We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists



185,000

200M



Our authors are among the

TOP 1% most cited scientists





WEB OF SCIENCE

Selection of our books indexed in the Book Citation Index in Web of Science™ Core Collection (BKCI)

### Interested in publishing with us? Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected. For more information visit www.intechopen.com



#### Chapter

# Plant Responses to Salt Stress

Mustafa Yildiz, İrem Poyraz, Aslinur Çavdar, Yasin Özgen and Ramazan Beyaz

# Abstract Cechopen

Salt stress is one of the harmful abiotic stress factors. It makes agricultural lands especially in arid and semi-arid regions useless despite the efforts. More than six percent of total world agricultural lands are on the edge of vanishing due to salt stress. Salinity in soil occurs as a result of the factors such as lack of drainage, improper irrigation, excessive accumulation of soluble salts. Salinity limits the growth of plants. Despite the main results, some results of plants due to these limitations vary from species to species. The negative effects get morphological, biochemical and physiological reactions from plants. Slowed or stopped growth of roots and shoots, closuring of stomata, germination slowing, decreased or stopped development of seedling, deterioration of photosynthetic activity are the main reactions of plants to stress. On the other hand, plants also develop tolerance mechanisms as a result of some auxiliaries for surviving under adverse conditions. Plants have tendency to protect themselves from salinity with osmotic protectants synthesized by them such as sugars, proline, amino acids, glycine betaine. In this review, the responses of plants to salt stress were investigated and gathered.

Keywords: salt stress, plant response, ion toxicity, osmotic stress, oxidative stress

#### 1. Introduction

The most important factor in the survival of humanity is food. A person, who cannot access to enough food for survive, cannot continue its development and eventually lose its life. For meeting the food needs of growing population, agricultural production has to be increased by 87% by 2050 [1]. For fulfilling the food needs of world besides increasing the cultivated lands, it is necessary to take maximum efficiency and benefit from the yield. Food, which can be called the main source of our lives, is produced by plants. When plants contain essential external and internal factors they go under phase of production the food that enables the living population of the world to survive. However, the needed food sometimes cannot be obtained from the plant due to external factors. In plants, the external factor reducing growth of plant, decreasing yield of plant, inhibition plant development, is called stress. Stress causes reactions in altered gene expression in plants, cell metabolism, growth rates, yield and many other areas. In addition to these factors, stress causes death of plant and the loss of quality and quantity in plants. Generally, stress can be biotic stress caused by living factors such as microorganisms, wild plants, pathogens or can be abiotic stress caused by non-living factors such as temperature, mineral toxicity, various gasses [2]. For surviving against these negative factors, plants develop some response mechanisms. Mostly they are in two tendencies. Plants can prevent the activities of stress factors with

developing mechanisms or they may try to continue their lives by protecting themselves against external factors with tolerance mechanisms. Soil salinity is one of the biggest problems that are considered among abiotic stress factors and decrease the usability of our agricultural lands today.

Soil salinity is considered as one of the most important problems of agriculture throughout history [3]. It limits agricultural production by especially harming the crop yields [4]. 1125 million ha of cultivated lands in world are coping with salinity, 76 million ha of agriculture lands are in the effect of human-induced salinity and sodicity [5]. One out of five irrigated lands are affected by salinity and every year 1.5 million ha agriculture lands lose their suitability for agricultural production. And if the conditions continue this way, 50% of the cultivated lands will be at the edge of loss by 2050 [6–7]. Salinity is a condition of the reason of high concentration soluble salts and when the ECe value is 4 dS/m<sup>-1</sup> and more, the soil is considered as salty. Soil salinity creates stress in two ways [4]. The salts with high concentrations in the soil complicate to get water to cells for roots and salts with high concentrations in the plant causes toxicity. The salt outside of plant root affects cell expansion and cell growth directly. Toxic concentrations of salt spend time for accumulation before affecting the plant [4].

The effect of salt on cell growth and expansion, plant membrane irregularity, ion toxicity, changing metabolic process, the mechanism of germination, photosynthetic activity, shoot and root lengths, leaf development is incontroversible [8, 9]. And plants develop some mechanisms to get rid of from these negative effects. Since NaCl is the most soluble and common salt, all plants develop mechanisms for regulating the accumulation of NaCl [10]. Halophytes, plant species of high salinity soils, maintain better this extracting from plant than glycophytes, which do not have any tolerance to high salinity soils [11]. Because the salinity is common in arid and semi-arid regions, adaptation mechanisms of plants occur according to these low water potentially areas [4]. For coping with harmful effects of salinity, plants create a lot of different morphological, physiological and biochemical adaptations [12].

