INTERNATIONAL
Agrophysics
www.international-agrophysics.org

Int. Agrophys., 2013, 27, 463-477
doi: 10.2478/intag-2013-0017

Review

Effect of drought and heat stresses on plant growth and yield: a review**

J. Lipiec[1], *C. Doussan*[2,3], *A. Nosalewicz*[1] *and K. Kondracka*[1]

[1]Institute of Agrophysics, Polish Academy of Sciences, Doświadczalna 4, 20-290 Lublin, Poland
[2]Mediterranean Environment and Modelling of Agro-Hydrosystems (EMMAH), UMR 1114 INRA-UAPV
[3]INRA - Domaine Saint Paul – Site Agroparc – F-84914 Avignon cedex 9, France

Received January 24, 2013; accepted August 30, 2013

Abstract. Drought and heat stresses are important threat limitations to plant growth and sustainable agriculture worldwide. Our objective is to provide a review of plant responses and adaptations to drought and elevated temperature including roots, shoots, and final yield and management approaches for alleviating adverse effects of the stresses based mostly on recent literature. The sections of the paper deal with plant responses including root growth, transpiration, photosynthesis, water use efficiency, phenotypic flexibility, accumulation of compounds of low molecular mass (*eg* proline and gibberellins), and expression of some genes and proteins for increasing the tolerance to the abiotic stresses. Soil and crop management practices to alleviate negative effects of drought and heat stresses are also discussed. Investigations involving determination of plant assimilate partitioning, phenotypic plasticity, and identification of most stress-tolerant plant genotypes are essential for understanding the complexity of the responses and for future plant breeding. The adverse effects of drought and heat stress can be mitigated by soil management practices, crop establishment, and foliar application of growth regulators by maintaining an appropriate level of water in the leaves due to osmotic adjustment and stomatal performance.

Keywords: water stress, high temperature, root and shoot growth, tolerance mechanisms, management practices

INTRODUCTION

Plants are frequently exposed to drought and heat stresses that reduce crop yield worldwide. The combined effect of both heat and drought on yield of many crops is stronger than the effects of each stress alone (Dreesen *et al*., 2012; Rollins *et al*., 2013).

Agricultural water deficit arises from both insufficient rainfall and soil water during the growing season to sustain a high crop yield (Sekhon *et al*., 2010; Vadez *et al*., 2011; 2012; Wahid *et al*,. 2007). Projections show an increase in intense rain events and at the same time reduction in the number of rain days that leads to increased risk of drought (Trenberth, 2011; Vadez *et al*., 2011). Therefore, under rainfed conditions water scarcity is one of the most widespread limitations to crop production.

A period of dry weather, injurious to crops, is often defined as ‘drought’ that is related to changes in soil and meteorological conditions and not with plant and tissue hydration. Drought stress occurs when the humidity of the soil and the relative air humidity are low and the ambient temperature is high.

Predisposition of plants to maintain a high potential of water in the tissues under drought is called dehydration avoidance, and tolerance that determines plant predisposition to survive water deficiency is called drought resistance (Blum, 2005; Vadez *et al*., 2011). Molecular biologists often report the effect of an exotic gene towards 'drought tolerance' and advertise its expected value in breeding (Blum, 2005).

Heat stress or heat wave is defined as the rise in temperature beyond a threshold level for a period sufficient to cause permanent damage to plant growth and development. Heat stress is a complex function of intensity, duration, and the rate of the increase in temperature (Wahid *et al*., 2007). Usually, a 10-15°C rapid rise above typical, ambient temperature may be considered as heat stress. A soil temperature increase resulting from an increase in air temperature may be even stronger when accompanied by a drought-induced decline in soil water content (Sekhon *et al*., 2010; Simoes-Araujo *et al*., 2003).

---

*Corresponding author e-mail: j.lipiec@ipan.lublin.pl

**The work was partly realized within the framework of an international research project: ‘FACCE Modelling European Agriculture with Climate Change for Food Security’ (2012-2015). We gratefully acknowledge financial support from the National Centre for Research and Development in Poland.

These effects can be enhanced by progressive and expected global warming (Fig. 1). According to the authors of the Intergovernmental Panel on Climatic Change (IPCC 2007), the temperature increase in the 20th century was assessed as 0.74°C with the steadily increasing rate. Model simulations suggest that an average increase in temperature of up to 2.5-5.4°C can be expected by year 2100 coupled with a decrease in precipitation of about 15% (Ciscar, 2012; Tadross *et al.*, 2007). Under climate of south-eastern Australia, it was predicted that every 1°C increase in air temperature will cause a 1.5°C increase of surface soil temperature (Ooi *et al.*, 2012).

Under field conditions, water shortage often occurs concurrently with high air temperature (say > 30°C in the low to mid-latitudes) and are threat limitations to plant growth (Farooq *et al.*, 2012; Mittler, 2006; Simoes-Araujo *et al.*, 2003; Vahid *et al.*, 2007) and sustainable agriculture (Ahuja *et al.*, 2010). Increasing frequency of water deficits, events of heat waves, and intra- and inter-seasonal variations as well as an increase in the atmospheric CO_2 concentration will add another layer of complexity to the effects of drought and heat stresses (Sekhon *et al.*, 2010; Vadez *et al.*, 2011; Vahid *et al.*, 2007). The heat wave effects can be anticipated to strengthen as the temperature progressively increases (Battisti and Naylor, 2009).

This paper provides a review of recent literature on plant responses and adaptations, including roots and shoots at the whole plant and cellular and sub-cellular levels, to drought and elevated temperature. Management approaches for alleviating the adverse effects of the stresses are discussed.

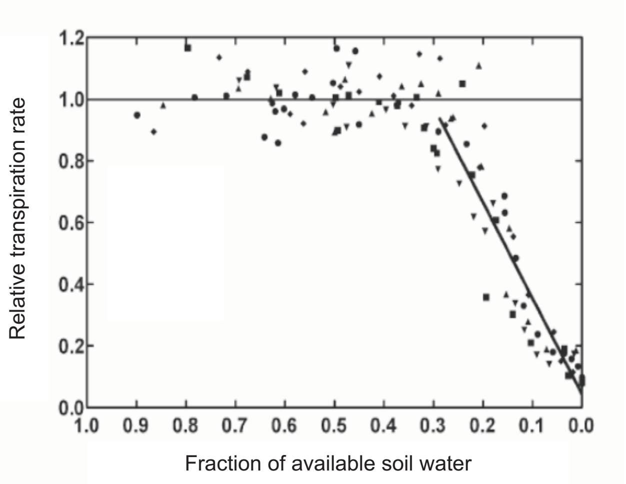

Fig. 1. Normalized daily transpiration rate of five Hibiscus sp. plants graphed against the fraction of transpirable soil water calculated from the endpoint (Sinclair *et al.*, 2005).

PLANT GROWTH AND DEVELOPMENT PROCESSES

Drought can be seen as the result of imbalance of the water flux rate between potential evapotranspiration (demand) and water transport into the soil-root system. This thus implies interactions between 3 actors: the soil, the root system and shoot, and the atmosphere, which are traversed by the water flux and connected as a series of resistances to water transfer.

Roots and root-soil interactions

For a given water potential gradient between the soil and the roots, water flux will be driven by the root hydraulic conductance (Lp). Variation of root system Lp with time and environmental stresses will give rise to root ‘hydraulic’ plasticity and acclimatization. Lp varies along the root according to tissue age and among root types (Doussan *et al.*, 1998) and will vary with growth of the root system and its plasticity. Lp can be modulated by cell membrane permeability and aquaporines (water channels). In the short term, with ongoing water deficit, an increase followed by a decrease in Lp is observed and ascribed to aquaporine activity and regulation (Maurel *et al.*, 2010). In the long terms of water deficit, a further decrease in Lp is observed due to increased suberization of root endodermis/exodermis (Vandeleur and Mayo, 2009). The decrease in Lp reduces water flux into the plant, but also prevents water losses from the plant to the dry soil. At a further longer time scale of drought, Lp can be further reduced in the plant by xylem embolism, a process by which air is sucked into the xylem vessels, interrupting the sap flow (Cruiziat and Cochard, 2002). Drought resistance can be related to a greater resistance to embolism (Li *et al.*, 2009). The increase in temperature increases Lp (rather the cell membrane permeability) in roots, but up to a deleterious point (harmful for plant functions).

During water shortage, the interactions between the soil and the root system will affect the level and dynamics of water stress. The first level of interaction originates from root system architecture and soil transfers: at a local scale, an increase in root clumping will decrease the efficiency of water uptake (Beudez *et al.*, 2013; Tardieu *et al.*, 1992); at the root system scale, vertical heterogeneity of soil water availability induced by water uptake combined with water transfer in the soil and in the plant leads to a water extraction front propagating downwards (Garrigues and Doussan, 2006). The extension and speed of this front can be modulated by the variation in Lp (aquaporines, suberization) of roots and helps in compensating the lower uptake in drier zones by an increase in the wetter zones. This effect can be further increased due to a decrease in soil-root hydraulic conductance related to root shrinkage, which severely hampers water flow to roots (Carminati *et al.*, 2009; Taylor and Willatt, 1983). Recent observations point to a rhizospheric effect onto the water relations of this soil-root interface, involving mucilages, root exudates and possibly solute accumulation (Carminati and Vetterlein, 2013; McCully *et al*., 2009; Read *et al*., 2003; Stirzaker and Passioura 1996), which would modulate soil-root contact and water uptake with variations in dry or moist soil (White and Kirkegaard, 2010).

