Australian Journal of
Crop Science
AJCS

AJCS 13(06):810-820 (2019) ISSN:1835-2707
doi: 10.21475/ajcs.19.13.06.p1286

Drought and salinity stresses in barley: Consequences and mitigation strategies

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Abstract

Recent trends show reductions in crop productivity worldwide due to severe climatic change. Different abiotic stresses significantly affect the growth and development of plants, leading to decreased crop yields. Salinity and drought stresses are the most common abiotic stresses, especially in arid and semi–arid regions, and are major constraints for barley production. The present review attempts to provide comprehensive information related to barley plant responses and adaptations to drought and salinity stresses, including physiological and agronomic, in order to alleviate the adverse effect of stresses in barley. These stresses reduce assimilation rates, as they decrease stomatal conductance, disrupt photosynthetic pigments, reduce gas exchange, enhance production of reactive oxygen species, and lead to decreased plant growth and productivity. This review focuses on the strategies plants use to respond and adapt to drought and salinity stress. Plants utilize a range of physiological and biochemical mechanisms such as adaptation strategies, through which the adverse effects can be mitigated. These include soil management practices, crop establishment, as well as foliar application of anti-oxidants and growth regulators that maintain an appropriate level of water in the leaves to facilitate adjustment of osmotic and stomatal performance. The present review highlighted the adverse effect of drought and salinity stresses barley and their mitigation strategies for sustainable barley production under changing climate. They review also underscored that exogenous application of different antioxidants could play a significant role in the alleviation of salinity and drought stress in plant systems.

Keywords: *Hordeum vulgare* L., water stress, salt stress, adaptation to stress, anti-oxidant.

Abbreviations: ABA_abscisic acid; AsA_Ascorbic acid; Ca^{2+}_calcium; chl, chlorophyll; chp_chloroplast; dS/m_deci Siemens per metre; EC_electrical conductivity; GB_glycine betaine; IAA_Indole Acetic Acid; K^+_potassium; MDA_malondialdehyde; Mg^{2+}_magnesium; MGT, N_nitrogen; Na^+_sodium; P_phosphorus; Pro_proline; QTL_quantitative trait loci; ROS_reactive oxygen species; SA_Salicylic acid.

Introduction

Barley (*Hordeum vulgare* L.) is ranked fourth for world cereal crops in both quantity produced and in acres of cultivation, after wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and maize (*Zea mays* L.) (FAO, 2016). It is mainly used as food and animal fodder, as well as for malting purposes. It provides an excellent source for genome mapping and genetic studies (Pour-Aboughadareh et al., 2013). It contributes in the study of heredity and helps improve the Information Systems. Barley is grown in regions experiencing low levels of soil moisture, where cereals such as maize and rice cannot grow well, especially in arctic or sub-arctic regions and in subtropical zones. For Example *Hordeum* spp. are grown in the Mediterranean region due to high tolerance against heat, drought, and salinity compared to other small grains (Zhou, 2009). Barley is considered an important cereal crop in several developing countries, including India, Nepal, Sri Lanka, and Bangladesh, where it is often subjected to severe drought stress that considerably influences crop productivity (Ceccarelli et al., 2007; El-Wahed et al., 2015). Drought experienced in the Mediterranean region is the result of low precipitation coupled with high temperatures in (Hossain et al., 2012a). Despite the success of modern agriculture, drought is one of the major problems wide affecting the growth and development of crops world-wide (Hasanuzzaman et. al., 2012; Hossain et al., 2012b). However, the severity of drought is a non-uniform phenomenon that adversely influences plants, depending on the plant's development stage at the time of its occurrence (Martiniello and Teixeira da Silva, 2011; Hossain et al., 2012b); high temperatures combined with drought cause considerable damage to on crops by shortening plant life span and consequently reducing yield (Vollenweider and Gunthardt-Goerg, 2005; Martiniello and Teixeira da Silva, 2011). Although barley is a salt-tolerant field crop, its growth and development is severely affected by ionic and osmotic potential (ψ) in predominantly saline soils (Izadi et al., 2014; Fayez and Bazaid, 2014). Salinity significantly reduces the production potential of most crops including barley also and can result in disruption of osmotic effects, ion-specific stress, ionic imbalance, and oxidative stress (Tabatabaei and Ehsanzadeh, 2016). Scarcity of water and salinity resulting from global climate change leads to severe summer droughts in many regions of the world (Hamdy et al., 2003; Munns, 2005). Excessive salinity in combination with water deficit has led to reduction in photosynthesis, transpiration, and other biochemical processes of crop plants (Tiwari et al., 2010). Salinity and drought lead to oxidative stress in plant cells, resulting in death of cells, due to high leakage of electrons towards O_2 during photosynthetic and respiratory processes enhance the generation of reactive oxygen species (ROS) (Mittler, 2002; Asada 2006; Fayez and Bazaid, 2014). However, knowledge and understanding of traits related to drought and salinity tolerance are important for exploring the tolerance mechanisms of crops. Responses to drought stress are becoming increasingly important, as the effects of climate change indicate that increasing areas of the globe will have semi-arid and arid climates in the near future (Petit et al., 1999; Reynolds et al., 2007). Breeding of stress-tolerant crops is the most efficient strategy to maintain productivity under conditions of environmental stress. It is thus necessary to screen the genetic resources of different populations with high tolerance to a biotic stresses and to understand their homeostatic mechanisms. The main objective of this review is to understand the production of barley under drought and saline soil conditions by understanding adverse effects as well as various adaptations to drought and saline soils. The review also attempts to explore impacts of the exogenous application of antioxidants that could play a significant role under stress conditions.

Adverse effect of drought on morphological, physiological, and biochemical processes of barley

Drought affects the morphological, physiological, and biochemical processes in plants, resulting in growth inhibition. Drought is characterized by reduction in water content, closure of stomata, and reduction in cell enlargement and growth (Ahmed et al., 2015); it is also associated with leaf senescence, which is an age-dependent deterioration process that ensures the translocation of nutrients from older leaves to developing tissues and seeds (Temel et al., 2017) and vary at different growth stages of barley (Wells and Dubetz, 1966). Under unfavorable conditions, stress caused by drought can induce senescence through breakdown of the chloroplast (chp) (Lim et al., 2007), decreased chlorophyll (chl) content, and reduced photosynthesis (Prochazkova et al., 2001). A decrease in chl content is also a symptom of drought-induced oxidative stress (Ahmed et al., 2015), while stability of chl content under drought conditions might be an indicator of drought tolerance (Li et al., 2006). Use of chl fluorescence from intact, attached leaves proved to be a reliable, non-destructive method in physiological studies of stress physiology of selected cereal crops (including wheat, oat, rice, sorghum and barley), namely water stress, heat stress, salt stress, and chilling stress (Sayed, 2003; Matouškova et al., 1999). Drought stress changes in the ratio of chl content and beta carotenoids in barley (Jaleel et al., 2009). Drought negatively influenced the chl content of different barley genotypes as reported by EL-Shawy et al. (2017; Fig. 1). While, severe drought reduced photosynthesis due to a decrease in Rubisco activity (Bota et al., 2004) that ultimately limit crop growth and yields (Dubey, 2005). Osmotic adjustment is highly dependent on photosynthesis to supply compatible solutes. Whereas dehydration becomes severe, photosynthesis is inhibited, resulting in a low quantity of solutes supplied for osmotic adjustment. Under conditions of continued water limitation, osmotic adjustment can delay, but cannot completely prevent, dehydration. The combined effects of salinity and drought on barley yield are more detrimental than the effects of each stress alone (Yousfi et al., 2010).

