

EXOGENOUS APPLICATION OF ABSCISIC ACID FOR DROUGHT TOLERANCE IN SUNFLOWER (*HELIANTHUS ANNUUS L.*): A REVIEW

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ABSTRACT

Sunflower has been successfully cultivated over a widely scattered geographical area in the world and also emerged as a crop, which has ability to adopt in a variety of environmental conditions. Sunflower is high yielding oilseed crop and has the potential to bridge up the gap existing between consumption and domestic production of edible oil. Water is essential at every stage of plant growth and development. Water deficit reduces crop yield regardless of the growth stage at which it occurs in field crops including sunflower. The productivity and spatial distribution of agronomic and horticultural crop plants of commercial importance are severely restricted by a variety of environmental factors. Among these factors, drought and salt play very significant role in reducing agricultural production. Water deficit effect is much pronounced at the vegetative and flowering stage. In sunflower water shortage at the flowering stage reduced yield by 29 %. Dwarf cultivars of sunflower have higher water potential i.e. least water stress as compared to intermediate and long stature cultivars. This is due to difference in canopy architecture and root penetration depth among different stature sunflower cultivars. Tall stature cultivars produced more leaf area, aerial biomass and deeper root system so they transpired more water. Major effect of drought in plant is reduction in photosynthesis, which is due to decrease in leaf expansion, impaired photosynthetic machinery, leaf senescence and finally reduction in assimilates production and partitioning. Sunflower exhibits a large varietal difference for osmotic adjustment in response to water shortage. Drought tolerance has been observed in all plant species, but its extent varies from species to species. One way to ensure future food needs of the increasing world populations should involve better use of water by the development of crop varieties those require lesser amounts of water and more tolerant to water shortage. Water deficit in root zone causes an increase in rate of root respiration which leads to an imbalance in the utilization of carbon resources, decrease in production of adenosine triple phosphate (ATP) and an increase in production of reactive oxygen species (ROS). Genotypic variation for osmotic adjustment has also been reported in sunflower. The dwarf sunflower cultivars have initiated osmotic adjustment earlier than intermediate and large stature cultivars which indicated better osmotic response of dwarf cultivars. The delay in osmotic adjustment in intermediate and tall stature sunflower genotypes is due to faster root penetration and more water extraction from deeper layer of soil. So, tall stature sunflower cultivars face water stress later as compared to short stature. Three growth stages of sunflower as heading, flowering and milking are sensitive to water shortage. In limited irrigation application study, water applied at different growth stages of sunflower significantly decreased seed yield, particularly during three growth periods: heading, flowering and milking. The role of abscisic acid (ABA) as plant stress hormone is well established. Under drought condition, ABA is synthesized in plant tissue and sent to the guard cell as a stress signal. Here ABA causes stomatal closure, which improves the water relations of plant. ABA entering a leaf can be metabolized rapidly. In response of water deficit, ABA begins to increase markedly in plant leaf tissues and to a lesser extent, in other tissues including roots. This leads to stomatal closure and decreased transpiration. It also inhibits shoot growth and root growth appears to be promoted which increased the water supply. It helps in promoting drought tolerance, both from the use of exogenous application to intact plants and from the measurement of the endogenous ABA concentration. In response to exogenous application of ABA in drought tolerant line of sunflower dehydrin protein accumulated in vegetative tissue. Dehydrin protects cytosolic structures from the deleterious effects of cellular dehydration. ABA plays a critical role in regulating plant water status through guard cells and growth as well as by induction of genes that encode enzymes and other proteins which create cellular dehydration tolerance. In plants stomata response to soil drying is mediated by ABA, originating from roots and transported to the shoot via the transpiration stream. ABA under drought is produced in dehydrated roots, transported to the xylem and regulates stomatal opening and leaf growth in the shoots. Stomata respond to the concentration of ABA in the guard cell apoplast. Screening of sunflower cultivars under drought applied at different crop growth stages and exogenous application of ABA will defiantly help in saving water for successful crop production.

Key Words: Sunflower cultivars, drought, growth stages, ABA application.

INTRODUCTION

Pakistan is chronically deficient in the production of edible oil and situation is getting worse day by day with alarming increase in population growth rate along with preferences of people for edible oils and deficient local production (Asif *et al.*, 2001). Pakistan is the third largest importer of edible oil in the world and spends huge foreign exchange on the import of edible oil, which is second to that spent on the import fuel oil. The consumer's demand has steadily increased from 0.3 million tons to 2.764 million tons during the last two and half decades with almost stagnant domestic production of 0.857 million tons. At present indigenous oil seed production meets only 27% of domestic requirement, while the remaining 73% is met through imports (Govt. of Pakistan, 2009a).

Domestic oil production during 2007-08 (July–March) was 0.833 million tons, while 2.23 million tons of edible oil was imported and 0.349 million tons recovered from imported oil-seeds. The total availability of edible oil from all sources amounted to be 3.066 million tons. The import of vegetable oils in increasing amounts is imposing a severe drain on national economy. The import bill of edible oil was Rs. 50 billion in 2006-07 and has risen up to Rs. 84 billions 2008-09 (Govt. of Pakistan, 2009b). All this necessitates concentrating on more efforts to increase domestic edible oil production to reduce drain on the foreign exchange reserves.

Edible oilseed crops in Pakistan can be classified as traditional (rapeseed, mustard, groundnut, sesame, cotton and non traditional (sunflower, soybean and safflower). Rapeseed and mustard oil is not regular cooking oil due to the presence of higher concentrations of erucic acid and thioglucoside could be more than 5% in oil blending for ghee manufacturing. Cottonseed contributes about 70-75% to the total domestic oil production only as a by-product. Cotton is mainly grown for fiber purpose and its oil content and fiber are negatively correlated with each other (Govt. of Pakistan, 2009b). Among the non-traditional oilseed crops sunflower can play an important role narrowing the wide gap between production of edible oils in the country and its import (Khan *et al.*, 2003). In Pakistan, area, production and yield per unit area of sunflower have increased tremendously with the passage of time. During 2007-08 area under sunflower cultivation was 1130 thousand acres with 683 thousand tons of seed yield and 264 thousand tons of oil production. During 2008-09 area of sunflower was provisionally estimated as 1250 thousand acres with 755 thousand tons seed and 287 thousand tons oil production (Govt. of Pakistan, 2009b).

As a plant of economic importance, sunflower seed contains 25-48% oil and 20-27% protein (Hatam and Abbasi, 1994). Its oil is called premium oil because of high %age of poly-unsaturated fatty acids (60%);

including oleic acid (16.2%) and linoleic acid (72.5%), which help to control cholesterol in blood (Satyabrata *et al.*, 1988). Sunflower oil is quite palatable and contains soluble vitamins A, D, E and K. It is also used in manufacturing of margarine. Sunflower cake is used as cattle feed.

Sunflower has been successfully cultivated over a widely scattered geographical area in the world and also emerged as a crop, which has ability to adopt in a variety of environmental conditions (Beard and Geng, 1982). Sunflower is high yielding oilseed crop and has the potential to bridge up the gap existing between consumption and domestic production of edible oil. Furthermore, it is a short duration crop (90-120 days) and can be grown twice a year. It fits well in existing cropping system and can be grown without replacing any major crop. Water is essential at every stage of plant growth and development. Water deficit reduces crop yield regardless of the growth stage at which it occurs in field crops including sunflower (Jensen and Mogenson, 1984; Hussain, 2010). The productivity and spatial distribution of agronomic and horticultural crop plants of commercial importance are severely restricted by a variety of environmental factors. Among these factors, drought and salt play very significant role in reducing agricultural production (Boyer, 1982). In the face of a global scarcity of water resources, drought has already become a primary factor in limiting crop production. Sunflower genotypes have performed differently in various environmental conditions. Different environmental conditions are required to evaluate the good yielding, better adaptive and stable crops varieties (Luquez *et al.*, 2002; Prusti *et al.*, 1999). Under drought sunflower head diameter, achene's yield, seed weight per head, 1000-seed weight, oil content and oil yield are significantly decreased (Jasinkas, 1999; Kazi *et al.*, 2002). At present, around 18% of the global farmland is irrigated (more than 240 million hectares) and up to 40% of the global food supply is produced on this land (Somerville and Briscoe, 2001).

Diminishing water resources in the world emphasize to limit irrigation for field crops. In some areas of the world the available water supply is not sufficient to produce the maximum yield on the irrigable area. While in other regions, the available moisture for irrigation is already regulated and requires deficit irrigation. For many surface water conservation projects, the annual supply of irrigation water is limited by reservoir capacity and the annual reservoir inflow. These adverse water available conditions highlight the need for deficit irrigation management for different crops (Martin *et al.*, 1989).

The role of abscisic acid (ABA) as plant stress hormone is well established. Under drought condition, ABA is synthesized in plant tissue and sent to the guard cell as a stress signal. Here ABA causes stomatal closure,

which improves the water relations of plant. ABA entering a leaf can be metabolized rapidly (Loveys, 1984; Gowing *et al.*, 1993; Jia *et al.*, 1996). In sunflower, stomatal control depends on the concentration of ABA in xylem sap (Tardieu *et al.*, 1996). Stomatal closure due to response of water shortage is one of the drought-adaptation mechanisms in plant. Physiological observations associated with the varieties differences in stress tolerance in field crops have been reported (Moons *et al.*, 1995; Pelah *et al.*, 1997) and ABA also produced genetic difference in drought tolerant and drought sensitive plants (Ouvrard *et al.*, 1996). Varietal differences in tolerance may be associated with increase of ABA in response to various environmental stresses. This includes drought tolerance of maize (Pekic and Quarrie, 1987), chilling tolerance of rice seedlings (Lee *et al.*, 1993) and salt tolerance of rice (Moons *et al.*, 1995). In wheat growth of dwarf stature cultivars (Dariel) is less sensitive to constant exogenous application of ABA than that of tall isolines (Bet Hashita) (Blum *et al.*, 1997).

Sunflower commercial cultivation: Sunflower (*Helianthus annuus* L.) is one of the important oil seed crops in the world. It originated in North America. Sunflower was “camp follower” of western Native American tribes who had domesticated the crop (possibly 1000 BC) and then took it coastward and southward of North America (Weiss, 2000). Firstly Europeans watched its cultivation at many places from Southern Canada to Mexico. It was first introduced in Europe through Spain, and spread in Europe as a curiosity until it approached to Russia where it was readily adapted. After the World War II high oil containing sunflower lines from Russia were introduced in America. It was the production of male sterile and restorer gene system that made hybrid cultivation feasible and increased commercial interest in sunflower and its use as an oil birdseed crop and human snack food crop.

Sunflower morphology: It is an annual, erect, broad leaf plant having strong, prolific and laterally spread tap root system. Stem is round in early season and becomes angular and woody later in the season. It normally remains un-branched. Leaves of sunflower are phototropic and follow the sun rays with a lag of 12° behind the sun azimuth. This feature has been contributed to enhance light interception and possibly increased photosynthesis (Putnam *et al.*, 1990).

The Sunflower head is made up of 1,000 to 2,000 individual flowers joined at a common receptacle. It has ligulate ray flowers around circumference which are without stamens and pistils, while the remaining flowers are perfect. Anthesis starts at the periphery and approach to the centre of the head.

In temperate regions, sunflower needs approximately 11 days from planting to emergence, 33 days from emergence to head formation, 27 days from

head visible to first anther formation, 8 days from first to last anther and 30 days from last anther to crop maturity. Varietal differences in maturity have been associated with changes in vegetative period before the head become visible.

Drought: Water is very essential for plant growth and makes up 75 to 95 percent of plant tissue. A vast amount of water moves throughout the plant daily. Plants use water and carbon dioxide to form sugars and complex carbohydrates. Water acts as a carrier of nutrients and also a cooling agent. It also provides an element of support through turgor and as an intercellular reaction medium (Ashraf and Harris, 2005).

Drought can be defined as an extended period of deficient rainfall relative to the statistical mean for a region. Drought can also be defined according to meteorological, hydrological or agricultural criteria. Meteorological drought is qualified by any significant deficit of precipitation, hydrological drought is manifested as reduced river and stream flow and critically deep ground water tables, while an agricultural drought indicates extended dry period that results in crop stress and harvest reduction. The impact of drought on agriculture is due to the shortage of moisture in the soil, when the moisture in the soil is no longer sufficient to meet the needs of growing crops. It results from a lack of input of moisture in soil from rainfall or irrigation to an extended period.

Among the environmental stress factors one of the most widely limiting for crop production on global basis is water. According to one estimate, around 28 percent of the world's land is too dry to support vegetation (Kramer and Boyer, 1995). On global basis, water is a paramount factor to determine the distribution of species, and the responses and adaptation of species to water stress are critical for their success in any environmental niche and for their use and productivity in agricultural ecosystem. Severe droughts occurred periodically in several major food producing countries, having far-reaching impacts on global food production and supply. The global production of grain has, in some years, been reduced by 5 percent or more as a result of severe droughts in key countries (Wisner and Chase, 1984). It has been estimated that droughts cause an average annual yield loss of 17 percent in the tropics (Edmeades *et al.*, 1999), but losses can be much more severe and total crop failure is also possible.