#### 2. Abiotic stress and salt stress

#### 2.1 Abiotic stress

Abiotic stress is a type of stress caused by environmental factors that affects plant growth, development, yield and seed quality in a negative way. Abiotic stress usually affects plant with factors like drought or floods, excessive light, excessive high or low temperature, lack of minerals, excessive pH in soil. Abiotic stress cannot directly occur, they are caused by multiple factor interactions. For example, "acid stress usually occurs because of the interaction aluminium toxicity" [13]. Plants create responses in 4 stages against abiotic stress effect. 1-Beginning alarm phase, 2-acclimation phase, 3-repair phase, 4-exhaustion phase [14]. The effect of stress is linked to plant sensitivity. When some species are so sensitive to external factors, some can tolerate it. From abiotic stresses, after drought stress the most effective factor on our world is mineral stress. In the occurrence of mineral stress, salinity is the most effective factor [2]. Big part of our agricultural lands suffer from salinity and each day this situation is getting impassable.

#### 2.2 Salinity and salt stress

Salinity occurs due to problems like wrong usage of agricultural lands, lack of rain, excess evaporation, lack of drainage. Soils that have salt concentrations that

prevent plant growth (Ece >  $4 \text{ dS/m}^{-1}$ ) and soils that do not have salt concentrations that disturb the structure of soil (ESP < 15) is called saline soil. Due to the excessive accumulations of these salts, affecting features like plant growth, development, yield, seed quality is called salt stress. Today, irrigation is being made in 17% of arid and semi-arid lands in the world and due to wrong treatments approximately 20% of these irrigated lands are being unproductive, plant presence is under negative cycle with it [2]. There is a little bit different situation in our country. Irrigation needed lands covers 2% of surface areas and 74% of these lands (approximately 12 thousand hectares) are exposed to negative effects of salt [15]. Soil salinity puts plant into stress with complicating ground-water flow from roots due to high concentrations of salts and with causing toxicity due to accumulation of high concentrations of salt in the plant [4]. The plants that struggles with salinity try to continue their life cycles by giving morphological, biochemical, physiological responses. More than 800 million ha agricultural lands are under negative effects of salinity in the world. This ratio composes more than 6% of world total agricultural lands [16]. Salinity separates as primary and secondary salinity. While primary salinity occurs by natural factors like oceans, corrosion of rocks, human induced secondary salinity occurs by excessive irrigation in agricultural lands, deterioration of agricultural land structure [4]. This situation shows its effect more day by day. Being estimated that 50% of cultivated agricultural lands will be under salt stress by 2050 [17]. NaCl and  $Na_2SO_4$  salts are the main reasons affecting the salinity of agricultural lands [18]. It is easier to understand whether the plant is salt tolerant at non-lethal salt concentrations during germination and early seedling stages, the most damages occurs in these stages [19]. Some factors should be considered in controlling salinity [20]. "In addition to well known principles such as drainage and management of irrigation resource, cultural practices and agricultural land development works are also important too. When it comes to cultural practices, fertilization, planting method, irrigation treatment, land leveling factors come to mind. Agricultural land developments are development of drainage, land leveling, breeding irrigations." [20]. The most important factor affecting salinity is lack of drainage. It causes million of fertile agricultural lands to be destroyed.

#### 3. Effect of salinity on plants

Salinity composes stress by damaging ionic and osmotic balances in plants. Osmotic stress caused by increasing the amount of salt in soil, decreases the amount of water that plant use and as a result physiological drought occurs. After these conditions, ionic stress occurs in the plant with deterioration of plant ion balance. Na and Cl ions which increases in medium with ionic stress, get in competition with essential nutrients such as K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup> lead to nutrient deficiency in plant. While the direct effect of salinity is osmotic and ionic stresses, deteriorations in structure and synthesis of toxic components composes secondary effect [21].

#### 3.1 Secondary effect of salt stress

The main secondary factors caused by NaCl are, complication in taking of K<sup>+</sup> into cells (it is efficient in closure of stomatas), decreasing photosynthetic activity, generation of reactive oxygen species (ROS) and programmed cell deaths [22]. K element is one of the most vital elements for plants for this reason Na<sup>+</sup> ions compete with K<sup>+</sup> ions for getting into the cell. Na<sup>+</sup> composes stress with blocking K<sup>+</sup> influx into the cell. Ion and hyperosmotic stress causes secondary metabolic effects in plant and the plant has to decrease these stresses for maintain its development [8].

#### 4. The chances caused by salt stress in plant

Salt stress occurs as a result of excessive salt accumulation in the soil and the plant cannot take water it needs with roots. Salt stress affects plants by toxicity caused by osmotic stresses and ions [23]. As a result of these effects, some negative changes occur in plants.