At longer time scales, not only plasticity in water relations but also in root growth will occur during water deficit, with a decrease in root length (reduced growth, increased mortality) in drier parts and an increase in wetter parts (Huang and Eissenstat, 2000; Sekhon *et al*., 2010). If an increase in root growth can be observed at the onset of water stress, the continuing drought will reduce the overall root growth, resulting from uncoupling between carbon production in leaves and use in root sinks (root apex) (Muller *et al*., 2011). The influence of soil water on root growth and function is closely related to the plant species and rooting depth (Vadez *et al*., 2012). In general, shallow-rooted crops such as potatoes are less drought tolerant than deep-rooted species such as alfalfa or maize. Under water stress, some plants develop short suberized roots, as the top soil becomes dry (Gliński and Lipiec, 1990), which helps surviving drought by reducing water loss from plant roots. A recent study has shown that in dry environments root cation exchange capacity and nutrient uptake can be significantly reduced, and the relative uptake of polyvalent cations (aluminium or heavy metals) may induce additional toxicity (Łukowska and Józefaciuk, 2013).

Root plasticity can be modulated by soil compaction and associated mechanical impedance. The negative effects of a heavily compacted subsoil layer on water uptake were partly compensated by increased uptake from looser top soil layers and significant contribution of thicker roots in water uptake. (Nosalewicz and Lipiec, 2013) Morphological and anatomical responses of the roots in dry and strong soil were related to the general shape of roots (circular or flattened) due to the spatial distribution of soil strength around the roots (Lipiec *et al*., 2012). Whalley and Clark (2011) reported that increases in soil strength sufficiently large to impede root elongation can occur after only a moderate degree of soil drying. For soils with little continuous macro- porosity, this can decrease root elongation and the maximum rooting depth attained, restraining further subsoil access to water and nutrients, and increase drought (Bengough, 1997).

Water scarcity and increased soil temperature substantially affect the formation, duration, and activity of pea nodules. In the study of Siczek and Lipiec (2011), improved soil water relations due to mulching significantly increased symbiotic nitrogen fixation as measured by nitrogenase activity, nodule diameter and dry weight, and seed yield.

Root-shoot signaling

Plants can transduce positive and negative signals among roots and shoots to coordinate growth rate and behaviour, and adapt to variable environments. When environmental stresses suppress root growth and change root distribution, shoot growth and functions may also be reduced as an effect of root-to-shoot signalling (Novák and Lipiec, 2012). The classical pattern for plant responses to dry soil is based on hydraulic signalling including a decline in root water uptake and then water potential and turgor in the leaves and stomatal closure, decreased leaf elongation, and osmotic adjustment (Clark *et al*., 2005). A number of plant hormones including abscisic acid (ABA), auxin, cytokinins, ethylene, gibberellins, and other factors (*eg* nitrogen, pH) have been shown to be involved in the regulation of physiological processes by acting as signal molecules under different environmental stresses (Dodd, 2005; Schachtman and Goodger, 2008). ABA has long been recognized as a major chemical root-to-shoot stress signal (Schachtman and Goodger, 2008). During soil drying, ABA is synthesized by the roots and transported in the xylem to the shoot, where it inhibits leaf expansion and induces stomatal closure before detectable changes in leaf water status and nutrient status (Dodd, 2005; Wang *et al*., 2000).

Moreover, transcription factors and their target genes are engaged in mediating ABA perception and signalling and modulating stomatal movement (Abe *et al*., 2003). Limitation of stomata is often considered the first step to cope with drought by maintaining sufficient cell turgor to continue plant metabolism. In a study of Wang *et al*. (2000) stomatal conductance and the transpiration rate under water stress conditions were lower under good than low fertility conditions. Also under the heat stress, soil fertility improved by application of some macronutrients like K and Ca and micronutrients like B, Mn, and Se modified stomatal function and activated physiological and metabolic processes that helped in upholding high tissue water potential and increasing heat stress tolerance (Waraich *et al*., 2012).

Biosynthesis of ABA is stimulated by decreased soil water content and plant turgor (Dodd, 2005; Vernieri et al., 2001). The effects of environmental stresses in the root zone on the shoot can be influenced by interaction between the chemical signals. For example, Yang *et al*. (2006) reported that the grain-filling rate in wheat is enhanced by an increase in the ratio of ABA to ethylene. Another study with wheat under water stress (Yang *et al*., 2003) suggested that ABA and cytokinins are involved in controlling plant senescence and enhanced carbon remobilization.

While shoot responses resulting from root exposure to environmental stresses are frequently studied, little is known about how shoot-subjected stresses affect root growth (Novák and Lipiec, 2012). The results of Parsons and Sunley (2001) indicate that N status in plants is likely to be most strongly sensed in the shoot and signals translocated to the roots may involve phloem-transported amino compounds or very low concentrations of specific signal molecules.

Shoot growth and functions

Transpiration and photosynthesis

Typical response of daily relative transpiration rate (rT: actuTypical response of the daily relative transpiration rate (rT: actual transpiration normalized by maximum transpiration) as a function of the fraction of available soil water content (FASW) is shown in Fig. 1. The fraction of available soil water content is defined as $FSW=(\theta-\theta_{\downarrow}pwp)/(\theta_{\downarrow}fc-\theta_{\downarrow}pwp)$; θ, θpwp, θ_{fc} being the actual, permanent wilting point and field capacity water contents, respectively. Figure 1 indicates that the onset of water stress depends on a threshold value (FASWt) at which rT starts to decrease more or less linearly (Sinclair et al., 2005). Such kind of a relationship has been shown for a large number of plants (Sadras and Milroy 1996) and form the basis of a number crop models for evaluating the impact of water deficit (Brisson and Mary, 1998; Steduto and Hsiao, 2009).

This relationship exhibits, however, variations not only with plant species but also with the level of potential evapotranspiration (Denmead and Shaw, 1962), the soil type/structure (Wu and Huang, 2011), the time-scale of stress in relation to acclimatization (Maurel *et al*., 2010), and/or the root profile and its dynamics (Brisson 1998) inducing intra-specific variations. Such environmental and plant variations in this relationship arise from the fact that plants do not sense directly the soil water content but rather the water potential, which is related to water flux (including transpiration), by its gradient and hydraulic conductances in the soil-root-plant system.

Summary of some results in Table 1 indicates that in general the photosynthesis rate and transpiration were substantially lower under water deficit than under well-watered conditions. The increase in temperature from 22 to 32°C resulted in a lower photosynthesis rate and transpiration under both well watered and water deficit conditions (Zhang *et al*., 2010). The decline was relatively greater under the well watered than water deficit conditions with greater absolute values at the former. In other studies it was shown that drought and heat stresses, irrespective of whether stomatal conductance was reduced or not, lead to a decrease in photosynthetic activity (Ashraf and Harris, 2013; Crafts-Brander and Salvucci, 2002; Zhou *et al*., 2007). The decline in the photosynthetic rate under both stresses are frequently attributed to lowered internal CO_2, inhibition of photosynthetic enzymes (*eg* Rubisco) and synthesis of ATP (Arasimowicz and Floryszak-Wieczorek 2007; Zlatev and

Table 1. Effect of soil water status and temperature onthe rate of photosynthesis (Pn), transpiration (E), and relative water content (RWC) in plants

Plant	Stress	Soil water content and/or temperature	Pn (μmol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	RWC (%)
Spring wheat (Superb) Zhang *et al*., 2010	Water deficit and high temperature	Well-watered^1			
		22/12°C	20.49	10.39	92.96
		32/22°C	11.46	3.68	91.11
		Water deficit^2			
		22/12°C	7.35	1.90	84.66
		32/22°C	6.37	1.79	85.37
Winter wheat (Zarrin) Roohi *et al*., 2013	Water stress	Well-watered^3	9.7 ± 0.02	6.0 ± 0.58	79.4 ± 1.93
		Water deficit^4	5.1 ± 1.19	3.51 ± 0.44	70.1 ± 3.25
Soybean (BPI Sy-4) Purwanto, 2003	Water stress	100%	17.45	11.6	
		50%	8.67	5.5	
		25%	1.81	0.7	
Winter barley (Bahman) Roohi *et al*., 2013	Water stress	Well-watered^4	7.9 ± 2.47	4.9 ± 0.91	77.4 ± 5.03
		Water deficit^3	3.6 ± 92	2.8 ± 0.41	59.8 ± 5.09
Spring triticale (Juanillo-092) Roohi *et al*., 2013	Water stress	Well-watered^4	8.8 ± 0.64	53 ± 0.26	83.5 ± 5.02
		Water deficit^3	5.3 ± 0.70	3.19 ± 0.38	71.3 ± 1.37

^{1}90-95%, ^{2}40%, ^{3}soil water potential = -300 kPa, ^{4}soil water potential = -1 200 kPa.

Lidon, 2012). However, it was also shown that mild water stress decreased biomass production without a significant effect on photosynthesis (Verelst *et al*., 2012). This demonstrates that plants reduce their growth as an adaptation response to stress rather than as a secondary consequence of resource limitations (Rollins *et al*., 2013).

Both stresses suppress particularly photochemical efficiency of photosystem PS II by decreasing electron transport, removal of external proteins, and release of calcium and magnesium ions from their binding (Barta *et al*., 2010; Wahid *et al*., 2007; Zlatev and Loden, 2012). Heat stress can also lead to damage to D1 and D2 proteins (Yoshioka *et al*., 2006). Damage to D1 protein is probably caused by singlet oxygen, which is produced by the reaction of chlorophyll (P680). Photosystem PS II is more sensitive to high temperatures than drought stress due to elimination of PS II in thylakoid membranes as a result of disruption of metabolic processes including inactivation of Rubisco activase (Prasad *et al*., 2008). Proper evaluation of the effect of drought and heat on photosynthesis is hampered by the protecting effect of water deficit on PS II against increased temperature, as reported by Lu and Zhang (1999).

