drought-resistant genotypes. Selecting for extreme values of gas exchange and relative water content under limited water availability has produced genotypes which have activated opposite mechanisms to resist drought. In fact, the genotypes selected for elevated physiological activity had a high vegetative growth, large leaf area per plant, elevated transpiration rates per unit leaf area and consequently an elevated water consumption per plant.

Belhassen *et al.* (1996) started breeding for drought tolerance from an interspecific cross with *H. argophyllus*. Four cycles of divergent selection using the physiological criterion of leaf cuticular transpiration (relative water loss) allowed the production of two contrasting genotypes: T- (low level of leaf cuticular transpiration) and T+ (high level of leaf cuticular transpiration). Field experiments showed better yield tolerance index combined with good potential yield for T- hybrids in some locations. Physiological analyses done in the field and in controlled conditions allowed to distinguish the two genotypes for only one parameter -osmotic adjustment. Molecular comparison revealed the existence of a cDNA differentiating T- from T+. This cDNA has high homology with an amino acid transporter. A quantification of the amino acid concentrations during water deficit in T- and T+ lines showed that the T- plants accumulate significantly more proline than T+ ones. RFLP and STS analysis using this cDNA allowed to differentiate the two lines.

Cellier *et al.* (1996) studied a sunflower genotype showing drought tolerance in field conditions (R1 genotype) and another one exhibiting drought sensitivity (S1 genotype). They found that R1 tolerance was characterized by a delay of both wilting and decrease of leaf water potential. To analyze R1 tolerance at a molecular level, they isolated different cDNAs (named SDI for Sunflower Drought Induced) corresponding to transcripts accumulated in water-stressed R1 leaves by subtractive hybridization. Analysis of transcripts accumulation in both genotypes upon drought stress suggested a differential expression of the *sdi* genes. Abscisic acid-mediated induction in the tolerant genotype was observed for four of the *sdi* genes and was found to differ among them. Sequence analysis of SDI clones showed high identity with known proteins, including nsLTPs, ELIPs or dehydrin, predicted to be involved in various physiological processes.

Studying interspecific hybrids, Griveau *et al.* (1996) discovered that germplasm derived from *Helianthus argophyllus* (Arg-rec and its issue, AA\7.2.4) through several intercross cycles was of great value for sunflower breeding for drought resistance. Arg-rec was found to be particularly interesting for its yield stability.

Menichincheri *et al.* (1996) investigated stability parameters for drought resistance in interspecific hybrids based on wild sunflower species and reported that head diameter, leaf area index, leaf area duration, oil percentage and seed yield were most stable characteristics. The most stable hybrids for seed yield and oil percentage were 887 × PNRM 6.5.1 and HA89 × Baracca.

Gomez-Sanchez *et al.* (1996) compared the behavior of interspecific hybrids based on different wild species under irrigation and drought conditions. A principal component analysis differentiated a set of seven morphophysiological traits that became activated only under drought conditions. That revealed an adaptive traits interaction system as the resistance mechanism for which plants can express direct or indirect correlations with seed yield. The stability or better response of genotypes in drought conditions depended on the kind and cumulative number of these traits.

Vannozzi *et al.* (1996) studied drought resistance in interspecific hybrids and found, based on ANOVA analysis, that there were significant differences among the traits studied depending on location, moisture level and genotype.

Parameswaran (1996) used leaf angle as an indicator for gauging water stress in sunflower. Relative water content and leaf water potential of the upper, middle and lower leaves were measured to quantify plant water status and the values were matched with the leaf angles. Altering plant water status resulted in clearly visible changes in leaf angle with the associated changes in leaf relative water content and leaf water potential.

Chimenti *et al.* (2004) investigated the influence of osmotic adjustment on yield expression in stress conditions and found that high osmotic adjustment families extracted more water from the profile during stress period and had greater grain yield and leaf area duration than families with a low degree of osmotic adjustment. There was no effect of osmotic adjustment on these variables in the irrigated controls. Grain size and number were the yield components most affected by the level of osmotic adjustment. The authors concluded that osmotic adjustment can contribute to post-anthesis drought tolerance in sunflower through increased water uptake, reduced impact on grain number, grain size and greater leaf area duration.

