Influence of abiotic stress on proline, Photosynthetic enzymes and growth

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ABSTRACT: Salt stress is one of the major abiotic stress factors that affect almost every aspect of physiology and biochemistry of a plant, resulting in a reduction in its yield. The salinity effect on the water stress of the plant, its gaseous exchanges and its metabolism has been analyzed over short periods. In plants under water or salt stress, proline content increases more than other amino acids, and this effect has been used as a biochemical marker to select varieties aiming to resist to such conditions. Salt and water stress affects germination percentage, germination rate and seedling growth in different ways depending on plant species.

Key words: Salt stress, water stress, potassium, ABA, Nutrient

INTRODUCTION

Salt stress

Salt stress is one of the major abiotic stress factors that affect almost every aspect of physiology and biochemistry of a plant, resulting in a reduction in its yield (Foolad, 2004). Thus it is a serious threat to agricultural productivity especially in arid and semi-arid regions (Parvaiz et al., 2008). Soil contaminated salts (ECe > 4 dS m⁻¹ or 40 mM NaCl or osmotic potential < 0.117 MPa) are defined as salinity land, which directly affects plant growth and development in vegetative growth prior to reproductive stage, especially crop species (Allakhverdiev et al., 2000; Sairam & Tyagi, 2004; Chinnusamy et al., 2005; Ashraf et al., 2008; Ashraf, 2009). Ayars (2003) observed that salinity in soil and water is irrevocably associated with irrigated agriculture throughout the world and salt management becomes an integral part of the production system. Many researchers shows that saline irrigation reduced the growth and yield of many crops (Pasternak et al., 1995; Li et al., 2006; Wichern, et al., 2006; Irshad et al., 2009), slow down growth and injure leaf cells (Munns, 2005) and causing saline stress (Hasegawa et al., 2000).

The salinity-induced crop yield reduction takes place due to a number of physiological and biochemical dysfunctions in plants grown under salinity stress which have been listed in a number of comprehensive reviews on salinity effects and tolerance in plants (Ashraf et al., 2008; Munns and Tester, 2008; Jamil et al., 2011; Krasensky and Jonak, 2012). Scientists have been vying for the last many decades to overcome the problem of salinity by employing a variety of strategies. Of the various strategies currently under exploitation, improvement in salinity tolerance of crops through exogenous application of different types of chemicals including plant growth regulators, osmoprotectants and inorganic nutrients seems to be an efficient, economical and shot-gun approach (Ashraf et al., 2008). The salinity effect on the water stress of the plant, its gaseous exchanges and its metabolism has been analyzed over short periods (see for example Osmond and Greenway, 1972; Longstreth and Strain, 1977; Albuzio, 1978; Yeo, et al., 1985; West, et al., 1986; Bowman and Strain, 1987). Some results mentioned that salinity decrease of sugars store and as a result it can distort the respiration metabolism of embryo growth (Kazerouni, 2005). Salinity with osmosis potential solution reduction can reduce plant growth. It’s reason is that alien with water molecules existence in environment, there are ions that preventing of water absorption by plants root and plant face with a water deficit (Tobe et al, 1999). Salinity stress has become an important problem regarding agricultural production in many regions of the world especially in arid and semi-arid regions. In Turkey, salinity and sodicity poses a problem for almost 1.5 million hectares of agricultural area. The negative effects of salinity stress on plants are explained as ion toxicity (Na⁺, Cl⁻); osmotic stress and nutritional disorders (Greenway & Munns, 1980; Lewitt, 1980a; Munns & Termaat, 1986; Yeo et al., 1991; Marschner, 1995). Salt stress causes hyperosmotic stress and
ion disequilibrium, thereby disabling the vital cellular functions of a plant. Reduced availability of water, increased respiration rate, altered mineral distribution, membrane instability, failure in the maintenance of turgour pressure are some of the events that prevails during this stress episode. Plants try to withstand these stresses either by tolerating it or by adopting a dormant stage (Cuartero et al., 2006). The salinity problems increase with increasing salt concentration in irrigation water (Cengiz, 2008). Crop growth reduction and certain phenological changes due to saline water in plants are reported by Abou-Hadid (2003) and environmental impacts of saline water use by Kandiah et al. (1998). Salinity decreased germination percent, root length, callus size, coleoptile length and seedling growth (Lallu and Dixit, 2005; Gandha et al., 2005; Bera et al., 2006 and Agnihotri et al., 2006). Plant height, stem diameter, dry weight decreased with increasing levels of salinity (Azo et al., 2004; Asha and Dhingra, 2007). Ecological variations in the aquatic macrophyte communities related to salinization are fully documented, which involves alterations in abundance, vegetation distribution in aquatic ecosystems (Kipriyanova et al., 2007; Watson and Byrne, 2009), variations in growth, reproduction and survival of macrophytes (Warwick et al., 1997; Muschal, 2006), and usually reduces species richness (Greenberg et al., 2006; Sharpe and Baldwin, 2009). Tolerances to environmental stresses as salinity of plants can be determined by using different parameters. Plants need to have special mechanisms for adjusting internal osmotic conditions and changing of osmotic pressure in the root environment. Stressed plants diminish osmotic potential by accumulating free amino acids, ions and dissolvable substances. In this way, osmotic adjustment is ensured (Salama et al., 1994; Weinberg, 1986, 1987). Salinity also delayed the emergence of panicle and flowering (Khatun et al., 1995) and decreased seed set through reduced pollen viability (Khatun and Flowers, 1995; Khatun et al., 1995). In contrast, rice was more salt tolerant at germination than at other stages (Narale et al., 1969; Heenan et al., 1988; Khan et al., 1997).