The world human population is expected to reach 8.0 billion by 2025 and 8.9 billion by 2050 (FAO, 2006). About 80 million people are being added to the population total each year and 97 percent of the predicted population growth will take place in the developing countries. It is projected that there is need to double world food production in order to feed 8.0 billion people by 2025. This will certainly place more pressure on the

environment. The developing countries, in particular, are confronted with severe food security challenges. With a severe limit to the amount of unused land available to bring in to cultivation, improving crop yields in both normal and less productive soils under limited water supply is an utter requirement to satisfy future world food needs.

Environmental stresses represent a major constraint to meet the world food demand. There are relatively few stress free areas where crops may approach their potential yields. For instance, up to 45% of the world agricultural lands are subject to continuous or frequent drought, wherein 38% of the world human population resides (Bot *et al.*, 2000). In the face of a global scarcity of water resources, drought has already become a primary factor in limiting crop production worldwide. Water-limited crop production depends on the intensity and the pattern of drought which vary from year to year. In some sub-tropical countries like Pakistan, however, there is a high probability that crop water deficits increase in severity as the season progresses, due to lack of rainfall and to the high evaporative demand (Ashraf and Foolad, 2006).

The severity of water shortage imposed on field crops also depends on the susceptibility of crops during different stages of their development. The general effects of drought on plant growth are well known. When soil moisture is deficient, crop establishment may be reduced, plant growth limited, normal development patterns disrupted and eventually, final yield is lowered (Manivannan *et al.*, 2007; Sankar *et al.*, 2007).

Abiotic stresses are considered to be the main source (71 %) of yield reductions (Boyer, 1982). The estimation of potential yield losses by individual abiotic stresses are estimated at 17 % by drought, 20 % by salinity, 40 % by high temperature, 15 % by low temperature and 8 % by other factors (Ashraf and Harris, 2005).

Water deficit plays a key role in reducing yields of field crops (Jaleel *et al.*, 2007a). Limitation in crop production due to water shortage depends on the intensity and the pattern of drought, which vary from year to year. The efficient use of limited water resources and better growth under limited moisture supply are desirable traits for crops in drought conditions. Crop production is severely constrained by water shortage during the growing period (Jaleel *et al.*, 2007b). In agriculture, water use productivity is associated with the amount of available water (Jaleel *et al.*, 2007c; Jaleel *et al.*, 2007d). Growth parameters showed reduction under salt and water stress condition. Salt stress together with moisture stress also adversely affected the growth rate (Hussain and Ismail, 1994)

Drought tolerance has been observed in all plant species, but its extent varies from species to species. One way to ensure future food needs of the increasing world

populations should involve better use of water by the development of crop varieties those require lesser amounts of water and more tolerant to water shortage (Jaleel *et al.*, 2007e).

Plant acclimation to drought has developed certain mechanisms necessary to sustain key physiological processes in plant. Maintenance of plant leaf turgor under deficit soil moisture is an important adaptation trait that attribute to drought tolerance (Hsiao *et al.*, 1976). Plant metabolic processes are more sensitive to turgor and cell volume than to absolute water potential (Jones and Corlett, 1992). The major physiological mechanism to maintain leaf turgor pressure by decreasing osmotic potential is osmotic adjustment (Jones and Turner, 1980). Sunflower exhibits a large varietal difference for osmotic adjustment in response to water shortage (Conroy *et al.*, 1988; Chimenti and Hall, 1994).

Drought has detrimental effects on plant growth and development. Cellular growth appears to be the most sensitive to water deficit. Decreasing the external water potential by only -0.1 M Pa or less might result in a perceptible decrease in cellular growth. The response of cellular growth to water deficit appears as a slowing of shoot and root growth. This is usually followed by a reduction in cell wall synthesis. Protein synthesis in the cell may be almost equally sensitive to drought. The activities of certain enzymes especially nitrate reductase, phenylalanine ammonia lyase decrease quite sharply as water deficit increase. A few enzymes, such as α -amylase and ribonuclease show increase in activities. Such hydrolytic enzymes might break down starches and other material to make the osmotic potential more negative, thereby resisting the drought. Nitrogen fixation and reduction also drop with water deficit, as nitrate reductase activity is reduced. At levels of water deficit that cause observable changes in enzyme activities, cell division is also inhibited. Stomata begin to close leading to reduction in transpiration and photosynthesis (Bradford and Hsiao, 1982).

Reduction in relative water content (RWC) and leaf water potential caused decrease in photosynthesis of higher plants (Lawlor and Cornic, 2002). Drought mainly limits photosynthesis by stomatal closure and through metabolic impairment (Tezara *et al.*, 1999; Lawson *et al.*, 2003). Drought can also affect growth of plant organs, which results in the alteration of the morphology of the plants (French and Turner, 1991).

Plants have different mechanisms to cope drought stress such as drought avoidance and drought tolerance. The ability of plants to delay harmful decrease in the water potential of the protoplasm is considered as avoidance of desiccation (Hussain, 2010). Desiccation tolerance means that plants have ability to maintain their normal functions even at low tissue water potentials. Both morphological and physiological diversity have

been developed in plants to tolerate the drought (Blum, 1997).

Sunflower is an adaptive species to available soil moisture. In water deficit conditions, high achene yield can be obtained by increasing total water use and harvest index while reducing soil evaporation and finally placing the crop at low vapor pressure deficit. Water is mostly localized deep in the profile in dry region, so the deep rooted species and cultivars with deep rooting should be used for maximum water utilization (Hoad *et al.*, 2001). Sunflower cultivars deplete available soil moisture differently. Mahal *et al.* (1998) conducted a trial about the effect of depletion of available soil moisture and nitrogen levels at Ludhiana, Indian Punjab. They reported that application of water at 40 % depletion of available soil moisture (ASMD), saved 8.2 cm (12.2 %) more water as compared to frequent irrigation (ASMD 20 %) with out any adverse effect on growth and yield.

Water deficit in sunflower has adverse effect on yield and its components while oil content is least affected. Seed yield has positive correlation with days to flowering, days to physiological maturity, head diameter, plant height, 1000-seed weight and oil yield under limited and normal irrigation (Razi and Asad, 1999). Water shortage also reduced total dry matter production, leaf area, relative water content, transpiration rate, total number of seeds per head, seed set percentage, grain yield and water use efficiency. Water deficit effect is much pronounced at the vegetative and flowering stage. In sunflower water shortage at the flowering stage reduced yield by 29 % (Velue and Palanisami, 2001).

There is evidence that ABA normally plays a role in resistance of mesophytes to water stress. Most studies have been done with drought sensitive cultivar of crop plants. Resistant cultivars have higher levels of ABA when they are exposed to water stress, and sensitive cultivars can be converted to resistant types by exogenous application of ABA (Quarrie, 1980; Cellier *et al.*, 1998). In response to water deficit, ABA begins to increase markedly in plant leaf tissues and, to a lesser extent, in other tissues including roots (Bradford and Hsiao, 1982; Salisbury and Marinos, 1985; Walton, 1980). This leads to stomatal closure and decreased transpiration. It also inhibits shoot growth, and root growth appears to be promoted which increased the water supply. Most of these adaptations involving ABA are best observed in mesophytes; xerophytes often have other adaptations (Kriedemann and loveys, 1974).

Drought, photosynthesis and respiration:

Photosynthesis is an important metabolic pathway which is responsible for growth and development. However, photosynthetic efficiency of particular plant is influenced by surrounding environmental conditions (Wise, 1995). The potential of plants to absorb light energy and funnel it to reaction center does not *get altered*, instead, the

capacity of plants to utilize the light absorbed by them declines significantly when they are exposed to environmental stresses such as drought, salinity, low temperature and high light intensity (Dubey, 1997; He *et al.*, 1995). Major effect of drought in plant is reduction in photosynthesis, which is due to decrease in leaf expansion, impaired photosynthetic machinery, leaf senescence and finally reduction in assimilates production (Wahid and Rasul, 2005). Drought stress reduced the crop yield due to changes in photosynthetic pigments (Anjum *et al.*, 2003) and diminished activities of calvin cycle enzymes (Monakhova and Chernyadev, 2002).

The earliest response to drought is closure of stomata at mild to moderate drought. In parallel, a progressive down-regulation or inhibition of metabolic processes leads to decreased RuBP content in leaf under severe drought, and finally inhibits photosynthetic CO₂ assimilation (Flexas and Medrano, 2002). The decreases in CO₂ assimilation and stomatal conductance are due to reduction in carboxylation and RuBP regeneration capacity. Although Rubisco specific activity decreases in severely stressed plant leaves, its content increase under prolonged drought. The increase of Rubisco content in the leaves of the drought-tolerant sunflower hybrid indicating that it could be the one factor which conferring better acclimation and good drought tolerance (Pankovic *et al.*, 1999; Hussain, 2010). Reaction of RuBP to 3-PGA decreased with reducing leaf relative water content (RWC), indicated regeneration of RuBP inhibited under drought stress. Water stressed leaves of sunflower has low RWC and ATP synthesis was known to limit photosynthesis rate because of the inhibition of photophosphorylation (Lawlor, 2002; Tezara *et al.*, 1999).

Relative water content, leaf water potential and osmotic potential of sunflower decreased with water shortage but there were no effects of elevated CO₂ on them. Increased *P_n* (net CO₂ assimilation rate) led to acclimation, with decreased Rubisco content and increased its activity; drought decreased *P_n* with metabolic inhibition involving loss of Rubisco activity (Tezara *et al.*, 2002).

Photosynthetic efficiency is reduced by drought stress which leads to photo-inhibition. Most prominent conditions of this phenomena are low and high temperature, osmotic and high light stress (Wise, 1995; Huner *et al.*, 1993). It may also be the result of activity of Reactive Oxygen Species (ROS) such as super-oxide anion radicals (O₂⁻), hydrogen peroxide (H₂O₂), hydroxyl radicals (OH⁻), alkoxy radicals (RO) and singlet oxygen (O₂⁻). When the electrons transferred from the PS- II reaction center molecules in the presence of light exceed the number of electrons accepted by NADP⁺, these are promptly accepted by O₂ through PS- I and lead to the formation of toxic oxygen species such as O₂⁻ and H₂O₂

(Asada, 1994). The generation of these toxic oxygen species is accelerated by the combined effect of salt and low temperature or drought and low temperature (Alscher and Hess, 1993). Toxic oxygen species i.e. singlet oxygen (O_2^{\cdot}) damaged the PS- II complex particularly, D1 protein of the reaction center of PS II. ROS react with proteins, lipids and deoxyribonucleic acid causing oxidative damage impairing the normal function of cells (Foyer and Fletcher, 2001). Photosynthesis in plants is also inhibited due to loss of balance between the production of reactive oxygen species and antioxidant defense (Fu and Huang, 2001; Reddy *et al.*, 2004).

Water deficit in root zone causes increase of root respiration rate which leads to an imbalance in the utilization of carbon resources, decrease in production of adenosine triphosphate (ATP) and an increase in production of ROS. In wheat, depending upon nutritional status, cultivar and growth stage, greater than 50% of the daily accumulated assimilates are transported to the root and 60% of this fraction is respired (Lambers *et al.*, 1996). In severe drought, sensitive wheat cultivar (Longchum, 8139-2) utilized relatively greater amount of glucose to absorb water (Liu *et al.*, 2004). Severe drought reduces the shoot and root biomass, photosynthesis and root respiration rate. In drying soil limited root biomass and respiration improves growth and physiological activities of drought tolerant line of wheat, which is advantageous over drought sensitive cultivar (Liu and Li, 2005).

Osmotic adjustment under drought: Osmotic adjustment (OA) is a common stress tolerance mechanism in plants accomplished by the production of different compatible organic solutes (Serraj and Sinclair, 2002). Osmotic adjustment (OA) has been considered as an important drought tolerance mechanism in plants which is helpful in postponement of dehydration stress (Morgan, 1990).

These compatible solutes including soluble sugars, sugar alcohols, proline and glycinebetaine are low molecular weight and highly soluble which are nontoxic for plant even at higher cytosolic concentration. They protect plants from cellular dehydration through detoxification of reactive oxygen species (ROS), stabilization of membranes, and structures of enzymes and proteins. Under drought stress, accumulation of compatible solutes occurs in the cell which lowered the osmotic potential and attracts water molecules into the cell and ultimately maintains the cell turgor. Due to OA plant organelles and cytoplasmic activities take place at about normal rate which help plants to perform well in terms of growth, photosynthesis and assimilate partitioning to grain filling (Ludlow and Muchow, 1990; Subbarao *et al.*, 2000).

Glycinebetaine (GB) is accumulated in diverse organisms under environmental stress such as drought,

salt, or cold. Glycinebetaine, a naturally occurring quaternary ammonium compound has received great attention as a compatible solute because under water stress it may aid in drought tolerance by maintaining turgor pressure (Agboma *et al.*, 1997). GB has been shown to protect functional proteins, enzymes (e.g. Rubisco), and lipids of the photosynthetic apparatus and to maintain electron flow through thylakoid membranes (Xing and Rajashekar, 1999; Allakhverdiev *et al.*, 2003). Plants with greater ability of glycinebetaine accumulation are more tolerant to water shortage (Monyo *et al.*, 1992).

In field crops accumulation of compatible solutes has been considered as a parameter of selection for stress tolerance. Accumulation of proline can be occurring in plants under stresses such as temperature, drought and starvation. Higher levels of proline enabled the plant to maintain low water potentials (Jalil *et al.*, 2007; Sankar *et al.*, 2007). Plant responses to drought stress include accumulation of ABA and proline which results in speculation that ABA may trigger proline increase in plant cells (Aspinall, 1980; Stewart, 1980).