In order to achieve the desired goal of sunflower breeding for drought resistance, one must first gain a thorough understanding of the relationship between drought resistance traits and yield. Once this has been done, a decision has to be made on whether to select for one or several traits, and then the screening methods for these traits must be properly developed. A similar view was proposed by Miller (1987). According to that author, it is important to identify and incorporate characteristics that contribute to physiological drought resistance, and characteristics that appear to be correlated with drought tolerance include deeper rooting depth and more efficient root uptake of water, tolerance to high osmotic pressure, low transpiration rates, and the ability to recover after wilting under heat stress.

When setting up a breeding program for sunflower resistance to drought, it is important to decide in advance whether to aim for adaptation to a specific environment, adaptation to a variable environment, or combined selection for drought resistance traits and high yield potential.

In sunflower breeding for drought resistance, best practical results have been achieved using the phenomenon of stay-green. Stay-green is used not only in breeding for drought resistance but also in breeding for resistance to *Macrophomina*, a fungal disease whose development is promoted by stress conditions. The stay-green trait is used in parallel to select genotypes resistant to *Phomopsis* as well (Škorić, 1989 and 1992). The great practical value of this character is confirmed by the large number of inbred lines (Ha-48, Ha-22, CMS-1-50, PH-BC-2-91, PR-ST-3, RHA-SES, RHA-583, *etc.*) and hybrids developed from them. The propriety of this approach was very much in evidence during the severely dry year 2007, when stay-green hybrids provided best performance in commercial sunflower production. The same views on the use of stay-green in sunflower breeding for drought resistance have been expressed by Vranceanu (2000).

Panković (1996) studied the stay-green hybrid NS-H-43 and the conventional hybrid NS-H-26-RM for physiological parameters in drought conditions and found that the former hybrid had a higher photosynthesis rate and quantum yield of photosynthesis in leaves thanks to its higher level of total soluble protein (especially the Rubisco protein), which resulted in better adaptability, *i.e.*, higher tolerance to drought conditions. The results of that study are another confirmation that the stay-green character can be used in sunflower breeding for drought resistance.

Use of wild *Helianthus* species in interspecific hybridization should have priority in sunflower breeding for drought resistance.

In breeding for drought resistance so far, it has been the wild sunflower species *H. argophyllus* that has been used most frequently and to greatest effect in breeding programs. Still, the significant positive results of these efforts have been somewhat marred by the failure to preserve the original structure of *H. argophyllus* leaves in the backcrosses (thickness of the epidermis, number of stomata, hairiness, *etc.*). The future use of wild sunflowers in selection for drought resistance should be expanded to include other wild species such as *H. deserticola, H. hirsutus, H. maximiliani, H. tuberosus*, and others. Their utilization and an increased use of molecular breeding will make it possible to identify genes controlling sunflower drought resistance and incorporate them into cultivated sunflower genotypes with good combining abilities.

Sunflower breeding for resistance to salinity, mineral deficiency and mineral toxicity

Abiotic stresses generated by mineral salts affect a considerable proportion of the arable land, ranking second after moisture stress. These stresses may occur in the form of a specific mineral deficiency or toxicity, or as accumulation of an excess amount of soluble salts in the root zone (Singh, 2000).

As sunflowers are grown in many countries on slightly to moderately saline soils, soil salinity is regarded as a limiting factors in sunflower production. There are a number of wild *Helianthus* species that grow on saline soils in the wild and thus represent a major source of genes for resistance to salinity. Using appropriate screening techniques, sunflower breeders should identify the wild species possessing genes for resistance to salinity and then incorporate these genes into the cultivated sunflower by best breeding methods available. In order for these goals to be realized, sunflower breeders must gain detailed knowledge of sunflower resistance to high salt concentrations.

Seiler (1992) stated that several wild species of *Helianthus* are native to salt-impacted habitats and may possess genes for salt tolerance. The same author reports that Chandler and Jan (1984) evaluated three wild *Helianthus* species for salt tolerance, namely *H. paradoxus, H. debilis*, and an *H. annuus* population native to salty desert areas, and obtained the following results. *Helianthus debilis* tolerated a salt concentration about the same as cultivated sunflower, wilting at a NaCl concentration of 250 to 400 mM. The wild ecotype of *H. annuus* had a higher tolerance, with some plants surviving the NaCl concentration of 800 mM. *Helianthus paradoxus* was highly salt tolerant, with some plants surviving at 1300 mM of NaCl. Salt tolerance was a dominant trait in hybrids between *H. paradoxus* and cultivated *H. annuus,* which did as well as the wild parent.