Effect of salt stress on proline

In plants under water or salt stress, proline content increases more than other amino acids, and this effect has been used as a biochemical marker to select varieties aiming to resist to such conditions (Bates, 1973). A large number of plant species accumulate proline in response to salinity stress and that accumulation may play a role in defense against salinity stress. However, data do not always indicate a positive correlation between osmolytes accumulation and an ability to adapt to stress (Ashraf and Harris, 2004, Mansour, 2000, Mansour et al. 2005). Moreover, there is additional evidence that these compatible solutes are accumulated in plants at high concentrations to alleviate enzyme inactivity or loss of membrane integrity due to water deficiency (Schwab and Gaff, 1990). The role of proline in cell osmotic adjustment, membrane stabilization and detoxification of injurious ions in plants exposed to salt stress is widely reported (Hare et al., 1999; Kavi Kishor et al., 2005; Ashraf & Foolad, 2007). The increase in proline content is the most remarkable parameter in rice grown under salt stress conditions (Roy et al., 1992). There are several techniques to enhance the endogenous proline accumulation for salt defense mechanism such as exogenous application (Santos et al., 1996; Hoque et al., 2007; Kaya et al., 2007), biosynthesis gene(s) overexpression (Zhu et al., 1998; Han & Hwang, 2003) and degradation gene(s) knock-out (Nanjo et al., 1999). Considering this feature, Roy et al. (1993) furnished exogen proline to rice seedlings, they found that 30 mol.m⁻³ proline avoided salt stress and toxicity caused by 100 mol.m⁻³ NaCl dose. The endogenous proline accumulation in salt stressed plants has been utilized as effective indicator for salt tolerance. Moreover, multivariate biochemical and physiological parameters, growth performances and yield have been applied to classify salt tolerant cultivars in maize (Neto et al., 2004), wheat (El-Hendawy et al., 2005), rice (Zeng, 2005), cowpea (Murillo-Amador et al., 2006), tomato (Juan et al., 2005), seashore paspalum (Lee et al., 2008), and chickpea (Malir et al., 2008). Marcum and Murdoch (1994) found that Cynodon dactylon x C. transvaalensis accumulated 103 mol.m⁻³ proline, when grown in 400 mol.m⁻³ NaCl.

