Mini Review

Bioscience Research, 6(1): 20-27, 2009
www.isisn.org

Drought stress in plants: A review on water relations

C. A. Jaleel[1]* and B. E. Llorente[2]

[1]Stress Physiology Lab, Department of Botany, Annamalai University, Annamalainagar 608 002, Tamil Nadu, **India**.
[2]Departamento Ciencias Básicas, Universidad Nacional de Luján, Rutas 5 y 7(6700) Luján, Buenos Aires, **Argentina**.
***Corresponding author**

The term stress is used, most often subjectively, with various meanings, the physiological definition, and appropriate term as responses in different situations. The flexibility of normal metabolism allows the development of responses to environmental changes which fluctuate regularly and predictable over daily and seasonal cycles. Thus every deviation of a factor form its optimum does not necessarily result in stress. Stress being with a constraint or with highly unpredictable fluctuations imposed on regular metabolic patterns that cause injury, disease, or aberrant physiology. Among the environmental stresses, drought stress is one of the most adverse factors of plant growth and productivity. The biochemical and molecular responses to drought is essential for a holistic perception of plant resistance mechanism to water limited condition in higher plants. In this review, we tried to describe some aspects of drought induced changes in water relations in higher plants.

Key words: Harvest Index, Transpiration rate, Net assimilation rate, Water stress, Water use efficiency

Environmental stresses trigger a wide variety of plant responses, ranging from altered gene expression and cellular metabolism to changes in growth rate and crop yield (Bhatt et al. 2005; Jaleel et al., 2007a; Farooq et al. 2008). Plant reactions exist to circumvent the potentially harmful effects caused by a wide range of both abiotic and biotic stresses, including light, drought, salinity and high temperatures (Chaves et al. 2002; Jaleel et al., 2007b, 2008a,b). Water stress is the major problem in agriculture and the ability to withstand such stress is of immense economic importance. Water stress tolerance involves subtle changes in cellular biochemistry. It appears to be the result of accumulation of compatible solutes and of specific proteins that can be rapidly induced by osmotic stress (Djibril et al. 2005; Farooq et al. 2008). The numerous physiological responses of plant to water deficits generally vary with the severity as well as the duration of water stress (Li, 2000; Correia et al., 2001; Pane and Goldstein, 2001; Pita and Pardes, 2001; Weigh, 2001; Edward and Wright, 2008).

Water is imperative for plant growth and development. Water deficit stress, permanent or temporary, limits the growth and distribution of natural vegetation and the performance of cultivated plants more than any other environmental factor (Soriano et al. 2002, 2004; Farooq et al. 2008, Jaleel et al., 2009a,b). Although research and practices aimed at improving water stress resistance and water use efficiency have been carried out for many years, the mechanism involved is still not clear (Jaleel et al., 2008c,d). Further understanding and manipulating plant water relations and water stress tolerance can significantly improve plant productivity and environmental quality.

Water deficit stress can be defined as situation in which plant water potential and turgor are reduced enough to interface with normal functions (Zhu, 2002). Water stress is considered to be a moderate loss of water which leads to stomatal closure and limitation of gas exchange. Desiccation is a much more extensive loss of water which can potentially lead to gross disruption of metabolism and cell structure and eventually to the cessation of enzyme catalyzed reaction (Kage et al. 2004). Water stress is characterized by reduction of water content, turgor, total water potential, wilting, closure of stomata, and decrease in cell enlargement and growth. Severe water stress may result in arrest of photosynthesis, disturbance of metabolism, and finally dying (Kamara et al. 2003).

Water stress influences plant growth at various levels of cell to community (Kiani et al. 2008). The quantity and quality of plant growth depend on cell division enlargement, and differentiation and all of these events are affected by water stress (Borsani et al. 2001; Kusaka et al. 2005; Jaleel et al., 2007c,d). It reduces plant growth inhibition of various physiological and biochemical processes, such as photosynthesis, respiration translocation, ion uptake, carbohydrates, nutrient metabolism and hormones (Lawlor et al. 2002).

