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REVIEW ARTICLE

Breeding sunflower (*Helianthus annuus* L.) for drought tolerance*

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ABSTRACT

Productivity of sunflower is strongly regulated by the availability of water and greatest yield losses occur when water shortage occurs at flowering. Therefore, it is critical to manage the deleterious effect of drought stress at this stage. Evolving crop genotypes which have enhanced drought tolerance are the most successful and cheapest strategy to cope with drought. However, progress in drought tolerance breeding is slow due to inappropriate selection criteria and faulty breeding strategies. Therefore, utility of potential physiological and morphological traits in drought stress breeding are discussed and progress in sunflower drought tolerance breeding at the molecular level is reviewed.

Key Words: *tolerance; genetic variability; osmotic adjustment; molecular marker.*

INTRODUCTION

Stress may be defined as any factor that causes reduction of yield when it is present or absent (Tollenaar and Wu, 1999). Similarly, drought can be imposed when a plant is unable to meet its evapo-transpirational demands. It may also be defined as “the inadequacy of water availability (including precipitation and soil moisture storage capacity) in quantity and distribution during the life cycle of a crop, thus restricting the expression of its full genetic yield potential (Sinha, 1996)”.

There are different types of drought; a drought may be meteorological when precipitation is significantly below expectation for the time of year and location. An agricultural drought is said to exist when water from all sources is sufficiently low enough to cause serious shortfalls in crop yield. A physiological drought occurs when water is present in the soil, but the plant cannot withdraw it due to lower osmotic potential of the soil caused by salts. Sometimes a plant shows temporary wilting of leaves due to a lower rate of water

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absorption by roots compared to the rate of water loss in the form of transpiration due to strong winds or high temperature. In addition, a plant can also experience permanent wilting by a micro-organism clogging vascular tissues.

Drought is a multidimensional stress affecting plants at various levels of their organization (Yordanov et al., 2000). Drought environments are characterized by wide fluctuations in precipitation, quantity of precipitation, and its distribution within and across seasons (Swindale and Bidinger, 1981). The effect of stress is usually manifested as a decrease in photosynthesis and growth (Yordanov et al., 2000). It is believed that drought is the largest single factor for reduction of yield globally (Fischer and Turner, 1978; Boyer, 1982).

DROUGHT: AN INTERNATIONAL DILEMMA IN SUNFLOWERS

It has been found that a world wide reduction in sunflower yield has been associated with drought (Dragovic and Maksimovic, 1995). According to a report, oilseed production in 2005 was down 2 percent from 2004 due to drier than normal weather. In Spain sunflower crops suffered substantially from the effects of drought with a 41 percent decrease in production (USDA, Agriculture Weather Facility). In Pakistan, a crippling drought for a period of three years from 2000-2002 resulted in a major reduction in sunflower area and production (Rauf and Sadaqat, 2007a). Similarly, Bosnjak (2004) analyzed water availability over a period of 39 years and found drought to be a predominant feature in summer, the results of which up to 50% yield losses in sunflower that could have been obtained in irrigated conditions. He also predicted that severe droughts may be expected in the future with global climatic changes.

EFFECTS OF DROUGHT STRESS

Sunflower is categorized as a low to medium drought sensitive crop. It has been found that both quantity and distribution of water has a significant impact on achene and oil yield in sunflower (Feres et al., 1986; Andrich et al., 1996; Krizmanic et al., 2003; Reddy et al., 2003; Iqbal et al., 2005;). However, oil quality of sunflower has not been significantly affected by drought treatment (Petcu et al., 2001). Intensity of yield reduction by drought stress depends on the growth stage of crop, the severity of the drought and tolerance of genotype (Lorens et al., 1987). Although drought stress affects every developmental stage of sunflower, maximum reduction in yield was experienced when drought occurred during the reproductive stage (Karaata, 1991; Reddy et al., 1998; Reddy et al., 2003; Vijay, 2004). Karaata (1991) conducted experiments to identify highly drought sensitive growth stages of sunflower, and it was found that maximum reduction in yield occurred when drought was imposed during flowering. Similarly, Vijay (2004) studied the response of achene yield to irrigation at four stages: initial at 15-20 days after seeding (DAS), capitulum initiation (30-35 DAS), flowering (50-60 DAS), and grain development (70-80 DAS). It was shown that maximum achene yield was obtained with irrigation at the flowering stage.

Drought during the vegetative phase of the plants affects both final biological and economic yields. During vegetative development, it reduces the main stem height, stem diameter, number of nodes or leaves and leaf area (Agele, 2003; Turhan and Baser, 2004) while an increase in root length occurs at the expense of above-ground dry matter. This has been observed by a higher root-to-shoot ratio obtained under drought stress (Sobrado and Turner, 1986). The reduction in vegetative biomass results in lower plant surface area which reduces the radiation use efficiency and photosynthetic activities (Stockle and Kiniry, 1990; Badr et al., 2004; Germ et al., 2005). This finally lowers assimilation of photosynthates during the reproductive phase which reduces head diameter. Reduction in head diameter further decreases the number of rows per head and number of achenes per head and results in correlation of yield components to severity of drought (Feres et al., 1986; Gimenez and Feres, 1986; Alza and Fernandez-Martinez, 1997; Rauf and Sadaqat, 2007a). On the other

hand, stress during the flowering stage causes abortion of ovaries, embryo, sterility of pollen and decreases in leaf area index. This reduces the number of achenes per head, 100-achene weight and fertile achenes per head (Baldini and Vannozzi, 1999; Reddy et al., 2003). It has been estimated that stress during the vegetative phase causes 15-25% yield reduction, whereas more than 50% reduction can occur if stress coincides with the flowering stage (Reddy et al., 2003). However, minimal damage has been found to occur if drought was imposed during the achene filling stage (Karam et al., 2007). At this stage, the plant responds to the stress by early, abrupt leaf senescence (Rauf and Sadaqat, 2007b) and mobilization of stem reserves to the developing achenes (Baldini and Vannozzi, 1999; Rauf and Sadaqat, 2007b). However, a reduction of 100-achene weight may occur due to lower photosynthate production as a result of excessive loss of leaves at this stage.

At the cellular level drought stress causes shrinkage of cells, cell membrane injury, and production of free radicals that cause damage to the cellular apparatus (Terbea et al., 1995; Sgherri et al., 1996; Kang and Zhang, 1997).

BREEDING FOR DROUGHT TOLERANCE

Drought can be managed to minimize its deleterious effects. Agronomically, the best approach for the management of drought stress is to irrigate the field. Other drought management techniques include the use of mulches to reduce evaporation losses, better weed control, crop rotations, improved cultivation methods to enhance infiltration rate, foliar sprays, efficient irrigation practices (e.g. drip, sprinkler) (Rachidi et al., 1993; Gajri et al., 1997; Unger and Howell, 1999). A basic philosophy for all these management practices is to relieve the deleterious effects of drought and to use the water efficiently. It has been found that all these agronomic practices can improve yield up to 15-25% under drought stress by improving water supplies (Edmeades & Bänziger, 1997). However, above mentioned agronomic practices increase costs and are dependent on input availability, infrastructure, access to market and skills in crop and soil management (Campos et al., 2004). As a result, such management practices cannot be exploited by the farmer with small holdings or who cannot afford these inputs.