Water relations of sunflower cultivars: The success of semi-dwarf genes in cereals has prompted scientist to consider height reduction in sunflower. Agronomic benefits of dwarf sunflowers have been reported (Miller, 1992; Johnston *et al.*, 1995). In sunflowers differential water relations response has been demonstrated by different stature genotypes. Dwarf cultivars of sunflower have higher water potential i.e. least water stress as compared to intermediate and long stature cultivars. This is due to difference in canopy architecture and root penetration depth among different stature sunflower cultivars (Angadi and Entz, 2002a). Tall stature cultivars produced more leaf area, aerial biomass and deeper root system so they transpired more water (Angadi and Entz, 2002b). Gimenez and Fereres (1986) have reported a negative correlation between leaf area and leaf water potential. Greater leaf overlap due to compact canopy in dwarf versus standard height sunflower has also been reported by Sadras *et al.* (1991). Compact crop canopies affect microclimate by reducing wind speed and light penetration by increasing relative humidity (Nobel, 1999), which in turn reduces transpiration loss from the canopy (Pataki *et al.*, 1998). An open canopy, with greater light penetration and better air circulation has potential to increase the plant water status (Nobel, 1999).

Genotypic variation for osmotic adjustment has also been reported in sunflower (Chimenti and Hall, 1994). The dwarf sunflower cultivars have initiated osmotic adjustment earlier than intermediate and large stature cultivars which indicated better osmotic response of dwarf cultivars. The delay in osmotic adjustment in intermediate and tall stature sunflower genotypes is due to faster root penetration and more water extraction from deeper layer of soil. So, tall stature sunflower cultivars

face water stress later as compared to short stature (Angadi and Entz, 2002b). At any rate, dwarf sunflower cultivars are quicker and more efficient in using osmotic adjustment to ameliorate the effects of drought stress (Angadi and Entz, 2002a). The superior osmotic adjustment and lower stress level enabled the dwarf sunflower cultivars to maintain the higher leaf pressure potential (Angadi and Entz, 2002b).

Genotypic variation in rooting depth has been noted in sunflower and deep root system of sunflower cultivars is usually associated with longer growth duration (Feres *et al.*, 1986; Schneiter, 1992). Short stature cultivars are gaining popularity among farmers due to ease in cultivation and shorter growth duration (Johnston *et al.*, 1995). Standard height sunflower hybrids have shown greater water depletion from soil as compared to dwarf open pollinated cultivars (Schneiter, 1992).

Drought in relation to crop growth stages: Sunflower is commonly grown as a rain fed crop in the world but it also responds well to irrigation. Three growth stages of sunflower as heading, flowering and milking are sensitive to water shortage (Doorenbos and Kassam, 1979). In limited irrigation application study, water applied at different growth stages of sunflower significantly decreased seed yield (Stone *et al.*, 1996), particularly at three growth periods of heading, flowering and milking (Demirenen, 1978), at three growth stages (heading, beginning of flowering and end of flowering) (Unger, 1983); and at 50 % ray flower stage (Alessi *et al.*, 1977). In rape seed response of drought stress mostly depend upon genotypes, weather conditions, intensity and duration of drought stress, growth and developmental stages (Robertson and Holland, 2004). Timing of water stress is most crucial than its intensity (Korte *et al.*, 1983).

Normal irrigations are essential for bumper crop production, but when there is scarcity of water, it becomes imperative to differentiate the critical growth stages of the crop, where irrigation could be missed, without reducing the grain yield significantly. In sunflower, irrigation missing at flowering drastically reduced achene yield (Demir *et al.*, 2006) and biological yield (Petchu *et al.*, 2003) as compared to achene yield (El-Tayeb, 2005) and biological yield (De-Guang *et al.*, 2001) obtained by irrigation missing at vegetative stage (Laghrab *et al.*, 2003) on account of reduction in number of achenes head⁻¹ (Kadayifei and Yildirim, 2000).

Sunflower irrigated at budding were 19cm taller than those irrigated only at flowering or late flowering. Irrigation at budding stage also favored leaf and stem dry matter production. Irrigation at flowering or late flowering was important for head and seed development. Highest seed and total dry matter yield were obtained with the full irrigation treatment, but they were not

always significantly higher than those resulting from less well timed irrigation, namely those at flowering and late flowering (Hussain, 2010). Irrigation treatments affected the rate of oil accumulation in seed and had a relatively small but significant effect on final oil percentage. Linoleic and oleic acid concentrations of oil were little affected by irrigation treatments (Unger, 1983).

Amount and timing of applied irrigation has pronounced effect on growth and yield of sunflower. Limited irrigations as one irrigation, at the “beginning flower stage” (BF) with 686 m³ ha⁻¹ of water or of two irrigations at “flower bud stage” (BF) and at “beginning flower stage” (BF) with 956 m³ ha⁻¹ or at “beginning flower stage” (BF) and at “middle seed growth stage” (MG) with 1155 m³ ha⁻¹, gave yields of 3.1, 3.3 and 3.5 t ha⁻¹ respectively. The achene yield (3.7 t ha⁻¹) obtained with three irrigations (volume 1509 m³ ha⁻¹), distributed in “FB”, “BF” and “MG” stages were higher than the yield obtained with the lesser irrigations volumes (D’Amato *et al.*, 1999).

Early sunflower growth was limited when the water availability was reduced during budding. Full irrigation was effective for maximum grain production. The corresponding yield increases were 1.4, 1.8 and 2.2 t ha⁻¹ as compared with medium inputs or moderately irrigated crop. The best yields (up to 4.0 t ha⁻¹) were observed in dry years under full irrigation. When drought occurred before anthesis, grain yield and achene number m⁻² were reduced. When drought occurred during the vegetative and flowering period the achene numbers per head decreased. In the absence of stressful environmental conditions during grain filling 3000-12000 achenes m⁻² and potential 1000-seed weight can be obtained. Oil concentration and grain yield increased together while oil and protein concentration were negatively related. So it was concluded that sufficient water is necessary during grain filling to achieve a high oil concentration (Debaeke *et al.*, 1998).

Supplemental water treatment applied to sunflower during vegetative, reproductive, or both growth stages has pronounced effect on seed yield. Seed yield ranged from 2100 to 2700 kg ha⁻¹, supplemental irrigation increased seed yields by 480 kg ha⁻¹ each year (Aiken and Stockton, 2001).

In sunflower irrigation application at heading, flowering and milking (HFM) is the best choice for maximum yield. Goksoy *et al.* (2004) applied irrigation at 60% heading, flowering and milking (H₆₀FM), 40% heading, flowering and milking (H₄₀FM), heading, 60% flowering and milking (HF₆₀M), heading, 40% flowering and milking (HF₄₀M), heading, flowering and 60% milking (HFM₆₀) and heading, flowering and 40% milking (HFM₄₀). They reported that seed yield and oil yield increases for the limited irrigation treatments were; 78.7 % and 77.4% for H₆₀FM; 77.4 % and 78.9% for H₄₀FM; 72.2 % and 75% for HF₆₀M; 76.4 % and 79.2%

for HF₄₀M; 72.7 and 73.6% for HFM₆₀; 77.6 and 76.1% for HFM₄₀.

Water deficit has significant effect on development stages of rapeseed. among six water deficit levels / stages *viz.* normal irrigation, no irrigation from germination to rosette, no irrigation at stem elongation, no irrigation at flowering, no irrigation at siliqua formation and no irrigation at seed filling, the siliqua number was decreased significantly when plants were exposed to water deficit at flowering stage (Rad *et al.*, 2005).

Daneshian *et al.* (2005a) conducted an irrigation control experiment based on 60mm evaporation from an evaporation basin. Second experiment irrigated when 180mm water was evaporated from evaporation basin. Drought stress started before the reproductive stage. Results showed that water stress reduced seed yield due to reduced head diameter, seed number, seed weight and plant height. The effective seed filling period, harvest index, leaf area index, and seed oil content were also decreased by drought. A reduction in leaf area of sunflower has been observed under continuous 30 day drought period, ending at anthesis than full irrigation (Hammadeh *et al.*, 2005).

Sunflower genotypes performed differently against drought at different growth stages. Maruthi *et al.* (1998) evaluated six genotypes of different growth period and their performance to rainfall distribution. All cultivars were subjected to moisture deficit at grain filling stage. They found that medium duration cultivars, despite encountering terminal drought, performed better as compared to other maturity groups. When water shortage in sunflower occurred for longer than 12 days at grain filling and flowering stage it reduced seed yield as compared with non stress plants (Reddy *et al.*, 1998). Seed yield in sunflower is also reduced in high oleic acid hybrids under limited water availability when irrigation was terminated at 100 % flowering or 10, 20 and 30 days later. Seed yield was adversely affected when irrigation was terminated at flowering than on later dates (Salera and Baldini, 1998; Singh *et al.*, 1999).

Irrigation interval has prominent effect on growth, development and yield of sunflower. Al-Ghamdi *et al.* (1991) irrigated sunflower with (a) 5 (b) 10 or (c) 15-days intervals corresponding to 40, 60 and 80% depletion of available soil moisture, respectively. Plant height and seed yield were significantly lower in (c) than in (a) or (b).

The influence of limited irrigation on growth, seed yield and yield components has well documented. Five irrigation treatments were applied, designated as T₁ full irrigation and T₂, T₃, T₄ and T₅ received 75, 50, 25 and 0% of applications of the fully irrigated treatment on the same day. Seed yields averaged the highest with full irrigation treatment (T₁) and differences between full irrigation and other treatments were significant (Erdem *et al.*, 2001). In sunflower when drought occurs during seed

filling it reduced seed yield, seed weight per head, 1000-seed weight and head diameter. Seed oil content and oleic acid also reduced but palmitic acid increased under water deficit conditions. (Jasinkas, 1999; Mekki *et al.*, 1999).

In canola 33.3% and 20.7% seed yield reduction were observed when drought stress applied at flowering and siliqua development stage, respectively. This yield reduction due to short term drought during flowering and siliqua development was associated with few siliques per plant and a reduction in seed weight (Sinaki *et al.*, 2007). Drought stress during vegetative or early reproductive stages in soybean reduces seed yield due to reduction in number of seeds per unit area, while water shortage during seed filling reduces seed size (Korte *et al.*, 1983; Brevedan and Egli, 2003).

Sunflower quality and yield under drought stress:

Sunflower genotypes have shown differential yield response under drought. Water stress increased the net assimilation rate while it decreased the leaf area ratio in sunflower. Water stress had no effect on relative growth rate. An inverse and negative correlation was found between net assimilation rate, achene yield and oil yield where as relative growth rate had a very low and positive correlation with both achene yield and oil yield. Leaf area ratio had positive and significant correlation with achene and oil yield (Hussain *et al.*, 2008). A decreasing trend in head diameter, number of achenes per head, 100-achene weight and achene yield per plant has been observed as the level of water stress increased from 100% to 25% of field capacity. Seed oil content was sensitive to even mild water stress but showed stability under increasing stress conditions (Khan *et al.*, 2000). Water deficit reduced harvest Index (HI). Excellent positive correlations were found between HI and grain yield under dry land conditions. The reduction in HI due to water deficits was mostly due to adjustments in seed number with less variation in individual seed weight. In turn, the reduction in seed number was due to a combination of reduced head size and of the area having viable seeds (Ferreter *et al.*, 1986). Water stress significantly decreased yield and its components; however, oil content did not differ significantly. Genotype and phenotype correlation revealed that seed yield had significant positive correlations with head diameter, plant height, 1000-seed weight and oil yield under normal and limited irrigation. Seed yield had significant correlations with oil content under normal irrigation regime, while these correlations were largely reduced under stress conditions and were not significant. The highest direct effect was exhibited by 1000-seed weight in normal and limited irrigation environments. Direct effect of oil was quite lower than its correlation with seed yield. The lowest direct effect was found for plant height and oil content under normal and stress environments, respectively (Razi and Asad, 1999).

A significant negative correlation of head diameter with fresh shoot weight was observed under water stress. Positive and significant correlation existed between dry shoot weight and seed yield per plant under water stress conditions (Tahir and Mehdi, 2001). Tahir *et al.* (2002) evaluated inbred lines of sunflower under water stress and normal irrigation. The maximum (34.13%) decrease in yield per plant was observed under water stress as compared with that of under normal irrigation condition followed by 25.56 % decrease in leaf area and 22.63 % decrease in 100-achene weight. Chimenti *et al.* (2002) also recorded a significant effect of drought on biomass at the end of anthesis, at physiological maturity, on grain yield and harvest index. Ardakani *et al.* (2005a) showed non-significant differences for biological yield, seed oil percent among water treatments. Water stress has significant effect on total dry matter, net assimilation rate, relative growth rate, crop growth rate, and leaf area index. Ardakani *et al.* (2005b) and Nasri (2005) also reported that water stress decreased seed number, seed weight; head diameter, harvest index, oil percent, oil yield and growth indices. Daneshian *et al.* (2005b) investigated the irrigated treatment as normal condition (60 mm evaporation from Pan) and irrigated as stress condition (180 mm

evaporation from pan). Normal condition showed the highest yield, high seeds per head and seed weight while oil seed content decreased under irrigated as stress condition.

Sunflower oil quality is affected under different water regimes. The major effect of irrigation was an increase of linoleic acid content and reduction in oleic acid. However oleic/linoleic acid ratio increased under water stress, especially when plants were subjected to soil water stress during elongation stage in standard genotypes (Flagella *et al.*, 2002).