Drought stress has adverse influence on water relations in *Arachis hypogeae* (Lawson et al. 2003), photosynthesis (Massacci, et al., 2008) and mineral nutrition, metabolism, growth and yield (Mohammadian, 2005). In addition, drought conditions influence the growth of weeds, agronomic management and nature and intensity of insects, pests and diseases (Monneveux et al., 2006; Nam et al., 2001).

Water use efficiency is traditionally defined as the ratio of dry matter accumulation to water consumption over a season. Increasing water use efficiency could theoretically affect plant growth. When water is limited, plants that use a finite water supply more efficient would positively affect plant productivity in peanut (Nayyar et al., 2006). Water use efficiency measurements may be made at three levels (i) in single leaf using gas exchange techniques (ii) in whole plants grown in containers and (iii) at the canopy level based on evapotranspiration in the field (Ogbonnaya et al., 2003).

Variation in water use efficiency amongest or within species can be assessed gravimetrically. However, reliable estimates of water use efficiency, under field conditions may be difficult, owing to the lack of technologies to asses the below ground biomass. But gravimetric technique can be adequately adopted to estimate in genotypic variation in pot culture experiments. Recent studies have shown that carbon isotope discrimination occurring during carbon assimilation by leaves is closely related to water use efficiency in various crops (Petropoulos et al. 2008), suggesting that carbon isotope discrimination technology can be used to screen genotypes for water use efficiency.

LEAF AREA DURATION

Monthly variations in leaf area index have been observed for some of the trees species in accordance with seasonal variation in multipurpose agroforestry tree species (Colom and Vazzana, 2001; Thakur and Kaur, 2001). This variation was found to be the main cause of variation in productivity. Leaf area duration is reduced by decreasing water potential in *Arachis hypogeae* (Reddy *et al*., 2003).

Leaf area index is the ratio of the total leaf area of plant to the ground area covered by the plant. Leaf area index, which indicates the photosynthetic surface per unit area were found to increase rapidly 30 to 60 days after sowing and thereafter declined in both the years irrespective of cropping systems and nitrogen levels in maize (Shivay *et al*., 2002). The significant variation was reported in leaf area index in water stressed sunflower plants with respect to plantation time (Soriano *et al*., 2004). Leaf area decreased in podded plants and further reduced by water stress in *Abelmoschus esculentum* (Bhatt and Srinivasa Rao, 2005).

CUMULATIVE WATER TRANSPIRED

Cowpea cultivars were found to have high mean stomatal frequency on lower surface of leaf than upper surface which leads to reduced transpiration rate (Razmjoo et al. 2008). The decline in transpiration with the ageing of the leaf plays a very important role in regulating transpirational losses (Thakur and Kaur, 2001). Similar results were observed in *barley* (Samarah 2005), *soybean* (Samarah et al. 2006) and in *Abelmoschus esculentus* (Sankar *et al*,. 2008).

WATER USE EFFICIENCY

Water use efficiency can be increased by systems and limited water and land resources, inorder to increase the food production with least quantity of water supply (Debaeke and Aboudrare, 2004). Water use efficiency is a non linear function that increases under conditions of water stress in peanut (Ferreyra *et al*., 2003). Under salinity condition there was no cultivar differences in wheat to WUE, if the plants were given sufficient water in wheat (Shaheen and Hood-Nowotny, 2005).

Water use efficiency was found to be varying with genotypic differences in groundnut (Sankar et al. 2008). Gaspar et al. (2002) considered water use efficiency as an important trait for selection of drought resistant varieties in plants. Water use efficiency was found to be varied in sunflower under water stress with respect to plantation time (Soriano *et al*., 2004).

Photosynthetic water use efficiency was found to be increased in potato during progressive soil drying in *Solanum tuberosum* (Liu *et al*., 2005). The existence of inter specific genetic differences in water use efficiency was reported in sympatric *Populus* species under water stress (Yin *et al*., 2005). When water is limited, plants that use a water supply more efficiently would grow more rapidly, in this case, high Water use efficiency would positively affect plant productivity in peanut (Wright *et al*., 1993). Similar results were observed in *Phaseolus vulgaris* (Martinez *et al*., 2007), *Eucalyptus microtheca* (Li *et al*., 2000), *Populus cathayana* (Tsialtas *et al*., 2001), *Sympatric* Oak species (Ponton *et al*., 2002) and *Eucalyptus microtheca* (Li and Wang, 2003). Under water stress water use efficiency were found to be increased in different species. Similar results were reported in previous studies (Li *et al*., 2000; Amdt *et al*., 2001; Marron *et al*., 2002; Siemens and Zwiazek, 2003; Zhang *et al*., 2004). Increased water use efficiency was found in relation to osmotic adjustment in two populations of *Atriplex halimus* (Martinez *et al*., 2003).