Drought can also be managed by modifying the plant morphology or incorporating some traits that help the plants to cope with drought stress successfully (Yordanov et al., 2000). Thus, genetic modification is usually the most successful and cheapest strategy to cope with drought. Since modifications within plant morphology and physiology introduced through breeding are heritable, once introduced into a breeding material it will be a permanent source of drought tolerance. Heritable changes within a crop with the aim of improving drought tolerance can be broadly considered as breeding for improved drought tolerance.

There are numerous strategies utilized in breeding for drought stress in a crop species such as induction of earliness for drought escape, modification of certain plant traits that leads toward drought resistance and introduction of drought tolerant traits associated with high yield. Strategy for breeding drought stress depends upon the intensity, frequency and timing of drought occurrence. Under typical Pakistani conditions rainfall is too low and agriculture is dependent on supplemental irrigations. To compound the problem, irrigation water availability has now become highly unpredictable due to a recent shortage of water. Since water availability is highly unpredictable and the sunflower flowering period is highly sensitive to drought, tolerance to drought at flowering must be developed to minimize the damaging effect of drought. A strategy to produce a high yielding genotype combined with traits leading toward drought tolerance during anthesis is desirable provided that traits conferring drought tolerance also show strong positive correlation with achene yield. A trait leading toward drought tolerance should be considered ideal if it shows strong positive correlation with achene yield (in case of sunflower), moderate to high heritability, cheaply

and easily measured, and hopefully determined before flowering so that undesirable plants may be rogued before crossing.

SUNFLOWER DROUGHT TOLERANCE BREEDING IN PAKISTAN

Breeding drought tolerance is a major objective for boosting sunflower yield worldwide and particularly in Pakistan. However, very few reports are available regarding the success of breeding sunflower against this stress. Most of the efforts have been intensified to cope with the drought through agronomic practices. The main focus of the research has been to ameliorate the effect of drought through soil conditioning, seed priming, exogenous foliar spray of certain osmo-protectants and deficit irrigation practice. These treatments have been shown to improve the performance of sunflower genotypes under drought stress conditions (Meo et al., 1999; Iqbal et al., 2005; Khaliq, 2004).

Apart from these studies, few studies have shown response of sunflower to the water stress. Qadir (2006) obtained maximum germination at 20-25°C at 0 bar in all the hybrids. Germination tended to decrease with increase in osmotic stress. Khaliq (2004) reports the response of sunflower hybrids to deficit irrigation practice and obtained near-maximum yield when sunflower was irrigated during the reproductive phase.

From a breeding point of view, efforts were restricted to the screening of breeding material and hybrids or formulation of selection criteria under the drought stress. Local and introduced genetic materials were evaluated for yield, yield components and physiological traits under drought conditions to discriminate between tolerant and sensitive lines (Tahir et al., 2002; Rauf and Sadaqat, 2007a; Rauf and Sadaqat, 2008a; Rauf et al., 2008a). Apart from the field or pot screening experiment, *in vitro* screening and selection for drought tolerant callus has also been carried out by plating the cell suspension on agar-solidified medium containing PEG (Hassan et al., 2004). It was reported that selected plants grew better than the non-selected lines under various levels of water deficit induced by PEG due to higher amounts of K⁺, Na⁺ and N, but lower amounts of Ca⁺⁺ and P than the non-selected lines.

GENETIC VARIABILITY: AN ESSENCE FOR DROUGHT TOLERANCE BREEDING

CULTIVATED GERMPLASM

Most cultivated hybrids or open pollinated varieties evolved under near optimum agronomic conditions and often have some common parentage and history of origin. Therefore, breeding for drought tolerance must expand genetic variability. This depends on the incorporation of diverse germplasm so that potential sources of drought tolerance may be identified and subsequently incorporated to ensure yield when drought occurs.

The first approach for the development of a drought tolerant line is to screen high yielding germplasm accompanied by superior yield contributing traits. It is likely that this germplasm may also contain extensive variation for stress tolerant traits (Vasal et al., 1997). Over the years, experience of handling plant material for drought tolerance at different research institutes (CIMMYT and ICARDA) indicates that improvement in drought tolerance can be made by screening both local and introduced germplasm belonging to various origins (Beck et al., 1990; Edmeades and Bänziger, 1997). However, the usefulness of introduced material depends on the performance under local conditions. Therefore, it is important to make selection of introduced material under local conditions, and a decision should be made accordingly: either it should be used as the source populations *per se* or to cross them with locally adapted materials or both (Beck et al., 1990).

Results showed significant variation existed between the sunflower genotypes for yield under drought stress. Fereres et al. (1986) conducted field experiments at Cordoba, Spain to evaluate the yield responses to drought of 53 sunflower genotypes and found substantial variability among genotypes both in dryland yield and under frequent irrigation. Similarly, water stress revealed a high genetic variability among traits related to water status, osmotic

adjustment, root characteristics, gas exchange parameters, seedling traits and drought susceptibility index when a large number of sunflower genotypes belonging to diverse origins were evaluated (Seiler, 1994; Chimenti et al., 2002; Lambrides et al., 2004; Turhan and Baser, 2004; Kiani et al., 2007a; Rauf and Sadaqat, 2007a; Rauf and Sadaqat, 2008a).

WILD RELATIVES

Wild species are a potentially important source of abiotic tolerance; therefore, it may be desirable to introgress drought tolerant genes from wild relatives. The genus *Helianthus* is comprised of 51 species and 19 subspecies with 14 annual and 37 perennial species (Seiler, 2007). According to Korrell et al. (1997), wild sunflower contains considerable variability for disease, insect pest resistance, and tolerance of abiotic stresses like drought and salinity. Similarly, fatty acid composition and protein quality can also be modified by introgression from wild species.

For drought tolerance breeding, specie *Helianthus argophyllus* has been extensively used by the sunflower breeders (Baldini and Vannozzi, 1998; Baldini et al., 1999; Griveau et al., 1998). In comparison with cultivated sunflower inbred lines and inbred lines obtained by a divergent selection for physiological traits from *Helianthus argophyllus*, it was found that lines obtained from *Helianthus argophyllus* had the highest water use efficiency, the best drought susceptibility index (S), and high harvest index (HI) value under drought conditions (Serieys, 1997; Baldini and Vannozzi, 1998; Baldini et al., 1999). However, a large genetic distance between the cultivated and wild sunflowers has decreased the introgression of the drought tolerant gene from wild relatives (Mohan and Seetharam, 2005). In addition, introgression from most of the wild species has also been found to be associated with the deterioration of oil yield in cultivated sunflower (Seiler, 2007).