It would therefore be possible for sunflower breeders to achieve high levels of resistance to salinity using *H. paradoxus* and perhaps some other wild *Helianthus* species. Naturally, it is important that they decide which selection criteria to use in their breeding programs, as these can include cell survival, seed germination, dry matter accumulation, leaf death or senescence, leaf ion content, leaf necrosis, root growth, and osmoregulation (Singh, 2000).

Sunflower breeding for resistance to mineral deficiency and mineral toxicity

Sunflowers require only ten macroelements (C, O, H, N, P, K, S, Ca, Fe, Mg) and six microelements (B, Mn, Cu, Zn, Mo, Co) for their growth and development. Air and water are the sources of carbon, oxygen and hydrogen. The rest of the elements are taken up from the soil or fertilizers and are divided into primary elements, secondary elements and microelements (Ćupina and Sakač, 1989). Sunflower nutrition has been the subject of many books and scientific papers, which have established optimum levels of each individual macro- and microelement needed for the normal growth and development of sunflower on different types of soil. There is also voluminous literature on the deficiencies or excess levels (toxicity) of individual elements and how they affect sunflower growth and development.

As there are unfortunately no major breeding programs anywhere in the world that deal specifically with sunflower resistance to mineral deficiency and mineral toxicity, sunflower breeders should consider a possibility of establishing one or more such programs. They would have to choose appropriate breeding methods and targets, define selection criteria and select potential resistance sources (most likely wild *Helianthus* species).

Sunflower breeding for heat and cold resistance

Each plant species, more particularly each genotype, has an optimum range of temperatures for its normal growth and development. These specific temperatures depend not only on the genotype but also on the stage of growth and development of a given genotype. When temperature moves beyond this optimal range, it generates temperature stress, *i.e.*, temperature interferes with plant performance. Temperature stresses may be grouped into the following three categories:

1. heat stress,
2. chilling stress, and
3. freezing stress (Singh, 2000).

Heat resistance

The adverse effect on plants of temperatures higher than the optimal is considered as heat stress. Heat affects:

1. survival,
2. growth and development, and
3. physiological processes in plants.

The nature and extent of the effects depends mainly on the temperature (Singh, 2000).

In order for sunflower breeders to be able to determine the right breeding methods, targets, and selection criteria and to choose their breeding materials for selection for heat resistance, they must have detailed knowledge of how sunflower organs respond to high temperature. Sunflower is exposed to high temperatures in arid and semi-arid conditions, which have been prevalent in much of Europe in 2007. High temperatures may be accompanied by high but also low humidity levels.

The present knowledge on sunflower heat resistance allows sunflower breeders to define more easily their selection criteria and to search for sources of heat resistance in wild *Helianthus* species.

Breeding for resistance to high temperatures should be combined with selection for drought resistance. Intensive breeding programs on sunflower heat resistance should be organized in countries where excessive temperatures are a regular occurrence. Selection for heat resistance is an integral part of many breeding programs and is often combined with breeding for increased productivity and resistance to dominant diseases and drought.

Cold resistance

In many environments, crop productivity is limited by low temperatures. When temperatures remain above freezing level, *i.e.*, $>0^{o}$C, it is called chilling, while freezing describes temperatures below freezing, *i.e.*, $<0^{o}$C.

For sunflower, it is important to increase its resistance to cold in the early stages of growth and development, *i.e.*, at germination, emergence and the stage of 2-3 leaf pairs, so as to enable successful early sowing. Cold resistance at maturation should be increased as well in order to enable sunflower growing at higher altitudes and in colder regions. Sources of cold resistance should be sought exclusively in the wild *Helianthus* species that are found growing wild in the mountains where winters are harsh and springs are cold.

There are unfortunately no significant breeding programs dealing with cold resistance in sunflower. What little work there is on this subject employs more of an empirical approach and does not constitute a major part of the programs concerned.

CONCLUSIONS

- Owing to the structure of its major organs (root, stem, and leaves), sunflower is more resistant to abiotic stresses than other field crops;
- In overall sunflower breeding for resistance to abiotic stresses, the greatest progress has been made in selection for drought resistance. This has been done using a large number of parameters, most of them physiological.
- The best method for sunflower screening for drought resistance is the use of

the stay-green character.