NET ASSIMILATION RATE

Net assimilation is found to be unaffected under water stress in *Asteriscus maritimus* plants (Rodriguez *et al*., 2005). Net assimilation rate is estimation of canopy photosynthesis per unit leaf area and can be used as a measure of photosynthetic efficiency. It's contribution of yield is not direct (Specht *et al*., 2001). The net assimilation rate was relatively lower under water stressed condition in Cluster bean (Vyas *et al*., 2001).

Net assimilation rate was found to be increased in maize plants when the cropping system and nitrogen levels were modified in the field (Amdt et al. 2001; Shivay *et al*., 2002). The decrease in photosynthetic rate strongly indicated stomatal closure as the factor for reduction during increased level of stress. The stomatal resistance significantly increased under water stress, whereas intercellular CO_2 concentration significantly reduced under severe stress condition (Meenakshi Sundaravalli *et al*., 2005). Sharp et al. (2002) noted that the leaf enlargement, stomatal opening and photosynthesis are directly affected by the water stress treatment in *Sorghum* leaves. Sinaki et al. (2007) also observed that water stress leads to decline in net photosnthesis and altered chloroplast capacity. Water stress can also negatively affect the photosynthetic activity of the plants through inactivation of enzymes (Cabuslay et al. 2002; Chaves *et al*., 2002; Lawlor, 2002).

MEAN TRANSPIRATION RATE

Rate of water loss was found to be decreased in *Avocado* cultivars under water deficit conditions due to increased some stomatal closure (Chartzoulakis *et al*., 2002). Similar case was found in *Vaccinium myrtillus* leaves (Chartzoulakis et al. 2002; Tahkokorpi *et al*., 2007). Transpiration efficiency with early plantings were consistently higher than those of late planting in sunflower under drought stress (Chaitanya et al. 2003; Soriano *et al*., 2004). Transpiration efficiency strongly influenced by the evaporative demand (Wu et al., 2008). Under rainfed condition with Cowpea genotyps belonging to different growth habit indicated that the determinate genotypes had higher values of transpiration rate as compared to indeterminate genotypes.

HARVEST INDEX

Harvest index found to be varied in drought stress sunflower with respect to plantation time (Soriano *et al*., 2004; Amarjit et al. 2005). In grain crops, avoiding the determinant effects of water deficits on the harvest index also minimizes the impact of the water limitation (Tahir et al. 2001). A two fold difference in harvest Index was imposed at different growth stages in water stressed sunflower (Soriano *et al*., 2002). A reduction in harvest Index was reported in sunflower during reproductive stages under water stressed conditions (Soriano *et al*., 2002). Long season genotype of sunflower has longer HI values than short season cultivars under rainfed conditions.

Greater plant fresh and dry weights under water limited conditions are desirable characters. A common adverse effect of water stress on crop plants is the reduction in fresh and dry biomass production. Plant productivity under drought stress is strongly related to the processes of dry matter partitioning and temporal biomass distribution (Kage *et al*., 2004). Diminished biomass due to water stress was observed in almost all genotypes of sunflower (Tahir & Mehid, 2001). However, some genotypes showed better stress tolerance than the others. Mild water stress affected the shoot dry weight while shoot dry weight was greater than root dry weight loss under severe stress in sugar beet genotypes (Mohammadian *et al*., 2005). Reduced biomass was seen in water stressed soybean (Specht *et al*., 2001), *Poncirus trifoliatae* seedlings (Wu *et al*., 2008), common bean and green gram and *Petroselinum crispum* (Petropoulos *et al*., 2008). A moderate stress tolerance in terms of shoot dry mass plants was noticed in rice (Lafitte *et al*., 2007).