#### 4.1 The changes in growth characteristics

Plants are the most sensitive at germination and seedling growth stages. In these stages, many activities expected to occur in natural course of the plant slow down or stop. Along with these limitations, many limitations such as physiological drought, sterility, stunted growth, reduction in leaf area, slow or lack blooming, irregularity of membrane, generation of reactive oxygen species (ROS), reduction in photosynthetic activity can happen. Also, high concentration of salinity causes reduction in leaf fresh and dry weights, with low humidity it causes reduction in shoot and root growth on plants. With affecting stomata, salt stress stops permanence of stomatal reactions. Formation of root nodules, plant sprouts and leaves are affected from salt stress. According to the studies, these negative results can be counted as the effects of salt stress on plants but the main responses of plants are still not fully known [24].

#### 4.2 Plant root and shoot length

Root length, root length density and thick roots which are the features of the root, are very vital in development of subsoil parts of plant by taking the existing water. A fertile root system during early seedling stage which is the most sensitive stage, provides advantage in accelerating growth. Since the water which is taken by plant in danger of being lost easily as a result it has to be taken from non-deep layers of soil [24].

Roots are one of the vulnerable parts of the plant. While under salt stress reduction in root length is being seen, in addition to salt stress not being able to use the existing water negatively affects root and shoot growth of plant. Besides all of these negative effects, roots are also known as surprisingly strong when they directly exposed to salt stress [24].

#### 4.3 Cell level effect

#### 4.3.1 Organelle level effect

Without doubt, the most affected organelle in plant from salt stress is chloroplast. Stress mostly affects thylakoids and stroma in chloroplast [2]. Chloroplasts tend to generate reactive oxygen species such as  $H_2O_2$ ,  $O_2^-$ ,  $OH^-$ . Reactive oxygen species seriously affects plant metabolic activities by causing oxidative damage to lipids that result in protein breakdown and membrane lipid peroxidation, causing the thylakoids to swell and turn into a wavy shape [2, 25]. The stress caused by salt, causes another negative situation starch accumulation which is not known how it occurred fully in chloroplast. Another negative situation caused by salt stress is deterioration of grana lamellae. Salt stress disrupts electrical charges that composes grana lamellae by changing ionic composition.

As a result of stress mitochondria, the another organelle affected from salt stress, is exposed to negative effects such as structural fragmentations, accelerations in vacuole forming, swelling and decrease in crystal [26].

#### 4.3.2 Effect of ion toxicity

Accumulation of Na<sup>+</sup> and Cl<sup>-</sup> ions in plant makes negative effect by developing competitive system with limiting intake of the other ions into the plant. Soluble salts with high concentrations in soil can cause physiological drought [23]. With accumulation of soluble salts in plant root area, decrease in plant water intake occurs. Accumulated salts in root area creates ion imbalance in cells by getting into plant cells and this imbalance causes growth problems in plant tissues such as leaves, seeds etc. Excessive Na<sup>+</sup> accumulation in plants causes necrosis in old leaves and high concentrations of Na<sup>+</sup> ions in shoots cause metabolic and osmotic problems [27]. Accumulation of soluble salts in high concentrations in soil causes negative effects.

#### 4.4 Effect to photosynthesis

It is known that the effect occurring in photosynthesis which is negatively affected by high and low salt concentrations, may be from stomata, non-stomata, or both limitations [2]. Several factors can be counted as a reason of decrease in photosynthetic activity. First reason is reduction in cell permeabilization of CO<sub>2</sub> as a result of dehydration of membranes. High concentration of salt in soil creates high osmotic potential in plant by limiting water reaching of plant but with decrease in water potential osmotic stress in plant occurs. Photosynthetic electron transport is affected negatively. With ion toxicity caused by Na<sup>+</sup> and Cl<sup>-</sup> ions, essential nutrients cannot be taken and this situation leads to limitation of photosynthesis and generation of reactive oxygen species (ROS). The changes in enzyme activities also cause decrease in photosynthesis ratio [24].

#### 4.4.1 Closure of stomata

High concentration salinity in soil causes osmotic stress formation by limiting water availability of plant with roots whereas closure of stomatas is a first response of plants. This response of plant limits transpiration and as a result stomata conductivity decreases [4]. Closure of stomata happens two ways as hydroactive closure and hydropassive closure [28]. Plants synthesis chemical signal molecules in occurring of hydroactive closure. ABA is one of the important synthesized chemical signal molecules and it is effective in plant growth and creating water balance. Under low water potential ABA molecules are transported into stomata by roots and old leaves via xylem. Low water potential is sensed by root tip and ABA molecules are synthesized at the root and transported to shoots with the help of xylem. The reason of synthesis of ABA molecules is ensuring regulation of stomata conductivity in low water potential conditions and as a result of this situation, it causes decrease in leaf water content [2].