Abscisic Acid (ABA): ABA has been associated as a stress hormone in vascular plants. It has been detected in mosses but absent in liverworts. Several genera of fungi make ABA as a secondary metabolite (Milborrow, 2001). ABA has been detected in every major organ of plant from the root cap to the apical bud and synthesized in almost all cells that contain chloroplast and amyloplasts. It is a 15-carbon compound that resembles the terminal portion of some carotenoid molecules. The orientation of carboxyl group at carbon 2 determines the *cis* and *trans* isomers of ABA. Nearly all the naturally occurring ABA is in the *cis* form, and by convention the name abscisic acid refers to that isomer (Taiz and Zeiger, 2003).

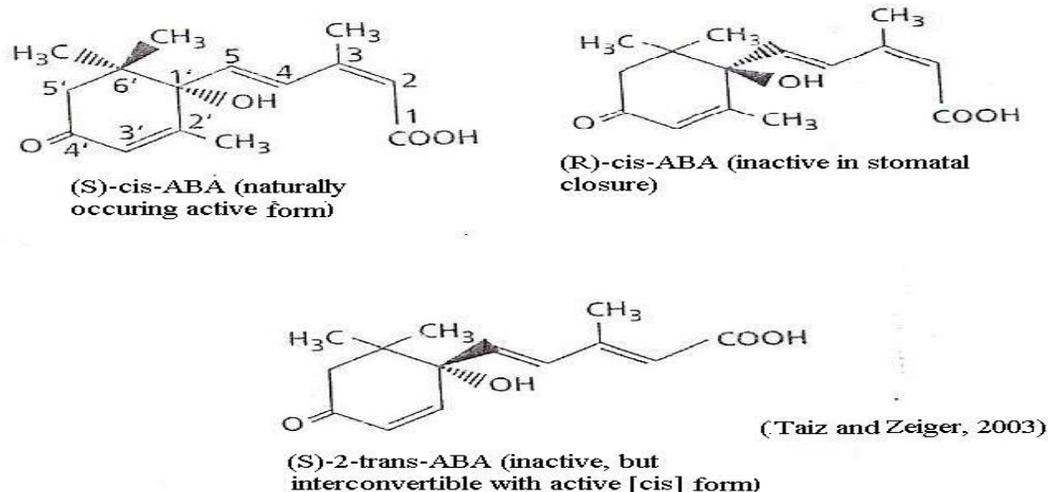


Figure 2-1. The chemical structures of the S (counterclockwise array) and R (clockwise array) forms of *cis*-ABA, and the (S)-2-trans form of ABA. The numbers in the diagram of (S)-*cis*-ABA identify the carbon atoms

Biosynthesis, metabolism and transport of ABA: ABA biosynthesis takes place in chloroplast and other plastids via the pathway as depicted in figure 2.2. The pathway begins with isopentenyl diphosphate (IPP), the biological isoprene unit, and leads to the synthesis of the violaxanthin. Synthesis of violaxanthin is catalyzed by zeaxanthin epoxidase (ZEP), converted to neoxanthin, which is then cleaved to form the C₁₅ compound

xanthoxal. The cleavage is catalyzed by 9-*cis*-epoxy-carotenoid dioxygenase (NCED). Synthesis of NCED is rapidly induced by water stress, suggesting that the reaction it catalyzes is a key regulatory step for ABA synthesis. The enzyme is localized in on the thylakoid, where the carotenoid substrate is located. Finally, xanthoxal is converted to ABA via oxidative steps involved the intermediate(s) ABA- aldehyde and or

possibly xanthoxic acid. This final step is catalyzed by a family of enzymes like aldehyde oxidases that synthesize ABA. Its biosynthesis is not the only factor that regulates ABA concentration in the tissue. The concentration of free ABA in the cell cytosol is also regulated by degradation, compartmentation, conjugation and transport (Hussain, 2010). For example, cytosolic ABA increases during water stress as a result of synthesis in the leaf, redistribution within the mesophyll cell, and import from the roots and recirculation from other leaves. The concentration of ABA declines after rewatering because of degradation and export from the leaf as well as a decrease in the rate of synthesis.

ABA is inactivated through oxidation, yielding the unstable intermediate 6-hydroxymethyl ABA, which is rapidly converted to Phaseic acid (PA) and dihydrophaseic acid (DPA). Free ABA is also inactivated by covalent conjugation to another molecule, such as a monosaccharide. A common example of an ABA conjugate is ABA-β-D-glucosyl ester (ABA-GE). Conjugation is not only renders ABA inactive as a

hormone but also alters its polarity and cellular distribution. Whereas free ABA is localized in the cytosol, ABA-GE accumulates in vacuoles and thus could theoretically serve as storage form of the hormone. When plants were subjected to a series of stress and re-watering cycles, suggesting that the conjugated form is not broken down during water stress (Taiz and Zeiger, 2003).

ABA is transported by both the xylem and the phloem, but it is normally much more abundant in phloem sap. When radioactive ABA is applied to a leaf, it is transported both up the stem and down toward the roots. Most of the radioactive ABA is found in the roots within 24 hours. Destruction of the phloem by a stem girdle prevents ABA accumulation in the roots, indicating that the hormone is transported in the phloem sap. ABA synthesized in the roots can also be transported to the shoot via the xylem. Whereas the concentration of ABA in the xylem sap of well watered sunflower plants is between 1.0 and 15.0 nM, while in water stressed sunflower plant it increases to as much as 3000 nM (3.0 μM) (Schurr *et al.*, 1992).

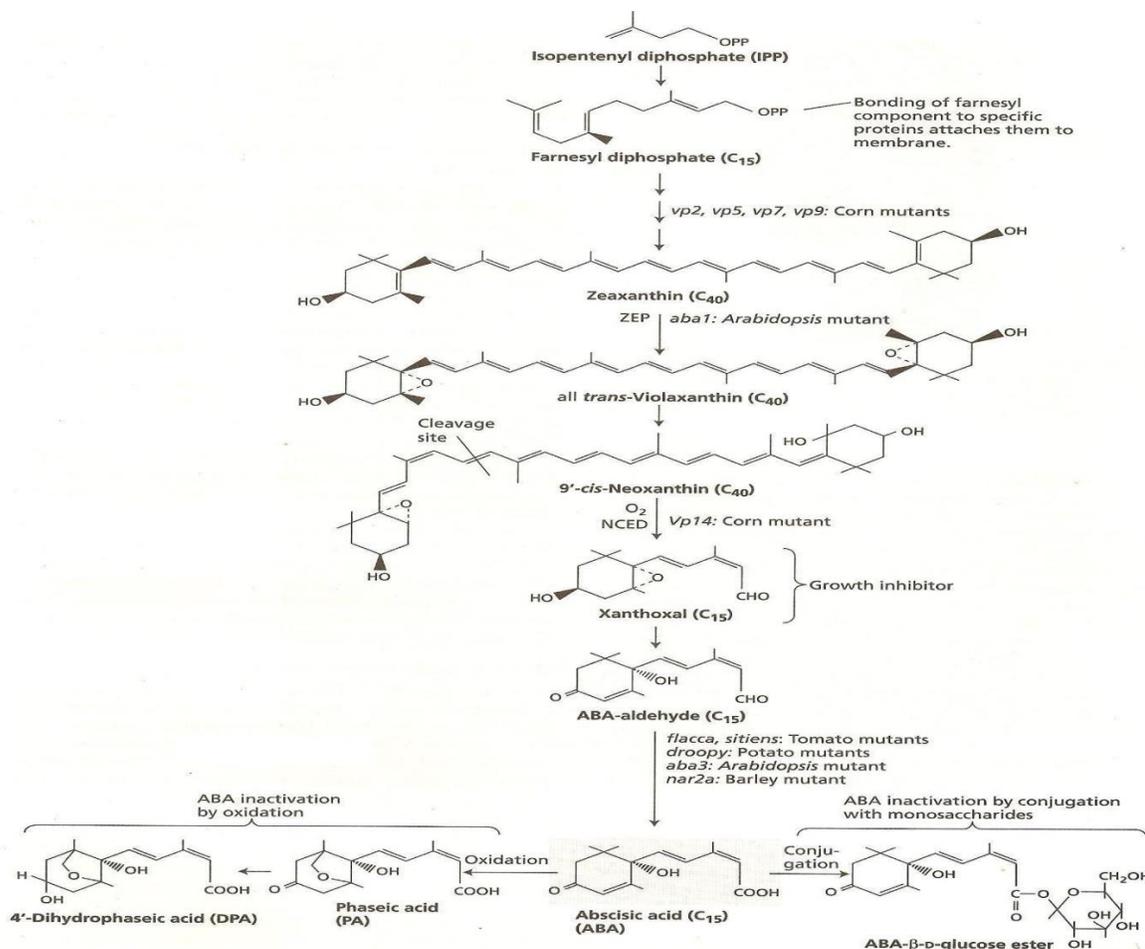


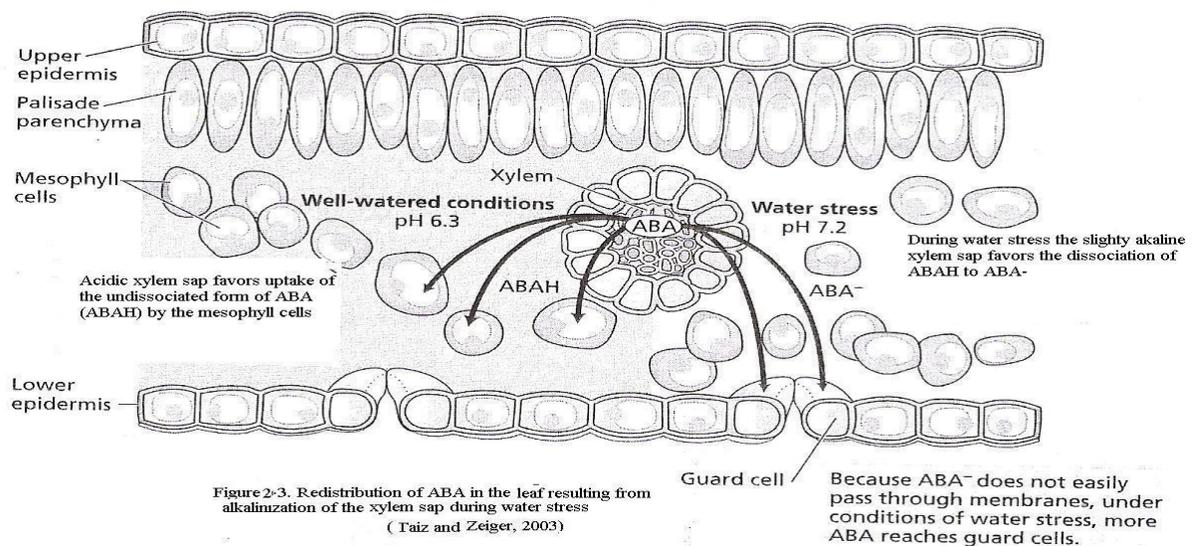
FIGURE 2-2.ABA biosynthesis and metabolism. In higher plants, ABA is synthesized via the terpenoid pathway. Some ABA-deficient mutants that have helped in elucidating the pathway are shown at the steps at which they are blocked. The pathways for ABA catabolism

include conjugation to form ABA-β-D-glucosyl ester or oxidation to form phaseic acid and then dihydrophaseic acid. ZEP = zeaxanthin epoxidase; NCED = 9'-cis-epoxycarotenoids dioxygenase. (Taiz and Zeiger, 2003)

The magnitude of stress induced change in xylem ABA content varies widely among species and it has been suggested that ABA also is transported in a conjugated form, and then released by hydrolysis in leaves although this has yet to be identified. As water stress begins, some of the ABA carried by the xylem stream is synthesized in roots that are in direct contact with the drying soil. Because this transport can occur before the low water potential the soil cause any measurable change in the water status of the leaves, ABA is believed to be a root signal that helps to reduce the transpiration rate by closing stomata in leaves (Davies and Zhang, 1991)

The $3.0\mu\text{M}$ ABA concentration in the apoplast is sufficient to close stomata but all of the ABA in the xylem stream does not reach the guard cells. Much of the

ABA in the transpiration stream is taken up and metabolized by the mesophyll cells. During the early stages of water stress, however, the pH of the xylem sap becomes more alkaline, increasing from pH 6.3 to about pH 7.2 (Wilkinson and Davies, 1997). Drought induced alkalization of the apoplast favors formation of the dissociated form of abscisic acid, ABA^- , which does not readily cross membranes. Hence, less ABA enters to the mesophyll cells and more reaches to the guard cells via the transpiration stream. In this way ABA is redistributed in the leaf without any increase in the total ABA level. This increase in xylem sap pH may function as a root signal that promoted early closure of the stomata (Taiz and Zeiger, 2003).



Abscisic Acid and drought: Plants are under periodic water stress due to unpredictable rainfall and limited availability of irrigation water. They have certain mechanisms which allow them to perceive the incoming stresses and rapidly regulate their physiology and metabolism to cope with these stresses. A good example of such mechanisms is the ability of plants to regulate their water loss through partial closure of stomata, reduced leaf development. It occurs long before loss in leaf turgor and irreversible damage to inner membrane systems (Jones, 1980; Cowan, 1982; Davies and Zhang, 1991). The plant hormone ABA is produced under water deficit conditions and plays a major role in response and tolerance to dehydration (Shinozaki and Yamaguchi Shinozaki, 1999).