Plant response to drought and heat stress differs in C3 (*eg* wheat) and C4 (*eg* maize) plants. C4 plants are more sensitive to water deficit due to stomatal closure and reduction of the photosynthetic enzyme (Alfonso and Brüggemann, 2012; Ghannoum, 2009). However, the effect of high temperature on the photosynthetic capacity is stronger with C3 than C4 plants due to different energy distribution and activities of carbon metabolism enzymes, particularly of rubisco (Salvucci and Crafts-Brandner, 2004). In a study of Crafts-Brander and Salvucci (2002), high leaf temperatures (> 38°C) in maize inhibited net photosynthesis to a higher extent when temperature was increased abruptly rather than gradually.

Negative effects of high temperature and vapour pressure deficit on leaf photosynthesis and water use efficiency (the ratio of photosynthetic and transpiration rates) can be partly offset by an increased atmospheric CO_2 concentration. This can be accomplished by maintaining the optimal CO_2 concentration in the substomatal chamber at a lower level of stomata opening, resulting in lower rates of transpiration saving water (Condon *et al*., 2002; Vadez *et al*., 2011), but this may induce heat stress as leaf temperature rises with reduced stomatal conductance and transpiration (Król, 2013).

Phenological changes

Crop adaptation to drought and high temperature is a function of the interaction of phenology with the pattern of water use (Sekhon *et al*., 2010; Wahid *et al*., 2007). Limited shoot growth by a decreased number of tillers in response to water limitation is considered as a strategy to reduce water use under stress (El Soda *et al*., 2010). Lower rates of plant water use under good water supply at first growth phases can maintain transpiration for longer periods, with significant consequences on later responses to water deficit. Such water-sparing behaviour should yield more water available for water uptake by roots at key stages like the grain-filling period (Vadez *et al*., 2011). It was observed that earlier heading in response to high temperature conditions is advantageous in retention of more green leaves at anthesis, leading to increased evapotranspiration and smaller reduction in yield (Tewolde *et al*., 2006; Vadez *et al*., 2011).

In general, short-duration varieties generally perform better under the stress conditions than long-duration ones, which could be due to their different root system (Singh *et al*., 2010). Studies under controlled growth conditions with various plants showed that high temperature is most harmful at gametogenesis (8-9 days before anthesis), anthesis, and fertilization (Foolad, 2005; Wahid *et al*., 2007). It should be emphasized that plant mechanisms protecting against stress such as reduced plant size or decreased stomatal conductance may be responsible for reduced productivity (Deikman *et al*., 2012).

Anatomical changes

Drought stress and high ambient temperature also result in anatomical changes (Wahid *et al*., 2007; Zhang *et al*., 2005). In general, the changes include reduced size and damaged cells, closure of stomata and curtailed water loss, increased stomatal and trichomatous densities, and larger xylem vessels. High temperature considerably affects anatomical structures not only at the tissue and cellular levels but also at the sub-cellular level. At the sub-cellular level, main modifications refer to the shape of chloroplasts, swelling of stromal lamellae, clumpy vacuoles that change the structural organization of thylakoids and form antenna-depleted PS II, and thereby reduced photosynthetic and respiratory activities (Zhang *et al*., 2005). The cumulative effects of all these changes under high temperature stress may contribute to poor plant growth and productivity.

Water and nutrient use

Water use efficiency, defined as the amount of biomass or grain produced per unit of water used, provides a quick and simple measure of how well available water can be converted into grain and thereby is the basic indicator for measuring the effectiveness of water-saving agriculture (Sekhon *et al*., 2010). Water use efficiency is often equated with drought resistance and the improvement of crop yield under stress (Blum, 2005). Due to a decreasing amount of water available for agriculture, it is essential to maximize water use efficiency, *ie* the amount of crop per drop (Vadez *et al*., 2011). In Australia, water use efficiency can be significantly improved by reduced soil evaporation using relevant genotypes and/or agronomic practices that stimulate earlier-developing canopies during winter and minimize in spring (Siddique *et al*., 2001). Another approach to increase crop WUE and root WUE is partial root drying, an approach using split root techniques, with one drying and one well-watered root half (Davies and Hartung, 2004). This approach is increasingly applied to a wide range of crops in many parts of the world (Jensen, 2013; Jovanovic *et al.*, 2010; Nardella *et al.*, 2012; Sarai *et al.*, 2012; Schachtman and Goodger, 2008).

Water stress is also of great importance in the mineral nutrition of plants since most of the nutrients are provided with water. Due to this, many studies showed that application of fertilizer has no significant effects in water stress conditions, while it significantly increased yield components at optimum soil moisture content. An example of interactive effects of soil moisture content and fertilizer level impacts on crop yield is given in Abayomi and Adefila (2008).

Application of potassium, known for regulating stomatal opening and closure, allows faster reopening of leaf stomata following drought-induced closure (Hu *et al.*, 2012). A decrease in the concentration of potassium ions results in membrane damage and distortion of ionic homeostasis (Kozłowska, 2007; Seyed *et al.*, 2012). Deficiency of water may cause a 50% decrease in the calcium concentration, which plays an important role in maintaining the integrity of cell membranes and other structures in maize leaves and roots.

Moreover, deficiency of water affects metabolism of nutrients *eg* inhibition of nitrate reductase activity and glutamine synthetase involved in intracellular assimilation of ammonium into organic compounds (Rizhysky *et al.*, 2004).

Biochemical and metabolic responses

Drought and high temperatures induce significant alterations in plant biochemistry and metabolism. Under drought stress, the responses deal with the stimulated production of reactive oxygen species (ROS), (*eg* singlet oxygen, superoxide radical, hydrogen peroxide, hydroxyl radical (Liu and Huang, 2000) that cause membrane injuries, protein degradation, enzyme inactivation and thus induce oxidative stress (Zlatev and Lidon, 2012). The main injuries under high temperatures include protein denaturation and increased fluidity of membrane lipids and inactivation of enzymes, reduced synthesis and degradation of proteins, and defaults in membrane integrity (Howarth, 2005; Kozłowska, 2007). Severe cellular injury or death may occur at moderately high temperatures after long-term exposure or within minutes at very high temperatures (Wahid *et al.*, 2007). These injuries may result in reduced ion flux and plant growth, and production of toxic compounds and reactive oxygen species (Howarth, 2005), likewise under water deficit. Application of such nutrients as N, K, Ca and Mg reduces the toxicity of ROS by increasing the concentration of antioxidants *eg* superoxide dismutase (SOD), catalase (CAT), and peroxidise (POD) in plant cells (Waraich *et al.*, 2012).

Prolonged exposure to high temperature causes a decrease in chlorophyll content, increased amylolytic activity, disintegration of thylakoid grana and disruption of assimilate transport (Kozłowska, 2007). To alleviate cellular injury, stressed plants produce antioxidant metabolites including enzymes, phenolics, flavonoids, anthocyanins, lignins, and other molecules (Wahid, 2007; Zlatev and Lidon, 2012). Wahid *et al* (2007) points out that also some signalling molecules may cause an increase in the antioxidant capacity of cells. Initial effects of heat stress can lead to induction of Ca_2^+ influx and cytoskeletal reorganization, resulting in upregulation of mitogen activated protein kinases (MAPK) and calcium dependent protein kinase (CDPK) cascades (Ashraf and Harris, 2013; Wahid *et al.*, 2007). This cascade signalling results in production of antioxidants and compatible osmolytes for adjusting water and osmotic balance and expression of heat shock proteins.

Expression of heat shock proteins

Expression of heat shock proteins (HSP) as well as other proteins is a strategy for adaptation to high temperatures, and HSP induction may be correlated with thermotolerance (Wahid *et al.*, 2007). An example can be enhanced expression of HSP 68 under heat stress in cells of many plant species (Neumann *et al.*, 1993). It is worth adding that expression of some heat shock proteins (*eg* HSPs 70) can be enhanced by abscisic acid (ABA) (Pareek *et al.*, 1998). Expression of genes inducing HSPs can be an important mechanism of increasing stress tolerance (thermotolerance) (Wahid *et al.*, 2007) through getting better photosynthesis and water and nutrient use efficiency (Camejo *et al.*, 2005) and cellular membrane stability (Ahn and Zimmerman, 2006) or hydration of cellular structures (Wahid and Close, 2007).

Recently, in their review, Ahuja *et al.* (2010) have indicated that during drought stress some genes *eg* dehydrin genes (in wheat) and superoxide dismutases (in alfalfa) were induced or upregulated whereas the protein concentration (in black poplar) decreased. The proteins have been involved in glycolysis and gluconeogenesis and proposed as putative biomarkers to define physiological effects at the molecular level and as targets for improving drought resistance in wheat. Systems biology approaches based on plant molecular stress respon- ses reveal the contribution of different signalling pathways defining plant '-omic' architectural responses in relation to changes in environmental stress factors (Ahuja *et al.*, 2010; Ashraf and Harris, 2013).