Effect of silicon on abiotic stress

Recently, numerous studies have shown that silicon can significantly alleviate manganese, aluminum, salt, drought, chilling, and freezing stresses, and is considered beneficial effects on plant growth and production (Ma and Yamaji, 2008). It has been observed that supplemental silicon improves yield and reduce the plant biotic and abiotic stresses (Epstein, 1999). In addition, some studies have shown that Si is effective in mitigating salinity in different plant species, such as barley (Liang et al., 1996; Liang et al., 2003), cucumber (Adatia and Besford, 1986; Zhu et al., 2004), maize (Moussa, 2006), tomato (Romero-Aranda et al., 2006), and wheat (Ahmad et al., 1992; Tuna et al., 2008). Some possible mechanisms through which silicon may increase salinity tolerance in plants (Liang et al., 2003) include: immobilization of toxic sodium ion (Liang et al., 2003), reduced sodium uptake in plants and enhanced potassium uptake (Liang et al., 2005) and higher potassium, sodium selectivity (Hasegawa et al., 2000). Studies on the effects of salinity stress on plants have primarily focused on growth, proline accumulation, chlorophyll content, K/Na, Ca/Na ratio, Na+ and Cl accumulation. It has been stated that genotypes with a high
proline accumulation and chlorophyll content, high K/Na ratio and low Na\(^{+}\) and Cl\(^{-}\) accumulation are more tolerant to salt (Mane et al., 2011).

**The relationship between potassium and sodium in salt stress**

Ayers and Eberhard (1960) found that increasing the concentration of sodium and calcium in soil resulted in a moderate decrease of potassium in the same order of magnitude for plants both broad bean and green bean plants. Uptake and accumulation of mg^{2+} and Na\(^{+}\) is increased by saline conditions (Samenia, et al., 1980), while accumulation of chloride may be localized in the plant (Hajrasulih, 1980). Maintenance of adequate levels of K\(^{+}\) is essential for plant survival in saline habitats. Under saline-sodic or sodic conditions, high levels of external Na\(^{+}\) not only interfere with K\(^{+}\) acquisition by the roots, but also may disrupt the integrity of root membranes and alter their selectivity. At the same time that K\(^{+}\) uptake is impaired by salinity, higher K\(^{+}\) levels in tissue are required for shoot growth (Grattana and Grattana, 1999). While increases in leaf-Na\(^{+}\) concentrations may help to maintain plant turgor, Na\(^{+}\) cannot completely substitute for K\(^{+}\) which is specifically required for protein synthesis and enzyme activation (Marschner, 1995). High K\(^{+}\) concentrations in the stroma are necessary for the maintenance of optimum photosynthetic capacity under stress conditions (Chow et al., 1990). Cellular injury also showed a significant positive correlation with Na\(^{+}\) and a negative correlation with K\(^{+}\) and grain yield (Farooq and Azam, 2005).

**Effect of salt on Seed Germination**

Salt stress affects germination percentage, germination rate and seedling growth in different ways depending on plant species (Ungar, 2005; Gul et. al., 1999). It was reported that maximum germination of the seeds of halophytes plants occurred in distilled water or under reduced salinity (Gul et. al.,1999;Khan et.al.,2003) and it has been found that germination percentage was reduced with a high NaCl concentrations (Tobe et al,2001; Pujol et al. 2000; Rubio-Casal et.al., 2003). Excess salinity with the plant root zone has a deleterious effect on plant growth and 8% germination at 1027mol/l level was reported by some workers (Mooring et al,1971).