Harvest index varied among cultivars of groundnut under water stressed condition (Nautiyal *et al*., 2002; Bhatt and Srinivasa Rao, 2005; Reddy *et al*., 2004; Jaleel et al. 2008e, 2009c-e). Grain yield in finger millet showed significant positive association with harvest index and negative association with dates to maturity**.** Harvest index drastically reduced under water stress in spring wheat (Zhu, 2002; Pan *et al*., 2003).

CONCLUSIONS

Drought is a worldwide problem, constraining global crop production and quality seriously, and recent global climate change has made this situation more serious. Drought is also a complex physical-chemical process, in which many biological macromolecules and small molecules are involved, such as nucleic acids, proteins, carbohydrates, lipids, hormones, ions, free radicals, and mineral elements. In addition, drought is related to salt stress, cold stress, high-temperature stress, acid stress, alkaline stress, pathological reactions, senescence, growth, development, cell circle, UV-B damage, wounding, embryogenesis, flowering, and signal transduction. Although physiological mechanisms of drought tolerance are relatively well understood, further studies are essential to determine the physiological basis of plant water relations under water deficit stress. In addition to other factors, changes in water relation parameters are of paramount importance to drought mechanisms.

REFERENCES

Amarjit, K. Nath., S. Kumari and D.R. Sharma. 2005. In vitro selection and characterization of water stress tolerant cultures of bell peper. *Indian J. Plant Physiol*. 10(1): 14-19.

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.

Bhatt, R.M. and N.K. Srinivasa Rao, 2005. Influence of pod load response of okra to water stress. *Indian J. Plant Physiol*., 10: 54–9

Borsani. O., P. Diaz, M.F. Agius., V. Valpuesta and J, Monza. 2001. Water stress generates an oxidative stress through the induction of specific Cu/Zn superoxide dismutase in *Lotus corniculatus* leaves. Plant science. 161: 757-763.

Cabuslay, G.S., O. Ito and A.A. Alejal. 2002. Physiological evaluation of responses of rice (*Oryza sativa L.*) to water deficit. *Plant Science*, 163: 815-827.

Chaves M.M., J.S. Pereira, J. Maroco, M.L. Rodriques, C.P.P. Ricardo, M.L. Osorio, I. Carvatho, T. Faria, C. Pinheiro, 2002. How plants cope with water stress in the field photosynthesis and growth? *Ann. Bot*., 89: 907–16

Debaeke, P and A. Aboudrare. 2004. Adaptation of crop management to water-limited environments. *Europe. J. Agronomy*. 21: 433-446.

Djibril, S., O.K. Mohamed, D. Diaga, D. Diégane, B.F. Abaye, S. Maurice and B. Alain, 2005. Growth and development of date palm (*Phoenix dactylifera* L.) seedlings under drought and salinity stresses. *African J. Biotechnol*., 4: 968–72

Edward, D. and D. Wright, 2008. The effects of winter waterlogging and summer drought on the growth and yield of winter wheat (*Triticum aestivum* L.) *European J. Agron.*, 28: 234-44

Farooq, M., S.M.A. Basra, A. Wahid, Z.A. Cheema, M.A. Cheema, A. Khaliq, 2008. Physiological role of exogenously applied glycinebetaine in improving drought tolerance of fine grain aromatic rice (*Oryza sativa* L.). *J. Agron. Crop Sci*., 194: 325–333.

Ferreyra. R.A., J.L. Dardanelli, L.B. Pachepsky, D.J. Collino, P.C. Faustinelli, G. Giambastiani, V.R. Reddy and J.W. Jones. 2003. Nonlinear effects of water stress on peanut photosynthesis at crop and leaf scales. *Ecological Modeling.* 168: 57-76.

Gaspar, T., T. Franck, B. Bisbis, C. Kevers, L. Jouve, J.F. Hausman, and J. Dommes, 2002. Concepts in plant stress physiology. Application to plant tissue cultures. *Plant Growth Regul*., 37: 263-85

Jaleel C.A., P. Manivannan, A. Kishorekumar, B. Sankar, R. Gopi, R. Somasundaram and R. Panneerselvam. Alterations in osmoregulation, antioxidant enzymes and indole alkaloid levels in Catharanthus roseus exposed to water deficit. Colloids and Surfaces B: Biointerfaces, 2007a; 59 150–157.