ABA plays a critical role in regulating plant water status through guard cells and growth as well as by induction of genes that encode enzymes and other proteins which create cellular dehydration tolerance (Luan, 2002; Zhu, 2002). In plants stomata response to

soil drying is mediated by ABA, originating from roots and transported to the shoot via transpiration stream (Davies and Zhang, 1991). ABA under drought is produced in dehydrated roots, transported to the xylem and regulates stomatal opening and leaf growth in the shoots (Zhang *et al.*, 1987; Zhang and Davies, 1990). Stomata respond to the concentration of ABA in the guard cell apoplast (Harris and Outlaw, 1991; Hornberg and Weiler, 1984; Anderson *et al.* 1994).

In gradual soil drying wilting of plant leaves and gradual stomatal closure are common phenomena. When soil drying prolonged ABA comes from two sources initially from the roots and later from the older plant leaves, which wilted earlier than the younger leaves (Zhang and Davies, 1989b). It appears that plants have evolved two responses to soil drying. Initial soil drying may be sensed by part of the root system and ABA in root xylem regulates stomatal conductance such that water loss in the shoot may be reduced and water deficit can be avoided (Zhang and Davies, 1989a). In severe soil

drying shoot water deficit becomes unavoidable and some older leaves may wilt, due to weak hydraulic link with the main stem or weaker control of the stomatal conductance. This wilting accounts for the accelerated ABA concentration in the xylem and much severe stomatal inhibition in the young leaves (Zhang and Davies, 1989b).

It has been shown that leaf conductance is closely related to xylem ABA concentration (Jia and Zhang, 1999). Closure of plant stomata depends upon the amount of xylem ABA that enters in leaves per unit time i.e. ABA flux (Raschke, 1975; Gowing *et al.*, 1993; Jarvis and Davies., 1997). This implies that ABA is helpful to regulate stomatal movement under normal conditions due to changes in transpiration under non stressed conditions, or that ABA's role is magnified after the soil drying has led to the very low transpiration. However, studies have strongly suggested that stomatal movement responds to xylem ABA concentration rather than its flux, like water stressed conditions when leaf conductance has decreased to low value (Zhang and Davies, 1991; Jackson *et al.*, 1995; Trejo *et al.*, 1995). The rapid metabolism of xylem derived ABA in the leaves is essential to prevent ABA accumulation and keep the stomata sensitivity regulated. ABA acts as stress hormone in root systems as it facilitates penetration of roots in compacted soil layers and increase desiccation tolerance in maize (Hartung *et al.*, 1994). Plants growing in arid and semi-arid climate often face some degree of drought stress. Due to which, plants have developed various mechanisms to enhance their tolerance including well-developed root systems, osmotic adjustments and certain leaf morphologies (Levitt, 1980; Kramer; 1983; Jones, 1992; Larcher, 1995; Blum, 1997; Kozłowski and Pallardy, 2002). ABA, a well-known stress induced plant hormone has long been studied as potential mediator for induction of drought tolerance in plants (Davies and Jones, 1991; Zeevart, 1999). It helps in promoting drought tolerance, both from the use of exogenous application to intact plants (Gibson *et al.*, 1991; Heschel and Hausmann, 2001; Xu *et al.*, 2002; Wang *et al.*, 2003) and from the measurement of the endogenous ABA concentration (Van Rensburg and Kruger, 1994; Li and Wang, 2003). Exogenous application of 5 μ M ABA to cotton under drought significantly increased seed number and lint mass per plant (Pandey *et al.*, 2003). Jia and Zhang (1999) has also shown 50 % decrease in leaf conductance in sunflower detached shoot fed with 5 μ M ABA solution for 30 minutes. In soybean, reproductive potential reduced considerably due to less pod set under drought stress. This problem has been alleviated by exogenous application of 0.1 mM abscisic acid (Liu *et al.*, 2004). Population variation due to exogenous application of ABA have been observed in well watered and stressed plants (Amtdt *et al.*, 2001; Tsialtas *et al.*, 2001; Ponton, *et al.*, 2001). Exogenous application of

ABA affected water use efficiency more in droughty plant than well-watered plants of jewel weed (Heschel and Hausmann, 2001). Plants would grow more rapidly by using a finite water supply more efficiently when water is limited, in this case high water use efficiency would positively affect plant productivity (Li, 1999).

The involvement of drought induced ABA and ethylene in shoot and root growth is still a controversial subject (Robert and LeNoble, 2002). Under drought-stressed conditions, stomata close in response to either a decline in leaf turgor and/or water potential, indicating that stomatal responses are closely linked to soil moisture content and leaf water status. Much is known about the role of ABA in closing the stomata as well as ABA production in dehydrating roots and ABA circulation in the plant (Wilkinson and Davies, 2002).

ABA-induced stomatal closure causes depression in net CO₂ uptake, which involves mechanisms at both the stomatal and chloroplast levels. The mid-day decline in stomatal conductance in several plant species under drought conditions may be due to increased sensitivity to xylem-carried ABA, which is induced by low leaf water potentials (Wilkinson and Davies, 2002). Also, the decline in intercellular CO₂ following stomatal closure apparently induces a down regulation of photosynthetic machinery to match the available carbon substrate. The amount of ABA in xylem sap can increase substantially as a function of reduced water availability in the soil and this might result in an increased ABA concentration in different compartments of the leaf. Zhang and Outlaw (2001) reported that stressing *Vicia faba* roots could change ABA concentrations at the guard cell apoplast and that the apoplastic guard cell ABA concentration correlated with changes in stomatal aperture more effectively than did the guard cell symplastic fraction. These studies indicate that apoplastically facing guard cell ABA receptors seem to be important in the responses to stress signals experienced by plants. Increases in the xylem sap ABA and leaf ABA were correlated with reduced stomatal conductance under partial root drying conditions in grape vines (Stoll *et al.*, 2000).

Abscisic Acid, drought and crop cultivars: Varietal differences in drought tolerance may be associated with changes in ABA in response to various environmental stresses. This includes drought tolerance of maize (Pekic and Quarrie, 1987), chilling tolerance of rice seedlings (Lee *et al.*, 1993) and salt tolerance of rice (Moons *et al.*, 1995). In wheat, growth of dwarf stature cultivars (Dariel) are less sensitive to constant exogenous application of ABA than that of tall isolines (Bet Hashita) (Blum *et al.*, 1997). Similarly higher accumulation of ABA in drought tolerant wheat cultivars C-306 and HW-24 than susceptible cultivar Hira have been reported (Chandrasekar *et al.*, 2000)

Cellier *et al.* (1998) studied a model system consisting of a drought tolerant line and a drought sensitive line of sunflower subjected to progressive drought. They described that in both lines exogenous application of 10 μ M ABA caused stomata closure within 6 hours. It displayed that stomata of both lines showed similar sensitivity to exogenous application of ABA. It is widely accepted that ABA mediates general adaptive responses to drought. There is also evidence to suggest that additional signals are involved in this process (Munns and King, 1988; Trejo and Davies, 1991; Munns *et al.*, 1993; Griffiths and Bray, 1996). In response to exogenous application of ABA in drought tolerant line of sunflower dehydrin protein accumulated in vegetative tissue (Labhilili *et al.*, 1995) and in wheat and poplar (Pelah *et al.*, 1997). Dehydrin protects cytosolic structures from the deleterious effects of cellular dehydration (Baker *et al.*, 1988; Dure *et al.*, 1989; Close, 1996).

ABA has pronounced effects on proline content and water status of different genotypes of sunflower. Unyayar *et al.* (2004) studied the effect of exogenous application of 10^{-5} M ABA on two sunflower genotypes (Nantio F1 and Ozdemirbey) exposed to drought and water logging. Leaf area and relative leaf water content decreased under drought stress but in ABA treated leaves relative water content had lower values than in non treated leaves of Nantio F1. Dry weight decreased under drought stress while it increased in ABA treated genotype Nantio F1. ABA and proline accumulation increased under water deficit conditions. Exogenous application of ABA increased proline and ABA content in treated leaves as compared to non treated leaves of Ozdemirbey. Genotypic response to ABA in drought is correlated with variation in ABA concentrations (Trejo *et al.*, 1995; Borel *et al.*, 1997; Blum and Sinmena, 1995; Cellier *et al.*, 1998). In Cassava under drought genotypic variation in accumulation of ABA among young, older, expanding and folded leaves have been observed which ultimately affect leaf expansion, growth and transpiration. Under both water shortage and well watered condition young leaves accumulated more ABA than mature leaves (Alfredo and Setter, 2000). In *Euphorbia Lathyrus* water stress increased 10-fold ABA concentration in expanding leaves and 5-fold in mature leaves (Sivakumaran and Hall, 1978), while in castor bean many fold increase in mature leaves and 11-fold increase in xylem sap ABA has been observed by Jokhan *et al.* (1996). This variation in accumulation of ABA in mature and young leaves under water stress is due to increase in rate of catabolism of ABA into biologically inactive products in mature leaves and slow ABA transport in them (Cornish and Radin, 1990). In droughty leaves an accumulation of high level of ABA soon comes to normal level after one day of re-watering (Alfredo and Setter, 2000; Hussain, 2010). This rapid return to normal level of ABA results in

recovery of plant growth and development. This behavior contributes to adoption of plants to cope periodic drought followed by renewed water application / rainfall (Connor and Cock, 1981; Palta, 1984). Genotypic variation in accumulation of ABA in field due to drought and other stresses have been observed which reflects gradual depletion of soil water. This genotypic variation also depends upon the extent to which leaf growth is arrested in response to mild and incipient water deficit and ability of crops to retain leaves during drought (Connor and Cock, 1981; Palta, 1984). Crop species like Cassava has ability to partially close the stomata and maintain well photosynthetic rate in low water potential. It is due to rapid accumulation of ABA and halting of leaf growth on the onset of drought and rapid recovery of growth after re-watering (Alfredo and Setter, 2000).

Conclusion: Drought is a serious menace to agriculture productivity. Drought stress at divergent growth stages of sunflower hybrids pounced severe damage to growth, development, oil quality and yield. ABA is a well-known stress hormone which improves drought tolerance in sunflower hybrids through osmotic adjustment and improving water relations. It is therefore suggested that screening of sunflower cultivars against drought should be done and exogenous application of ABA will defiantly help in conserving water within plants which is necessary for successful crop production under water deficit conditions.

REFERENCES

- Agboma, P., T. Sinclair, K. Jokinen, P. Peltonen-Sainio and E. Pehu (1997). An evaluation of the effect of exogenous glycinebetaine on the growth and yield of soybean. *Field Crops Res.*, 54:51-64.
- Aiken, R. M. and R. D. Stockton (2001). Effect of supplemental water on sunflower productivity in northwest Kansas. Performance tests with sunflower hybrids, Report of Progress. Pp. 888.
- Alessi, J., J. F. Power and D. C. Zimmerman (1977). Sunflower yield and water use as influenced by planting date, population and row spacing. *Agron. J.*, 69:465-469.
- Alfredo, A. C. A. and T. L. Setter (2000). Response of cassava to water deficit: Leaf area growth and abscisic acid. *Crop Sci.*, 40: 131-137.
- Allakhverdiev, S. I., H. Hayashi, Y. Nishiyama, A. G. Ivanov, J. A. Aliev, V. V. Klimov, N. Murata and R. Carpentier (2003). Glycinebetaine protects the D1/D2/Cytb559 complex of photosystem II against photo-induced and heat-induced inactivation. *J. Plant Physiol.*, 160:41-49.
- Alscher, R. G. and J. L. Hess (1993). Antioxidants in higher plants. CRC, Press, Boca Raton, FL.