**Mechanisms of salt tolerance**

Mechanisms of salt tolerance, not yet completely clear, can be explained to some extent by stress adaptation effectors that mediate ion homeostasis, osmolyte biosynthesis, toxic radical scavenging, water transport and long distance response co-ordination (Hasegawa et al. 2000 ). However, attempts to improve yield under stress conditions by plant improvement have been largely unsuccessful, primarily due to the multigenic origin of the adaptive responses. Therefore, a well-focused approach combining the molecular, physiological, biochemical and metabolic aspects of salt tolerance is essential to develop salt-tolerant crop varieties. Exploring suitable ameliorants or stress alleviant is one of the tasks of plant biologists. In recent decades exogenous protectant such as osmoprotectants (proline, glycinebetaine, trehalose, etc.), plant hormone (gibberellic acids, jasmonic acids, brassinosteroids, salicylic acid, etc.), antioxidants (ascorbic acid, glutathione, tocopherol, etc.), signaling molecules (nitric oxide, hydrogen peroxide, etc.), polyamines (spermidine, spermine, putrescine), trace elements (selenium, silicon, etc.) have been found effective in mitigating the salt induced damage in plant (Hoque et al. 2007; Ahmad et al. 2010a, 2012; Azzedine et al. 2011; Hasanuzzaman et al. 2011a, b; Hayat and Ahmad 2011; Hossain et al. 2011; Poór et al. 2011; Ioannidis et al. 2012; Nourjan et al. 2012; Rawia et al. 2011; Iqbal et al. 2012; Tahir et al. 2012; Yusuf et al. 2012).

**Water stress**

Water is an important factor in agricultural and food production yet it is a highly limited resource and is becoming increasingly more important over time for optimal crop production (O'Shaughnessy et al., 2011; Wang et al., 2012). Therefore, research on irrigation and water management has focused on crop yield responses to water supply (Chen et al., 2010a; Köksal, 2011). Water stress can affect photosynthesis directly by causing changes in plant metabolism or indirectly by limiting the amount of CO2 available for fixation (Lawlor and Cornic, 2002). Plant productivity under drought stress is strongly related to the processes of dry matter partitioning and temporal biomass distribution (Kage et al., 2004). Water evaporation from leaf surfaces induces root water uptake, which in turn ensures turgor maintenance. Closing the stomata will prevent water loss but also slows down evaporative cooling. Continuing high temperatures and low humidity may therefore increase the risk of heat stress. Dryness of the atmosphere, as represented by saturation deficit, reduces dry matter production through stomatal control and leaf water potential. Upon transpiration the humidity immediately surrounding the leaves will become saturated with water vapour, such that additional water cannot evaporate and that water and nutrients are not being drawn from the root zone. High humidity may therefore cause root and nutrient deficiencies. Insights into the water regulation of growth have shown that plant parts are differentially sensitive to reduced water potential, as explained by their
solute accumulation (Davies, 2007). The yield components such as grain number and grain size were decreased under pre-anthesis drought stress treatment in wheat (Edward and Wright, 2008). Plant may be affected by drought at any time of life, but certain stage such as germination and seedling growth are critical (Pessarakli, 1999). Rajaram et al. (1996) suggested that simultaneous evaluation of germplasm should be carried-out both under near optimum condition (to utilize high heritability and identify genotypes with high yield potential) and under stress conditions (to preserve alleles for drought tolerance). In wheat, yield is greatly reduced mostly when drought stress occurs during the heading or flowering and soft dough stages. Drought stress during maturity resulted in about 10% decrease in yield, while moderate stress during the early vegetative period had essentially no effect on yield (Bauder, 2001). Gupta et al. (2001) studied physiological and yield attributes of two wheat genotypes with stress at boot and anthesis. They reported that number of grains, grain yield, biological yield and harvest index decreased to a greater extent when water stress was imposed at anthesis stage.

**Drought resistance**

Drought resistance of a plant is related to its ability to maintain higher relative water content in the leaves under water stress. Many changes in gene expression occur in plants growing under limited water conditions (Bray, 2002).

**Photosynthetic enzymes under water stress**

The data on water stress induced regulation of the activity of photosynthetic enzymes other than Rubisco are scarce. Thimmanaik et al. (2002) studied the activity of several photosynthetic enzymes under progressive water stress in two different cultivars of Morus alba. Unlike Rubisco, which is highly stable and resistant to water stress, the activity of some enzymes involved in the regeneration of ribulose-1,5-bisphosphate (RuBP) are progressively impaired from very early stages of water stress. Thus, these results present the possibility that some enzymes involved in the regeneration of RuBP could play a key regulatory role in photosynthesis under water stress. During water stress induced by polyethilenglycole, Rubisco activity significantly increased in young potato leaves, while decreased in mature leaves (Bussis et al., 1998). Similarly, some reports have shown strong drought-induced reductions of Rubisco activity per unit leaf area (Maroco et al., 2002) and per mg showed that the decrease of Rubisco activity in vivo was not connected with the protein content. It occurs because of CO2 concentration decrease in the carboxylation center in consequence of the partly closing of stomata (Flexas et al., 2006).