The flag leaf and ear of barley and wheat are the main photosynthetic organs to provide assimilates for grain filling, particularly in environments where drought is encountered at the end of plant life cycle (Sanchez-Diaz et al., 2002). Drought stress suppresses photochemical efficiency in particular by decreasing electron transport, removing external proteins, and releasing $Ca^{2+}$and Mg^{2+} from their binding sites (Zlatev and Lidon, 2012). Drought induces important alterations in plant biochemistry and metabolism. Under drought stress, responses involve production of ROS. ROS are chemically reactive chemical species containing oxygen), which cause membrane injuries, protein degradation, enzyme inactivation, and induce oxidative stress (Zlatev and Lidon, 2012).

Agronomic traits such as grain yield and associated yield components (productive tillering, grain yield per spike, no of grains per spike are the major selection criteria for evaluating drought tolerance (Lopes et al., 2012). Barley

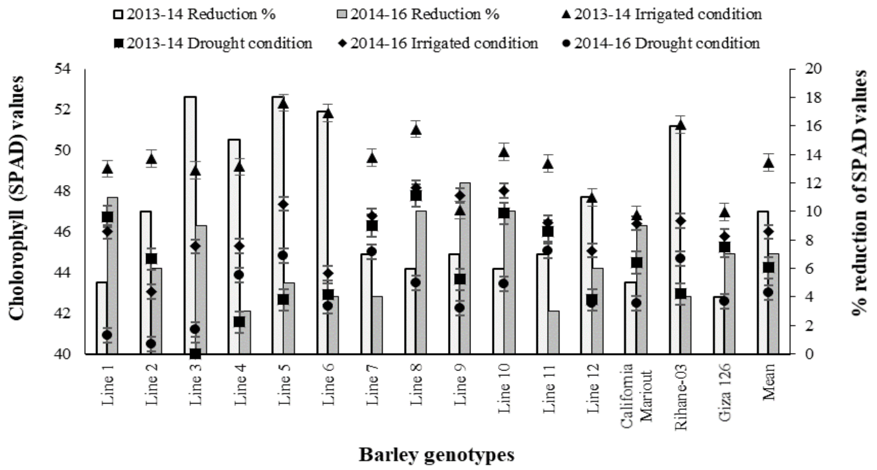

Fig 1. In primary axis indicate the chlorophyll content (SPAD value) of barley genotypes is influenced by drought stress, in secondary axis indicate the reduction of SPAD value due to drought stress (Adapted from EL-Shawy et al., 2017).

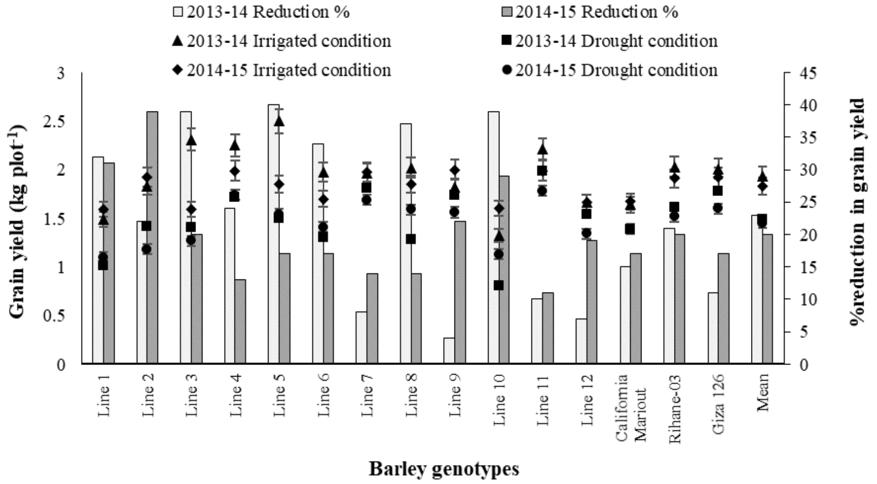

Fig 2. Yield of barley genotypes as influenced by drought stress. In secondary axis indicate the % yield reduction of barley under drought stress (Adapted from EL-Shawy et al., 2017).

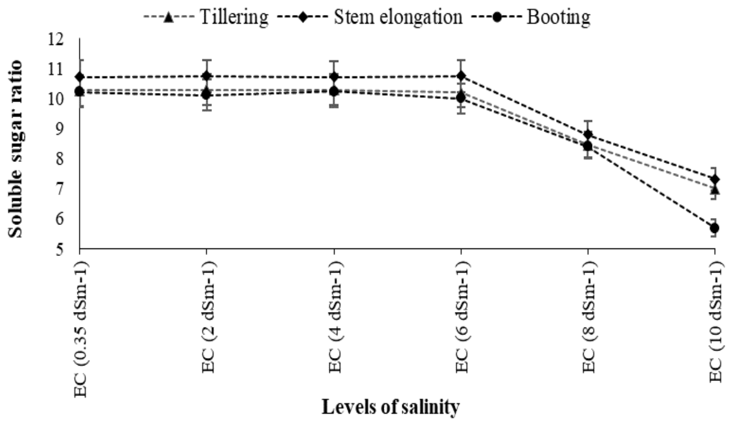

Fig 3. Soluble sugar ratio of barley is influenced by different levels of salinity at tillering, stem elongation and booting stage of barley (Adapted from Abd El-Wahed et al., 2015).

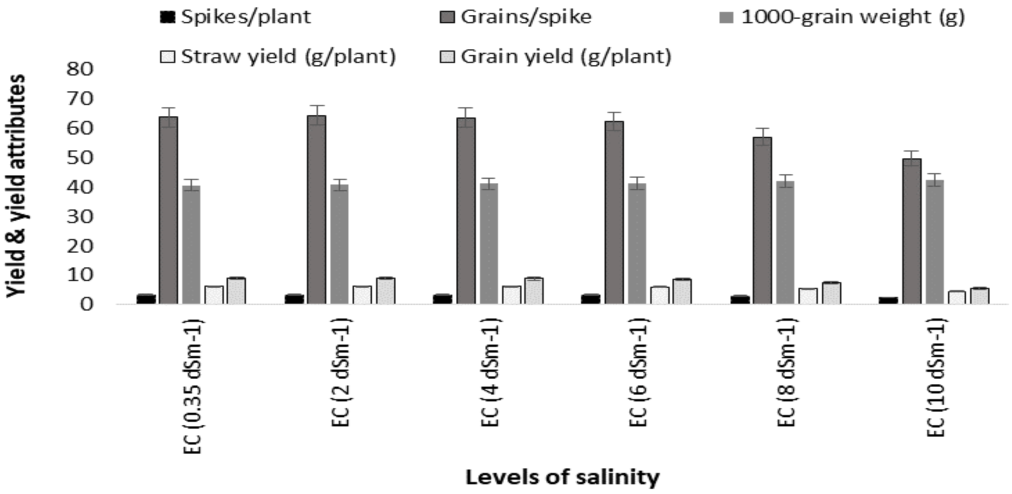

Fig 4. Yield attributes of barley as influenced by different levels of salinity that ultimately lead to decrease the final grain weight of barley (Adapted from Abd El- Wahed et al., 2015).