STRATEGIES FOR THE GENETIC IMPROVEMENT OF DROUGHT TOLERANCE

IMPOSING DROUGHT STRESS

Since a field experiment assures optimum vigor, growth and reproduction of genetic material, for evaluations drought stress has been imposed in the field during the reproductive phase which has been considered as the best strategy for improvement of genetic material against this stress (Baldini et al., 1999; Rauf and Sadaqat, 2007a; Rauf and Sadaqat, 2008a). However, performance in the field under drought stress should be considered a cumulative effect of some other biotic and abiotic stresses. In sunflower, drought stress results in higher intensity of fungal diseases, inter genotype competition, bird attack, injuries due to heat stress, and reduced soil thermal conductivity when compared with irrigated conditions (Alexandrov and Koteva, 2001; Rauf et al. 2008b). A controlled experiment on the other hand provides better control over these variables, but does not indicate optimum growth, vigor and reproduction. In pot experiments soil masses are too low, while in hydroponic conditions growth is restricted due to toxicity caused by differential genotypic absorption of polyethylene glycol (Blum, 1979). Therefore, ideal experiments should be designed to optimize the results both in field and controlled conditions.

YIELD AS A SELECTION CRITERION

There are two thoughts regarding the selection for high yielding genotypes. According to one group, selection for high yield should be practiced under non stress conditions, where genotypes may show their full genetic potential and environmental effects are minimal. A genotype with alleles responsible for high yield under non stress conditions may also show promise under stress conditions due to its high residual yield (Blum, 1979). However, another group is of the opinion that selection for a high yielding genotype should be carried out under the target environment. The presence of significant genotype x environment (G x E) interaction in most studies shows the desirability of the second approach. A significant G x E means changes occur in relative performance of genotypes across environments. As a

result, a genotype showing promise in one environment may not be exceptional in another environment. However, improvement by direct selection of yield under the target environment has been slow due to low narrow sense heritability of trait under stress. Since yield is a resultant trait that is maximized by cumulative effects of a large number of yield contributing traits. The contribution of these traits to the yield is expected to be different under variable environments. Based on this fact, better improvement of the yield may occur if selection is based on a yield contributing trait that shows highest association with yield in a specific environment.

For drought tolerance breeding, emphasis should be on traits that confer drought tolerance in the plant and also show positive association with yield. Over the past decades, plant breeders have focused on some traits that were incorporated to plant survival under stress conditions such as lower leaf canopy and reduced transpiration (Fischer and Wood, 1979; Karamanos and Papatheohari, 1999). Often, traits were not necessarily positively associated with high yield. As a result breeders continue to develop cultivars which yield poorly under stress conditions. Therefore, analysis of plant traits with significant effects on drought tolerance and high yield potential under stress conditions seems to be necessary (Richards, 2004).

APPROPRIATE TRAITS FOR DROUGHT TOLERANCE BREEDING

SEEDLING TRAITS

Selection of suitable genotypes on the basis of seedling traits has been considered a reliable technique for evaluating a large number of genotypes for drought tolerance (Tomar and Kumar 2004; Basal et al., 2005; Longenberger et al., 2006).

The effects of stress, environment and genotype on seedling traits have been identified and well documented. Pace et al. (1999) reported that drought-stressed seedlings showed some increase in root length but a reduced diameter. Prior et al. (1995) showed that inadequate soil moisture reduced root elongation, while Plaut et al. (1996) found that soil moisture deficit reduced root length and density. A number of different seedling traits have been suggested as important relative to drought tolerance. These include lateral and tap root weight, lateral root number and root-to-shoot ratios (Cook 1985; Pace et al., 1999). Singh et al. (1999) adopted a simple method of screening germplasm lines by seedling survivability, which accurately discriminated between drought tolerance and susceptibility under artificial moisture stress conditions. Rauf et al. (2008a) conducted experiments under two moisture regimes to study their modifying effects on phenotypic expression and combining ability of seedling traits and their genotypic correlation with achene yield. The moisture stress regime was favorable for the expression of additive genetic variability. All seedling traits except shoot length showed a significant correlation with achene yield, which also signified their importance for improving achene yield under drought regimes. From a breeding point of view, it was shown that seedling recovery % and root weight were useful traits for evaluating sunflower genotypes for drought tolerance.

HARVEST INDEX

A higher harvest index was shown as a better translocation of photosynthates to the reproductive part under drought stress (Rauf and Sadaqat, 2008b). The suppressing effect of drought stress on the harvest index has been reported previously in sunflower, and only drought tolerant genotypes showed stability or increase in the value of this trait, indicating harvest index as a useful trait in discriminating between drought sensitive or tolerant lines (Baldini and Vannozzi, 1998; Fereres, 1986). The harvest index has also shown a significant positive relationship with achene yield under drought stress, signifying the importance of this trait for improving achene yield under stress conditions (Reddy et al., 1995; Baldini et al., 1999). Moreover, significant genetic variability and high narrow sense heritability for harvest index has been reported in sunflower (Alza and Fernandez-Martinez, 1997; Baldini and

Vannozzi, 1998; Reddy et al., 2003; Rauf and Sadaqat, 2008b). However, narrow sense heritability was found to be higher than achene yield within a drought stress environment but found to be lower than achene yield when calculated combined across environments showing specificity of this trait under drought stress (Alza and Fernandez-Martinez, 1997). Rauf and Sadaqat (2008b) compared high and low osmotic adjustment genotypes and found superiority of high osmotic adjustment genotypes due to higher harvest index.

DROUGHT SUSCEPTIBILITY INDEX

Drought susceptibility index (DSI) is calculated on the basis of a ratio obtained from yield under drought stress condition to the yield under non stress condition (Fischer and Maurer, 1978). It has been calculated to determine the difference of yield potential under irrigated conditions and yield under drought for each genotype (Vannozzi et al., 1999). A higher value of susceptibility index indicates higher susceptibility of a genotype to the stress. Conversely, Andrich et al. (1996) calculated drought resistance index on the basis of a ratio between the weights of the kernels of the mean achenes grown in un-irrigated and irrigated conditions, with a value close to 1 indicating resistant cultivars and a reduced ratio indicating drought sensitivity. A significant negative relationship or genetic correlation has been observed between the drought susceptibility index and yield under drought stress conditions, indicating that the drought susceptibility index may prove a very useful selection criterion for drought-tolerance breeding in sunflower (Feres et al., 1986; Baldini et al., 1992; Alza and Fernandez-Martinez, 1997; Rauf and Sadaqat, 2007a). However, a significant correlation between the DSI and yield under non stress conditions was absent (Feres et al., 1986; Baldini et al., 1992; Rauf and Sadaqat, 2007a). This indicated that yield under irrigated conditions could not be considered a prediction of its yield under drought conditions, and that yield under irrigated conditions should not be used as a selection criterion to improve yield under drought (Baldini et al., 1992). Therefore, yield in low and high yielding environments can be considered as two separate traits that are not necessarily maximized by identical sets of alleles (Falconer, 1990). Consequently, plant breeding strategies should be different when targeting stress and non-stress environments (Ceccarelli et al., 1991; Ceccarelli et al., 1998).