- Amdt, S. K., S. C. Clifford, W. Wanek, H.G. Jones and M. Popp (2001). Physiological and morphological adaptations of the fruit tree *Ziziphus rotundifolia* in response to progressive drought stress. *Tree Physiol.*, 21: 705–715.
- Anderson, B. E., J. M. Ward and J. I. Schroeder (1994). Evidence for an extra cellular reception site for abscisic acid in *Commelina* guard cells. *Plant Physiol.*, 104:1177-1183.
- Angadi, S. V. and M. H. Entz (2002a). Agronomic performance of different stature sunflower cultivars. *Can. J. Plant Sci.*, 202:117-125.
- Angadi, S. V. and M. H. Entz (2002b). Water relation of standard height and dwarf sunflower cultivars. *Crop Sci.*, 42: 152-159.
- Anjum, F., M. Yaseen, E. Rasul, A. Wahid, and S. Anjum (2003). Water stress in barley. I. Effect on chemical composition and chlorophyll content. *Pakistan J. Agric. Sci.*, 40: 45-9.
- Ardakani, M. R., A. H. S. Rad, D. Habibi and S. Jahed (2005a). Effect of drought stress on quantitative and qualitative characteristics of oilseed rape (*Brassica napus* L.). Interdrought-II, the second international conference on integrated approaches to sustain and improve plant production under drought stress; Rome, Italy, September, 24-28 pp-132.
- Ardakani, M. R., A. H. S. Shirani and D. Habibi (2005b). Drought stress effects on quantitative characters of commercial sunflower cultivars and hybrids. Interdrought-II, the second international conference on integrated approaches to sustain and improve plant production under drought stress; Rome, Italy, September, 24-28. Pp-132.
- Asada, K. (1994). Production and action of active oxygen species in photosynthetic tissues. In: Foyer, C.H. and P.M. Mullineaux (Eds.), Causes of photooxidative stress and amelioration of defense systems in plants. CRC Press, Boca Raton, FL., pp. 77-104.
- Ashraf, M. and M. R. Foolad (2006). Roles of glycinebetaine and proline in improving plant abiotic stress resistance. *Environ. Exp. Bot.*, 59:206-216.
- Ashraf, M. and P. J. C. Harris (2005). Abiotic stresses: plant resistance through breeding and molecular approaches. Haworth press, New York.
- Asif, M., N. Hussain and M. B. Khan (2001). Effect of K on the growth and seed yield of spring sunflower (*Helianthus annuus* L.). *Pakistan J. Biol. Sci.*, (Supplementary Issue 1):100-101.
- Aspinall, D. (1980). Role of abscisic acid and other hormones in adaptation to water stress. In NC Turner, PJ Kramer, (Eds) Adaptation of Plants to Water and High Temperature Stress. Wiley and Sons, New York, pp. 155-172.
- Baker, J., C. Steele and LIII. Dure (1988). Sequence and characterization of 6 Lea protein and their genes from cotton. *Plant Mol. Biol.*, 11: 277-291.
- Beard, B. H. and S. Geng (1982). Interrelationship of morphological and economic characters of sunflower. *Crop Sci.*, 22: 817-822.
- Blum, A. (1997). Crop responses to drought and the interpretation of adaptation. In: Belhassen, I. (Ed.), Drought Tolerance in Higher Plants: Genetically, Physiological, and Molecular Biological Analysis. Kluwer Academic Publish, Dordrecht, pp. 57–70.
- Blum, A. and B. Sinmena (1995). Isolation and characterization of variant wheat cultivars for ABA sensitivity. *Plant Cell Environ.*, 18: 77-83.
- Blum, A., C. Y. Sullivan and H. T. Nguyen (1997). The effect of plant size on wheat response to agents of drought stress. II. Water deficit, heat and ABA. *Aust. J. Plant Physiol.*, 24: 43-48.
- Borel, C., T. Simonneau, D. and F. Tradieu (1997). Stomatal conductance and ABA concentration in the xylem sap of barley lines of contrasting genetic origin. *Aust. J. Plant Physiol.*, 24: 607-615.
- Bot, A.J., F.O. Nachtergaele and A. Young (2000). Land resource potential and constraints at regional and country levels. World Soil Resources Reports 90. Land and Water Development Division, Food and Agriculture Organization, Rome.
- Boyer, J. S. (1982). Plant Productivity and Environment. *Sci.*, 218:443-448.
- Bradford, K. J. and T. C. Hsiao (1982). Physiological responses to moderate water stress. In Lange, O. L., P.S. Nobel, C. B. Osmond and H. Ziegler (Eds) , Physiological Plant Ecology II, water relations and carbon assimilation. Pp.263-324. in A. Person, M.H. Zimmermann (Eds) Encyclopedia of plant physiology, new series. 12B. Springer-verlag, Berlin, Heidelberg, New York.
- Brevedan, R. E. and D. B. Egli (2003). Short periods of water stress during seed filling, leaf senescence and yield of soybean, *Crop Sci.*, 43: 2083-2088.
- Cellier, F., G. Conejero., J.C. Bretiler and F. Casse (1998). Molecular and physiological responses to water deficit in drought sensitive lines of sunflower. *Plant Physiol.*, 116: 319-328.
- Chandrasekar, V., R. K. Sairam and G. C. Srivatava (2000). Physiological and biochemical responses of hexaploid and tetraploid wheat to drought stress, *J. Agron. Crop Sci.*, 185: 219-227.
- Chimenti, C. A. and A. J. Hall (1994). Responses to water stress of apoplastic water fraction and bulk modulus of elasticity in Sunflower (*Helianthus annuus* L.) genotype of contrasting

- capacity for osmotic adjustment. *Plant Soil*, 166: 101-107.
- Chimenti, C. A., J. Pearson and A. J. Hall (2002). Osmotic adjustment and yield maintenance under drought in sunflower. *Field Crops Res.*, 75:235-246.
- Close, T. J. (1996). Dehydrins: emergence of a biochemical role of a family of plant dehydration Proteins, *Physiol. Plant.*, 97: 795-803.
- Connor, D. J. and J. H. Cock (1981). Response of cassava to water shortage. II. Canopy dynamics. *Field Crops Res.*, 4: 285-296.
- Conroy, J. P., J. M. Virgona, R. M. Smillie and E. W. Barlow (1988). Influence of drought acclimation and CO₂ enrichment on osmotic adjustment and chlorophyll a fluorescence of sunflower during drought. *Plant Physiol.*, 86:1108-1115.
- Cornish, K. and J. W. Radin (1990). From metabolism to organism: An integrative view of water stress emphasizing ABA. Pp. 89-112. In Katterman, F. (Ed). *Environmental injury to plants*. Academic Press, San Diego, CA.
- Cowan, I. R. (1982). Water use and optimization of carbon assimilation. In: Lange, *et al.* (Eds.), *Physiological Plant Ecology II*, II. Springer-Verlag, Berlin, pp. 589-613.
- D'Amato, A., I. Giordano and L. Concilio (1999). Irrigation of the sunflower in conjunction with the phenological stages in relation to the availability of water in the soil; Symposium on scheduling of irrigation for vegetable crops under field condition. *ISHS Acta Horticulturae*, 278.
- Daneshian J., R. Ardakani, D. Habibi and E. Gafaripour (2005a). Drought stress effects on yield, quantitative and qualitative characteristics of new sunflower hybrids. *Interdrought-II*, the second International Conference on integrated approaches to sustain and improve plant production under drought stress; Rome, Italy, September, 24-28 pp-175.
- Daneshian, J., E. Farrokhi, M. Khani and A. H. S. Rad (2005b). Evaluation of sunflower hybrids, CMS and restorer lines to drought stress. *Interdrought-II*, the second International Conference on integrated approaches to sustain and improve plant production under drought stress; Rome, Italy, September, 24-28 pp-137.
- Davies, W. J. and H. G. Jones (1991). *Abscisic Acid: Physiology and Biochemistry*. BIOS Scientific Publishers, Oxford, UK, pp.266.
- Davies, W. J. and J. Zhang (1991). Root signals and the regulation of growth and development of plants in drying soil. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 42: 55-76.
- Debaeke, P., M. Cabelguenne, A. Hilaire and D. Raffailac (1998). Crop management systems for rainfed and irrigated sunflower (*Helianthus annuus*) in South Western France. *J. Agric. Sci. Cambridge* 131:171-185.
- De-Guang, Y., S. Xiuying and Z. Tianhong (2001). The role of active oxygen scavengers in increasing drought resistant of maize. *J. Shengang Agric. Univ.*, 33(1):3-5.
- Demir, A. O., A. T. Goksoy, H. Buyukcangaz, Z. M. Turan and E. S. Koksak (2006). Deficit irrigation of sunflower in a humid climate. *Irrig. Sci.*, 24: 279-289.
- Demiroren, T. (1978). Détermination of evapotranspiration of sunflower in Ttokat, 25. *J. Tokat Region Soil Water Research Institute, Tokat*, pp. 27.
- Doorenbos, J. and A. H. Kassam (1979). *Yield responds to water*. Pub. 33. United Nations FAO, Rome. Pp. 193.
- Dubey, R. S. (1997). *Handbook of photosynthesis*, In Pessaraki, M. (Ed.). Marcel Dekker, New York. pp. 859-876.
- Dure L III, M. Crouch, J. Harada, J. Mundy, R. Quatrano, T. Thomas and Z. R. Sung (1989). Common amino acid sequence domains among the LEA proteins of higher plants. *Plant Mol. Biol.*, 12: 475-486.
- Edmeadas, G. O., J. O. Balanos, S. C. Chapman, H. R. Lafitte and M. Banziger (1999). Selection improves drought tolerance in tropical maize population. I. Grains in biomass, grain yield and harvest index. *Crop Sci.*, 39:1306-1315.
- El- Tayeb, M. A. (2005). Response of barley grains to the interactive effect of salinity and salicylic acid. *Plant Growth Regulator*. 45: 215-224.
- Erdem, T., L. Delba and A. H. Orta (2001). Water-use characteristics of sunflower (*Helianthus annuus* L.) under deficit irrigation. *Pakistan J. Biol. Sci.*, 4(7):766-769.
- FAO. (2006). *World agriculture: Towards 2030/2050*. Prospects for food, nutrition, agriculture and major commodity groups. Global perspective studies unit food and agriculture organization of the United Nations, Rome, Italy.
- Fereres, E., C. G. Gimenez and J. M. Fernandez (1986). Genetic variability in sunflower cultivars under drought .I. yields relationships. *Aust. J. Agric. Res.*, 37(6):573-582.
- Flagella, Z., T. Rotunno, E. Tarantino, R. Di Caterina and A. De Caro (2002). Changes in seed yield and fatty acid composition of high oleic sunflower hybrids in relation to the sowing date and water regime. *Eur. J. Agron.*, 17: 221-230.
- Flexas, J. and H. Medrano (2002). Drought-inhibition of photosynthesis in C₃ plants: Stomatal and non-

- stomatal limitations revisited. *Ann. Bot.*, 89:183-189.
- Foyer, C. H. and J. M. Fletcher (2001). Plant antioxidants: color me healthy biologist 48: 115-120.
- French, R. J. and N. C. Turner (1991). Water deficits changes dry matter partitioning and seed yield in narrow-leaved lupins (*Lupinus angustifolius* L.). *Aust. J. Agric.*, 42(3):471-484.
- Fu, J. and B. Huang (2001). Involvement of anti oxidants and lipid peroxidation in the adaptation of two cool season grasses to localized drought stress. *Environ. Exp. Bot.*, 45: 105-114.
- Gibson, A., K. T. Hubick and E. P. Bachelard (1991). Effects of abscisic acid on morphological and physiological responses to water stress in *Eucalyptus camaldulensis* seedlings. *Aust. J. Plant Physiol.*, 18: 153-163.
- Gimenez, C., and E. Fereres (1986). Genetic variability of sunflower cultivars under drought. II. Growth and water relations. *Aus. J. Agric. Res.*, 37: 583-597.
- Goksoy, A. T., A. O. Demir, Z. M. Turan and N. Dagustu (2004). Response of sunflower (*Helianthus annuus* L.) to full and limited irrigation at different growth stage. *Field Crop Res.*, 87: 167-1780.
- Govt. of Pakistan (2009b). Economic Survey of Pakistan. Ministry of Food, Agriculture and Livestock, Finance Division, Economic Advisor's wing, Islamabad, Pakistan, p: 23.
- Govt. of Pakistan (2009a). Economic Survey of Pakistan. Ministry of Food, Agriculture and Livestock, Finance Division, Economic Advisor's wing, Islamabad, Pakistan, p: 3-4.
- Gowing, D. J. G., H. G. Jones and W. J. Davies (1993). Xylem transported abscisic acid; the relative importance of its mass and its concentration in the control of stomatal aperture. *Plant Cell Environ.*, 16: 453-459.
- Griffiths, A. and E. A. Bray (1996). Shoot induction of ABA requiring genes in response to soil drying. *J. Exp. Bot.*, 47: 1525-1531.
- Hammadeh, I., P. Maury, P. Debaeke, J. Lecoq, L. Nouri, S.P. Kiani and P. Grieu (2005). Canopy nitrogen distribution and photosynthesis during grain filling in irrigated and water stressed sunflower genotypes. Interdrought-II, the second International Conference on integrated approaches to sustain and improve plant production under drought stress; Rome, Italy, September, 24-28 pp-94.
- Harris, M. J and W. H. Outlaw (1991). Rapid adjustment of guard-cell abscisic acid levels to current leaf-water status. *Plant Physiol.*, 95:171-173.
- Hartung, W., J. Zhang and W. J. Davies (1994). Does abscisic acid play a stress physiological role in maize plants growing in heavily compacted soil? *J. Exp. Bot.*, 45:221-226.
- Hatam, M. and G. Q. Abbasi (1994). Oilseed Crops. In: Crop production.(Eds): Nazir, M S. and E. Bashir, National Book Foundation, Islamabad, Pakistan. Pp 343.
- He, J. X., J. Wang and H. G. Liang (1995). Effects of water stress on photochemical functions and protein metabolism of photosystem II in wheat leaves. *Physiol. Plant.*, 93: 771-777.
- Heschel, M. S. and N. J. Hausmann (2001). Population differentiation for abscisic acid responsiveness in *Impatiens capensis* (Balsaminaceae). *Inter. J. Plant Sci.*, 162: 1253-1260.
- Hoad, S. P., G. Russell, M. E. Lucas and I. J. Bingham (2001). The management of wheat, barley and oats root systems. *Adv. Agron.*, 74:193-246.
- Hornberg, C., E. W. Weiler (1984). High affinity binding sites for abscisic acid on the plasmalemma of *Vicia faba* guard cells. *Nature*. 310: 321-324.
- Hsiao, T. C., R. Acevedo, E. Fereres and D. W. Henderson (1976). Stress, growth and osmotic adjustment. *Phil. Trans. R Soc. Lond. B*. 273: 479-500.
- Huner, N. P. A., G. Oquist, V. M. Hurry, M. Korel, S. Falk and M. Griffith (1993). Photosynthesis, photoinhibition and low temperature acclimation in cold tolerant plants. *Photosyn. Res.*, 37:19-39.
- Hussain, M., M. A. Malik, M. Farooq, M. Y. Ashraf and M. A. Cheema (2008). Improving drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. *J. Agron. Crop Sci.*, 194: 193-199.
- Hussain, S. (2010). Enhancement of drought tolerance in sunflower (*Helianthus annuus* L.) by exogenous application of abscisic acid, Ph. D. dissertation, Department of Agronomy, University of Agriculture, Faisalabad, Pakistan.
- Hussain, S. and S. Ismail (1994). Effect of salt and water stress on growth and biomass production in *Helianthus annuus* L. *Pakistan J. Bot.*, 26(1):127-138.
- Jackson, G. E., J. Irvine, J. Grace, A. A. M. Khalil (1995). Abscisic acid concentrations and fluxes in drought conifer saplings. *Plant Cell Environ.*, 18: 13-22.
- Jaleel, C. A, P. Manivannan, B. Sankar, A. Kishorekumar, R. Gopi, R. Somasundaram, R. Panneerselvam (2007c). Induction of drought stress tolerance by ketoconazole in *Catharanthus roseus* is mediated by enhanced antioxidant potentials and secondary metabolite accumulation, *Colloids Surf. B: Biointerfaces* 60: 201-206.