To increase plant tolerance to abiotic stresses and maintain a high relative water content, plants may accumulate compounds of low molecular mass such as proline (amino acid) and gibberellins (compatible osmolytes) (Kavi Kishor *et al.*, 2005; Zlatev and Lidon, 2012), possibly through buffering the cellular redox potential (Wahid and Close, 2007). The accumulation capacity of the compounds

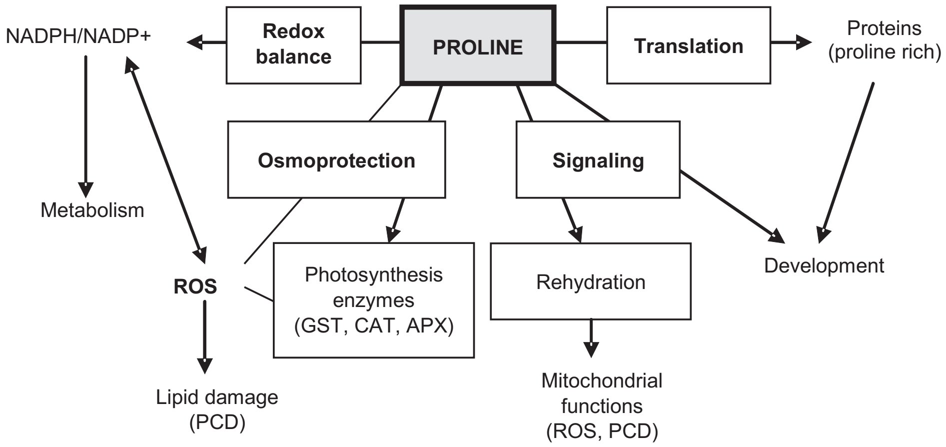

Fig. 2. Proline functions in plants (Szabo and Savoure, 2010).

protects protein structures as cells dehydrates and is linked to genetic variability of plants for moisture stress tolerance (Monica *et al*., 2007; Zlatev and Lidon, 2012). Some authors indicated that the relationship between turgor and proline accumulation could be a useful drought-injury sensor (Iannucci *et al*., 2000), since during stress the proline level can be as much as 100-fold higher than in normal conditions (Bellinger and Larher, 1987). Most proline accumulates in leaves (especially young ones) and the least in the roots. Recent studies show that proline may differently affect stress tolerance, increase the activity of many enzymes, and stabilize protein integrity (Fig. 2). Proline contributes to maintenance of the redox balance, can regulate development, and is a component of metabolic signalling networks controlling mitochondrial functions, stress relief, and development. In addition, biosynthesis of cuticular waxes in the aerial parts of land plants is also closely associated with drought resistance responses (Lee and Suh, 2013).

Plant biomass and yield

The decrease in the duration of developmental growth phases caused by heat and drought stresses is partly responsible for yield reduction of cereals by reduction in light interception over the shortened life cycle (Barnabás *et al*., 2008). Effects of drought and high temperature were reflected in reduced accumulation in plant mass, shorter first internode, increased tillering, early senescence and premature death, and fruit discoloration and damage in various plants (Vahid *et al*., 2007; Vollenweider and Gunthardt-Goerg, 2005; Zlatev and Lidon, 2012). Response of dry compared to fresh plant biomass to water deficit is relatively lower and thereby dry the mass/fresh mass ratio is used as a stress parameter at the plant level (Augé *et al*., 2001; Zlatev and Lidon, 2012). Water stressed compared to well-watered plants showed a higher value of the maximum leaf bulk elastic modulus, probably due to lower solute potentials at full turgor rather than the increase in the cell wall rigidity (Zlatev and Lidon, 2012).

Different indices are used to quantify the stress level experienced by a crop and associated grain yield. They are based on both plant and soil water status. In the studies of Abayomi *et al*. (2012), cereal grain yield was related to water stress index (WSI) (Rizza *et al*., 2004) and drought susceptibility index (DSI). The WSI integrates the actual plant available soil water content (soil water content minus water content at permanent wilting) during the growing season, and the DSI is based on the grain yield ratios under water stress and at normal soil moisture (Golabadi *et al*., 2006). Both indices showed a significant negative relationship between grain yield and water stress of barley (Rizza *et al*., 2004) and maize (Abayomi *et al*., 2012) (Figs 3, 4).

Another approach, the least limiting water range (LLWR), combines soil water holding capacity, soil strength, and soil aeration into one factor to describe management effects on soil potential productivity (da Silva *et al*.

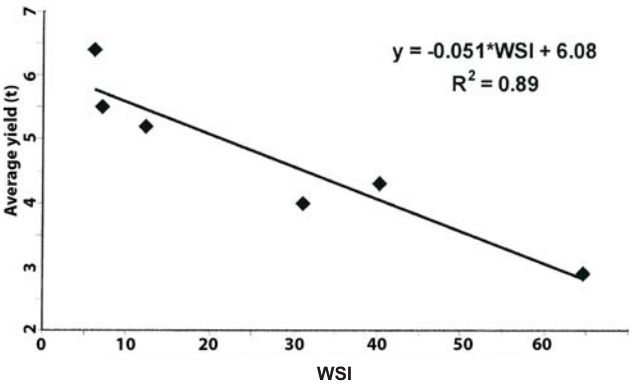

Fig. 3. The relationship between barley grain yield and the water stress index (WSI) (Rizza *et al*., 2004).

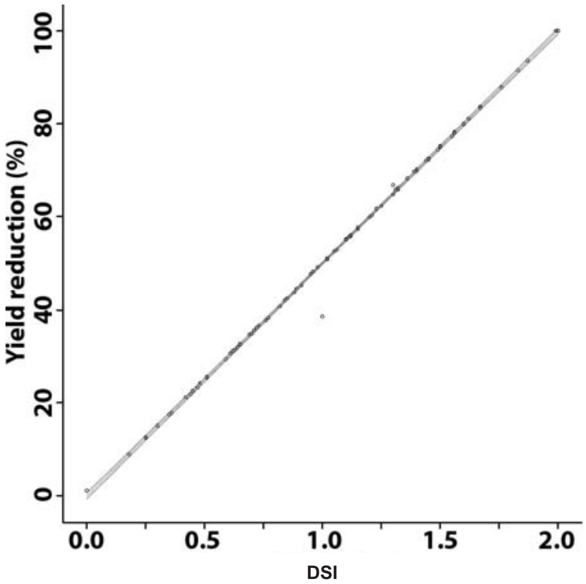

Fig. 4. The relationship between percent reduction in maize grain yield due to soil moisture deficit and drought susceptibility index (Abayomi *et al*., 2012).

(1994). Using the differences of actual water contents in the field from the limits identified by the LLWR during the growing season, Benjamin *et al*. (2003) proposed water stress day (WSD) to identify critical periods of water stress in crop production.

The effect of heat stress from flowering to grain filling often limits final crop yield in temperate regions due to reduction in kernel growth (Guilioni *et al*., 2003). Moreover, heat stress during grain filling can modify the seed N concentration in grain legumes (Sekhon *et al*., 2010), decrease starch granules, protein and oil contents in wheat and maize grains (Wilhelm *et al*., 1999), and affect grain composition of other cereals (Maestri *et al*., 2002; Wardlaw *et al*., 2002) and thus baking quality of flour (Balla *et al*., 2011). Drought and drought+heat were found to have a much greater influence on the yield and quality than heat stress alone (Balla *et al*., 2011; Mittler, 2006).

The effect of high temperature on plant growth is particularly important in tropical and subtropical climates, where heat stress may become a major limiting factor for field crop production (Wahid *et al*., 2007). Rising temperatures may lead to altered geographical distribution and growing season of agricultural crops by allowing the threshold temperature for the start of the season and crop maturity to reach earlier (Porter, 2005). In general, tropical crops often have higher threshold temperature values compared to cool season and temperate crops (Wahid *et al*., 2007).

Management practices towards alleviating drought and heat stresses

There are many management practices to alleviate negative effects of drought and heat stresses. They include, among others, soil management practices, irrigation, crop residues and mulching, and choice of crops and varieties to be grown.

Soil management and irrigation

Changes in the soil surface affect soil water and heat balance in terms of soil water evaporation and infiltration and heat exchange between soil and atmosphere (Ferrero *et al*., 2005; Sekhon *et al*., 2010). They can be induced by tillage, surface residue management, or mulching through the effect on the soil surface roughness, surface-energy partitioning, gradients in temperature and water vapour, infiltration, the amount of water stored in the soil and water uptake by plants (Lipiec *et al*., 2006; Sekhon *et al*., 2010). Research has shown that, compared to ploughed ones, soils after direct drilling are characterized by a greater number of longitudinally continuous biopores (made by soil fauna and plant roots), which offer greater potential for undisturbed root growth, because roots can bypass the zones of high mechanical impedance (Lipiec and Hatano, 2003) and affect soil water retention and movement (Sławiński *et al*., 2011, 2012). A significant increase in rooting depth in soils with definite hard subsoils can be attained by deep tillage. Because of the high cost of the operation, it is usually recommended only in most dense soil areas (Martínez *et al*., 2012).

The use of the surface organic mulch diminishes soil temperature due to low thermal conductivity (Khan *et al*., 2000), favourably influences the water content by controlling evaporation from the soil surface and absorbing water vapour onto mulch tissue (Mulumba and Lal, 2008; Sekhon *et al*., 2010), and aggregation of soil particles (Jordan *et al*., 2010; Kęsik *et al*., 2010) affects the quantity of rainwater entering the soil and evaporation (Ghosh *et al*., 2006) and crop yield (Siczek and Lipiec, 2011). Furthermore, mulch significantly increases symbiotic nitrogen fixation as measured by nitrogenase activity, nodule diameter, and dry weight (Siczek and Lipiec, 2011).

Supplemental irrigation during the growing season can result in a significant increase in water use efficiency (WUE) and grain yield. The modern irrigation techniques including sprinkling, drip, and film hole irrigation compared to surface irrigation are more effective in terms of water saving (up to more than 50%), grain yield, and water use efficiency and less effective in terms of cost and energy requirements (Sekhon *et al*., 2010; Jensen, 2013). Therefore, the modern techniques are mostly suitable for cash crops and on sloppy lands with amounts of water synchronized with plant growth stage and water use. The research revealed that WUE can be increased by soil management practices or supplemental irrigation by 25-40% and grain yield by up to 75% by irrigation at the reproductive growth phase (Sekhon *et al*., 2010).