ROOT SYSTEM

The root system of a plant is important when considering drought tolerance breeding, since certain root characteristics such as root length, root biomass, and lateral root density would determine the efficiency of water extraction from soil. A deeper root system would allow water extraction from lower soil profiles and, thus, it is expected that the plant will perform better under moisture stress when its growth is dependent on water stored deeper in soil. Sunflower has a deep and extensive root system that can extract water up to 270 cm (Gimenez and Fereres, 1986; Connor and Sadras, 1992; Rachidi et al., 1993). Its root growth depends upon several factors such as plant genotype, water availability, plant population and soils. Limited research literature is available on the intraspecific variations for the root system in sunflower (O'Toole and Bland, 1987), since determination of root characteristics in the field is very laborious and time consuming. Few reports have characterized heritable variation in sunflower for root length and any greater root length associated with longer growth duration (Feres et al., 1986; Schreiner, 1992; Rauf and Sadaqat, 2008b). Angadi and Entz (2002) compared root system characteristics and water extraction patterns of dwarf hybrids with hybrids of standard height. Most of the dwarf sunflower hybrids showed lower root length, root length density and root distribution, thus showing a positive correlation between plant height and root characteristics studied. Other studies showed effect of water availability on root characteristics. An increase in root length and root-to-shoot ratio in response to moisture stress along with the decrease in lateral root length as an adoptive measure for drought stress can be generalized from experiments conducted on sunflower (Petcu and Stanciu, 2001; Gomes et al., 2005; Rauf and Sadaqat, 2008b). Soil characteristics

such as compaction and depth also have significant impacts on root growth. A decrease in root area and biomass had been observed with the increase in soil depth and compaction under moisture stress conditions (Petcu and Petcu, 2006). Soil compaction limits root growth by directly posing physical injuries and indirectly by reducing water infiltration. Petcu and Petcu (2006) showed maximum root area and biomass of sunflower in soil depth of 0-10 cm along with a progressive decrease in the values of both these traits as the depth and compaction increased under water stress.

LEAF HYDRAULICS

Leaves can be considered as a sink for water absorbed by the plant; therefore, leaf water status may accurately define the demand and supply of water. Characteristics of leaves that define moisture content of leaves may also accurately discriminate between drought tolerance and susceptibility. These traits include relative water contents, leaf water potential, turgor pressure, osmotic potential and stomatal conductance. These physiological traits are collectively called 'water relations'. In sunflower, genotypes selected for these elevated physiological traits under drought had greater vegetative growth, elevated water consumption and increased root-to-shoot ratio. They avoid drought stress by continued water uptake from deeper soil layers (Perniola, 1994; Baldini et al., 1997). Among the traits used for the evaluation of plant water-status, relative leaf water contents (RWC) gives best measure of the level of the water deficit in the plant at a specific time-point. As RWC is related to cell volume, it may closely reflect the balance between water supply to the leaf and transpiration rate (Sinclair and Ludlow, 1985). Significant variability and heritability has been reported in sunflower for this trait (Baldini et al., 1997). Other traits such as leaf turgor, water and osmotic potential are related to the osmotic adjustment (Perniola, 1994). Osmotic adjustment (OA) is a phenomenon in which plants accumulate a certain type of compatible solute under stress conditions to lower its potential. As a result of this lower potential, plant may regain its turgor and attract more water from the soil. Compatible solutes help in maintaining the cell turgor, protect against denaturing of important structural molecules and cell organelle, and their high concentration does not cause toxicity in the cell. There are many molecules which may be considered as candidates of compatible solutes such as K^+ , Ca^{++} , proline, HSPs, and dehydrins. However, in sunflower large number of studies depicted that proline has been an important osmolyte under drought stress. It was shown that its content tended to increase in young leaves in response to drought stress (Terbea et al., 1995; Badr et al., 2004; Cechin et al., 2006).

Significant genetic variability between genotypes has been observed in sunflower for OA (Chimenti and Hall, 1993; Chimenti and Hall, 1994; Angadi and Entz, 2002; Rauf and Sadaqat, 2008a). In sunflower, different studies have shown a significant relationship of OA with leaf turgor, RWC and root growth, which signified the importance of OA in maintaining leaf turgor and relative water contents through better root growth (Conroy et al., 1988; Rauf and Sadaqat, 2008a; Rauf and Sadaqat, 2008b). As a result, plants were able to maintain a photosynthetic rate and stomatal conductance at lower leaf water potentials (Maurey et al., 2000). The value of OA as a yield contributing trait has been established in sunflower. It is inferred from the studies that sunflower genotypes with higher OA extracted more water from the soil during the stress period due to greater root growth. They had greater shoot biomass and harvest index (HI) at physiological maturity and greater grain yield. There was no effect of OA on these variables in the irrigated controls (Chimenti et al., 2002; Rauf and Sadaqat, 2008a; Rauf and Sadaqat, 2008b).

MOLECULAR BREEDING FOR DROUGHT TOLERANCE IN SUNFLOWER

The advent of emerging and novel technologies of plant cell and molecular biology provided us a powerful means to supplement and complement the traditional methods of plant improvement. Therefore, in the recent past much of the research has been devoted to

isolation and testing the expression of drought tolerant genes. Novel stress responsive genes were identified following subtractive hybridization of cDNA synthesized from RNA isolated from drought stress and unstressed plants. Identified genes related to drought tolerance such as SunTIP, HaDhn1, HaDhn2, Sdi (sunflower drought induced), Gdi15, Hahb-4 and HAS1 or HAS1.1 showed an abundance of their transcript levels under drought stress, and it was proposed that they play a role in the sunflower response to drought (Ouvrard et al., 1996; Cellier et al., 1998; Sarda et al., 1999; Gopalakrishna et al., 2001; Liu and Baird, 2003; Dezar et al., 2005; Herrera Rodriguez et al., 2007). Furthermore, they only showed expression in drought tolerant types when compared to drought sensitive genotypes (Roche et al., 2007). Expression of these genes was not confined to a single organ. However, gene *sdis* and Ha-RPS28 showed highest expression in fully expanded leaves and they were linked to the production of certain ACC oxidase antioxidant or dehydrins while HAS1 and HAS1.1 showed more expression in root when compared with leaves. A few genes were shown to effect the expression of other genes to induce drought tolerance. Manavella et al. (2006) found that plants over-expressing Hahb-4 were less sensitive to external ethylene and entered the senescence pathway later. Expression of this transcriptional factor has a major repressive effect on genes related to ethylene synthesis, such as ACO and SAM, and on genes related to ethylene signalling, such as ERF2 and ERF5.

Drought stress triggers the production of abscisic acid. A part from its differential effect on biomass partitioning (Rauf and Sadaqat, 2007b) it also mediates the expression of certain drought tolerant genes such as HaDhn2, *Sdis* (*sdi1*, *sdi5*, *sdi9*, *sdi6*, *sdi8*), Ha-RPS28, and Hahb-4 (Ouvrard et al., 1996; Cellier, 1998). However, Giordani et al. (1999) indicated the existence of two regulation pathways of HaDhn1a transcripts accumulation, an ABA-dependent and an ABA-independent one, which may have cumulative effects. Its expression was not uniform during day/night cycle and maximum HaDhn1 transcript accumulated during the mid day time (Cellier et al., 2000).