Jaleel C.A., P. Manivannan, B. Sankar, A. Kishorekumar, R. Gopi, R. Somasundaram, R. Panneerselvam. Pseudomonas fluorescens enhances biomass yield and ajmalicine production in Catharanthus roseus under water deficit stress. Colloids and Surfaces B: Biointerfaces, 2007b; 60, 7–11.

Jaleel C.A., Paramasivam Manivannan, B. Sankar, A. Kishorekumar, Ragupathi Gopi, R. Somasundaram, R. Panneerselvam. Water deficit stress mitigation by calcium chloride in Catharanthus roseus; effects on oxidative stress, proline metabolism and indole alkaloid accumulation. Colloids and Surfaces B: Biointerfaces. 2007c; 60, 110–116.

Jaleel C.A., P. Manivannan, B. Sankar, A. Kishorekumar, Ragupathi Gopi, Rajaram Somasundaram, R. Panneerselvam. Induction of drought stress tolerance by ketoconazole in Catharanthus roseus is mediated by enhanced antioxidant potentials and secondary metabolite accumulation. Colloids and Surfaces B: Biointerfaces. 2007d; 60(2), 201-206.

Jaleel C.A., P. Manivannan, G.M.A. Lakshmanan, M. Gomathinayagam, R. Panneerselvam. Alterations in morphological parameters and photosynthetic pigment responses of Catharanthus roseus under soil water deficits. Colloids and Surfaces B: Biointerfaces. 61/2 (2008a) 298-303.

Jaleel C.A., B. Sankar, P.V. Murali, M. Gomathinayagam, G.M.A. Lakshmanan, R. Panneerselvam, Water deficit stress effects on reactive oxygen metabolism in Catharanthus roseus; impacts on ajmalicine accumulation, Colloids and Surfaces B: Biointerfaces. 2008b; 62/1 pp. 105-111.

Jaleel C.A., P. Manivannan, P.V. Murali, M. Gomathinayagam, R. Panneerselvam. Antioxidant potential and indole alkaloid profile variations with water deficits along different parts of two varieties of Catharanthus roseus. Colloids and Surfaces B: Biointerfaces. 62 (2008c) 312–318

Jaleel C.A., R. Gopi, B. Sankar, M. Gomathinayagam, R. Panneerselvam. Differential responses in water use efficiency in two varieties of Catharanthus roseus under drought stress. Comptes Rendus Biologies (2008d) 331/1: 42-47.

Jaleel C.A., R. Gopi, P. Manivannan, M. Gomathinayagam, Shao Hong-Bo, Chang-Xing Zhao, R. Panneerselvam. Endogenous hormonal and enzymatic responses of Catharanthus roseus with triadimefon application under water deficits. Comptes Rendus Biologies. 331 (2008e) 844-852.

Jaleel C.A., R. Gopi, P. Manivannan, M. Gomathinayagam, Ksouri Riadh, Jallali Inès, Zhao Chang-Xing, Shao Hong-Bo, R. Panneerselvam. Antioxidant defense responses: Physiological plasticity in higher plants under abiotic constraints. Acta Physiologiae Plantarum. 31/3, (2009a) 427-436.

Jaleel C.A., P. Manivannan, Abdul Wahid, Muhammad Farooq, R. Somasundaram, R. Panneerselvam. Drought Stress in plants: A Review on Morphological Characteristics and Pigments Composition. International Journal of Agriculture and Biology. (2009b), 11: 100–105.

Jaleel C.A., M.M. Azooz, P. Manivannan, Rajaram Panneerselvam. Involvement of Paclobutrazol and ABA on Drought-Induced Osmoregulation in Cajanus cajan. American-Eurasian Journal of Botany (2009c) 2/1: 30-36.