cultivars differ considerably in their response and adaptation to drought stress (Beigzadeh et al., 2013; Křen et al., 2014). Drought stress during the reproductive stage decreased grain yield by decreasing the number of grains per spike and kernel weight (González et al., 1999). A decrease in the duration of developmental phases caused by drought stress is partly responsible for yield reduction in cereals (maze, rice, wheat due to the reduction in light interception over the shortened life cycle (Barnabás et al., 2008). These studies indicated that the cereal plant was most sensitive to drought stress just before spike emergence. Another peak of barley sensitivity to drought was during anthesis and the initial stages of kernel development. The severity of drought stress from the beginning of grain filling to maturity may be detrimental to grain development (i.e. causing grain abortion) and to crop yields. Post-an thesis drought stress may decrease the fertility of late tillers; although how these tillers contribute to grain number and yield of barley needs to be studied (Samarah, 2005). Drought stress reduces the grain yield of barley through negative effects on yield and yield components such as number of plants per unit area, number of spikes and kernels per plant or unit area, and single grain weight, which are determined at different growth stages of the crop (Beigzadeh et al., 2013; Haddadin, 2015). The number of grains per unit area is set immediately after anthesis (this can be affected by environmental factors on spike, for example, Spike Terminal sterility), while grain filling and accumulation of grain biomass take place in the remaining post-anthesis period (Ugarte et al., 2007). The reduction in yield and yield components of barley in response to late and continuous water stress was previously reported by Samarah et al. (2009). Moustafa et al. (1996) confirmed that mid-and late-season drought stress shortened the grain filling period by up to 11 days. The number of spikes per plant and the number of kernels per spike were more sensitive to drought than the measure of 100-kernel weight.

Yield of Yield components (kernels spike^{-1}; spikes per m^{2}) are most sensitive to drought, while kernel weight remains stable due to high remobilization of carbohydrates assimilated in kernels (Abedl-Ghani, 2008). Samarah (2005) attributed the reduction in number of spikes per plant under drought conditions to an increase in the number of sterile spikes per plant and corresponding decrease in number of fertile spikes per plant. They also noticed that Reduction in kernel yield was attributed to a decrease in the number of fertile florets and the number of grains per spike as well as an increase in the number of tillers bearing sterile spikes and grains (Samarah, 2005). Grain yield of different barley genotypes is significantly influenced by limitation and variation of soil moisture regimes (EL-Shawy et al., 2017) as presented in Fig. 2.

Adverse effects of salinity on morphological, physiological, and biochemical processes of barley

Salinity stress adversely affects almost all stages of plant growth and development, i.e. germination, growth, and vigor of the seedlings; tillering; flowering; and fruit set, ultimately causing diminished economic yield of products of barley (Ahmed, 2009; Abd El-Monem et al., 2013). High salt concentrations trigger secondary stress factors including osmotic, ionic, and oxidative stresses, resulting in the disruption of ionic homeostasis (Zhu, 2001) and cell membrane integrity by damaging structural and functional proteins (Wang et al., 2003). Growth, physiological activities and water use efficiency are significantly reduced when salinity rates exceed 6 deciSiemens per metre (dS/m) (Fig. 3), this is due to water and nutrient stress occurring under high salinity stress (Abd El-Wahed et al., 2015); these processes may cause the shoot to remain small. Salinity leads to disturbances in plant metabolism (Diurnal Carbohydrate Metabolism or Glutamine Metabolism) which consequently result in reduction of plant growth and productivity (Shafi et al., 2009). In salt stressed plants, the osmotic potential of vacuoles is decreased due to accumulation of the stress-related amino acid proline (Yeo, 1998). Accumulations of osmotic compounds such as proline are often used as a parameter for selection of crops including barley with high salt stress tolerance (Ashraf, 2004; Ashraf and Foolad, 2007). Proline may act as a signaling molecule, able to activate multiple responses that are components of the adaptation process (Maggio et al., 2002).

Increasing soluble proteins might be due to the synthesis of osmotin-like proteins or structural proteins, in particular synthesis of those proteins that are involved in modification of the cell wall (it may be due to synthesis of osmotic-like proteins or structural proteins) (Ashraf, 2004). Reduction in protein content at the highest salinity level Electrical Conductivity (EC of 13 dS m^{-1}) in some cultivars may reflect a feature of salinity stress in plants in which salt reduces photosynthesis (Munns et al., 2006). It is well documented that a greater degree of salt tolerance in plants is associated with a more efficient system for selective uptake of K^+ over Na^+ (Tester and Davenport, 2003; Islam et al.,2011). The decrease in K^+ occurs due to the presence of excessive Na^+ in the growth medium; high external Na^+ content is known to have an antagonistic effect on K^+ uptake in plants (Ashraf, 2004; Izadi et al., 2014). It was reported that antagonism between the absorption of K^+ and Na^+ occurs at the root surface under salinity stress (Ahmadi et al., 2009). Leaf growth is affected by salt stress due to changes in transpiration, plasma membrane potential, abscisic acid (ABA) content, and osmolality in barley (Fricke and Peters, 2002). A slight decrease in the relative water content of roots in a hydroponic system was observed in salt-stressed barley plants at lower concentrations of NaCl (Vysotskaya et al., 2010). Reduction in gas exchange as a whole and leaf stomata closure could be due to (a) toxic Na^+ and Cl^- ions that decrease photosynthetic electron transport and stomatal conductance, (b) reduction in absorption and metabolism of carbon, and (c) oxidative damage during photosynthesis II under salt stress (Ashrafi et al., 2014; Pirasteh-Anosheh et al., 2016). A decrease in Cl content in some genotypes of barely under salt stress could be due to pigment photo-oxidation (Patterson et al., 2009; Yang et al., 2009). However, excessive swelling and loss of chlp membranes (Ceccarelli et al., 2010), damage to chlp (Gill and Tuteja, 2010), and slower photosynthesis, faster breakdown, or dissociation of chlp, due to the production of ROS under salinity stress (Kim et al., 2005).

A desirable genotype produces a satisfactory yield when subjected to stress conditions but demonstrates high productivity under ideal growing conditions. Abiotic stresses generally affect morphological parameters in most crops (Ashraf and Foolad, 2007). Within phenology, plants are most sensitive to salinity during vegetative and early reproductive stages and less sensitive at flowering and grain filling stages (Mass and Poss, 1989). Osmotic adjustment is defined as a lowering of osmotic potential (ψ_π) due to net solute accumulation in response to water stress that has been considered to be a beneficial drought tolerance mechanism in some crop species including barley also. However, organic solutes such as carbohydrates can play an important role in balancing osmotic pressure in cytoplasm (Keles and Öncel, 2004).

Salinity stress causes the reduction in grain weight (Santamaria et al., 1990), ultimately reduced that the grain yield per unit area (Munns et al., 1995; El-Tayeb, 2005) through negative effects on enlargement of barley cells (James et al., 2002), reduces the number of tillers, spike length, number of spikelets $spike^{-1}$, biomass $plant^{-1}$, and finally grain yield $plant^{-1}$ (Ahmad et al., 2013; 2015). Yield and yield attributes of barley are influenced by levels of salinity are presented in Fig. 4, which revealing that productivity and water use efficiency reduced when salinity rates exceeded 6 dS m^{-1} (Abd El-Wahed et al., 2015). A better understanding of agronomical responses under conditions of salinity may help programs aiming to improve the salt tolerance of barley.