#### 4.5 Oxidative stress

With decrease in photosynthesis formation, reactive oxygen species increases and increasing of reactive oxygen species increases production of enzymes that enable detoxify of these reactive oxygen species. While plants adapt to changing environment, they undergo the activation of biochemical processes that prevent oxidative damages against photosystem, leaf morphology, chloroplast pigment composition and many other changes. Reactive oxygen species can divide the activities of plant. For example, DNA, proteins and lipids make negative effects by mixing into plant metabolism [29].

#### 5. Effect of salinity on some crops

Until 2050, for fulfilling the food needs of increasing population and developing world, the yield of the crops obtained from crops, which have undeniable effects in human life, has to increase by 50% [30]. The most effective factor in limiting product yield is undoubtedly salt stress. Plants try to tackle with stress for removing the pressure on them. But the method of tackle and the effect of each species differ. The process of field crops under salinity and their responses vary from species to species.

#### 5.1 Rice (Oryza sativa L.)

Rice is a monocotyl warm-season cereal crop. It is grown in many parts of the world, especially Asia, it is an indispensable food of approximately 50% of the world population [23]. Rice shows more different responses to salt stress compared to other field crops. Rice crop is severely affected by salinity stress. Especially in the early growth stage, reduction is observed in the plant growth. In high concentration of salt, reduction is observed in plant seed growth and plant wet weight [31]. The first organ of the plant affected by salinity is root. As a result of excessive accumulation of Na<sup>+</sup> in the root, reduction is observed in plant root and shoot growth [32]. Salinity has negative effects on cell division and cell wall. As a result of high concentration of salt, the salt effect is severely observed in leaf length, root and yield [9]. Rice gives very rapid response under salinity stress. For example, in early response to stress, production of ethylene phytohormone contributes to plant survival [23, 33]. Salt stress causes poor development of inner and outer spikelets and sterility of cluster, this situation results in decreased grain yield [23].

#### 5.2 Wheat (*Triticum aestivum* L.)

Wheat is a cereal genus belonging to the *Poaceae* family. In today, approximately 36% of humans use wheat as main product [34]. Salt stress affects wheat too. Yield in wheat starts to decrease in 6 dS/m<sup>-1</sup> salinity ratio [35]. The presence of highly concentrated salts in the soil prevents the plant from bringing water to cells through its roots, causing osmotic stress and causing ion stress as a result of ion irregularity in plant. As a result of accumulation of Na<sup>+</sup> ion in plants in high concentrations, causes plant ionic stress more toxic by becoming dominant against other ions [34]. Osmotic stress caused by the absence of water to the plant causes a decrease in germination rates of the wheat varieties against the salt stress they are exposed to [12]. In addition to the negativities occurring in germination, there are some reductions in the shoot and roots, leaves and cells of the plant. Most sensitive stages against salt stress in wheat plants are early growth stages [23]. Excessive accumulation of Na<sup>+</sup> and Cl<sup>-</sup> ions in chloroplast, which is the organelle most affected by salt stress, leads to decrease in photosynthetic ratio [36]. Decreases and stops in photosynthetic activity occurs when the salinity falls below 150 mM NaCl concentration [37].

#### 5.3 Maize (Zea mays L.)

Maize plant which is not very sensitive to salinity, is a C4 plant belonging to *Poaceae* family [38]. The ratio of salt that allows maize to live without harming its growth and development, without causing any harm, is 0.25 mM NaCl or 1.8 dS/m<sup>-1</sup> [39]. When there is salt accumulation above this ratio, disruptions in plant life cycle occurs. Like the other field crops, maize plant is most susceptible against salt stress

during early growth stages including germination and seedling stages [40]. Salinity in seed germination may lead to fatal results by a) causing toxicity of Na<sup>+</sup> or Cl<sup>-</sup> or both ions, b) preventing the plant from retaining water [39]. Early stages of stress, the typical reaction of plant before Na<sup>+</sup> ions reaches toxic degrees is decrease in growth as a result of the osmotic reaction [41]. Shoot growth in maize is also disrupted by osmotic stress [23]. The only reason for maize that the stress is caused by ion imbalance and that it increases and turns into a toxic effect is that Na<sup>+</sup> ions make it difficult to absorb ions such as K<sup>+</sup> and Ca<sup>2+</sup> and as a result of this, it causes water loss and causes necrosis [41].