Choice of Crops and Varieties

Crops do vary in their ability to tolerate drought and heat stresses. Plant growth and yield under water-limited conditions can be determined by genetic factors controlling resistance to drought and high temperature conditions and/or WUE (Blum, 2005; Rizza *et al*., 2004; Singh *et al*., 2010). Some crops/genotypes are more suitable than others to tolerate stress. In general, crop types and varieties that mature earlier perform better in drought-prone areas by escaping terminal drought as a result of early phenological stages such as flowering, which affects final crop yield (Singh *et al*., 2010). Moreover, crops and varieties with good stand establishment and canopy structure perform better in drought and heat prone areas through reduction in soil evaporation and heating (Sekhon *et al*., 2010).

Plant tolerance to drought is enhanced by more extensive root systems (Rizza *et al*., 2004), including root hairs that help keeping root-soil contact in shrink soil due to drying (Gliński and Lipiec, 1990; White and Kirkegaard, 2010). Additionally, greater hydraulic resistance of the root system related to smaller xylem vessels would increase drought tolerance of plants due to decreasing the rate of extraction of water from the soil without rapid decreasing the amount of available water. The number of seminal roots, root hair length, and an increase in the root hydraulic resistance that can be modified through breeding was indicated (Bengough *et al*., 2011), However, when crops are irrigated, extensive root systems using a large quantity of photosynthates are unnecessary. In a hydroponic experiment (unlimited water availability), Vysotskaya *et al*. (2004) showed that only one out of five wheat roots can maintain transpiration and stomatal conductivity at the same level as control plants with an intact root system. Therefore, different genotypes are required under irrigated and rain fed conditions or other farming practices.

The effect of drought on crop growth is related to stress intensity and yield potential. Under moderate stress, varieties with high yield potential can be suitable whereas under severe stress varieties with high drought tolerance and low yield potential would be more beneficial (Panthuwan *et al*., 2002; Rizza *et al*., 2004).

Plant tolerance to abiotic stresses can be improved using traditional and contemporary molecular breeding protocols and transgenic approaches or genetic engineering (Mittler and Blumwald, 2010; Wahid and Close, 2007). Genetic improvement of crops for stress tolerance is a relatively new effort and has been considered only since the last 3 decades. The use of molecular and transgenic approaches is still limited due to insufficient knowledge and availability of genes with known effects on plant tolerance to the abiotic stresses (Wahid *et al*., 2007). Therefore, several recent studies have aimed at identification of most stress-tolerant plant genotypes for breeding purposes using new tools, such as markers for quantitative trait loci (QTLs) and single genes for genotype, rather than phenotype selection (Abayomi *et al*., 2012; Hossain *et al*., 2013). Currently, both approaches including cultural practices and genetic improvements are often suggested to be employed simultaneously in order to minimize adverse effects of the environmental stresses on crop production (Wahid *et al*., 2007). Moreover, agroforestry including concurrent production of trees and agricultural crops from the same piece of land can be useful for sustaining stresses in the cropping zone (Kędziora, 2011).

Changes in temperatures and water limitations expected under climate change may have a significant effect on geographical distribution and occurrence of insect pests and diseases, as well as expansion of new pathogens limiting crop production (Vadez *et al*., 2011). This implies a need for development new control measures.

Foliar application of growth regulators and expression of aquaporins

The adverse effects of the abiotic stresses can be mitigated by foliar application of natural and synthetic growth regulators. The drought stress effect was reduced by the use of exogenous gibberellic acid (Taiz and Zeiger 2006), 1-aminocyclopropane-1-carboxylic acid (Brownfield *et al*., 2008), external glycinebetaine (Farooq *et al*., 2009), and maintaining an appropriate level of water in the leaves due to osmotic adjustment and stomatal performance (Sakamoto and Murata, 2002). Jasmonic acid belonging to the natural growth regulators also protects plants against the stress through expression of relevant genes (Farooq *et al*., 2009). Gibberellic acid improves also seed germination under warm temperature (Rojas-Aréchiga *et al*., 2011).

Another way for regulating water flow at the root level is trough aquaporin activity, which facilitates water transport across cell membranes in the root (Parent *et al*., 2009; Vadez *et al*., 2011) and leaves (Prado and Maurel, 2013; Sadok and Sinclair 2010). It appears that ABA has a role in regulating expression of aquaporins (Beaudette *et al*., 2007; Parent *et al*., 2009). Törnroth-Horsefield *et al*. (2006) reported that aquaporins can be quickly activated or deactivated by mechanisms of phosphorylation/dephosphorylation. The effect of ABA and other compounds on the role of aquaporins in control of root hydraulic conductance and adaptation of crops to water deficit require further research (Vadez *et al*., 2011).

CONCLUSIONS AND RESEARCH NEEDS

Crop production under field conditions can be decreased by several abiotic stresses. This gives studies on multifactor interactions greater importance than analyses of only one stress. Plant reaction to a combination of drought and heat stress cannot be directly extrapolated from the response of plants to each of these different stresses applied individually. Co-occurrence of heat and drought stress affects plants to a larger degree than the summary effect of both stresses.

Plant roots and shoots manifest numerous adaptive changes in response to drought and heat stresses. The decrease in root hydraulic conductivity induced by drought reduces water flux into the plant, but also prevents water losses from the plant to the dry soil. High soil temperatures may increase root hydraulic conductivity up to a level harmful for plant functions.

Root growth under initial drought and high temperature conditions is generally enhanced for better access to water and dehydration avoidance. However, prolonged drought results in root shrinkage, anatomical deformations, and weak root-soil contact that limits water and ion supply. In legume crops, the stresses decrease nodule size and weight and nitrogenase activity.

The alterations in root growth and distribution reduces shoot growth and functions as an effect of root-to-shoot signalling with contribution of plant hormones and other factors (*eg* nitrogen, calcium, pH) acting as signal molecules. The plant stress hormone, ABA, has long been recognized to act as a major chemical root-to-shoot stress signal under both stresses. Both stresses induce stomatal closure, decrease the transpiration rate and photosynthesis activity particularly through the effect on photosystem PS II, and lead to earlier crop maturity and poor productivity. Other responses include accumulation of compounds of low molecular mass (*eg* proline and gibberellins), anatomical deformations at the tissue, cellular, and sub-cellular levels. Expression of heat shock proteins and other proteins is an adaptation strategy to high temperatures. C3 (*eg* wheat) compared to C4 (*eg* maize) plants are more sensitive to drought and less sensitive to heat stress.

Soil-plant water relations and heat balance can be influenced by tillage, surface residue management or mulching through the effect on the soil surface roughness, surface-energy partitioning, gradients in temperature and water vapour, infiltration and amounts of water stored in the soil, and water uptake by plants. The partial root drying approach has been recently applied to increase crop WUE and root WUE in many regions. Crops and varieties with good stand establishment and an extensive root system perform better in drought and heat prone areas. Foliar application of growth regulators can alleviate the adverse effects of drought and heat stresses through keeping an appropriate level of water in the leaves due to osmotic adjustment and stomatal performance.

There is relatively little information about the effects of the drought and heat stresses along with other environmental threats, such as soil compaction, erosion salinity, and acidification. Further research involving determination of plant assimilate partitioning (from source to sink) and phenotypic plasticity is essential for understanding the complexity of the responses and for breeding using molecular protocols or genetic engineering of plants that can tolerate abiotic stresses.

REFERENCES

Abayomi Y.A. and Adefila O.E., 2008. Interactive effects of soil moisture content and fertilizer level on growth and achene yield of sunflower (*Helianthus annuus* L.). J. Agronomy, 7, 182-186.

Abayomi Y.A., Awokola C.D., and Lawal Z.O., 2012. Comparative evaluation of water deficit tolerance capacity of extra-early and early maize genotypes under controlled conditions. J. Agric. Sci., 4, 54-71.

Abe H., Urao T., Ito T., Seki M., Shinozaki K., and Yamaguchi-Shinozaki K., 2003. Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. Plant Cell, 15, 63-78.

Ahn Y.-J. and Zimmerman J.L., 2006. Introduction of the carrot HSP17.7 into potato (*Solanum tuberosum* L.) enhances cellular membrane stability and tuberization in vitro. Plant Cell Environ., 29, 95-104.

Ahuja I., De Vos R.C., Bones A.M., and Hall R.D., 2010. Plant molecular stress responses face climate change. Trends Plant Sci., 15, 664-674.

Alfonso S.U. and Bruggemann W., 2012. Photosynthetic responses of a C3 and three C4 species of the genus *Panicum* (s.l.) with different metabolic subtypes to drought stress Photosynth. Res., 112, 175-191.

Arasimowicz M. and Floryszak-Wieczorek J., 2007. Nitric oxide as a bioactive signalling molecule in plant stress responses. Plant Sci., 172, 876-887.

Ashraf M. and Harris P.J.C., 2013. Photosynthesis under stressful environments: An overview. Photosynthetica, 51(2), 163-190.

Augé R.M., Kubikova E., and Moore J.L., 2001. Foliar dehydration tolerance of mycorrhizal cowpea, soybean and bush bean. New Phytol., 151, 535-541.

Balla K., Rakszegi M., Li Z.G., Bekes F., Bencze S., and Veisz O., 2011. Quality of winter wheat in relation to heat and drought shock after anthesis. Czech J. Food Sci., 29, 117-128.