3. Combined effect of drought and salinity on crop physiology and yield of barley

Salinity and drought stress show a high degree of similarity with respect to physiological, biochemical, molecular, and genetic effects on plants (Sairam and Tyagi, 2004). Plants usually share a common response to salinity and drought stress: as both stresses reduce water potential in the soil, water deficits or osmotic effects are the most common physiological mechanisms that cause growth reduction. In addition to the toxic effects of Na^+ and Cl^- ions, salinity disturbs water processes in plants due to the decreased availability of water in the soil as a result of reduced osmotic potential (Munns, 2005). Both salinity and drought stresses lead to reduction in photosynthesis, transpiration, and other biochemical processes associated with plant growth, development, and productivity (Reddy et al., 2004; Anjum et al., 2011). These stresses cause oxidative stress in plant cells, resulting in greater leakage of electrons towards O_2 during photosynthetic and respiratory processes, which in turn leads to enhancement of ROS generation (Asada, 2006). Much of the injury incurred by plants under abiotic stress is linked with oxidative damage at the cellular level, leading to cell death (Mittler, 2002). It is also important to investigate the physiology of drought and salinity tolerance in well-adapted wild barley, in order to understand the limits and tradeoffs between drought and salinity tolerance as well as to determine traits that are associated with high tolerance to both factors (Ahmed et al., 2013). An increase in Na^+ concentration and a decrease in K+ ion uptake interrupt ionic balances, as observed in most species exposed to salinity stress (Qiu et al., 2011). Increases in Na^+ concentrations and Na^+/K^+ ratios were observed in roots, stems, and leaves in both wild and cultivated barley genotypes under conditions of salinity alone and combined drought and salinity (D+S) stress, when compared with controls. Accumulation of malondialdehyde (MDA) is an indicator of the lipid peroxidation level, which reflects the extent of tolerance to abiotic stresses such as drought and salinity (Ahmed et al., 2013; 2015). It has been reported that cultivars with high drought tolerance have low MDA content when subjected to stress (Reddy et al., 2004; Anjum et al., 2011). The decrease in water potential occurring with both abiotic stresses results in reduced cell, root, and shoot growth and also causes inhibition of cell expansion and reduction in cell wall synthesis (Liang et al., 2003; Türkan et al., 2005). For water stress, the severity, duration, and timing of stress; the responses of plants after stress removal; and the interaction between the stress and other factors are extremely important (Plaut, 2003).The effects of salinity and drought have raised the question of whether the same change in the plant's water status, caused either by salinity or by drought, leads to the same yield reduction (Parida and Das, 2005; Fayez and Bazaid, 2014).

Strategies for enhancing survival capability under drought and salinity stress

Using quantitative trait loci (QTL) mapping

Tolerance to drought involves a complex of mechanisms working in combination to avoid or tolerate water deficits (Diab et al., 2004). In addition, physiological traits such as relative water content, proline accumulation, and osmotic adjustment are considered to be associated with plant adaptability to drought-prone environments (Cattivelli et al., 2008; Farooq et al., 2009). QTL mapping is a first step towards unraveling the molecular basis of drought resistance, i.e. through map-based cloning (Frary et al., 2000). QTL analysis can be performed to statistically analyze the association between genetic markers and traits of interest. This identifies regions of chromosomes that influence these traits. QTL maps have been made for traits thought to be involved in drought tolerance in many species, including *O. sativa, H. vulgare* and *T. aestivums* (Ashraf and Foolad, 2013; Teulat et al., 2001; 2002; Langridge et al., 2006); a review of progress in breeding for drought tolerance suggested that markers tightly linked to traits of drought tolerance could improve breeding efficiency. The identification of these QTLs with linked markers allows breeders to use marker-assisted, instead of traditional, selection as a complementary tool for the selection of suitable parental lines and the development of new lines or complementary tool to DNA Markers. In a study conducted by Ahmadi-Ochtapeh et al. (2015), an interesting QTL, QTwg4Hc, was localized on chromosome 4H in the XE41-M61 marker distance that controls several traits including shoot and coleoptile lengths and shoot fresh mass under salt stress. They further concluded that a dense marker cluster around a resistance gene could offer a starting point for positional cloning.

Use of plant growth regulators and compatible solutes

Many metabolic factors contribute to the inhibitory effects of water stress on plant growth (Chaves et al., 2003). The adverse effects of abiotic stresses can be mitigated by foliar application of natural and synthetic growth regulators. The effect of drought stress has been reduced by the use of exogenous external glycine betaine (GB) (Farooq et al., 2009; Sakamoto and Murata, 2002). Treatment of plants with osmolytes remarkably improves their tolerance to stress conditions (Ashraf and Foolad, 2007). In addition to their roles as osmoprotectants, proline and betaine might perform a protective function by scavenging ROS. Proline's ability to quench ROS, particularly hydroxyl radical ($OH^\bullet$), has been demonstrated convincingly (Signorelli et al., 2013). Soluble sugar accumulation has been reported with salt and drought stresses (Munns, 2005); likewise, phenolic compounds help in scavenging free radicals and protecting plants against the damaging effects of increased ROS levels due to salt and drought stresses (Petridis et al., 2012). Proline accumulation counter balances the deleterious effects of water deficit and salinity (Tani and Sasakawa, 2006; Ashraf and Foolad, 2007) and may serve as an organic nitrogen reserve that can be utilized during recovery from stress (Sairam and Tyagi, 2004). Proline accumulation co-occurred with higher activities of antioxidant enzymes (glutathione peroxidase) in younger seedlings, proving proline's role in activating antioxidant defenses in plants (Rejeb et al., 2014). Proline is widely distributed in plants and accumulates in larger amounts than other amino acids, when plants are subjected to stress (Irigoyen et al., 1992). Shevyakova et al. (2009) suggest that NaCl and *paraquat*-induced accumulation of proline had both osmo-protective and antioxidant functions. Proline's implication in the protection of protein integrity (Szabados and Savoure, 2009) may contribute to the ability of seedlings to survive in early growth stages under highly saline conditions (Hayat et al., 2012). Proline application improved the salt tolerance in tobacco BY-2 cells by increasing the activity of enzymes involved in antioxidant defense (Hoque et al., 2007).