- Jaleel, C. A., B. Sankar, P. V. Murali, M. Gomathinayagam, G. M. A. Lakshmanan and R. Panneerselvam (2007d). Water deficit stress effects on reactive oxygen metabolism in *Catharanthus roseus*; impacts on ajmalicine accumulation, Colloids Surf. B: Biointerfaces doi:10.1016/j.colsurfb.2007.09.026.
- Jaleel, C. A., P. Manivannan, A. Kishorekumar, B. Sankar, R. Gopi, R. Somasundaram, and R. Panneerselvam (2007a). Alterations in osmoregulation, antioxidant enzymes and indole alkaloid levels in *Catharanthus roseus* exposed to water deficit, Colloids Surf. B: Biointerfaces 59: 150–157.
- Jaleel, C. A., P. Manivannan, B. Sankar, A. Kishorekumar, R. Gopi, R. Somasundaram and R. Panneerselvam (2007b). Water deficit stress mitigation by calcium chloride in *Catharanthus roseus*: Effects on oxidative stress, proline metabolism and indole alkaloid accumulation, Colloids Surf. B: Biointerfaces. 60:110–116.
- Jaleel, C. A., P. Manivannan, G. M. A. Lakshmanan, M. Gomathinayagam and R. Panneerselvam (2007e). Alterations in morphological parameters and photosynthetic pigment responses of *Catharanthus roseus* under soil water deficits, Colloids Surf. B: Biointerfaces doi:10.1016/j.colsurfb.2007.09.008.
- Jaleel, C. A., R. Gopi, B. Sankar, P. Manivannan, A. Kishorekumar and R. Sridharan (2007). Studies on germination, seedling vigor, lipid peroxidation and proline metabolism in *Catharanthus roseus* seedlings under salt stress. South Afr. J. Bot., 73:190-195.
- Jarvis, A. J. and W. J. Davies (1997). Whole-plant ABA flux and the regulation of water loss in *Cedrella odorata*. Plant Cell Environ., 20: 521–527.
- Jasinkas, A. (1999). Investigation of change of mass and moisture content of energy plants. Egyptian J. Agron., 21: 67-85.
- Jensen, H. E. and V. P. Mogenson (1984). Yield and nutrient content of spring wheat subjected to water stress at various growth stages. Acta Agric., 34:527-533.
- Jia W., J. Zhang and D. Zhang (1996). Effect of leaf water status and xylem pH in metabolism of xylem-transported abscisic acid. J. Exp. Bot., 47: 1085-1091.
- Jia, W and J. Zhang (1999). Stomatal closure is induced rather by prevailing xylem abscisic acid than by accumulated amount of xylem derived abscisic acid. Physiol. Plant., 106: 268-275.
- Johnston, A. M., S. A. Brandt and D. A. Derksen (1995). Relative performance of canola, sunola, and mustard. P.208-215. In Proc. Western Canada Agron. Workshop, 5-7 July, Red Deer, AB, Canada.
- Jokhan, A. D., M. A. Else and M. B. Jackson (1996). Delivery rates of abscisic acid in xylem sap of *Ricinus communis* L. plants subjected to part drying of soil. J. Exp. Bot., 47: 1595-1599.
- Jones, H. G. (1980). Interaction and integration of adaptive responses to water stress: the implications of an unpredictable environment. In: Turner, N.C., Kramer, P.J. (Eds.), Adaptation of Plants to Water and High Temperature Stress. Wiley, New York, pp. 353–365.
- Jones, H. G. (1992). Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology. Cambridge University Press, Cambridge, UK. Pp. 428.
- Jones, H. G. and J. E. Corlett (1992). Current topics in drought physiology. J. Agric. Sci., 119:291-296.
- Jones, M. M and N. C. Turner (1980). Osmotic adjustment in expanding and fully expanded leaves of sunflower in response to water deficit. Aust. J. Plant. Physiol., 7:181-192.
- Kadayifei, A. and O. Yildirim (2000). Response of sunflower seed yield to water. Turkish J. Agri. Foresrty, 24(2): 137-145 (CAB Absts., 2000-2002).
- Kazi, B. R., F. C. Oad, G. H. Jamro, L. A. Jamil and N. L. Oad (2002). Effect of water stress on growth, yield and oil content of sunflower. Pakistan J. Appl. Sci., 2 (5): 550-552.
- Khan, M. S., M. S. Swati, I. H. Khali and A. Iqbal (2000). Heterotic studies for various characters in sunflower. Asian J. Plant Sci., 2(14):1010-1014.
- Khan, M. S., M. S. Swati, I. H. Khali and A. Iqbal (2003). Heterotic studies for various characters in sunflower. Asian J. Plant Sci., 2(14):1010-1014.
- Korte, L. L., J. H. Williams, J. E. Specht and R. C. Sorenson (1983). Irrigation of soybean genotypes during reproductive ontogeny: II. Yield components responses. Crop Sci., 23:528-533.
- Kozlowski, T. T. and S. G. Pallardy (2002). Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev., 68 (2): 270–334.
- Kramer, P. J. (1983). Water Relations of Plants. Academic Press, New York, pp.489
- Kramer, P. J. and J. S. Boyer (1995). Water relations of plants and soils. San Diego, CA: academic press.
- Kriedemann, P. E. and B. R. Loveys (1974). Hormonal mediation of plant responses to environmental stress. Pp. 461-465. In Bieleski, R. L., A.R. Ferguson, and M.M. Creswell (Eds), Mechanism

- of regulation of plant growth, The royal society of New Zealand, Vellingyton.
- Labhili, M., P. Joudrier and M. F. Gautier (1995). Characterization of cDNAs encoding *Triticum durum* dehydrins and their expression patterns in cultivars that differ in drought tolerance. *Plant Sci.*, 112: 219-230.
- Laghrab, M. H., F. Nouri and H. Z. Abianeh (2003). Effect of the reduction of drought stress using supplementary irrigation for sunflower in dry farming conditions. In *Agronomy and Horticulture*. 59: 81-86 (CAB Absts., 2000-2002).
- Lambers, H., O. K. Atkins and I. Scheureater (1996). Respiratory patterns in roots in relation to their function in: Waisel Y. (Ed.), *Plant roots, The Hidden Half*, Marcel Dekker, New York. USA.
- Larcher, W. (1995). *Physiological Plant Ecology*. Springer-Verlag, Berlin, pp. 506.
- Lawlor, D. W. (2002). Limitations to photosynthesis in water stressed leaves: stomata vs. metabolism and the role of ATP. *Ann. Bot.*, 89:1-15.
- Lawlor, D. W. and G. Cornic (2002). Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ.*, 25:275-294.
- Lawson, T., K. Oxborough, J. I. L. Morison and N. R. Baker (2003). The responses of guard and mesophyll cell photosynthesis to CO₂, O₂, light and water stress in range of species are similar. *J. Exp. Bot.*, 54:1743-1752.
- Lee, T. M., H. S. Lur and C. Chu (1993). Role of abscisic acid in chilling tolerance of rice (*Oryza sativa* L.) seedlings. I. Endogenous abscisic acid levels. *Plant Cell Environ.*, 16: 481-490.
- Levitt, J. (1980). Responses of plants to environmental stress, 2nd ed., 2. Academic Press, New York. pp.497.
- Li, C. (1999). Carbon isotope composition, water use efficiency and biomass productivity of *Eucalyptus microtheca* populations under different water supplies. *Plant Soil.*, 214:165-171.
- Li, C. and K. Wang (2003). Differences in drought responses of three contrasting *Eucalyptus microtheca* F. Muell. Populations. *For. Ecol. Manage.*, 179: 377-385.
- Liu, F., C. R. Jensen and M. N. Andersen (2004). Pod set related to photosynthetic rate and endogenous ABA in soybean subjected to different water regimes and Exogenous ABA and BA at early reproductive stage. *Annals of Bot.*, 94: 405-411.
- Liu, H. S. and F. M. Li (2005). Root respiration, photosynthesis and grain yield of two spring wheat in response to soil drying, *Plant growth regul.*, 46: 233-240.
- Liu, H. S., F. M. Li. and H. Xu (2004). Deficiency of water can enhance root respiration rate of drought sensitive but not drought tolerant spring water. *Agri. Water Manage.*, 64: 41-48.
- Loveys, B. R. (1984). Abscisic acid transport and metabolism in grapevine. *New Phytol.*, 98: 575-582.
- Luan, S. (2002). Signalling drought in guard cells. *Plant Cell Environ.*, 25: 229-237.
- Ludlow, M. M. and R. C. Muchow (1990). A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.*, 43: 107-153.
- Luquez, J. E., L. A. N. Aguirrezebal, M. E. Augero and V. R. Pereyra (2002). Stability and adaptability of cultivars in non balanced yield trials, comparison of methods for selecting high oleic sunflower hybrids for grain yield and quality. *J. Agron. Crop Sci.*, 188 (4): 225-234.
- Mahal, S. S., H. S. Uppal and B. S. Mankotia (1998). Performance of spring sunflower under different levels of soil moisture regimes and nitrogen. *Environ. Eco.*, 16(3): 599-602.
- Manivannan, P. C. A. Jaleel, A. Kishorekumar, B. Sankar, R. Somasundaram, R. Sridharan and R. Panneerselvam (2007). Changes in antioxidant metabolism of *Vigna unguiculata* (L.) Walp. by propiconazole under water deficit stress, *Colloids Surf. B: Biointerfaces* 57: 69-74.
- Martin, D., J. Van. Brochin and G. Wilmes (1989). Operating rules for deficit irrigation management. *ASAE*. 22: 1207-1215.
- Maruthi, V., S. G. Reddy and M. Vanaja (1998). Evaluation of sunflower genotypes under late sown characters of sunflower. *Crop Sci.*, 22:817-822.
- Mekki, B. B., M. A. El-Kholy and E. M. Mohamad (1999). Yield, oil and fatty acids content as affected by water deficit and potassium fertilization in two sunflower cultivars. *Egyptian J. Agron.*, 35(2): 67-85.
- Milborrow, B. W. (2001). The pathway of biosynthesis of abscisic acid in vascular plants: A review of the present state of knowledge of ABA biosynthesis. *J. Exp. Bot.*, 52: 1145-1164.
- Miller, J. F. (1992). Update on inheritance of sunflower characteristics. P.905-945. In *Proc. Of 13th Int. Sunflower Conf.* 7-11 Sept. Pisa, Italy, 1, Int. Sunflower Association, Toowoomba, Australia.
- Monakhova, O. F. and I. I. Chernyadev (2002). Protective role of kartolin-4 in wheat plants exposed to soil drought, *Appl. Biochem. Micro.*, 38:373-380.
- Monyo, E. S., G. Ejeta and D. Rhodes (1992). Genotypic variation for glycinebetaine in sorghum and its relationship to agronomic and morphological traits. *Media*, 37:283-286.