Barnabás E., Jager K., and Feher A., 2008. The effect of drought and heat stress on reproductive processes in cereals. Plant, Cell Environ., 31, 11-38.

Barta C., Dunkle A.M., Wachter R.M., and Salvucci M.E., 2010. Structural changes associated with the acute thermal instability of Rubisco activase. Arch. Biochem. Biophys., 499(1-2), 17-25.

Battisti D.S. and Naylor R.L., 2009. Historical warnings of future food insecurity with unprecedented seasonal heat. Sci., 323, 240-244.

Beaudette P.C., Chlup M., Yee J., and Emery R.J.N., 2007. Relationships of root conductivity and aquaporin gene expression in *Pisum sativum*: diurnal patterns and the response to HgCl2 and ABA. J. Exp. Bot., 58, 1291-1300.

Bellinger Y. and Larher F., 1987. Proline accumulation in higher plants: A redox buffer? Plant Physiol. (Life Sci Adv.), 6, 23-27.

Bengough A.G., 1997. Modelling rooting depth and soil strength in a drying soil profile. J. Theoret. Biol., 186(3), 327-338.

Bengough A.G., McKenzie B.M., Hallett P.D., 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. J. Experim. Botany 62(1), 59-68.

Benjamin J.G., Nielsen D.C., and Vigil M.F., 2003. Quantifying effects of soil conditions on plant growth and crop production. Geoderma, 116, 137-148

Beudez N. and Doussan C., 2013. Influence of three root spatial arrangement on soil water flow and uptake. Results from an explicit and an equivalent, upscaled, model. Procedia Environ. Sci., 19(0), 37-46.

Blum A., 2005. Drought resistance, water-use efficiency, and yield potential – are they compatible, dissonant, or mutually exclusive?. Aust. J. Agric. Res., 56, 1159-1168.

Brisson N., 1998. An analytical solution for the estimation of the critical available soil water fraction for a single layer water balance model under growing crops. Hydrol. Earth System Sci., 2(2-3), 221-231.

Brisson N. and Mary B., 1998. STICS: a generic model for the simulation of crops and their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. Agronomie, 18(5-6), 311-346.

Brownfield D.L., Todd C.D., and Deyholos M.K., 2008. Analysis of *Arabidopsis arginase* gene transcription patterns indicates specific biological functions for recently diverged paralogs. Plant Mol. Biol., 67, 429-440.

Camejo D., Rodriguez P., Morales M.A., Dell'amico J.M., Torrecillas A., and Alarcon J.J., 2005. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J. Plant Physiol., 162, 281-289.

Carminati A. and Vetterlein D., 2009. When roots lose contact. Vadose Zone J., 8(3), 805-809.

Carminati A. and Vetterlein D., 2013. Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. Ann. Botany, 112(2), 277-290.

Ciscar J.-C., 2012. The impacts of climate change in Europe (the PESETA research project). Climatic Change, 112, 1-6.

Clark L.J.G., Gowing D.J., Lark R.M., Leeds-Harrison P.B., Miller A.J., Wells D.M., Whalley W.R., and Whitmore A.P., 2005. Sensing the physical and nutritional status of the root environment in the field: a review of progress and opportunities. J. Agric. Sci., 143, 347-358.

Condon A.G., Richards R.A., Rebetzke G.J., and Farquhar G.D., 2002. Improving intrinsic water-use efficiency and crop yield. Crop Sci., 42, 122-131.

Crafts-Brander C. and Salvucci M.E., 2002. Sensitivity to photosynthesis in the C4 plant maize to heat stress. Plant Cell, 12, 54-68.

Cruiziat P. and Cochard H., 2002. Hydraulic architecture of trees: main concepts and results. Ann. Forest Sci., 59(7), 723-752.

da Silva A.P., Kay B.D., and Perfect E., 1994. Characterization of least limiting ranges of soils. Soil Sci. Soc. Am. J., 58, 1775-1781.

Davies W.J. and Hartung W., 2004. Has extrapolation from biochemistry to crop functioning worked to sustain plant production under water scarcity? New directions for a diverse planet. Proc. 4th Int. Crop Sci. Congr., September 26 – October 1, Brisbane, Australia.

Deikman J., Petracek M., and Heard J.E., 2012. Drought tolerance through biotechnology: improving translation from the laboratory to farmers' fields. Curr. Opin. Biotechnol., 23, 243-250.

Denmead O.T. and Shaw R.H., 1962. Availability of soil water to plants as affected by soil moisture content and meteorological conditions. Agron. J., 54, 385-390.

Dodd I.C., 2005. Root-to-shoot signalling: assessing the roles of "up" in the up and down world of long-distance signalling in planta. Plant Soil, 274, 251-270.

Doussan C., Vercambre G., and Pages L., 1998. Modelling of the hydraulic architecture of root systems: an integrated approach to water absorption: distribution of axial and radial conductances in maize. Ann. Botany, 81, 225-232.

Dreesen P.E, De Boeck H.J., Janssens I.A., and Nijs I., 2012. Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. Environ. Exp. Bot., 79, 21-30.

El Soda M., Nadakuduti S.S., Pillen K., and Uptmoor R., 2010. Stability parameter and genotype mean estimates for drought stress effects on root and shoot growth of wild barley pre-introgression lines. Molecular Breeding, 26, 583-593.

Farooq M., Aziz T., Wahid A., Lee D.J., Siddique K.H.M., 2009. Chilling tolerance in maize: agronomic and physiological approaches. Crop Past Sci., 60, 501-516.

Farooq M., Hussain M., Wahid A., and Siddique K.H.M., 2012. Drought stress in plants: An Overview. In: Plant Responses to Drought Stress(Ed. R. Aroca), Springer Press, Berlin -Heidelberg.

Ferrero A., Usowicz B., and Lipiec J., 2005. Effects of tractor traffic on spatial variability of soil strength and water content in grass covered and cultivated sloping vineyard. Soil Till. Res., 84, 127-138.

Foolad M.R., 2005. Breeding for abiotic stress tolerances in tomato. In: Abiotic Stresses: Plant Resistance Through Breeding and Molecular Approaches (Eds M. Ashraf, P.J.C. Harris). The Haworth Press, New York, USA.

Garrigues E. and Doussan C., 2006. Water uptake by plant roots: I - Formation and propagation of a water extraction front in mature root systems as evidenced by 2D light transmission imaging. Plant Soil, 283(1-2), 83-98.

Ghannoum O., 2009. C4 photosynthesis and water stress. Ann. Bot., 103, 635-644.

Ghosh P.K., Dayal D., Bandyopadhyay K.K., and Mohanty M., 2006. Evaluation of straw and polythene mulch for enhancing productivity of irrigated summer groundnut. Field Crops Res., 99, 76-86.

Gliński J. and Lipiec J., 1990. Soil Physical Conditions and Plant Roots. CRC Press, Boca Raton, FL, USA.

Golabadi M., Arzani A., and Mirmohammadi Malbody S.A.M., 2006. Assessment of drought tolerance in segregating populations in Durum wheat. African J. Agric. Res., 1(5), 162-171.

Guilioni L., Wery J., and Lecoeur J., 2003. High temperature and water deficit may reduce seed number in field pea purely by decreasing plant growth rate. Funct. Plant Biol., 30, 1151-1164.

Hossain A., Sarker M.A.Z., Saifuzzaman M., Teixeira da Silva J.A., Lozovskaya M.V., and Akhter M.M., 2013. Evaluation of growth, yield, relative performance and heat susceptibility of eight wheat (*Triticum aestivum* L.) genotypes grown under heat stress. Int. J. Plant Production, 7, 615-636.

Howarth C.J., 2005. Genetic improvements of tolerance to high temperature. In: Abiotic Strsses Plant Resistance Through Breeding and Molecular Approaches (Eds M. Ashraf, P.J.C. Harris). Howarth Press, New York, USA.

Hu L., Wang, Z., and Huang, B., 2011. Effects of cytokinin and potassium on stomatal and photosynthetic recovery of Kentucky Bluegrass from drought stress. Crop Sci. 2013 53: 221–231.

Huang B. and Eissenstat D.M., 2000. Root plasticity in exploiting water and nutrient heterogeneity. Plant-Environment Interactions (Ed. R.E. Wilkinson). Dekker Press, New York, USA.

Iannucci A., Rascio A., Russo M., Di Fonzo N., and Martiniello P., 2000. Physiological responses to water stress following a conditioning period in berseem clover. Plant Soil, 223, 217-227.

IPCC, **2007.** Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change Core Writing Team (Eds R.K. Pachauri, A. Reisinger) IPCC, Geneva, Switzerland.

Jensen Ch.R., 2013. Some options for securing water resources for agricultural production In: Plant Functioning under Environmental Stress (Eds M. Grzesiak, A. Rzepka, T. Hura, S. Grzesiak). Institute of Plant Physiology, PAS, Cracow, Poland.

Jordan A., Zavala L.M., and Gil J., 2010. Effects of mulching on soil physical properties and runoff under semi-arid conditions in southern Spain. Catena, 81, 77-85.

Jovanovic Z., Stikic R., Vucelic-Radovic B., Paukovic M., Brocic Z., Matovic G., Rovcanin S., and Mojevic M., 2010. Partial root zone drying increases WUE, N and antioxidant content in field potatoes. Eur. J. Agron., 33, 124-131.

Kavi Kishor P.B., Sangam S., and Amrutha R.N., 2005. Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: Its implications in plant growth and a biotic stress tolerance. Curr. Sci., 88, 424-438.