Jaleel C.A., Non-Enzymatic Antioxidant Changes in Withania somnifera with Varying Drought Stress Levels. American-Eurasian Journal of Scientific Research 4 (2): 64-67, 2009d

Jaleel C.A., Physiological Basis of Defense Mechanisms in Withania somnifera under Water Deficit Stress. Global Journal of Environmental Research 3 (2): 82-86, 2009e

Kage, H., M. Kochler, H. Stützel, 2004. Root growth and dry matter partitioning of cauliflower under drought stress conditions: measurement and simulation. European J. Agron., 20: 379–94

Kamara, A.Y., A. Menkir, B. Badu-Apraku and O. Ibikunle, 2003. The influence of drought stress on growth, yield and yield components of selected maize genotypes. J. Agric. Sci., 141, 43-50

Kiani, S.P., P. Maury, A. Sarrafi, P. Grieu, 2008. QTL analysis of chlorophyll fluorescence parameters in sunflower (Helianthus annuus L.) under well-watered and water-stressed conditions. Plant Sci., 175: 565-73

Kusaka, M., A.G. Lalusin and T. Fujimura. 2005. The maintenance of growth and turgor in pearl millet (Pennisetum glaucum (L.) Leeke) cultivars with different root structures and osmo-regulation under drought stress, Plant Science. 168: 1-14.

Lafitte, H.R., G. Yongsheng, S. Yan and Z.K. Li, 2007. Whole plant responses, key processes, and adaptation to drought stress: the case of rice. J. Exp. Bot., 58: 169-75

Lawlor D.W. 2002. Limitation to photosynthesis in water stressed leaves: Stomata Vs metabolism and role of ATP: *Ann. Bot*. 89: 871-885.

Lawson, T., K. Oxborough, J.I.L. Morison and N.R. Baker, 2003. The responses of guard andmesophyll cell photosynthesis to CO_2, O_2, light, and water stress in a range of species are similar. *J. Exp. Bot*., 54: 1743–52

Li, C. 2000. Population differences in water use efficiency of *Eucalyptus microtheca* seedling under different watering regimes. *Physiol. Plant*. 108: 134-139.

Li, C. and K. Wang. 2003. Differences in drought responses of three constrating *Eucalyptus microtheca* F. Muell. Populations. *For. Ecol. Manage*. 179: 137-385.

Li, C., F. Berninger, J. Koskela and E. Sonninen. 2000. Drought responses of *Eucalyptus microtheca* F. Muell. Provenances depend on seasonality of rainfall in their place of origin: Aust. *J. Plant Physiol*. 27: 231-238.

Liu, F., R. Christian, J.A. Shahanzari., Mathias N. Andersen. and E.E. Jacobsen. 2005. ABA Regulated stomata control and photosynthetic water use efficiency of potato (*Solanum tuberosum* L.) during progressive soil drying. *Plant Science.* 168: 831-836.

Marron, N., D. Delay, J.M. Petit, E. Dreyer, G. Kahlem, F.M.Delmotte and F. Brignolas. 2002. Physiological traits of two *populus* x *euramericana* clones, *Luisa avanzo* and dorskamp, during water stress and re-watering cycle. *Tree Physiol*. 22: 849-858.

Martinez, J.P., H. Silva, J.F. Ledent and M. Pinto, 2007. Effect of drought stress on the osmotic adjustment, cell wall elasticity and cell volume of six cultivars of common beans (*Phaseolus vulgaris* L.). *European J. Agron*., 26: 30–8

Martinez, J.P., J.F. Ledent, M. Bajji, J.M. Kinet and S. Lutts. 2003. Effect of water stress on growth, Na^+ and K^+ accumulation and water use efficiency in relation to osmotic adjustment in two population of *Atriplex halimus* L. *Plant Growth Regulation.* 41: 63-73.

Massacci, A., S.M. Nabiev, L. Pietrosanti, S.K. Nematov, T.N. Chernikova, K. Thor, J. Leipner, 2008. Response of the photosynthetic apparatus of cotton (*Gossypium hirsutum*) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. Plant Physiol. Biochem., 46: 189-95

Meenakshi Sundaravalli, V., K. Paliwal and A. Ruckmani. 2005. Effect of water stress on photosynthesis, protein content and nitrate reducates activity of *Albizzia* seedlings. *J. Plant. Biol*. 32(1): 13-17.