#### 5.4 Sorghum (Sorghum bicolor L.)

Sorghum which is mostly grown in Australia in the world, is a monocotyl C4 plant that belongs to the *Poaceae* family. Even though sorghum has a high tolerance against salt concentrations, salt stress has a big role in plant growth deceleration [42]. In soils with high salinity, ion toxicity and toxicity-induced mineral deficiency are observed [43]. Tolerable salt concentration for grain sorghum is 6.8 dS/m<sup>-1</sup> and when salinity reaches 7 dS/m<sup>-1</sup> 25% decrease is observed in yield and when salinity reaches 10 dS/m<sup>-1</sup> a 50% decrease is observed [44]. Under salinity, while germination rate decreases, germination time increases [45]. Plant stem yield and soluble carbohydrate decrease with increasing salinity [46].

#### 5.5 Cotton (Gossypium hirsutum L.)

Production of cotton in the world, one of the most important fiber and oil plants, has increased by 2.5% compared to previous season with 121.6 million bales [47]. 35% of world fiber usage provided by cotton. Cotton cultivation and production is mostly done in arid and semi-arid regions [48]. Salinity causes negative effects on leaf area affected by osmotic stress, plant growth, root and shoot growth, in addition to these effects salinity causes decreases in photosynthetic activity, fiber quality, metabolic activities [49]. Salinity after flowering stage causes decrease in fiber quality of plant [23]. Undoubtedly, these occurring negative effects tend to change depending on the type of cotton, magnitude and time of stress exposed to.

#### 6. Responses of plant to salt stress

In order to determine the responses of plants to salt stress, firstly we have to know the factors cause this stress. It is a priority to know whether the toxic effect caused by excessive salt accumulation in the plant or the osmotic stress caused by soluble salts in the soil in which the plant is restricting growth. While plants give rapid responses to external induced osmotic stress, they give slower responses to accumulation of Na<sup>+</sup> ions in the leaves [4, 50].

There are 2 types of struggle with salinity, human-help responses and the plant's natural adaptation responses. Natural struggle strategies among plants leans on 3 strategies. 1) extracting Na<sup>+</sup> ions from cytoplasm due to low intake, 2) the desire of Na<sup>+</sup> ion to enter the vacuole, 3) accumulation in leaves due to preference. Genotypes with high concentrations of Na<sup>+</sup> ions in leaves have proven to be highly susceptible to salinity, generally those who tolerate high concentrations are those that transmit Na<sup>+</sup> ions to the vacuoles of leaf cells. Salt tolerant plants get rid of harmful effects of NaCl [23].

#### 6.1 Morphological adaptation responses against salinity in plants

The factors such as the type of plant (halophyte) that can adapt to the environment in which the plant is located or the type of plant (glycophyte) that is poorly affected by environment, the time it is exposed to salinity, salt concentrations in irrigation water have effects on growth and these factors cause plants to develop different mechanisms against negative effects [4].

#### 6.1.1 Germination

Seed germination is one of the vital stages for the plant but it is prevented by salinity. Salt stress causes negative effects on plant imbibition and root growth [51]. Salinity induced decrease in germination and reduction in plant root growth are connected to ion toxicity and osmotic stress [52]. Decrease in germination is observed in plants growing under salinity. Especially wheat among field crops, is severely affected by salinity and decrease in germination is observed. Salinity also delays germination time [53].

#### 6.1.2 Seedling development

In order for the plant to continue its vital events, seedling development under salinity stress play an important role. Plant biomass accumulation and stunted growth of plant are among the results of salinity, the most impact is its role in leaf area expansion [51]. Although some salt tolerant plants appear to increase biomass combination under high salinity, there is an inverse relationship between seedling development and salinity. Salinity also negatively affects seedling fresh and dry weights, plant length, and root surface area in plant [51].

#### 6.1.3 Photosynthesis

Plant produce their foods with photosynthesis [51]. Photosynthesis is affected by salinity in long-term or short-term. While it can get rid of the effects in shortterm with stomata restrictions that cause a decrease in carbon accumulation, it can get rid of the effects caused by salt accumulation in the leaves in long term [4, 54]. Closure of stomata prevents plant from losing water through transpiration. Deteriorations in thylakoid membranes and decrease in activities of Calvin cycle enzymes are the most important factors caused by salinity [51]. As a result of salinity, deterioration in PSII receptors cause yield loss in PSII [51]. Reduced chlorophyll content due to salinity may be depend on increased pigment degradation or impaired biosynthesis. Generally, the plant shows its response to salinity by decreasing photosynthetic activity and restricting the production of the factors that make up this activity [51].