K^+ plays an important role in balancing membrane potential and turgor, activating enzymes, regulating osmotic pressure, and maintaining stoma movement, and membrane polarization (Kaya et al., 2007). Supplying low levels of KNO_3 alleviated the effect of stress-induced NaCl that had decreased seed germination of certain grass species (Neid and Biesboer, 2005). As K^+ is involved in multiple plant activations, the K^+/Na^+ ratio has been proposed as an effective indicator of salinity tolerance (Fayez and Bazaid, 2014). However, overproduction of ROS caused by salinity usually leads to lipid peroxidation and induces K^+ leakage from cells by activating K^+ efflux channels (Cuin and Shabala, 2007; Demidchik et al., 2014). External application of low exogenous concentrations of GB and proline maintained higher K^+ concentrations in salt-stressed leaves of plant (Ashraf and Foolad, 2007; Demidchik et al., 2010) and decreased salt-induced K^+ efflux from barley roots (Cuin and Shabala, 2007). Although some researchers have reported positive correlation between the capacity for GB and/or proline accumulation and salinity tolerance (Yamaguchi and Blumwald, 2005), others have challenged the value of these solutes as definite indicators for resistance to salt stress (Ashraf and Harris, 2004; Ashraf and Foolad, 2013). Under salt stress, GB and proline reduced membrane injury, improved K^+ uptake and growth, and increased chl content (Demiral and Türkan, 2006). GB can protect the photosynthetic apparatus from stress-induced damage (Sakamoto and Murata, 2002). Leaves of plants (old or young) have higher GB accumulation in a stressed environment (Agboma et al., 1997). As explained by Yang and Lu (2005), the CO_2 assimilation rate increased in stressed maize plants under low GB concentration (from 2 to 20 mM), which allowed the maize plants to grow normally. Increased stomatal conductance due to a high concentration of GB decreased both CO_2 assimilation and growth in cotton plants (Sulian et al., 2007). Salicylic acid (SA) is considered as a hormone-like substance, which plays an important role in photosynthetic rate, stomatal conductance, and transpiration (Arfan et al., 2007; Fayez and Bazaid, 2014), increasing anti-oxidative protection (Xu et al., 2008) and inhibiting Na^+ and Cl accumulation (Gunes et al., 2007). Several lines of evidence demonstrate the beneficial role of SA during salinity (Shakirova et al., 2003) and drought (Singh and Usha, 2003). However, in the case of salt stress, the effect of SA on plant growth and metabolism is still a matter of controversy, considering different plant species, salt stress intensity and duration, as well as SA doses applied (Horva´th et al., 2007). Exogenous SA regulates activities of antioxidant enzymes and increases plant tolerance to abiotic stresses (Kaydan et al., 2007; Ashraf et al., 2010). SA plays an important role in plant growth and development, photosynthesis-related processes, stomatal regulation, and ion uptake and transport under saline conditions. Enhanced number of tillers, plant height, spikelets ear^{-1}, grains ear^{-1}, biological yield, and grain yield have been reported as a result of SA application on two wheat genotypes under saline conditions (Jafar et al., 2012). Ashraf et al. (2010) indicated that SA foliar applications could alleviate adverse effects of salinity via promotion of seedling growth, restoration of plant growth, and promotion of the accumulation of proline, ABA, indole acetic acid (IAA), and cytokinin. Ascorbic acid (AsA) is an organic acid with antioxidant properties, which has the capability of counteracting the adverse effects of salt and drought stress in crop plants (Khan et al., 2011). AsA also plays a role in stress signaling and other physiological processes (Wolucka et al., 2005). Significant effort has been made to study the application of AsA to the foliar parts of plants in order to promote shoot growth under various stresses (Muramoto et al., 1999; Jiang and Huang, 2001; Parvaiz and Satyawati, 2008; Abdelaal et al.,2017). As previously discussed, the physiological activities and agronomical performance of barley grown under stress conditions have been evaluated to consider the role of protective agents in mitigating the negative impacts of environmental stresses.

Conclusions and future research to mitigate drought and salinity under changing climate

Drought and salinity stresses progressively reduce assimilation rates due to decreased stomatal conductance. Both of these stresses disrupt photosynthetic pigments and reduce both the gas exchange as well as the production of ROS causing a decrease in plant growth and productivity. Several adaptation strategies are required to cope with salinity and drought stress. Application of plant growth regulators and compatible solutes could play a significant role in alleviating salinity and drought stress in plants. Water deficit and salinity affect the development, growth, and yield in barley, but tolerance of the crops varies remarkably. Changes in morphological, physiological, biochemical, and molecular aspects are generally noted in response to drought and salinity stress. Understanding these responses to abiotic stress is important for screening various genotypes' tolerance to environmental stress conditions. This review provided evidence supporting the potential of barley cultivation under drought stress conditions due to its traits demonstrating high capacity for growth. The review also evaluated the impact of drought on the photosynthetic performance of barley. This review provides potential responses correlated with increasing drought stress and enhances understanding of stress avoidance mechanisms of barley that affect stress tolerance.

Disclaimer statement

We hereby declare that this the review article submitted to 'Australian Journal of Crop Science' have been approved by all co-authors who have seen and approved the final version. The review has not been submitted nor is it being considered for publication in other journal and to the best of our knowledge the review contains no copy of any material previously published or written by another person except where due reference is made in the text. We also declare that this review contains no material which has been accepted for the award of any degree or diploma in any university.

Acknowledgement

We are very grateful to all the editors and reviewers, for their good comments and suggestions which have allowed us to make additional improvements to the review.

Conflicts of interest

The authors declare no conflicts of interest.

References

Abd El-Wahed MH, EL Sabagh A, Mohammed HH, Ueda A, Saneoka H, Celaleddin B (2015) Evaluation of Barley Productivity and Water Use Efficiency under Saline Water Irrigation in Arid Region. Int J Agric Crop Sci. 8: 765-773.

Abdelaal KA, Hafez YM, El Sabagh A, & Saneoka H (2017) Ameliorative effects of Abscisic acid and yeast on morpho-physiological and yield characteristics of maize plant (*Zea mays* L.) under water deficit conditions. Fresen. Environ. Bull, 26(12), 7372-7383.

Abedl-Ghani A (2008) Genetic variation, heritability and interrelationships of agro-morphological and phenological traits in Jordanian Durum wheat landraces. Jordan J Agric Sci. 4: 350-366.

Abd El-Monem AA, El-Habbasha SF, Hozayn M (2013) Mitigation Salinity Stress Effects on Barley (*Hordeum vulgare* L.) Growth, Yield and Some Physiological Aspects by Hemin. J Appl Sci Res. 9(3): 2411-2421.

Agboma PC, Jones MG, Peltonen-Sainio P, Rita H, Pehu E (1997) Exogenous glycinebetaine enhances grain yield of maize, sorghum and wheat grown under two supplementary watering regimes. J Agron Crop Sci. 178(1): 29-37.

Ahmadi-Ochtapeh H, Soltanloo H, Ramezanpour SS, Naghavi MR, Nikkhah HR, Rad SY (2015) QTL mapping for salt tolerance in barley at seedling growth stage. Biol Plant. 59(2): 283-90.

Ahmadi A, Emam Y, Pessarakli M (2009) Response of various cultivars of wheat and maize to salinity stress. J Food Agric Environ. 7: 123-128.

Ahmed S (2009) Effect of Soil Salinity on the Yield and Yield Components of Mungbean. Pak J Bot. 41(1): 263-268.

Ahmed IM, Cao F, Zhang M, Chen X, Zhang G, Wu F (2013) Difference in yield and physiological features in response to drought and salinity combined stress during anthesis in Tibetan wild and cultivated barleys. PloS one 8(10):e77869.

Ahmed IM, Nadira UA, Bibi N, Zhang G, Wu F (2015) Tolerance to combined stress of drought and salinity in barley. In: Combined Stresses in Plants Physiological, Molecular, and Biochemical Aspects; Mahalingam, R., Ed.; Springer: Basel, Switzerland, 2015; pp. 93–121.

Anjum, S.A., Xie, X.Y., Wang, L.C., Saleem, M.F., Man, C. and Lei, W., 2011. Morphological, physiological and biochemical responses of plants to drought stress. Afr J Agric Res 6(9): pp.2026-2032.

Anjum SA, Xie XY, Wang LC, Saleem MF, Man C, Lei W (2011) Morphological, physiological and biochemical responses of plants to drought stress. African J Agric Res. 6(9): 2026-2032.

Arfan M, Athar HR, Ashraf M (2007) Does exogenous application of salicylic acid through the rooting medium modulate growth and photosynthetic capacity in two differently adapted spring wheat cultivars under salt stress?. J Plant Physiol. 164(6): 685-694.

Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol. 141: 391–396.

Ashraf M (2004) Some important physiological selection criteria for salt tolerance in plants. Flora. 199: 361–376.

Ashraf M, Foolad MR (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environ Exp Bot. 59: 206-216.

Ashraf M, Foolad MR (2013) Crop breeding for salt tolerance in the era of molecular markers and marker-assisted selection. Plant Breed. 132(1): 10-20.