**Seed germination**

Seed germination and seedling growth traits are extremely important factors in determining yield (Rauf et al., 2007). Dhandas et al. (2004) indicated that seed vigor index and plumule length are the most sensitive traits to drought stress. The rate of seed germination and the final germination percentage as well as amount of water absorption by seeds were considerably lowered with the rise of osmotic stress level at grain growth (Heikal et al., 1981). There are many studies such as the selecting plant species or the seed treatments that are helpful for alleviating the negative effect of drought stress on different plants (Almansouri et al. 2001).

**Accumulation of proteins and ABA under water stress**

Some proteins are up-regulated under water stress while others are degraded or down regulated. According to Ashraf et al. (2003) accumulation of proteins in leaves under water stress conditions might be an adaptive mechanism. Abscisic acid (ABA) is a plant stress hormone that is observed to accumulate under drought stress and mediates many stress responses. ABA also expresses the gene encoding enzymes that participate in the repair of spontaneous protein damage (Mudgett and Clark, 1994). Moreover, ABA induced increase in the osmolyte might also help in stabilizing the proteins under water stress (Noiraud et al., 2001).

**Reduces plant growth under water stress**

Severe water stress may result in the arrest of photosynthesis, disturbance of metabolism and finally death of plant (Jaleel et al., 2008a). It reduces plant growth by affecting various physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism and growth promoters (Jaleel et al., 2008b; Farooq et al., 2008). It has been established that drought stress is a very important limiting factor at the initial phase of plant growth and establishment. It affects both elongation and expansion growth (Anjum et al., 2003; Bhatt & Srinivasa Rao, 2005; Kusaka et al., 2005; Shao et al., 2008).
Effect of water stress on root growth

A developed root system is constitutive feature in many environments. The roots help the plants to absorb water and minerals for their better use. Roots are also important component of drought tolerance at the various growth stages of plant (Blum, 1996; Weerathaworn et al., 1992). The maximum accumulated water in the root zone depends on the anchorage of roots in the soil volume. Under the limited supply of water resource allocation pattern changes; root tissues gain more assimilates as compare to leaf tissues. If drought stress prevails at the early seedling stage the root-shoot changes (Nielsen and Hinkle, 1996a) and commonly increases (Sharp and Davies, 1989). Investigation work showed that root weight enhance while shoot weight reduce with the application of water deficit stress (Morizet et al., 1983). It was found that drought reduced fresh and dry shoot and root weight by 40 and 58 %, respectively. Drought stress decreased the length and fresh weight of shoot in maize (Thakur and Rai, 1984).

Nutrient relations

Decreasing water availability under drought generally results in limited total nutrient uptake and their diminished tissue concentrations in crop plants. An important effect of water deficit is on the acquisition of nutrients by the root and their transport to shoots. Lowered absorption of the inorganic nutrients can result from interference in nutrient uptake and the unloading mechanism, and reduced transpirational flow (Garg, 2003; McWilliams, 2003). However, plant species and genotypes of a species may vary in their response to mineral uptake under water stress. In general, moisture stress induces an increase in N, a definitive decline in P and no definitive effects on K (Garg, 2003). As nutrient and water requirements are closely related, fertilizer application is likely to increase the efficiency of crops in utilizing available water. This indicates a significant interaction between soil moisture deficits and nutrient acquisition. Studies show a positive response of crops to improved soil fertility under arid and semi-arid conditions. Currently, it is evident that crop yields can be substantially improved by enhancing the plant nutrient efficiency under limited moisture supply (Garg, 2003).

MATHERIALS AND METHODS

This paper is a review of the literature search on ISI, Scopus and the Information Center of Jahad and MAGIRAN, SID is also abundant. Search library collection of books, reports, proceedings of the Congress was also performed. All efforts have been made to review articles and abstracts related to internal and external validity.

REFERENCES


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