#### 6.1.4 Water relations

Excessive amounts of Na<sup>+</sup> and Cl<sup>-</sup> ions prevents water intake of plant by increasing osmotic potential of soil, this situation causes negativities in plant growth by decreasing water consent in plant cells [9]. Under the salinity increase, inverse correlation against stress between osmotic potential and water potential occurs, which means that while salinity increases, decrease in both of these factors is observed [51]. Water based osmotic stress causes closure of stomata and by going further causes disruption in photosynthesis by preventing CO<sub>2</sub> flow. Regulation of water flow is the key solution in eliminating these negative factors [55].

In addition, in tackling salinity especially in field crops using canal waters instead of salty groundwater can be preferred. Gypsum usage is also among the options where canal water is not accessible [56].

#### 6.1.5 Ion toxicity

Salt stress occurs due to accumulation of high amounts of Cl<sup>-</sup> or Na<sup>+</sup> ions in soil and causes ion toxicity in plant. Although plant responses against salinity varies from species to species, generally excessive intake of Na<sup>+</sup> causes nutrient imbalance [51–57]. Na<sup>+</sup> ion has toxic concentration earlier than Cl<sup>-</sup> ion [4]. While high concentrations of Na<sup>+</sup> ions cause negative effects in photosynthetic activity, they may lead to worse results in salt sensitive plants [58]. While the effect of Na<sup>+</sup> ions may be negative in some plants, Cl<sup>-</sup> ion may be more negative in plants such as soybean and citrus [59]. Cl<sup>-</sup> ions can also deteriorate photosynthetic activity and may cause ion toxicity in plants like Na<sup>+</sup> ions. In response to ion toxicity ABA hormone, which is produced by plant itself, is important. The amount of synthesis increases during stress, it is used to prevent disruption in the growth and development mechanisms of cell [60–61].

#### 6.1.6 Osmotic stress

Root water conductivity is impaired as the plant's high salinity restricts water intake from the soil, resulting in osmotic stress [4–10]. Salinity related osmotic stress causes closure of stomata [50]. Cell division and elongation are negatively affected in decreasing turgor pressure [62]. Cell permeability decreases, water intake to plant deteriorates and this decreases water intake and transpiration rate in leaf water potential [63]. Most of these effects are observed in maize plants, which are sensitive to salt stress, from field crops. But when the responses to salt stress are examined, responses of each plant are different.

#### 6.1.7 Oxidative stress

Salt stress constitutes reactive oxygen species (ROS). Reactive oxygen species such as  $H_2O_2$ ,  $O^{2^-}$ ,  $OH^-$  are produced in plant cells, in chloroplast and mitochondria [64]. Decrease in photosynthesis rate increases formation of reactive oxygen species [65]. Reactive oxygen species increase under stress and balance between antioxidant defense systems deteriorates and as a result oxidative stress occurs [66]. Under salt stress the negative effects such as disruption in membrane integrity, oxidation of carbohydrates and nucleic acids are observed as most harmful effects of reactive oxygen species [51]. Disruption of a gene related to oxidative stress tolerance may block the plant's tolerance to any abiotic stress [4]. Malondialdehydes are considered as important symptoms of oxidative stress, accumulation of high concentrated malondialdehyde in cells also cause oxidation of complementary structural components of cells [9].

## 6.2 Physiological and biochemical adaptation responses against salinity in plants

#### 6.2.1 Ion homeostasis

In plant growth, some ions must be inside of cell. Although ions such as nitrogen, potassium, calcium are present in soil, they cannot enter the plant cells as a result of competition with other ions with high concentrations. Presence of salt with high

concentration in soil complicates the intake of these ions which are effective in plant development. Plants make some responses to ensure that this negative effect is eliminated and for the continuity of low ion concentration. Dividing the ions to be added to plants instead of intaking them inside of cells as one time is considered as important action for plant growth and development [51]. In maintaining the low concentration of ions, in transportation to plants the cell membrane is important [67]. Thanks to proteins, channel proteins and semptomers, ions can be moved to the plant [68]. Antiporters are also used in transportation. These transporters are located in vacuolar membranes. V-ATPase are known as channels needed for the continuity of plant under salt stress [69]. Due to the excessive accumulation in the soil, when Na<sup>+</sup> ion enters the cytoplasm, it wants to move to vacuoles and this transport is carried out by Na<sup>+</sup>/H<sup>+</sup> antiporters. In the cell metabolism of plant, the other role is cytoplasmic K<sup>+</sup> homeostasis. Under salinity, K<sup>+</sup> concentration undergoes a severe decrease [64]. K<sup>+</sup> ions, which can be transmittable to cells by K<sup>+</sup> transporters and membrane channels, have low concentration under salinity stress. There is an important factor in cell recruitment. When the extracellular K<sup>+</sup> concentration is low, K<sup>+</sup> transporters mediating high affinity of K<sup>+</sup> uptake mechanisms allow affinity if extracellular K<sup>+</sup> concentration is high. As a result of this, concentration of Na<sup>+</sup> ion increases under salinity and with this increase Na<sup>+</sup> competes with K<sup>+</sup> and reduces K<sup>+</sup> uptake into the cell [4, 51]. More K<sup>+</sup> retention of roots in plants such as wheat, maize, beans have been observed as one of the mechanisms applied by plants to withstand salt stress [51–64]. Accumulation of K<sup>+</sup> ions in cell increases under salinity stress [51, 70].