Mohammadian, R., M. Moghaddam, H. Rahimian and S.Y. Sadeghian, 2005. Effect of early season drought stress on growth characteristics of sugar beet genotypes. *Turkisk J. Bot*., 29: 357–68

Monneveux, P., C. Sánchez, D. Beck and G.O. Edmeades, 2006. Drought tolerance improvement in tropical maize source populations: evidence of progress. *Crop Sci*., 46: 180–91

Nam, N.H., Y.S. Chauhan and C. Johansen, 2001. Effect of timing of drought stress on growth and grain yield of extra-short-duration pigeonpea lines. *J. Agric. Sci.*, 136, 179-89

Nautiyal, P.C., Ravindra, V. and Y.C. Joshi. 2002. Dry matter partitioning and water use efficiency under water-deficit during various growth stages in groundnut. *Indian J. Plant Physiol*. 7(2): 135-139.

Nayyar, H., S. Kaur, S. Singh and H.D. Upadhyaya, 2006. Differential sensitivity of Desi (small-seeded) and Kabuli (large-seeded) chickpea genotypes to water stress during seed filling: effects on accumulation of seed reserves and yield. *J. Sci. Food Agri.,* 86: 2076-82

Ogbonnaya, C.I., B. Sarr, C. Brou, O, Diouf, N.N. Diop and H. Roy-Macauley, 2003. Selection of cowpea genotypes in hydroponics, pots, and field for drought tolerance. *Crop Sci.*, 43: 1114–20

Pan, X.Y. G.X. Wang., H.M. Yang. and X.P. Wei. 2003. Effect of water deficits on within-plot variability in growth and grain yield of spring wheat in north west china. *Field Crops Research*. 80: 195-205.

Pane, J.A. and A.H. GoldStein. 2001. Response of stomatal conductance to drought in ponderosa pine: implications for carbon and ozone uptake. *Tree Physiol*. 21: 377-344.

Petropoulos, S.A., Dimitra Daferera, M.G. Polissiou, H.C. Passam, 2008. The effect of water deficit stress on the growth, yield and composition of essential oils of parsley *Sci. Hort*., 115: 393-7

Pita, P. and J.A. Pardes. 2001. Growth, leaf morphology, water use and tissue water relation of *Eucalyptus globules* clones in response to water deficit. *Tree Physiol*. 21: 599-607.

Ponton, S., J.L. Dupouey, N. Breda and E. Dreyer. 2002. Comparison of water use efficiency of seedlings from two sympatric oak species: genotype X environment interactions. *Tree Physiol*. 22: 413-422.

Razmjoo, K., P. Heydarizadeh and M.R. Sabzalian, 2008. Effect of salinity and drought stresses on growth parameters and essential oil content of *Matricaria chamomile*. *Int. J. Agri. Biol*., 10: 451–4

Reddy, A.R., K.V. Chaitanya and M. Vivekanandan. 2004. Drought induced responses of photosynthesis and antioxidant metabolism in higher plants. *J. of Plant Physiol*., 161: 1189-1202.

Reddy, T.Y., V.R. Reddy and V. Anbumozhi. 2003. Physiological responses of groundnut (*Arachis hypogea* L.) to drought stress and its amelioration: A critical review. *Plant Growth Regulation*. 41: 75-88.

Rodriguez, P., A. Torrecillas, M.A. Morales, M.F. Ortuno and M.J.S. Blanco. 2005. Effects of NaCl salinity and water stress on growth and leaf water relations of *Asteriscus maritimus* plants. *Environmental and Experimental Botany.* 53: 113-123.

Samarah, N.H., 2005. Effects of drought stress on growth and yield of barley. *Agron. Sustain. Dev.*, 25: 145-9

Samarah, N.H., R.E. Mullen, S.R. Cianzio and P. Scott, 2006. Dehydrin-like proteins in soybean seeds in response to drought stress during seed filling. *Crop Sci.*, 46: 2141-50

Sankar, B., C.A. Jaleel, P. Manivannan, A. Kishorekumar, R. Somasundaram, R. Panneerselvam, 2008. Relative efficacy of water use in five varieties of *Abelmoschus esculentus* (L.) Moench. under water-limited conditions. *Colloids Surf. B: Biointerfaces*, 62: 125-9

Shaheen, R., and R.C. Hood-Nowotny. 2005. Effect of drought and salinity on carbon isotope discrimination in wheat cultivars. *Plant Science*. 168: 901-909.