- Moons, A., G. Bauw, E. Prinsen, M. Van, Montagu and D. Van Der Straeten (1995). Molecular and physiological responses to abscisic acid and salts in roots of salt-sensitive and salt-tolerant indica rice varieties. *Plant Physiol.*, 107: 177-186.
- Morgan, P. W. (1990). Effects of abiotic stresses on plant hormone systems, In: stresses response in plants: adaptation and acclimation mechanisms, Wiley-Liss, Inc., pp. 113-146.
- Munns R. and R. W. King (1988). Abscisic acid is not the only stomatal inhibitor in the transpiration stream of wheat plants. *Plant Physiol.*, 88: 703-708.
- Munns R., R. W. Passioura, B. V. Milborrow, R. A. Jmes and T. J. Close (1993). Stored xylem sap from wheat and barely in drying soil contains a transpiration inhibitor with a large molecular size. *Plant Cell Environ.*, 16: 867-872.
- Nasri, M. (2005). Interaction of nutrient elements and drought stress in cultivars of *Brassica napus*. The second international conference on integrated approaches to sustain and improve plant production under drought stress. Rome, Italy, September 24-28, pp-109.
- Nobel, P. S. (1999). *Physicochemical and environmental plant physiology*. P.474. 2nd Ed., Academy Press, San Diego, CA, USA.
- Ouvrard, O., F. Cellier, K. Ferrare, D. Tusch, T. Lamaze, J.M. Dupuis and F. Casse-Delbart (1996). Identification and expression of water stress- and abscisic acid-regulated genes in a drought-tolerance sunflower genotype, *Plant Mol. Biol.*, 31: 819-829.
- Palta, J. A. (1984). Influence of water deficits on gas exchange and the leaf area development of cassava cultivars. *J. Exp. Bot.*, 35: 1441-1449.
- Pandey, D. M., C. L. Goswami and B. Kumar (2003). Physiological effects of plant hormones in cotton under drought. *Biologia Plantarum*, 47 (4): 535-540.
- Pankovic, D., Z. Sakac, S. Kevresan and M. Plesnicar (1999). Acclimation to long-term water deficit in the leaves of two sunflower hybrids: Photosynthesis, electron transport and carbon metabolism. *J. Exp. Bot.*, 50: 127-138.
- Pataki, D. E., R. Orem., and N. Phillips (1998). Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *J. Exp. Bot.*, 49: 871-878.
- Pekic, S. and S. A. Quarrie (1987). Abscisic acid accumulation in maize differing in drought resistance: a comparison of intact and detached leaves. *J. Plant Physiol.*, 127: 203-217.
- Pelah D., W. Wang. A. Altman., O. Shoseyov and D. Bartels (1997). Differential accumulation of water stress-related proteins, sucrose synthase and soluble sugars in *Populus* species that differ in their water stress response. *Physiol. Plant.* 99: 153-159.
- Petchu, E., A. Arsintescu and D. Stanciu (2003). Studies regarding the hydro stress effect on sunflower plants. *Analele Institutului de Cereale si Plante Technice, Fundulea*, 70:347-356.
- Ponton, S., J. L. Dupouey, N. Breda and E. Dreyer (2001). Comparison of water-use efficiency of seedlings from two sympatric oak species: genotype environment interactions. *Tree Physiol.*, 22:413-422.
- Prusti, A. M., R. K. Bajaj, B. Subbalakshmi and V. S. Dev (1999). Stability analysis for oil yield and its components in sunflower. *J. Environ. Ecol.*, 17(1): 94-96.
- Putnam, D. H., E. S. Oplinger, D. R. Hicks, B. R. Durgan, D. M. Noetzel, R. A. Meronuck, J. D. Doll and E. E. Schutle (1990). *Alternative Field Crops Manual*, University of Wisconsin Coop. Ext. Serv., Univ. of Minnesota, Ex. Serv., Cent. for Alternative Plant and Animal Products.
- Quarrie, S. A. (1980). Genotypic difference in leaf water potential, abscisic acid and proline concentration in spring wheat during drought stress. *Annals of Bot.*, 46: 383-394.
- Rad, A. H. S., J. Daneshian and A. R. Valadabadi (2005). Water deficit stress effect at grain filling seed stages of rapeseed. The second international conference on integrated approaches to sustain and improve plant production under drought stress, Rome, Italy, September 24-28, pp-243.
- Raschke, K. (1975). Simultaneous requirement of carbon dioxide and abscisic acid for stomatal closing in *Xanthum strumarium* L. *Planta*. 125: 243-259.
- Razi, H. and M. T. Asad (1999). Comparison of selection criteria in normal and limited irrigations in sunflower. *Euphytica*. 105: 83-90.
- Reddy, A. R., K. V. Chaitanya and M. Vivekanandan (2004). Drought induced responses of photosynthesis and antioxidant metabolism in higher plants, *J. Plant Physiol.*, 161:1189-1202.
- Robert, E. S. and M. E. LeNoble (2002). ABA, ethylene and the control of shoot and root growth under water stress. *J. Exp. Bot.*, 53:33-37.
- Robertson, M. J. and J. F. Holland (2004). Production risk of canola in the semi-arid subtropics of Australia. *Aust. J. Agric. Res.*, 55: 525-538.
- Sadras, V. O., D. M. Whitefield and D. J. Connor (1991). Regulation of evapotranspiration and its partitioning between transpiration and soil evaporation by sunflower crops: a comparison between hybrids of different stature. *Field Crops Res.*, 28:17-37.

- Salera, E. and M. Baldini (1998). Performance of high and low oleic acid hybrids of sunflower under different environmental conditions. Note-II, *Helia*, 21(28):55-67.
- Salisbury, B. F. and N. G. Marinos (1985). The ecological role of plant growth substances in Pharis, R. P. and D.M. Reid (Eds), *Encyclopedia of plant physiol.*, 11. Springer- verlag, Berlin, Heidelberg, New York.
- Sankar, B., C. A. Jaleel, P. Manivannan, A. Kishorekumar, R. Somasundram and R. Panneerselvam (2007). Drought-induced biochemical modifications and proline metabolism in *Abelmoschus esculentus* (L.) Moench. *Acta Bot. Croat.*, 66:43-56.
- Satyabrata, M., M. R. Hedge and S. B. Chattopodhay (1988). *Hand Book of Annual Oilseed Crops*, Oxford IBH Pub.Co., (Pvt) Ltd., New Dehli. pp.176.
- Schneiter, A. A. (1992). Production of semi dwarf and dwarf sunflower in the northern great plains of United States. *Field Crops Res.*, 30: 391-401.
- Schurr, U., T. Gollan and E. D. Schulze (1992). Stomatal response to drying soil in relation to changes in xylem sap composition of sunflower, II. Stomatal sensitivity to abscisic acid imported from the xylem sap. *Plant Cell Environ.*, 15: 561-567.
- Serraj, R. and T. R. Sinclair (2002). Osmolyte accumulation: can it really help increase crop yield under drought conditions? *Plant Cell Environ.*, 25: 333-341.
- Shinozaki, K. and K. Yamaguchi-Shinozaki (1999). Molecular responses to drought stress. In: Yamaguchi-Shinozaki, (Ed). *Molecular responses to cold, drought, heat and salt stress in higher plants*. Austin, TX: R.G.Landes Company. pp. 11-28.
- Sinaki J. M., E. M. Heravan, A. H. S. Rad, G. Noormohammadi and G. Zarei (2007). The effect of water deficit during growth stages of canola. *American-Eurasian J. Agric. Environ. Sci.*, 2(4): 417-422.
- Singh, B., G. S. Sandha, R. K. Bajaj, N. Kaur and S. Bhardwaj (1999). Genotype environment interactions for seed yield and its components in sunflower. *Crop Improv.*, 26(1):99-102.
- Sivakumaran, S. and M. A. Hall (1978). Effects of age and water stress on endogenous levels of plant growth regulators in *Euphorbia lathyris* L. *J. Exp. Bot.*, 29: 195-205.
- Somerville, C. and J. Briscoe (2001). Genetic engineering and water. *Sci.*, 292:2217.
- Stewart, C. R. (1980). The mechanism of abscisic acid-induced proline accumulation in barley leaves. *Plant Physiol.*, 66: 230-233.
- Stoll, M., B. Loveys and W. J. Davies (2000). Hormonal changes induced by partial root zone drying of irrigated grape vine. *J. Exp. Bot.*, 51:1627-1634.
- Stone, L. R., A. J. Schlenge, R. E. Gwin and A. H. Khan (1996). Response of corn, grain sorghum and sunflower to irrigation in the high plains of Kansas, *Agric. Water Management*. 30:251-259.
- Subbarao, G. V., N. H. Num, Y. S. Chauhan and C. Johansen (2000). Osmotic adjustment, water relation and carbohydrates remobilization in pigeon pea under water deficits. *J. Plant Physiol.*, 157: 651-659.
- Tahir, M. H. N and S. S. Mehdi (2001). Evaluation of open pollinated sunflower (*Helianthus annuus* L.) populations under water stress and normal condition. *Int. J. Agric.* 3(2):236-238.
- Tahir, M. H. N., M. Imran and M. K. Hussain (2002). Evaluation of sunflower (*Helianthus annuus* L.) inbred lines for drought tolerance. *Int. J. Agric. Biol.*, 04(3):398-400.
- Taiz, L. and E. Zeiger (2003). *Plant physiology; In; Abscisic acid: A seed maturation and anti-stress signal*. Panama Publishing Corporation, New Delhi, India. pp. 540-544.
- Tardieu, F., T. Lafarge and T. Simonneau (1996). Stomatal control by fed or endogenous xylem ABA in sunflower: interpretation of correlations between leaf water potential and stomatal conductance in arnsohydric species. *Plant Cell Environ.*, 19: 75-84.
- Tezara, W., V. J. Mitchell, S. D. Driscoll and D. W. Lawlor (1999). Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature*, 401:914-917.
- Tezara, W., V. Mitchell, S. P. Driscoll and D. W. Lawlor (2002). Effects of water deficit and its interaction with CO₂ supply on the biochemistry and physiology of photosynthesis in sunflower. *J. Exp. Bot.*, 53:1781-1791.
- Trejo, C. L. and W. J. Davies (1991). Drought-induced closure of *Phaseolus vulgaris* L .stomata precedes leaf water deficit and any increase in xylem ABA concentration. *J. Exp. Bot.*, 42:1507-1515.
- Trejo, C. L., A. L. Clephan and W. J. Davies (1995). How do stomata read abscisic acid signals? *Plant Physiol.*, 109: 803-811.
- Tsialtas, J. T., L. L. Handley, M. T. Kassioumi, D. S. Veresoglou and A. A. Gagianas (2001). Inter-specific variation in potential water use efficiency and its relation to plant species abundance in water-limited grassland. *Funct. Ecol.*, 15: 605-614.

- Unger, P. W. (1983). Irrigation effects on sunflower growth, development and water use. *Field Crops Res.*, 3:181-194.
- Unyayar, S., Y. Keles and E. Unal (2004). Proline and ABA levels in two sunflower genotypes subjected to water stress. *Bulg. J. Plant Physiol.*, 30(3-4): 34-47.
- Van Rensburg, L. and G. H. J. Kruger (1994). Applicability of abscisic acid and (or) proline accumulation as selection criteria for drought tolerance in *Nicotiana tabacum*. *Can. J. Bot.*, 72:1535– 1540.
- Velue, G. and K. Palanisami (2001). Impact of moisture stress and ameliorants on growth and yield of sunflower. *Madras Agric. J.*, 88(10-12):660-665.
- Wahid, A. and E. Rasul (2005). Photosynthesis in leaf, stem, flower and fruit In: Pessarakli M. (Ed). *Hand book of Photosynthesis*, 2nd Ed., CRC Press, Florida, pp: 479-497.
- Walton, D. C. (1980). Biochemistry and physiology of abscisic acid. *Annual review of plant physiology*: 31: 453-489.
- Wang, Z. L., B. R. Huang and Q. Z. Xu (2003). Effects of abscisic acid on drought responses of *Kentucky bluegrass*. *J. Am. Soc. Hort. Sci.*, 128 (1): 36–41.
- Weiss, E. A. (2000). *Oil Seed Crops*. Blackwell Science Ltd. London. Pp. 218.
- Wilkinson, S. and W. J. Davies (2002). ABA-based chemical signaling: the coordination of responses to stress in plants. *Plant Cell Environ.* 25: 195–210.
- Wilkinson, S. and W. J. Davies (1997). Xylem sap pH increase: A drought signal received at the apoplastic face of the guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. *Plant Physiol.*, 113: 559-573.
- Wise, R. R. (1995). Chilling enhanced phototoxidation: the production. *Photosyn. Res.*, 45:79-97.
- Wisner, T. N. and C. A. Chase (1984). World food trade and US agriculture 1960-1983.
- Xing, W. and C. B. Rajashekar (1999). Alleviation of water stress in beans by exogenous glycinebetaine. *Plant Sci.*, 148:185-195.
- Xu, X., G. Q. Zheng, X. P. Deng and H. Medrano (2002). Effects of exogenous abscisic acid and water stress on the growth response of subterranean clover of different genotypes. *Acta Bot. Sinica.*, 44(12):1425–1431.
- Zeevart, J. A. D. (1999). Abscisic acid metabolism and its regulation. In: Hooykaas, P.J.J., M.A. Hall, K.R. Libbenga. (Eds.), *Biochemistry and Molecular Biology of Plant Hormones*. Elsevier Science, Amsterdam, pp. 189–207.
- Zhang, J. and W. J. Davies (1989a). Abscisic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. *Plant Cell Environ.*, 12: 73–81.
- Zhang, J. and W. J. Davies (1989b). Sequential responses of whole plant water relations towards prolonged soil drying and the mediation by xylem sap ABA concentrations in the regulation of stomatal behavior of sunflower plants. *New Phytol.*, 113: 167–174.
- Zhang, J. and W. J. Davies (1990). Changes in the concentration of ABA in the xylem sap as a function of changing soil water status can account for changes in leaf conductance and growth. *Plant Cell Environ.* 13: 277–285.
- Zhang, J. and W. J. Davies (1991). Anti-transpiration activity in xylem sap of maize plants. *J. Exp. Bot.*, 42: 317–321.
- Zhang, J., U. Schurr and W. J. Davies (1987). Control of stomatal behavior by abscisic acid which apparently originates in roots. *J. Exp. Bot.*, 38:1174– 1181.
- Zhang, S. Q. and W. H. Outlaw Jr. (2001). Abscisic acid introduced into transpiration stream accumulates in the guard cell apoplast and causes stomatal closure. *Plant Cell Environ.*, 24:045–54.
- Zhu, J. K. (2002). Salt and drought stress signal transduction in plants. *Annu. Rev. Plants Physiol. Plant Mol. Biol.*, 53: 247–273.