Genes related to drought stress such as dehydrins (Dhn1) have also been used to study the phylogenetic and genetic variability between cultivated and wild sunflower for this gene. The expressed protein showed diversification of biochemical properties between annual and perennial *Helianthus* species. However, cultivated sunflower contained lower genetic variability for dehydrin genes than wild sunflower (Giordani et al., 2003; Natali et al., 2003). It was also concluded that the stress responsive gene (Dhn1) can also be used to study the phylogeny of *Helianthus*.

The concept of DNA-based markers has revolutionized our ability to directly access any part of the plant genome, and has led to new opportunities such as screening a large number of segregating population for QTL's related to the drought tolerance without actually exposing them to drought and independence of plant growth stage. In nature, the vast majority of physiological traits are quantitative trait loci (QTL). Quantitative traits show continuous phenotypic distributions affected by a large number of loci and show significant interaction with environment (Tanksley, 1993). However, in sunflower very few studies have been carried out to determine the development of a molecular marker for QTL's related to drought tolerance (Jamaux et al., 1997; Hervé et al., 2001; Kiani et al., 2007b). Hervé et al. (2001) used the AFLP linkage map for the identification of QTL related to net photosynthesis, stomatal movements and water status (transpiration and leaf water potential). Using an AFLP linkage map, 19 QTL were detected explaining 8.8–62.9% of the phenotypic variance for each trait. Among these, two major QTL for net photosynthesis were identified on linkage group IX. One QTL co-location was found on linkage group VIII for stomatal movements and water status. Coincidental locations for QTL regulating photosynthesis, transpiration and leaf water potential were described on linkage group XIV. On the other hand, Kiani et al. (2007b) detected 24 QTLs under well-watered conditions, of which 5 (about 21%) were also detected in the water-stressed treatment. The percentage of phenotypic variance explained by the QTLs ranged from 6% to 29%. Among the eight QTLs detected for

OA, four of them (50%) were co-located with the QTLs for turgor potential ($\Psi(t)$) on linkage group IV (OA.4.1), with the QTL for osmotic potential at full turgor ($\Psi(sFT)$) in well-watered RILs on linkage group VII (OA. 12.2) and with QTLs of several traits on linkage group V (OA.5.1 and OA.5.2). The four other QTLs for OA (50%) were very specific. However, they concluded that these QTLs were identified in greenhouse conditions and the usefulness of these QTLs for marker-assisted selection should therefore be evaluated under field conditions and validated in other genetic backgrounds. Similarly, Jamaux et al. (1997) identified RFLP and STS molecular markers of relative water loss and osmotic adjustment by RAPD bulked analysis.

REFERENCES

- Agele, S.O. (2003). Sunflower responses to weather variations in rainy and dry, cropping seasons in a tropical rainforest zone. *International Journal of Biotronics* 32, 17–33.
- Alexandrov, V., Koteva, V. (2001). Attack on sunflower by charcoal rot (*Sclerotium bataticola* T.) under the influence of climate and mineral fertilization. *Bulgarian Journal of Agricultural Science* 7(3), 271–274.
- Alza, J.O., Fernandez-Martinez, J.M. 1997. Genetic analysis of yield and related traits in sunflower (*Helianthus annuus* L.) in dry land and irrigated environments. *Euphytica* 95, 243–251.
- Andrich, G., Balzini, S., Zinnai, A., Silvestri, S., Galoppini, C. (1996). The effect of drought stress on some characteristics of sunflower seeds. *Agricoltura Mediterranea* 126 (3), 285–291.
- Angadi, S.V., Entz, M.H. (2002). Root System and water use patterns of different height sunflower cultivars. *Agronomy Journal* 94, 136–145.
- Badr, N.M., Thalooth, A.T., Mohamed, M.H. (2004). Effect of foliar spraying with the nutrient compound "Streen" on the growth and yield of sunflower plants subjected to water stress during various stages of growth. *Bulletin of the National Research Centre Cairo* 29(4), 427–439.
- Baldini, M., Vannozzi, G.P., Turi, M., Gomez-Sachez, D. (1997). Results of a physiological selection approach to improve drought resistance in sunflower. *Genetika-a-Slechtenti* 33: 3, 181–195.
- Baldini, M., Cecconi, F., Cecchi, A., Martorana, F., Vannozzi, G.P., Benventi, A. (1992). Drought resistance in sunflower. Factor affecting yield and their variability under stress. *Proceedings 13th International Sunflower Conference, 8-12 September, Pisa, Italy*. International Sunflower Association, Paris, France, 513–521.
- Baldini, M., Vannozzi, G.P. (1998). Agronomic and physiological assessment of genotypic variation for drought tolerance in sunflower genotypes obtained from a cross between *H. annuus* and *H. argophyllus*. *Agricultural Medicine* 128, 232–240.
- Baldini, M., Vannozzi, G.P. (1999). Yield relationships under drought in sunflower genotypes obtained from a wild population and cultivated sunflowers in rain-out shelter in large pots and field experiments. *Helia* 22 (30), 81–96.
- Baldini, M., Vannozzi, G.P., Berville, A., Tersac, M. 1999. Yield relationships under drought in sunflower genotypes obtained from a wild population and cultivated sunflowers in rain-out shelter in large pots and field experiments. *Helia* 22 (30), 81–96.
- Basal, H., Smith, C.W., Thaxton, P.S., Hemphill, J.K. 2005. Seedling drought tolerance in upland cotton. *Crop Science* 45, 766–771.
- Beck, D.L., Vasal, S.K., Crossa, J., 1990. Heterosis and combining ability of CIMMYT's tropical early and intermediate maturity maize germplasm. *Maydica*, 35, 279–285.
- Blum, A. (1979). Genetic improvement for drought resistance in crop plants: A case for sorghum. In: Musell, H., Staples, R.C. (Eds.) *Stress physiology in crop plants*, 430–445.