Kęsik T., Błażewicz-Woźniak M., and Wach D., 2010. Influence of conservation tillage in onion production on the soil organic matter content and soil aggregate formation. Int. Agrophys., 24, 267-273.

Khan A.R., Chandra D., Quraishiand S., and Sinha R.K., 2000. Soil aeration under different soil surface conditions. J. Agron. Crop Sci., 185, 105-112.

Kozłowska M., 2007. Plant Physiology. From theory to applied sciences (in Polish). PWRiL, Warsaw, Poland.

Król A., 2013. The growth and water uptake by yellow seed and black seed rape depending on the state of soil compaction. . Ph.D. Thesis, Bohdan Dobrzański Institute of Agrophysics PAS, Lublin, Poland.

Lee S.B. and Suh M.C., 2013. Recent Advances in Cuticular Wax Biosynthesis and Its Regulation in Arabidopsis, Mol. Plant, 6(2), 246-249.

Li Y.Y., Sperry J.S., and Shao M., 2009. Hydraulic conductance and vulnerability to cavitation in corn (*Zea may*s L.) hybrids of differing drought resistance. Environ. Exp. Botany, 66(2), 341-346.

Lipiec J. and Hatano R., 2003. Quantification of compaction effects on soil physical properties and crop growth. Geoderma, 116, 107-136.

Lipiec J., Horn R., Pietrusiewicz J., and Siczek A., 2012. Effects of soil compaction on root elongation and anatomy of different cereal plant species. Soil Till. Res., 121, 74-81.

Lipiec J., Kuś J., Słowińska-Jurkiewicz A., and Nosalewicz A., 2006. Soil porosity and water infiltration as influenced by tillage methods. Soil Till. Res., 89, 210-220.

Liu X. and Huang B., 2000. Heat stress injury in relation to membrane lipid peroxidation in creeping bent grass. Crop Sci., 40, 503-510.

Lu C. and Zhang J., 1999. Effects of water stress on photosystem II photochemistry and its thermostability in wheat plants. J. Exp. Botany, 50(336), 1199-1206.

Łukowska M. and Józefaciuk G., 2013. Unknown mechanism of plants response to drought: low soil moisture and osmotic stresses induce severe decrease in CEC and increase in acidity of barley roots. J. Agric. Sci., 5(10), 204-213 .

Maestri E., Klueva N., Perrotta C., Gulli M., Nguyen H.T., and Marmiroli N., 2002. Molecular genetics of heat tolerance and heat shock proteins in cereals. Plant Mol. Biol., 48, 667-681.

Martínez I. G., Prat C., Ovalle C., del Pozo A., Stolpe N., and Zagal E., 2012. Subsoiling improves conservation tillage in cereal production of severely degraded Alfisols under Mediterranean climate. Geoderma, 189-190, 10-17.

Maurel C., Simonneau T., and Sutka M., 2010. The significance of roots as hydraulic rheostats. J. Exp. Botany, 61(12), 3191-3198.

McCully M.E. and Cann M.J., 2009. Cryo-scanning electron microscopy (CSEM) in the advancement of functional plant biology. Morphological and anatomical applications. Functional Plant Biol., 36(2), 97-124.

Mittler R., 2006. Abiotic stress, the field environment and stress combination. Trends Plant Sci., 11, 15-19.

Mittler R. and Blumwald E., 2010. Genetic engineering for modern agriculture: Challenges and perspectives. Ann. Rev. Plant Biol., 61, 443-62.

Monica R., Consortium L., and Consortium L., 2007. Breeding temperate legumes: Advances and challenges. Lotus Newsl., 37(3), 105.

Muller B., Pantin F., Génard M., Turc O., Freixes S., Piques M., and Gibon Y., 2011. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. J. Exp. Bot., 62, 1715-1729.

Mulumba L.N. and Lal R., 2008. Mulching effects on selected soil physical properties. Soil Till. Res., 98, 106-111.

Nardella E., Giuliani M.M., Gatta G., and De Caro A., 2012. Yield response to deficit irrigation and partial root-zone drying in processing tomato (*Lycopersicon esculentum* Mill.). J. Agric. Sci. Technol., A 2, 209-219.

Neumann D.M., Emmermann M., Thierfelder J.M., Zur Nieden U., Clericus M., Braun H.P., Nover L., and Schmitz U.K., 1993. HSP68-a DNAK-like heat-stress protein of plant mitochondria. Planta, 190, 32-43.

Nosalewicz A. and Lipiec J., 2013. The effect of compacted soil layers on vertical root distribution and water uptake by wheat. Plant and Soil (in press).

Novák V. and Lipiec J., 2012. Water extraction by roots under environmental stresses. In: Pollution and Water Resources, Columbia University Seminar Proceedings: Impact of Anthropogenic Activity and Climate Changes on the Environment of Central Europe and USA (Eds J. Halasi-Kun, V. Stekauerová, I. Fodor, V. Nagy, B. Sinóros-Szabó, R. Lo Pinto). Slovak Academy of Sciences – Hungarian Academy of Sciences – Columbia University .

Ooi M.K.J., Auld T.D., and Denham A.J., 2012. Projected soil temperature increase and seed dormancy response along an altitudinal gradient: implications for seed bank persistence under climate change. Plant Soil, 353, 289-303.

Panthuwan G., Fukai S., Cooper M., Rajatasereekul S., and Toole J.C., 2002. Yield response of rice (*Oryza sativa* L.) genotypes to different types of drought under rainfed lowlands. Part 1. Grain yield and yield components. Field Crop Res., 73, 153-168.

Pareek A., Singla S.L., and Grover A., 1998. Proteins alterations associated with salinity, desiccation, high and low temperature stresses and abscisic acid application in seedlings of Pusa 169, a high-yielding rice (*Oryza sativa* L.) cultivar. Curr. Sci., 75, 1023-1035.

Parent B., Hachez C., Redondo E., Simonneau T., Chaumont F., Tardieu F., 2009. Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: A trans-scale approach. Plant Physiology, 149, 2000-2012.

Parsons R. and Sunley R.J., 2001. Nitrogen nutrition and the role of root-shoot nitrogen signalling particularly in symbiotic systems. J. Exp. Botany, 52, 435-443.

Porter J.R., 2005. Rising temperatures are likely to reduce crop yields. Nature, 436, 174.

Prado K. and Maurel C., 2013. Regulation of leaf hydraulics: from molecular to whole plant levels. Front. Plant. Sci., 4, 255. doi:10.3389/fpls.

Prasad P.V.V., Pisipati S.R., Ristic Z., Bukovnik U., and Fritz A.K., 2008. Impact of nighttime temperature on physiology and growth of spring wheat. Crop Sci., 48, 2372-2380.

Purwanto E., 2003. Photosynthesis activity of soybean (*Glycine max* L.) under drought stress. Agrosains J., 5(1), 13-18.

Read D.B., Bengough A.G., Gregory P.J., Crawford J.W., Robinson D., and Scrimgeour C.M., 2003. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. New Phytol., 157, 315-326.

Rizhysky L., Liang H., Shuman J. , Shulaev V., Davletova S., and Mittler R., 2004. When defense pathways collide: The response of Arabidopsis to a combination of drought and heat stress. Plant Physiol., 134, 1683-1696.

Rizza F., Badeck F.W., Cattivelli L., Li Destri O., Di Fonzo N., and Stanca A.M., 2004. Use of a water stress index to identify barley genotypes adapted to rainfed and irrigated conditions. Crop Sci., 44, 2127-2137.

Rojas-Aréchiga M., Aguilar K.M., Golubov J., and Mandujanoa M.C., 2011. Effect of Gibberellic Acid on Germination of Seeds of Five Species of Cacti From the Chihuahuan Desert, Northern Mexico. The Southwestern Naturalist, 56(3), 393-400.

Rollins J.A., Habte E., Templer S.E., Colby T., Schmidt J., and von Korff M., 2013. Leaf proteome alterations in the context of physiological and morphological responses to drought and heat stress in barley (*Hordeum vulgare* L.). J. Exp. Botany, 64(11), 3201-3212.

Roohi E., Tahmasebi-Sarvestani Z., Modarres-Sanavy S.A.M., and Siosemardeh A., 2013. Comparative Study on the effect of soil water stress on photosynthetic function of triticale, bread wheat, and barley. J. Agr. Sci. Tech., 15, 215-228.

Sadok W. and Sinclair T.R., 2010. Transpiration response of 'slow-wilting' and commercial soybean (*Glycine max*, L. Merr.) genotypes to three aquaporin inhibitors. J. Exp. Botany, 61, 821-829.

Sadras V.O. and Milroy S.P., 1996. Soil-water thresholds for the responses of leaf expansion and gas exchange: A review. Field Crops Res., 47(2-3), 253-266.

Sakamoto A. and Murata N., 2002. The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. Plant Cell Environ., 25, 163-171.

Sakamoto A. and Murata N., 1998. Metabolic engineering of rice leading to biosynthesis of glycinebetaine and tolerance to salt and cold. Plant Mol. Biol., 38(6), 1011-1019.

Salvucci M.E. and Crafts-Brandner S.J., 2004. Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. Plant Physiol., 134, 1460-1470.

Sarai Tabrizi M., Parsinejad M., and Babazadeh H., 2012. Efficacy ofpartial root drying technique for optimizing soybean crop production in semi-arid regions. Irrig. Drain., 61(1), 80-88.

Schachtman D.P. and Goodger J.Q.D., 2008. Chemical root to shoot signaling under drought. Trends Plant Sci., 13, 281-287.