#### 6.2.2 Biosynthesis of osmoprotectants

Osmoprotectants are high rated soluble compounds [71]. Certain organic compounds, which are sugars, amino acids, proline and osmoprotectants that are interchangeable compounds, are synthesized by plants under stress conditions according to their stress levels. Osmolytes are in charge of providing adaptation of plant to salt stress [71]. Quaternary ammonium compounds as betalain betanin which is synthesized only by a few members of *Plumbaginacease* family [72]. Amino acids like proline present in plant types are present in different type of plants from ammonium compounds like betalain betanin present in plant types. These osmoprotectant compounds can replace each other [73]. While accumulation of compounds varies with salt stress, most of the osmolytes try to make it easier to maintain osmotic balance and structure of plant cells with an uninterrupted water flow [8].

#### 6.2.2.1 Amino acids

Free amino acids take part in reducing osmotic stress caused by high concentrations of salt [74]. Amino acids such as arginine, glycine, alanine, proline, leucine, valine, serine take part in regulation of cell [75]. Accumulation of these amino acids is done for solving the problems that the plant creates against salt stress. But amino acids such as methionine, arginine, which make up the majority of amino acids, decreases under stress condition unlike proline, which increases under salinity [51].

#### 6.2.2.2 Proline

Proline, which has wide usage, is one of the most common osmolytes [76]. In high plants, which are found to be abundant, even under salt stress this content does not decrease, conversely it tends to increase [57]. Accumulation of proline

is accepted as an important precaution to avoid salinity stress [76–77]. The effect of proline accumulation under salinity conditions varies from species to species. Increasing the proline content in plant cells is a positive factor in preventing negative effects occurring at cell level [76]. Even in negative conditions, the accumulation of proline helps the plant to grow [76].

#### 6.2.2.3 Glycine betain

Glycine betain, the variety of which is known to be found in organisms as well as plants, is accepted as the most common quaternary ammonium compound [78]. Under salt stress, it takes part in protecting membrane structure of plant, regulation of plant cells [76–79]. According to the studies, glycine betain accumulated in chloroplast is more effective than its accumulation in cytosol [79]. In conducted study, while in rice seedlings, which are under 150 mM salt stress, fragmentation of grana, swelling of thylakoids, deterioration in mitochondria may be observed, it is observed that these effects disappear with the pretreatment of glycine betaine [80]. As a result of accumulation of exogenously applied glycine betain, the plant has a stronger system against stress [76].

#### 7. Conclusion

With increasing population, satisfying the food need of humanity is important. Responding to this need gets harder day by day. Most of the agricultural lands in the world are exposed to salt stress. Other than the natural factors causing salt stress, unfortunately the wrong practices made by people also invite salt stress. Plants develop some response mechanisms for surviving against the negative effects occurring on them. These mechanisms which we can group as physiological, morphological, biochemical, depend on the magnitude and effect of stress and vary from species to species. As a result of these responses, the tolerance of plants to the environment they live in increases, they may be affected less by external factors and they may continue their life cycle.

#### **Conflict of interest**

The authors declare no conflict of interest.

# Intechopen

#### **Author details**

Mustafa Yildiz<sup>1\*</sup>, İrem Poyraz<sup>2</sup>, Aslinur Çavdar<sup>3</sup>, Yasin Özgen<sup>1</sup> and Ramazan Beyaz<sup>4</sup>

1 Department of Field Crops, Faculty of Agriculture, Ankara University, Ankara, Turkey

2 Department of Field Crops, Graduate School of Natural and Applied Sciences, Ankara University, Ankara, Turkey

3 Biotechnology Institute, Ankara University, Ankara, Turkey

4 Department of Soil Science and Plant Nutrition, Faculty of Agriculture, Kirşehir Ahi Evran University, Kirşehir, Turkey

\*Address all correspondence to: myildiz@ankara.edu.tr

#### **IntechOpen**

© 2020 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/3.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

#### References

[1] Kromdjik J, Long SP. One crop breeding cycle from starvation? How engineering crop photosynthesis for rising  $CO_2$  and temperature could be one important route to alleviation. Proceedings of the Royal Society B: Biological Sciences. 2016;283(1826)20152578. DOI: 10.1098/ rspb.2015.2578

[2] Çulha Ş, Çakırlar H. Tuzluluğun bitkiler üzerine etkileri ve tuz tolerans mekanizmaları. Afyon Kocatepe University Journal of Sciences. 2011;11:11-34.