- Bosnjak, D.J. (2004). Drought and its relation to field crops production in Vojvodina Province (Serbia, Serbia&Montenegro). *Zbornik-radova-Naucni-institut-za-ratarstvo-i-povrtarstvo (Serbia and Montenegro)* 40, 45–55.
- Boyer, J.S. (1982) Plant productivity and environment. *Science* 218, 443–448.
- Campos, H., Cooper, M., Habben, J.E., Edmeades, G.O., Schussler, J.R. (2004) Improving drought tolerance in maize: a view from industry. *Field Crops Research* 90, 19–34.
- Ceccarelli, S., Acevedo, E., Grando, S. (1991). Breeding for yield stability in unpredictable environments: Single traits interaction between traits architecture of genotypes. *Euphytica* 56, 159–185.
- Ceccarelli, S., Grando, S., Impiglia, A. (1998). Choice of selection strategy in breeding barley for stress environments. *Euphytica* 103, 297–318.
- Cechin, I., Rossi, S.C., Oliveira, V.C., Fumis, T.F. (2006). Photosynthetic responses and proline content of mature and young leaves of sunflower plants under water deficit. *Photosynthetica* 44(1), 143–146.
- Cellier, F., Conejero, G., Breitler, J.C., Casse, F. (1998). Molecular and physiological responses to water deficit in drought-tolerant and drought-sensitive lines of sunflower. Accumulation of dehydrin transcripts correlates with tolerance. *Plant Physiology* 116(1), 319–328.
- Cellier, F., Conejero, G., Casse, F. (2000). Dehydrin transcript fluctuations during a day/night cycle in drought-stressed sunflower. *Journal of Experimental Botany* 51(343), 299–304.
- Chimenti, C.A., Hall, A.J. (1993). Genetic variation and changes with ontogeny of osmotic adjustment in sunflower (*Helianthus annuus* L.) *Euphytica* 71 (3), 201–210.
- Chimenti, C.A., Hall, A.J. (1994). Responses to water stress of apoplastic water fraction and bulk modulus of elasticity in sunflower (*Helianthus annuus* L.) genotypes of contrasting capacity for osmotic adjustment. *Plant and Soil* 166 (1), 101–110.
- Chimenti, C.A., Pearson, J., Hall, A.J. (2002) Osmotic adjustment and yield maintenance under drought in sunflower. *Field Crops Research* 75 (2-3), 235–246.
- Connor, D.J., Sadras, V.O. (1992). Physiology of yield expression in sunflower. *Field Crops Research* 30, 333–389.
- Conroy, J.P., Virgona, J.M., Smillie, R.M., Barlow, E.W. (1988). Influence of drought acclimation and CO₂ enrichment on osmotic adjustment and chlorophyll a fluorescence of sunflower during drought. *Plant Physiology* 86, 1108–1115.
- Cook, C.G. (1985). Identifying root traits among MAR and non-MAR cotton, *Gossypium hirsutum* L. cultivars that relate to performance under limited moisture conditions. *Master's thesis submitted to A&M University, College Station, TX.*
- Dezar, C.A., Gago, G.M., Gonzalez, D.H., Chan, R.L. (2005). Hahb-4, a sunflower homeobox-leucine zipper gene, is a developmental regulator and confers drought tolerance to *Arabidopsis thaliana* plants. *Transgenic Research* 14(4), 429–440.
- Dragovic, S., Maksimovic, L. (1995). Drought phenomenon and impact on crop yields in the Vojvodina Province, Yugoslavia. *Proceedings of the international workshop on Drought in the Carpathian Region, Budapest*, 207–217.
- Edmeades, G.O., Bänziger, M. (1997). Conclusion: What have we learned and where do we go? In: Edmeades, G.O., Bänziger, M., Mickelson, H.R., Penavaldiva, C.B. (Eds.), *Developing Drought and Low N-Tolerant Maize. Proceedings of a Symposium, March 25-29, 1996, CIMMYT, El Batan, Mexico.* Mexico, D.F., 557–563.
- Falconer, D.S. (1990) Selection in different environments, effects on environmental sensitivity (reaction norm) and on mean performance. *Genetics Research* 56, 57–70.
- Fereres, E. Gimenez, C., Fernandez, J.M. (1986). Genetic variability in sunflower cultivars under drought. I. Yield relationships. *Australian Journal of Agricultural Research* 37, 573–582.

- Fischer R.A., Wood, J.T. (1979). Drought resistance in spring wheat cultivars. III. Yield association with morpho-physiological traits. *Australian Journal of Agricultural Research* 30, 1001-1020.
- Fischer, R.A., Turner, N.C. (1978). Plant productivity in the arid and semi-arid zone. *Annual Review of Plant Physiology* 29, 277-317.
- Fischer, R.A., Maurer, R. (1978). Drought resistance in spring wheat cultivar: I. Grain yield responses. *Australian Journal of Agricultural Research* 29, 897-912.
- Gajri, P. R., Gill, K.S., Chaudhary, M.R., Singh, R. (1997). Irrigation of sunflower (*Helianthus annuus*) in relation to tillage and mulching. *Agricultural Water Management* 34 (2), 149-160.
- Germ, M., Berčič, O.U., Ačko, D.K. (2005). The response of sunflower to acute disturbance in water availability. *Acta Agriculturae Slovenica* 85, 135-141.
- Gimenez, C., Fereres, E. (1986). Genetic variability in sunflower cultivars under drought II. Growth and water relations. *Australian Journal of Agricultural Research* 37, 573-582.
- Giordani, T., Natali, L., Cavallini, A. (2003). Analysis of a dehydrin encoding gene and its phylogenetic utility in helianthus. *Theoretical and Applied Genetics* 107(2), 316-325.
- Giordani, T., Natali, L., D'Ercole, A., Pugliesi, C., Fambrini, M., Vernieri, P., Vitagliano, C., Cavallini, A. (1999). Expression of a dehydrin gene during embryo development and drought stress in ABA-deficient mutants of sunflower (*Helianthus annuus* L.). *Plant Molecular Biology* 39(4), 739-748.
- Gomes, E.M., Ungaro, M.R.G., Vieira, D.B. (2005). Sunflower root system under water stress. *Embrapa Soja* 261, 15-18.
- Gopalakrishna, R., Ganesh, K., Krishnaprasad, B.T., Mathew, M.K., Kumar, M.U., Kumar, G. (2001). A stress-responsive gene from groundnut, Gdi-15, is homologous to flavonol 3-O-glucosyltransferase involved in anthocyanin biosynthesis. *Biochemical and Biophysical Research Communications* 284(3), 574-579.
- Griveau, Y., Serieys, H. Cleomene, J., Belhassen, E. (1998). Field evaluation of sunflower genetic resources in relation to water supply. *Czech Journal of Genetics and Plant Breeding* 34(1), 11-16.
- Hassan, N.S., Shaaban, L.D., Hashem, E.S.A., Seleem, E.E. (2004). In vitro selection for water stress tolerant callus line of *Helianthus annuus* L. cv. Myak. *International Journal of Agriculture and Biology* 6(1), 13-18.
- Herrera Rodriguez M.B., Perez Vicente, R., Maldonado, J.M. (2007). Expression of asparagine synthetase genes in sunflower (*Helianthus annuus*) under various environmental-stresses. *Plant Physiology and Biochemistry* 45(1), 33-38.
- Hervé, D., Fabre, F., Berrios, E.F., Leroux, N., Chaarani, G.A., Planchon, C., Sarrafi, A., Gentzbittel, L. (2001). QTL analysis of photosynthesis and water status traits in sunflower (*Helianthus annuus* L.) under greenhouse conditions. *Journal of Experimental Botany* 52(362), 1857-1864.
- Iqbal, N., Ashraf, M., Ashraf, M.Y., Azam, F. (2005). Effect of exogenous application of glycinebetaine on capitulum size and achene number of sunflower under water stress. *International Journal of Biology and Biotechnology* 2(3), 765-771.
- Jamaux, I., Steinmetz, A., Belhassen, E., Farrar, J. (1997). Looking for molecular and physiological markers of osmotic adjustment in sunflower. Putting plant physiology on the map: genetic analysis of development and adaptive traits. *Proceedings of the Second New Phytologist symposium, held in Bangor, UK, April 1997.* 137(1), 117-127.
- Kang, S.Z., Zhang, J.H. (1997). Hydraulic conductivities in soil-root system and relative importance at different soil water potential and temperature. *Transactions of Chinese Society of Agricultural Engineers* 13 (2), 76-81.