Ashraf MP, Harris PJ (2004) Potential biochemical indicators of salinity tolerance in plants. Plant Sci. 166(1): 3-16.

Ashraf M, Akram NA, Arteca RN, Foolad MR (2010) The physiological, biochemical and molecular roles of brassinosteroids and salicylic acid in plant processes and salt tolerance. Critical Reviews in Plant Sci. 29(3): 162-90.

Ashrafi E, Razmjoo J, Zahedi M, Pessarakli M (2014). Selecting alfalfa cultivars for salt tolerance based on some physiochemical traits. Agron J. 106(5): 1758-64.

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

Beigzadeh S, Fatahi K, Sayedi A, Fatahi F (2013) Study of the effects of late-season drought stress on yield and yield components of irrigated barley lines within Kermanshah province temperate regions. World Appl Program. 3(6): 226-231.

Bota J, Medrano H, Flexas J (2004) Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress?. New Phytologist. 162: 671–681.

Cattivelli L, Rizza F, Badeck FW, Mazzucotelli E, Mastrangelo AM, Francia E, Mare C, Tondelli A, Stanca AM (2008) Drought tolerance improvement in crop plants: an integrated view from breeding to genomics. Field Crops Res. 105(1-2): 1-14.

Ceccarelli S, Grando S, Maatougui M, Michael M, Slash M, Haghparast R, Rahmanian M, Taheri A, Al-Yassin A, Benbelkacem A, Labdi M (2010) Plant breeding and climate changes. J Agric Sci. 148: 627-637.

Ceccarelli S, Grando S, Baum M (2007) Participatory plant breeding in water-limited environments. Exp Agric. 43: 1-25.

Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought—from genes to the whole plant. Funct Plant Biol. 30(3): 239-264.

Cuin TA, Shabala S (2007) Compatible solutes reduce ROS-induced potassium efflux in Arabidopsis roots. Plant, Cell Environ. 30(7): 875-885.

Diab AA, Teulat-Merah B, This D, Ozturk NZ, Benscher D, Sorrells ME (2004) Identification of drought-inducible genes and differentially expressed sequence tags in barley. Theor Appl Genet. 109(7): 1417-1425.

Demiral T, Türkan I (2006) Exogenous glycinebetaine affects growth and proline accumulation and retards senescence in two rice cultivars under NaCl stress. Environ Exp Bot 56(1): 72-79.

Demidchik V, Cuin TA, Svistunenko D, Smith SJ, Miller AJ, Shabala S, Sokolik A, Yurin V (2010) Arabidopsis root K+-efflux conductance activated by hydroxyl radicals: single-channel properties, genetic basis and involvement in stress-induced cell death. J Cell Sci. pp.jcs-064352.

Demidchik V, Straltsova D, Medvedev SS, Pozhvanov GA, Sokolik A, Yurin V (2014) Stress-induced electrolyte leakage: the role of K+-permeable channels and involvement in programmed cell death and metabolic adjustment. J Exp Bot. 65(5):1259-70.

Dubey RS (2005) Photosynthesis in plants under stressful conditions. In Handbook of Photosynthesis (Ed. M Pessarakli), pp. 717–737. London: Taylor & Francis.

EL-Shawy EE, EL Sabagh A, Mansour M, Barutcular C (2017) A comparative study for drought tolerance and yield stability in different genotypes of barley (*Hordeum vulgare* L.). J Exp Biol Agric Sci. 5(2): 151.162.

El-Tayeb MA (2005) Response of barley grains to the interactive e. ect of salinity and salicylic acid. Plant Growth Regul. 45(3): 215-224.

El-Wahed MA, Sabagh AE, Saneoka H, Abdelkhalek A, Barutçular C (2015) Sprinkler irrigation uniformity and crop water productivity of barley in arid region. Emirates J Food Agric. 27(10): 770-775. doi.org/10.9755/ejfa.2015-05-209

FAO (2016) FAOSTAT. Online statistical database (available at http://faostat.fao.org)

Farooq M, Aziz T, Wahid A, Lee DJ, Siddique KH (2009) Chilling tolerance in maize: agronomic and physiological approaches. Crop Past Sci. 60: 501-516.

Fayez KA, Bazaid SA (2014) Improving drought and salinity tolerance in barley by application of salicylic acid and potassium nitrate. J Saudi Soc Agric Sci. 13(1): 45-55.

Fricke W, PetersWS (2002) The biophysics of leaf growth in salt stressed barley. A study at the cell level. Plant Physiol. 129: 374-88.

Frary A, Nesbitt TC, Frary A, Grandillo S, Van Der Knaap E, Cong B, Liu J, Meller J, Elber R, Alpert KB, Tanksley SD (2000). fw2. 2: a quantitative trait locus key to the evolution of tomato fruit size. Sci. 289(5476): 85-88.

Gill SS, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem. 48: 909-930.

González A, Martín I, Ayerbe L (1999) Barely yield in water-stress conditions. The influence of precocity, osmotic adjustment and stomatal conductance. Field Crop Res. 62: 23–34.

Gunes A, Inal A, Alpaslan M, Eraslan F, Bagci EG, Cicek N (2007) Salicylic acid induced changes on some physiological parameters symptomatic for oxidative stress and mineral nutrition in maize (*Zea mays* L.) grown under salinity. J Plant Physiol. 164: 728–736.

Haddadin MF (2015) Assessment of drought tolerant barley varieties under water stress. Int J Agric For. 5(2): 131-137.

Hamdy A, Ragab R, Scarascia-Mugnozza, E (2003) Coping with water scarcity: water saving and increasing water productivity. Irrig Drain. 52: 3–20.

Hasanuzzaman M, Hossain MA, Teixeira da Silva JA, Fujita M (2012) Plant response and tolerance to abiotic oxidative stress: antioxidant defense is a key factor. In: Bandi V, Shanker AK, Shanker C, Mandapaka M. (Eds.), Crop Stress and its Management: Perspectives and Strategies. Springer, The Netherlands, pp. 261–315.

Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A (2012) Role of proline under changing environments: A review. Plant Signal Behav. 7: 1-11.

Hoque MA, Okuma E, Banu MNA, Nakamura Y, Shimoishi Y, Murata Y (2007) Exogenous proline mitigates the detrimental effects of salt stress more than exogenous betaine by increasing antioxidant enzyme activities. J Plant Physiol. 164: 553-561.

Horva´th E, Szalai G, Janda T (2007) Induction of abiotic stress tolerance by salicylic acid signalling. J Plant Growth Regul. 26: 290– 300.

Hossain A, Teixeira da Silva JA*,* Lozovskaya MV, Zvolinsky VP (2012ª) High temperature combined with drought affect rainfed spring wheat and barley in South-Eastern Russia: I. Phenology and growth. Saudi J Biol Sci 19(4): 473-487.

Hossain A, Teixeira da Silva JA*,* Lozovskaya MV, Zvolinsky VP, Mukhortov VI (2012b) High temperature combined with drought affect rainfed spring wheat and barley in south-eastern Russia: yield, relative performance and heat susceptibility index. J Plant Breed Crop Sci. 4(11): 184-196.

Irigoyen JJ, Einerich DW, Sánchez-Díaz M (1992) Water stress induced changes in concentrations of proline and total soluble sugars in nodulated alfalfa (*Medicago sativd*) plants. Physiol plant. 84(1): 55-60.