Sekhon H.S., Singh G., Sharma P., and Bains T.S., 2010. Water Use Efficiency Under Stress Environments In: Climate Change and Management of Cool Season Grain Legume Crops (Eds S.S. Yadav, D.L. Mc Neil, R. Redden, and S.A. Patil). Springer Press, Dordrecht-Heidelberg-London-New York.

Seyed Y., Lisar S., Rouhollah Motafakkerazad, Mosharraf M. Hossain and Ismail M. Rahman M., 2012. Water Stress in Plants: Causes, Effects and Responses, Water Stress (Ed. Ismail Md. Mofizur Rahman), Intech Europe, Rijeka, Croatia.

Siczek A. and Lipiec J., 2011. Soybean nodulation and nitrogen fixation in response to soil compaction and surface straw mulching. Soil Till. Res., 114, 50-56.

Siddique K.H.M., Regan K.L., Tennant D., and Thomson B.D., 2001. Water use and water use efficiency of cool season grain legumes in low rainfall mediterranean-type environments. Eur. J. Agron., 15, 267-280.

Simoes-Araujo J.L., Rumjanek N.G., and Margis-Pinheiro M., 2003. Small heat shock proteins genes are differentially expressed in distinct varieties of common bean. Braz. J. Plant Physiol., 15, 33-41.

Sinclair T.R., Holbrook N.M., and Zwieniecki M.A., 2005. Daily transpiration rates of woody species on drying soil. Tree Physiol., 25(11), 1469-1472.

Singh V., van Oosterom E.J., Jordan D.R., Messina C.D., Cooper M., and Hammer G.L., 2010. Morphological and architectural deve- lopment of root systems in sorghum and maize. Plant Soil, 333, 287-299.

Sławiński C., Cymerman J., Witkowska-Walczak B., and Lamorski K., 2012. Impact of diverse tillage on soil moisture dynamics. Int. Agrophys., 26, 301-309.

Sławiński C., Witkowska-Walczak B., Lipiec J., and Nosalewicz A., 2011. Effect of aggregate size on water movement in soils. Int. Agrophys., 25, 53-58.

Steduto P. and Hsiao T.C., 2009. AquaCrop - the FAO crop model to simulate yield response to water: I. Concepts Underlying Principles. Agron. J., 101(3), 426-437.

Stirzaker R.J. and Passioura J.B., 1996. The water relations of the root-soil interface. Plant Cell Environ., 19(2), 201-208.

Szabo L. and Savoure A., 2010. Proline: a multifunctional amino acid. Trends Plant Sci., 15(2), 89-97.

Tadross M., Suarez P., Lotsch A., Hachi gonta S., Mdoka M., Unganai L., Lucio F., Kamdonyo D., and Muchinda M., 2007. Changes in growing-season rainfall characteristics and downscaled scenarios of change over southern Africa: implications for growing maize. IPCC regional Expert Meet. Regional Impacts, Adaptation, Vulnerability, and Mitigation, June 20-22, Nadi, Fiji.

Taiz L. and Zeiger E., 2006. Plant physiology. Sinauer Associates Press, Sunderland, MA, USA.

Tardieu F., Bruckler L., and Lafolie F., 1992. Root clumping may affect the root water potential and the resistance to soil-root water transport. Plant Soil, 140, 291-301.

Taylor H.M. and Willatt S.T., 1983. Shrinkage of soybean roots. Agron. J., 75(5), 818-820.

Tewolde H., Fernandez C.J., and Erickson C.A., 2006. Wheat cultivars adapted to post-heading high temperature stress. J. Agron. Crop Sci., 192, 111-120.

Törnroth-Horsefield S., Wang Y., Hedfalk K., Johanson U., Karlsson M., Tajkhorshid E., Neutze R., and Kjellbom P., 2006. Structural mechanism of plant aquaporin gating. Nature, 439, 688-694.

Trenberth K.E., 2011. Changes in precipitation with climate change. Clim. Res., 47, 123-138.

Vadez V., Berger J.D., Warkentin T., Asseng S., Ratnakumar P., Rao K.P.C., Gaur P.M., Munier-Jolain N., Larmure A., Voisin A.S., Sharma H.C., Pande S., Sharma M., Krishnamurthy L., and Zaman M.A., 2012. Adaptation of grain legumes to climate change: a review. Agron. Sustain. Dev., 32, 31-44.

Vadez V., Kholova J., Choudhary S., Zindy P., Terrier M., Krishnamurth L., Kumar P.R., and Turner N.C., 2011. Whole plant response to drought under climate change. In: Crop adaptation to climate change (Eds S.S. Yadav, R. Redden, J.L. Hatfield, H. Lotze-Campen, A.E. Hall). Chichester-Wiley-Blackwell.

Vandeleur R.K. and Mayo G., 2009. The Role of Plasma Membrane Intrinsic Protein Aquaporins in Water Transport through Roots: Diurnal and Drought Stress Responses Reveal Different Strategies between Isohydric and Anisohydric Cultivars of Grapevine. Plant Physiol., 149(1), 445-460.

Verelst W., Bertolini E., De Bodt S., Vandepoele K., Demeulenaere M., Pé M.E., and Inzé D., 2012. Molecular and physiological analysis of growth-limiting drought stress in Brachypodium distachyon leaves. Mol. Plant., 6, 311-322.

Vernieri P., Lenzi A., Figaro M., Tognoni F., and Pardossi A., 2001. How the roots contribute to the ability of *Phaseolus vulgaris* L. to cope with chilling-induced water stress. J. Exp. Bot., 52, 2199-2206.

Vollenweider P. and Gunthardt-Goerg M.S., 2005. Diagnosis of abiotic and biotic stress factors using the visible symptoms in foliage. Environ Pollut., 137, 455-465.

Vysotskaya L.B., Arkhipova T.N., Timergalina L.N., Dedov A.V., Veselov S.Y., and Kudoyarova G.R., 2004. Effect of partial root excision on transpiration, root hydraulic conductance and leaf growth in wheat seedlings. Plant Physiol. Biochem., 42, 251-255.

Wahid A., 2007. Physiological implications of metabolites biosynthesis in net assimilation and heat stress tolerance of sugarcane sprouts. J. Plant Res., 120, 219-222.

Wahid A. and Close T.J., 2007. Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. Biol. Plant., 51, 104-109.

Wahid A., Gelani S., Ashraf M., and Foolad M.R., 2007. Heat tolerance in plants: an overview. Environ. Exp. Bot., 61, 199-223.

Wang Z., Xiong Y., and Wang M., 2000. Study on expert system of irrigation forecast and decision making for water saving. Institute of Agricultural Soil Water Engineering of North West Science and Technology University of Agriculture Forestry, Yangling, Shaanxi.

Waraich E.A., Ahmad R., Halim A., and Aziz T., 2012. Alleviation of temperature stress by nutrient management in crop plants: a review. J. Soil Sci. Plant Nutrition, 12(2), 221-244.

Wardlaw I.F., Blumenthal C., Larroque O., and Wrigley C.W., 2002. Contrasting effects of chronic heat stress and heat shock on kernel weight and flour quality in wheat. Functional Plant Biol., 29, 25-34.

WhalleyW.R. and Clark L.J., 2011. Drought stress, effect on soil mechanical impedance and root (crop) growth. In: Encyclopedia of Agrophysics (Eds J. Gliński, J. Horabik, J. Lipiec), Springer Press, Dordrecht-Heidelberg-London-New York.

White R.G. and Kirkegaard J.A., 2010. The distribution and abundance of wheat roots ina dense, structured subsoil-implications for water uptake. Plant Cell Environ., 33, 133-148.

Wilhelm E.P., Mullen R.E., Keeling P.L., and Singletary G.W., 1999. Heat stress during grain filling in maize: effects of kernel growth and metabolism. Crop Sci., 39, 1733-1741.

Wu Y.Z. and Huang M.B., 2011. Transpirational response to water availability for winter wheat as affected by soil textures. Agric. Water Manag., 98(4), 569-576.

Yang J., Zhang J., Wang Z., Liu K., and Wang P., 2006. Abscisic acid and ethylene interact in wheat grains in response to soil-drying during grain filling. New Phytol., 171, 293-303.

Yang J.C., Zhang J.H., Wag Z.Q., Zhu Q.S., and Liu L.J., 2003. Involvement of abscisic acid and cytokinins in the senescence and remobilization of carbon reserves in wheat subjected to water stress during grain filling. Plant, Cell Environ., 26, 1621-1631.

Yoshioka M., Uchida S., Mori H., Komayama K., Ohira S., Morita N., Nakanishi T., and Yamamoto Y., 2006. Quality control of photosystem II: cleavage of reaction center D1 protein in spinach thylakoids by FtsH protease under moderate heat stress. J. Biol. Chem., 281, 21660-21669.

Zhang J.-H., Huang W.D., Liu Y.-P., and Pan Q.-H., 2005. Effects of temperature acclimation pretreatment on the ultrastructure of mesophyll cells in young grape plants (*Vitis vinifera* L. *cv.* Jingxiu) under cross-temperature stresses. J. Integr. Plant Biol., 47, 959-970.

Zhang B., Liu W., Chang S.X., and Anyia A.O., 2010. Water-deficit and high temperature affected water use efficiency and arabinoxylan concentration in spring wheat. J. Cereal Sci., 52, 263-269.

Zhou J., Wang X., Jiao Y., Qin Y., Liu X., He K., Chen C., Ma L., Wang J., and Xiong L., 2007. Global genome expression analysis of rice in response to drought and high-salinity stresses in shoot, flag leaf, and panicle. Plant Mol. Biol., 63, 591-608.

Zlatev Z. and Lidon F.C., 2012. An overview on drought induced changes in plant growth, water relations and photosynthesis. Emir. J. Food Agric., 24, 57-72.