- Karaata, H. (1991). Water-production functions of sunflower under Kırklareli conditions. Village Affair Research Institute, Kırklareli Turkey, *Report No 24, (PhD Thesis)*. (in Turkish).
- Karam, F., Lahoud, R., Masaad, R., Kabalan, R., Breidi, J., Chalita, C., Roupheal, Y. (2007). Evapotranspiration, seed yield and water use efficiency of drip irrigated sunflower under full and deficit irrigation conditions. *Agricultural Water Management* 90(3), 213–223.
- Karamanos, A.J., Papatheohari, A.Y. (1999). Assessment of drought resistance of crop genotypes by means of the water potential index. *Crop Science* 39, 1792–1797.
- Khaliq, A. (2004). Irrigation and nitrogen management effects on productivity of hybrid sunflower (*Helianthus annuus* L.). *Ph.D. Thesis. University of Agriculture, Faisalabad*.
- Kiani, S.P., Talia, P., Maury, P., Grieu, P., Heinz, R., Perrault, A., Nishinakamasu, V., Hopp, E., Gentzbittel, L., Paniego, N., Sarrafi, A. (2007a). Genetic-analysis of plant water status and osmotic adjustment in recombinant inbred lines of sunflower under 2 water treatments. *Plant Sciences* 172(4), 773–778.
- Kiani, S.P., Grieu, P., Maury, P., Hewezi, T., Gentzbittel, L., Sarrafi, A. (2007b). Genetic variability for physiological traits under drought conditions and differential expression of water stress-associated genes in sunflower (*Helianthus annuus* L.). *Theoretical and Applied Genetics* 114 (2), 193–207.
- Korrell, M., Brahm, L., Friedt, W., Horn, R. (1996). Interspecific and intergeneric hybridization in sunflower breeding. II. Specific uses of wild germplasm. *Plant Breeding Abstracts* 66(8), 1081–1091.
- Krizmanic, M., Liovic, I., Mijic, A., Bilandzic, M., Krizmanic, G. (2003). Genetic potential of OS sunflower hybrids in different agroecological conditions. *Sjemenarstvo*. 20(5/6): 237–245.
- Lambrides, C.J., Chapman, S.C., Shorter, R. (2004). Genetic variation for carbon isotope discrimination in sunflower: association with transpiration efficiency and evidence for cytoplasmic inheritance. *Crop Science* 44, 1642–1653.
- Liu, X., Baird, W.V. (2003). The ribosomal small-subunit protein S28 gene from *Helianthus annuus* (Asteraceae) is down-regulated in response to drought, high salinity, and abscisic acid. *American Journal of Botany* 90(4), 526–531.
- Longenberger, P.S., Smith, C.W., Thaxton, P.S., McMichael, B.L. (2006). Development of a screening method for drought tolerance in cotton seedlings. *Crop Science* 46, 2104–2110.
- Lorens, G.F., Bennet, J.M., Loggale, L.B. (1987). Differences in drought resistance between two corn hybrids. II. Component analysis and growth rates. *Agronomy Journal* 79, 808–813.
- Manavella, P.A., Arce, A.L., Dezar, C.A., Bitton, F., Renou, J.P., Crespi, M., Chan, R.L. (2006). Cross-talk between ethylene and drought signaling pathways is mediated by the sunflower Hahb-4 transcription factor. *Plant Journal* 48(1), 125–137.
- Maury, P., Berger, M., Mojayad, F., Planchon, C. (2000). Leaf water characteristics and drought acclimation in sunflower genotypes. *Plant and Soil* 223 (1–2), 153–160.
- Meo, A.A., Baig, F., Khan, Z., Naseem, W. (1999). Effect of urea and sporadic drought on dry matter and yield of sunflower (*Helianthus annuus* L.). *Sarhad Journal of Agriculture* 15(5), 443–446.
- Mohan, G.S.R., Seetharam, A. (2005). Studies on genetic relationships among cultivated and wild sunflowers through RAPD markers. *Cytologia* 70 (3), 267–273.
- Natali, L., Giordani, T., Cavallini, A. (2003). Sequence Variability of a dehydrin gene within *Helianthus annuus*. *Theoretical and Applied Genetics* 106 (5), 811–818.
- O'Toole, J.C., Bland, W.L. (1987). Genotypic variation in crop plant root systems. *Advances in Agronomy* 41, 91–145.

- Ouvrard, O., Cellier, F., Ferrare, K., Tusch, D., Lamaze, T., Dupuis, J.M., Casse-Delbart, F. (1996). Identification and expression of water stress- and abscisic acid-regulated genes in a drought-tolerant sunflower genotype. *Plant Molecular Biology* 31(4), 819–829.
- Pace, P.F., Cralle, H.T., El Halawaney, S.H.M., Cothorn, J.T., Sensemen, S.A. (1999). Drought induced changes in shoot and root growth of young cotton plants. *Journal of Cotton Science* 3, 183–187.
- Perniola, M. (1994). Ecophysiological parameters and water relations of sweet sorghum, cotton and sunflower during drought cycles. *International Conference on Land and Water Resources Management in the Mediterranean Region, Valenzano, Bari, Italy 4–8 September*. 5, 97–115.
- Petcu, E., Arsintescu, A., Stanciu, D. (2001). The effect of drought stress on fatty acid composition in some Romanian sunflower hybrids. *Romanian Agricultural Research* 15, 39–42.
- Petcu, G.H., Petcu, E. (2006). Effect of cultural practices and fertilizers on sunflower yields in long term experiments. *Helia* 29(44), 135–144,
- Plaut, Z., Carmi, A., Grava, A. (1996). Cotton root and shoot response to subsurface drip irrigation and partial wetting of the upper soil profile. *Irrigation Science* 16, 107–113.
- Prior, S.A., Rogers, H.H., Runion, G.B., Kimball, B.A., Mauney, J.R., Lewin, K.F., Nagy, J., Hendry, G.R. (1995). Free-air carbon dioxide enrichment of cotton: Root morphological characteristics. *Journal of Environmental Quality* 24, 678–683.
- Qadir, G. (2006) Morpho-genetic expression of sunflower under varied temperature and moisture regimes. *PhD thesis, University of Arid Agriculture, Rawalpindi*.
- Rachidi, F., Kirkham, M.B., Stone L.R., Kanemasu, E.T. (1993). Soil water depletion by sunflower and sorghum under rainfed conditions. *Agricultural Water Management* 24 (1), 49–62.
- Rauf, S., Sadaqat, H.A., Khan, I.A. (2008a). Effect of moisture regimes on combining ability variations of seedling traits in sunflower (*Helianthus annuus* L.). *Canadian Journal of Plant Science* 88, 323–329.
- Rauf, S., Sadaqat, H.A., Naveed, A. (2008b). Effect of moisture stress on combining ability variation for bird resistance traits in sunflower (*Helianthus annuus* L.). *Pakistan Journal of Botany* (submitted).
- Rauf, S., Sadaqat, H.A. (2007a). Sunflower (*Helianthus annuus* L.) germplasm evaluation for drought tolerance. *Communications in Biometry and Crop Science* 2 (1), 8–16.
- Rauf, S., Sadaqat, H.A. (2007b). Effects of varied water regimes on root length, dry matter partitioning and endogenous plant growth regulators in sunflower (*Helianthus annuus* L.). *Journal of Plant Interactions* 2 (1), 41–51.
- Rauf, S., Sadaqat, H.A. (2008a) Identification of physiological traits and genotypes combined to high achene yield in sunflower (*Helianthus annuus* L.) under contrasting water regimes. *Australian Journal of Crop Science* 1(1), 23–30.
- Rauf, S., Sadaqat, H.A. (2008b). Effect of osmotic adjustment on root length and dry matter partitioning in sunflower (*Helianthus annuus* L.) under drought stress. *Acta Agriculturae Scandinavica, Section B. Soil and Plant Science* (article in press).
- Reddy, G.K.M., Dangi, K.S., Kumar, S.S., Reddy, A.V. (2003). Effect of moisture stress on seed yield and quality in sunflower, *Helianthus annuus* L. *Journal of Oilseeds Research* 20(2), 282–283.
- Reddy, G.S., Maruthi, V., Vanaja, M., Rao, D.G. (1998). Effect of moisture stress and management practices on productivity of rainfed sunflower (*Helianthus annuus*). *Indian Journal of Agronomy* 43(1), 149–153.
- Reddy, Y.A.N., Shaanker, R.U., Virupakshappa, K. (1995). Studies on the sunflower genotypes under moisture stress conditions. *Journal of Oilseeds Research* 12(2), 292–294.