Islam MS, Akhter MM, El Sabagh A, Liu LY, Nguyen NT, Ueda A, Masaoka Y, Saneoka H (2011) Comparative studies on growth and physiological responses to saline and alkaline stresses of Foxtail millet (*Setaria italica* L.) and Proso millet (*Panicum miliaceum* L.). Aust. J. Crop Sci., 5 (2011), pp. 1269-1277.

Izadi MH, Rabbani J, Emam Y, Pessarakli M, Tahmasebi A (2014) Effects of salinity stress on physiological performance of various wheat and barley cultivars. J. Plant Nutr 37(4): 520-531.

Jafar MZ, Farooq M, Cheema MA, Afzal I, Basra SM, Wahid MA, Aziz T, Shahid M (2012) Improving the performance of wheat by seed priming under saline conditions. J Agron Crop Sci. 198(1): 38-45.

Jaleel CA, Manivannan PA, Wahid A, Farooq M, Al-Juburi HJ, Somasundaram RA, Panneerselvam R (2009) Drought stress in plants: a review on morphological characteristics and pigments composition. Int J Agric Biol, 11(1): 100-105.

James RA, Rivelli AR, Munns R, von Caemmerer S (2002) Factors affecting CO_2 assimilation, leaf injury and growth in salt-stressed durum wheat. Funct Plant Biol. 29: 1393-1403.

Jiang Y, Huang, B (2001) Drought and heat stress injury to two cool-season turfgrasses in relation to antioxidant metabolism and lipid peroxidation. Crop Sci. 41(2): 436-442.

Kaya C, Tuna AL, Ashraf M, Altunlu H (2007) Improved salt tolerance of melon (Cucumis melo L.) by the addition of proline and potassium nitrate. Environ Exp Bot. 60(3): 397-403.

Kaydan D, Yagmur M, Okut N (2007) Effects of salicylic acid on the growth and some physiological characters in salt stressed wheat (*Triticum aestivum* L.). Tarim Bilimleri Dergisi. 13: 114-119.

Keles Y, Oncel I (2004) Growth and solute composition in two wheat species experiencing combined influence of stress conditions. Russ. J Plant Physiol. 51: 203-209.

Khan T, Mazid M, Mohammad F (2011) A review of ascorbic acid potentialities against oxidative stress induced in plants. J Agrobiol. 28: 97–111.

Kim SY, Lim JH, Park MR, Kim YJ, Park TI, Seo YW, Choi KG, Yun SJ (2005) Enhanced antioxidant enzymes are associated with reduced hydrogen peroxide in barley roots under saline stress. BMB Reports. 38(2): 218-24.

Kramer PJ, Boyer, J. S (1995) Water relations of plants and soils. Academic Press. San Diego.

Křen J, Klem K, Svobodová I, Míša P, Neudert L (2015) Yield and grain quality of spring barley as affected by biomass formation at early growth stages. Plant, Soil Environ. 60(5):221-227.

Langridge P, Paltridge N, Fincher, G (2006) Functional genomics of abiotic stress tolerance in cereals. Briefings Funct Genom. 4(4): 343-354.

Liang Y, Chen QI, Liu Q, Zhang W, Ding R (2003) Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (*Hordeum vulgare* L.). J Plant Physiol. 160(10): 1157-64.

Li RH, Guo PG, Michael B, Stefania G, Salvatore C (2006) Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. Agric Sci China. 5: 751–757.

Lim PO, Kim HJ, Nam, HG (2007) Leaf senescence. Annu Rev Plant Biol. 58, 115–136.

Lopes MS, Reynolds MP, Jalal-Kamali MR, Moussa M, Feltaous Y, Tahir IS, Barma N, Vargas M, Mannes Y, Baum M (2012) The yield correlations of selectable physiological traits in a population of advanced spring wheat lines grown in warm and drought environments. Field Crops Res. 128: 129–136.

Maggio A, Miyazaki S, Veronese P, Fujita T, Ibeas JI, Damsz B, Narasimhan ML, Hasegawa PM, Joly RJ, Bressan RA (2002) Does proline accumulation play an active role in stress induced growth reduction? Plant J. 31: 699–712.

Martiniello P, Teixeira da Silva JA (2011) Physiological and bio–agronomical aspects involved in growth and yield components of cultivated forage species in Mediterranean environments: A review. European J Plant Sci Biotech. 5(Special Issue 2): 64–98.

Maas EV, Poss JA (1989) Salt sensitivity of cowpea at various growth stages. Irrigat Sci. 10(4): 313-320.

Matouškova M, Bartoškova H, Nauš J, Novatný R (1999) Reaction of photosynthetic apparatus to dark desiccation sensitivity detected by the induction of chlorophyll fluorescence quenching, J Plant Physiol. 155: 399–406.

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci. 7: 405–410.

Moustafa MA, Boersma L, Kronstad WE (1996) Response of four spring wheat varieties to drought stress. Crop Sci. 36: 982-986.

Munns R (2005) Genes and salt tolerance: bringing them together. New Phytol. 167: 645-663. doi:10.1111/j.1469-8137.

Munns R, James RA, Lauch A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot. 57: 1025–1043.

Munns R, Schachtman DP, Condon AG (1995) The significance of a two-phase growth response to salinity in wheat and barley. Funct Plant Biol. 22(4): 561-569.

Muramoto Y, Watanabe A, Nakamura T, Takabe T (1999) Enhanced expression of a nuclease gene in leaves of barley plants under salt stress. Gene. 234(2): 315-321.

Neid SL, Biesboer DD (2005) Alleviation of salt-induced stress on seed emergence using soil additives in a greenhouse. Plant and Soil. 268(1): 303-307.

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf. 60(3): 324-349.

Parvaiz A, Satyawati S (2008) Salt stress and phyto-biochemical responses of plants-a review. Plant Soil Environ. 54(3): 89-99.

Patterson JH, Newbigin ED, Tester M, Bacic A, Roessner U (2009) Metabolic responses to salt stress of barley (Hordeum vulgare L.) cultivars, Sahara and Clipper, which differ in salinity tolerance. J Exp Bot. 60(14): 4089-4103.

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola JM, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nat. 399 (6735): 429–436.

Petridis A, Therios I, Samouris G, Tananaki C (2012) Salinity-induced changes in phenolic compounds in leaves and roots of four olive cultivars (*Olea europaea* L.) and their relationship to antioxidant activity. Environ Exp Bot. 79: 37-43.

Pirasteh-Anosheh H, Ranjbar G, Pakniyat H, Emam Y (2016) Physiological mechanisms of salt stress tolerance in plants: An overview. In: Mahgoub-Azooz M, Ahmad P (ed.): Plant Environment Interaction: Responses and Approaches to Mitigate Stress. Chapter 8. Pp. 141-160. John Wiley & Sons, Ltd, Jammu and Kashmir.

Plaut Z (2003) Plant exposure to water stress during specific growth stages. In: Trimble WS (ed.). Encyclopedia of water science. London: Taylor & Francis.

Pour-Aboughadareh AR, Naghavi MR, Khalili M (2013) Water deficit stress tolerance in some of barley genotypes and landraces under field conditions. Not Sci Biol. 5: 249–255.

Prochazkova D, Sairam RK, Srivastava GC, Singh DV (2001) Oxidative stress and antioxidant activity as the basis of senescence in maize leaves. Plant Sci. 161: 765–771.

Qiu L, Wu D, Ali S, Cai S, Dai F, Jin X, Wu F, Zhang G (2011) Evaluation of salinity tolerance and analysis of allelic function of *HvHKT1* and *HvHKT2* in Tibetan wild barley. Theor Appl Genet. 122: 695-703.