Sharp, R.E. and M.E. LeNoble, 2002. ABA, ethylene and the control of shoot and root growth under water stress. *J. Exp. Bot*., 53: 33–37.

Siemens, J.A. and J.J. Zwiazek. 2003. Effects of water deficit stress and recovery on the root water relations of trembling aspen (*Populus tremuloides*) seedlings. *Plant Sci*. 165:113-120.

Sinaki, J.M., E.M. Heravan, A.H.S. Rad, G. Noormohammadi and G. Zarei, 2007. The effects of water deficit during growth stages of canola (*Brassica napus* L.). *American-Eurasian J. Agri. Environ. Sci.*, 2: 417-22

Soriano, M.A., F. Orgaz., F.J. Villalobos and E. Fereres. 2004. Efficiency of water use of early plantings of sunflower. *Europe. J. Agronomy.* 21: 465-476.

Soriano, M.A., F.J. Villalobos and E. Fereres, 2002. Stress timing effects on sunflower harvest index. In: F.J. Villalobos and L. Testi (Eds.). *VII Congress of the European Society for Agronomy*, Sevilla, Spain JA, Consejería de Agricultura y Pesca pp. 141–2

Specht, J.E., K. Chase, M. Macrander, G.L. Graef, J. Chung, J.P. Markwell, M. Germann, J.H. Orf and K.G. Lark, 2001. Soybean response to water. A QTL analysis of drought tolerance. *Crop Sci*., 41: 493–509

Tahir, M.H.N. and S.S. Mehid, 2001. Evaluation of open pollinated sunflower (*Helianthus annuus* L.) populations under water stress and normal conditions. *Int. J. Agric. Biol*., 3: 236–8

Tahir, M.H.N., M. Imran and M.K. Hussain, 2002. Evaluationof sunflower (Helianthus annuus L) inbred lines for drought tolerance. *Int. J. Agric. Biol*., 3: 398–400

Tahkokorpi, M., K. Taulavuori, K. Laine, and E. Taulavuori, 2007. After-effects of drought-related winter stress in previous and current year stems of *Vaccinium myrtillus* L. *Environ. Exp. Bot.*, 61: 85–93

Thakur, P.S. and H. Kaur. 2001. Variation in photosynthesis, transpiration, water use efficiency, light transmission and leaf area index in multipurpose Agroforestry tree species. *Indian J. Plant Physiol*. 6(3): 249-253.

Tsialtas, J.T., L.L. Handley, M.T. Kassioumi, D.S. Veresoglou and A.A. Gagianas. 2001. Interspecific variation in potential water use efficiency and its relation to plant species abundance in a water limited grass land. *Funct. Ecol*. 15: 605-614.

Vyas, S.P., B.K. Garg, S. Kathju and A.N. Lahiri 2001. Influence of potassium on water relations, photosynthesis, nitrogen metabolism and yield of cluster bean under soil moisture stress. *Indian J. Plant Physiol*. 6(1): 30-37.

Weigh, M. 2001. Evidence for increased sensitivity to nutrient and water stress in a fast-growing hybrid willow compared with a natural willow clone. *Tree Physiol*. 21: 1141-1148.

Wu, Q.S., R.-X. Xia, Y.-N. Zou, 2008. Improved soil structure and citrus growth after inoculation with three arbuscular mycorrhizal fungi under drought stress. *European J. Soil Biol*., 44: 122-8

Yin, C., X. Wang, B. Duan, J. Luo and C. Li. 2005. Early growth, dry matter allocation and water use efficiency of two Sympatric *populus* species as affected by water stress. *Environmental and Experimental Botany*. 53: 315-322.

Zhang, X., R. Zang and C. Li. 2004. Population differences in physiological and morphological adaptations of *Populus davidiana* seedlings in response to progressive drought stress. *Plant. Sci*. 166: 791-797.

Zhu J.K. 2002. Salt and drought stress signal transduction in plants. *Annu Rev Plants Biol.* 53: 247-273.