- Wild *Helianthus* species are used as sources of genes for resistance to drought. The most widely utilized of these species is *H. argophyllus*, which has been used to develop new sunflower germplasm by interspecific hybridization. Several other wild sunflower species should be included in these efforts as well.
- The screening of cultivated sunflower genotypes, interspecific hybrids and wild sunflower species at the molecular level has given significant results lately.
- Sunflower resistance to salinity can be significantly increased using the wild species *H. paradoxus*.
- Sunflower selection for resistance to mineral deficiency and mineral toxicity has so far produced modest results.
- More progress has been made in sunflower breeding for heat resistance than in that for cold resistance. Wild species can be used as sources of desirable genes in these efforts.

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MEJORAMIENTO DE GIRASOL POR RESISTENCIA A ESTRESES ABIÓTICOS

RESUMEN

Debido a la estructura de sus órganos principales (raíz, hojas, tallo, capítulo), el girasol puede cultivarse exitosamente en suelos marginales y condiciones semiáridas y es más resistente a estreses abióticos que otros cultivos. En lo referido a mejoramiento de girasol por resistencia a estreses abióticos, el mayor progreso logrado ha sido en mejoramiento por resistencia a sequía. Los mejoradores utilizan más de 30 parámetros diferentes en la evaluación de girasol por resistencia a sequía, siendo los atributos fisiológicos los caracteres predominantes. Los mejores resultados del mejoramiento se han alcanzado a través de la utilización del fenómeno stay-green, con el bonus agregado de que este método no sólo incorpora resistencia a sequía en el girasol cultivado, sino también resistencia a *Macrophomina* y *Phomopsis*. La riqueza encontrada entre las especies silvestres del género *Helianthus* ofrece grandes posibilidades de incrementar la resistencia genética del girasol cultivado a los estreses abióticos. Los mejores resultados en la utilización de especies silvestres en mejoramiento de girasol por resistencia a sequía y salinidad se han alcanzado mediante la utilización de *H. argophyllus* y *H. paradoxus*, respectivamente. El mejoramiento de girasol por resistencia a estreses abióticos debería hacer un mayor uso de las herramientas moleculares disponibles, además del uso de especies silvestres del género *Helianthus*. Ha habido un mayor progreso en la obtención de resistencia a estrés por alta temperatura en girasol que por resistencia a frío. Todavía falta establecer programas específicos por resistencia a deficiencias minerales y toxicidad por minerales. Los mejoradores de girasol a lo largo del mundo deberían comprometerse a hacer un mayor uso de las especies silvestres del género *Helianthus* en mejoramiento por resistencia a estreses abióticos.

SÉLECTION DU TOURNESOL POUR LA RÉSISTANCE AUX STRESS ABIOTIQUES

RÉSUMÉ

Du fait de la structure spécifique de ses principaux organes (racine, tige, feuilles, capitule), le tournesol peut être cultivé avec succès sur des sols marginaux et dans des conditions semi-arides, et est plus résistant aux stress abiotiques que les autres plantes de grande culture. Dans l'amélioration génétique du tournesol pour sa résistance aux stress abiotiques, les plus grands progrès ont été réalisés pour sa résistance à la sécheresse. Les sélectionneurs ont utilisé plus de 30 paramètres différents dans le screening du tournesol pour sa résistance à la sécheresse, et parmi ceux-là, les critères physiologiques ont été prédominants. Les meilleurs résultats ont été obtenus par l'utilisation du phénomène de "stay green", par le bonus que cette méthode apporte non seulement pour la résistance à la sécheresse mais encore pour la résistance à *Macrophomina* et à *Phomopsis*. La richesse des espèces sauvages du genre *Helianthus* offre de grandes possibilités pour augmenter la résistance du tournesol cultivé aux stress abiotiques. Par l'utilisation des formes sauvages dans l'amélioration du tournesol pour la résistance à la sécheresse et à la salinité , les meilleurs résultats ont été obtenus avec *H. argophyllus* et *H. paradoxus*, respectivement. En addition à l'utilisation de ces formes sauvages, l'améliora-

tion génétique devrait faire un usage plus important des techniques de sélection moléculaire. Des progrès plus importants ont été réalisés pour la résistance aux fortes températures que pour la résistance au froid. Des programmes spécifiques pour la résistance à des déficits et toxicités minérales doivent maintenant être mis en place. Les sélectionneurs de tournesol de part le monde devraient consacrer des efforts plus importants à l'utilisation des formes sauvages pour l'amélioration génétique de la résistance aux stress abiotiques.