- Richards, R.A. (2004). Defining selection criteria to improve yield under drought. *Plant Growth Regulation* 157–166.
- Roche, J., Hewezi, T., Bouniols, A., Gentzbittel, L. (2007). Transcriptional profiles of primary metabolism and signal transduction-related genes in response to water-stress in field-grown sunflower genotypes using a thematic cDNA microarray. *Planta* 226(3), 601–617.
- Sarda, X., Tusch, D., Ferrare, K., Cellier, F., Alcon, C., Dupuis, J.M., Casse, F., Lamaze, T. (1999). Characterization of closely related delta-TIP genes encoding aquaporins which are differentially expressed in sunflower roots upon water deprivation through exposure to air. *Plant Molecular Biology* 40(1), 179–191.
- Schneiter, A.A. (1992). Production of semidwarf and dwarf sunflower in the northern Great Plains of the United States. *Field Crops Research* 30, 391–401.
- Seiler, G.J. (1994). Primary and lateral root elongation of sunflower seedlings. *Environmental and Experimental Botany* 34, 409–418.
- Seiler, G.J. (2007). Wild annual *Helianthus anomalus* and *H. deserticola* for improving oil content and quality in sunflower. *Industrial Crops and Products* 25(1), 95–100.
- Serieys, H. (1997). Use of wild relatives in sunflower improvement. *Oleoscope* 42, 14–17.
- Sgherri, C.L.M., Pinzino, C., Navari-Izzo, F. (1996). Sunflower seedlings subjected to increasing stress by water deficit: changes in O₂ production related to the composition of thylakoid membranes. *Plant Physiology* 196(3), 446–452.
- Sinclair, T.R., Ludlow, M.M. (1985). Who taught plants thermodynamics? The unfulfilled potential of plant water potential. *Australian Journal of Plant Physiology* 12, 213–217.
- Singh, B., Mai-Kodomi, Y., Terao, T. (1999) A simple screening method for drought tolerance in cowpea. *Indian Journal of Genetics* 59, 211–220.
- Sinha, H.A. (1996). Breeding for abiotic resistance. In: Singh, B.D. (Ed.) *Plant Breeding-Principles and Methods*. Kalyani Publishers, Ludhiana, Punjab, India.
- Sobrado, M.A., Turner, N.C. (1986). Photosynthesis, dry matter accumulation and distribution in the wild sunflower *Helianthus petiolaris* and the cultivated sunflower *Helianthus annuus* as influenced by water deficits. *Acta Oecologia* 69, 181–187.
- Stockle, C.O., Kiniry, K.R. (1990). Variability in crop radiation-use efficiency associated with vapour-pressure deficit. *Field Crops Research* 25, 171–181.
- Swindale, L.D., Bidinger, F.R. (1981). The human consequences of drought and crop research priorities for their alleviation. In: Pleg, L.G., Aspinall, D. (Eds.) *The Physiology and Biochemistry of Drought Resistance in Plants*. New York, Academic Press. USA, 1–13.
- Tahir, M.H.N., Muhammad, I., Hussain, M.K. (2002). Evaluation of sunflower (*Helianthus annuus* L.) inbred lines for drought tolerance. *International Journal of Agriculture and Biology* 4(3), 398–400.
- Tanksley, S.D. (1993). Mapping polygenes. *Annual Review of Genetics* 27, 205–233.
- Terbea, M., Vranceanu, A.V., Petcu, E., Craiciu, D.S., Micut, G. (1995). Physiological response of sunflower plants to drought. *Romanian Agricultural Research* 3, 61–67.
- Tollenaar, M., Wu, J. (1999). Yield improvement in temperate maize is attributable to greater stress tolerance. *Crop Science* 39, 1597–1604.
- Tomar, S.M.S., Kumar, G.T. (2004). Seedling survivability as a selection criterion for drought tolerance in wheat. *Plant Breeding* 123, 392–394.
- Turhan, H., Baser, I. (2004). In vitro and In vivo water stress in sunflower (*Helianthus annuus* L.). *Helia* 27, 227–236.
- Unger P.W., Howell, T.A. (1999). Agricultural water conservation- A global perspective. In: Khirkharm, M.B. (Ed.) *Water use in crop production*, Food Products Press, Binghamton, NY.
- USDA (2005). *Agricultural weather facility. Global crop production review*. 1–5.

- Vannozi, G.P., Baldini, M., Gomez-Sanchez, D. (1999). Agronomic trait useful in sunflower for drought resistance. *Helia* 22(30), 97-124.
- Vasal, S.K., Cordova, H., Beck, D.L., Edmeades, G.O. (1997). Choices among breeding procedures and strategies for developing stress tolerant maize germplasm. In: Edmeades, G.O., Bänziger, M., Mickelson, H.R., Pena-Valdiva, C.B. (Eds.), *Developing drought and low N tolerant maize*.
- Vijay, K.L. (2004). *Irrigation strategies for crop production under water scarcity*. International Commission on Irrigation and Drainage, New Delhi 110-021, 89-109.
- Yordanov, I., Velikova, V., Tsonev, T. (2000). Plant responses to drought, acclimation, and stress tolerance. *Photosynthetica* 38, 171-186.