Reddy AR, Chaitanya KV, Vivekanandan M (2004) Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J Plant Physiol. 161(11): 1189-1202.

Rejeb KB, Abdelly C, Savoure, A (2014) How reactive oxygen species and proline face stress together. Plant Physiol Biochem. 80: 278-284.

Reynolds LV, Ayres MP, Siccama TG, Holmes RT (2007) Climatic effects on caterpillar fluctuations in northern hardwood forests. Canadian J For Res. 37: 481–491.

Sairam R, Tyagi A (2004) Physiology and molecular biology of salinity stress tolerance in plants. Curr Sci Bangalore. 86: 407–21.

Sairam RK, Shukla DS, Saxena DC (1997) Stress induced injury and antioxidant enzymes in relation to drought tolerance in wheat genotypes. Biol Plant. 40: 357–364.

Sakamoto A, 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.

Samarah H, Mullen E, Anderson I (2009) Soluble sugar contents, germination and vigour of soybean seeds in response to drought stress. J New Seeds. 10: 63–73.

Samarah NH (2005) Effects of drought stress on growth and yield of barley. Agron Sustain Dev. 25: 145–149.

Sánchez-Díaz M, García JL, Antolín MC, Araus JL (2002) Effects of soil drought and atmospheric humidity on yield, gas exchange, and stable carbon isotope composition of barley. Photosynthetica. 40: 415–421.

Santamaria JM, Ludlow MM, Fukai S (1990) Contribution of osmotic adjustment to grain yields in sorghum under water-limited conditions water stress before anthesis. Aust J Agric Res. 41: 51-65.

Sayed OH (2003) Chlorophyll fluorescence as a tool in cereal crop research. Photosynthetica. 41: 321–330.

Shafi M, Raziuddin J, Zhang G (2009) Effect of Cadmium and Salinity stresses on growth and antioxidant enzymes activity of wheat genotypes. J Environ Toxicol. 82(6): 772-776.

Shakirova FM, Sakhabutdinova AR, Bezrukova MV, Fatkhutdinova RA, Fatkhutdinova DR (2003) Changes in the hormonal status of wheat seedlings induced by salicylic acid and salinity. Plant Sci. 164: 317–322.

Shevyakova NI, Bakulina EA, Kuznetsov VV (2009) Proline antioxidant role in the common ice plant subjected to salinity and paraquat treatment inducing oxidative stress. Russian J Plant Physiol. 56(5): 663-669.

Signorelli S, Coitiño EL, Borsani O, Monza J (2013) Molecular mechanisms for the reaction between OH radicals and proline: insights on the role as reactive oxygen species scavenger in plant stress. J Phys Chem B. 118(1): 37-47.

Singh B, Usha K (2003) Salicylic acid induced physiological and biochemical changes in wheat seedlings under water stress. Plant Growth Regul. 39(2): 137-141.

Sulian LV, Yang A, Zhang K, Wang L, Zhang J (2007) Glycinebetaine synthesis improved drought tolerance in cotton. Mol Breed. 3: 233-248

Szabados L, Savoure A (2009) Proline: a multifunctional amino acid. Trends Plant Sci. 15: 89-97.

Tabatabaei S, Ehsanzadeh P (2016) Photosynthetic pigments, ionic and antioxidative behaviour of hulled tetraploid wheat in response to NaCl. Photosyntheica 54: 340-350.

Tani C, Sasakawa H (2006) Proline accumulates in Casuarina equisetifolia seedlings under salt stress. Soil Sci Plant Nut. 52(1): 21-25.

Temel A, Janack, B, Humbeck, K (2017) Drought Stress-Related Physiological Changes and Histone Modifications in Barley Primary Leaves at HSP17 Gene. Agron 7(2): 43. doi:10.3390/agronomy7020043

Tester M, Davenport R (2003) Na+ tolerance and Na+ transport in higher plants. Ann Bot. 91: 503–527.

Teulat B, Merah O, Souyris I, This, D (2001) QTLs for agronomic traits from a Mediterranean barley progeny grown in several environments. Theor Appl Genet. 103(5): 774-787.

Teulat B, Merah O, Sirault X, Borries C, Waugh R, This, D (2002) QTLs for grain carbon isotope discrimination in field-grown barley. Theor Appl Genet. 106(1): 118-126.

Tiwari JK, Munshi AD, Kumar R, Pandey RN, Arora A, Bhat JS, Sureja AK (2010) Effect of salt stress on cucumber: Na+/K+

ratio, osmolyte concentration, phenols and chlorophyll content. Acta Physiol Plant 32: 103–114.

Türkan I, Bor M, Özdemir F, Koca H (2005) Differential responses of lipid peroxidation and antioxidants in the leaves of drought-tolerant *P. acutifolius* Gray and drought-sensitive *P. vulgaris* L. subjected to mediated water stress. Plant Sci. 168(1): 223-231.

Ugarte C, Calderini DF, Slafer GA (2007) Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. Field Crop Res. 100: 240-248.

Vollenweider P, Gunthardt–Goerg MS (2005) Diagnosis of abiotic and biotic stress factors using the visible symptoms in foliage. Environ Pollut. 137: 455–465.

Vysotskaya L, Hedley PE, Sharipova G, Veselov D, Kudoyarova G, Morris J, Jones HG (2010) Effect of salinity on water relations of wild barley plants differing in salt tolerance. AoB PLANTS, https://doi.org/10.1093/aobpla/plq006

Wang WX, Vinocur B, Arie A (2003) Plants responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta. 218: 1-14.

Wells SA, Dubetz S (1966) Reaction of barley varieties to soil water stress, Can J Plant Sci. 46: 507–512.

Wolucka BA, Goossens A, Inzé D (2005) Methyl jasmonate stimulates the *de novo* biosynthesis of vitamin C in plant cell suspensions. J Exp Bot. 56: 2527–2538.

Xu Q, Xu X, Zhao Y, Jiao K, Herbert JS, Hao L (2008) Salicylic acid, hydrogen peroxide and calcium-induced salinity tolerance associated with endogenous hydrogen peroxide homeostasis in naked oat seedlings. Plant Growth Regul. 54: 249–259.

Yamaguchi T, Blumwald E (2005) Developing salt-tolerant crop plants: challenges and opportunities. Trends Plant Sci. 10(12): 615-620.

Yang X, Lu C (2005) Photosynthesis is improved by exogenous glycinebetaine in salt-stressed maize plants. Physiol. Plant. 124: 343-352.

Yang CW, Xu HH, Wang LL, Liu J, Shi DC, Wang DL (2009) Comparative effects of salt-stress and alkali-stress on the growth, photosynthesis, solute accumulation, and ion balance of barley plants. Photosynthetica. 47(1): 79-86.

Yeo A (1998) Molecular biology of salt tolerance in the context of whole plant Physiology. J Exp Bot. 49: 915–929.

Yousfi S, Serret MD, Araus JL, Draye X, Foulkes J, Hawkesford M, Murchie E (2010) A comparative effect of salinity and drought on growth, ion concentration and Delta13C and Delta15N in barley. Aspects Appl Biol. 105: 73–81.

Zhou MX (2009) Barleyproduction and consumption. In: Genetics and Improvement of Barley Malt Quality (pp. 1-17 Zhang G, Li C (eds),). Springer, Berlin, Heidelberg.

Zhu JK (2001) Plant salt tolerance. Trends Plant Sci. 6: 66-71, 2001.

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