[3] Nandal M, Hooda, R. Salt tolerance and physiological response of plants to salinity: A review. International Journal of Scientific & Engineering Research. 2013;4:44-67.

[4] Munns R, Tester M. Mechanisms of salinity tolerance. The Annual of Plant Biology. 2008;651-681.

[5] Wicke B, Smeets E, Dornburg V,
Vashev B, Gaiser T, Turkenburg WC,
Faaij APC. The global technical and
economic potential of bioenergy
from salt-affected soils. Energy &
Environmental Science. 2011;4(8):
2669-2681. DOI: 10.1039/C1EE01029H

[6] Hasanuzzaman M, Nahar K, Alam M, Bhowmik PC, Hossain A, Rahman MM, Majeti P, Ozturk M, Fujita M. Potential use of Halophytes to remediate saline soils. Journal of Biomedicine and Biotechnology. 2014;2014(8):1-12. DOI: 10.1155/2014/589341

[7] Hossain S. Present scenario of global salt affected soils,its management and importance of salinity research. International Research Journal of Biological Sciences. 2019;1(1):1-3.

[8] Hasegawa PM, Zhu JK, Bressan RA, Bohnert JH. Plant cellular and molecular responses to high salinity. Annual Review of Plant Physiology and Plant Molecular. 2000;51:463-499. DOI: 10.1146/annurev.arplant.51.1.463

[9] Munns R. Comparative physiology of salt and water stress. Plant Cell and Environment. 2002; 25(2): 239-250. DOI: 10.1046/j.0016-8025.2001.00808.x

[10] Munns R. Genes and salt tolerance:Bringing them together. NewPhytologist.2005;167(3):645-663. DOI:10.1111/j.1469-8137.2005.01487.x

[11] Garthwaite AJ, Colmer TD, Bothmer RV. Salt tolerance in Wild Hordeum species is associated with restricted entry of Na<sup>+</sup> and Cl<sup>-</sup> into the shoots. Journal of Experimental Botany.2005;56(419):2365-2378. DOI: 10.1093/jxb/eri229

[12] Motos JA, Ortuño MF, Vivancos PD, Vicente AB, Hernandez JA, Sánchez BM. Plant responses to salt stress: Adaptive mechanisms. Agronomy.2017;7(1):18. DOI: 10.3390/agronomy7010018

[13] Rhodes D, Nadolska-Orczyk A. Plant Stress Physiology. Encyclopedia of life sciences. Nature Publishing Group. 2001;10. DOI: 10.1038/npg. els.0001297

[14] Kosová K, Renaut J, Prasil IT, Vítámvás P.Plant protome changes under abiotic stress. Journal of Proteomics. 2011;74(8):1301-1322. DOI: 10.1016/j.jprot.2011.02.006

[15] Kendirli B, Çakmak B, Uçar Y. Salinity in the Southeastern Anatolia Project (GAP), Turkey: issues and options. Irrigation and Drainage. 2005;54(1):115-122. DOI: 10.1002/ ird.157

[16] Roy RN, Finck A, Blair GJ, Tandon HLS. Plant nutrition for feed security: A guide for integrated nutrient management.FAO; 2006. 348 pages. [17] FAO. How to feed the World in 2050. In: Proceedings of the Expert Meeting on How to Feed the World in 2050;24-26 June 2009; Rome; 2009.

[18] Pessarakli M, Szabolcs I. Soil Salinity and Sodicity as Particular Plant/Crop Stress Factors. In: Pessarakli M,editor. Handbook of Plant and Crop Stress . 4th ed. Routledge Handbooks Online; 2010. p .1-19. DOI: 10.1201/B10329-3

[19] Munns R, Gilliham M. Salinity tolerance of crops- what is the cost ? New Phytologist. 2015;208(3):668-673. DOI: 10.1111/nph.13519

[20] Ayers RS, Westcot DW. Water quality for agriculture. 2nd ed. FAO Irrigation and Drainage; 1985. 174 pages.

[21] Botella MA, Rosado A, Bressan R, Hasegawa PM. Plant adaptive responses to salinity stress. In: Jenks MA, Hasegawa PM editors. Plant Abiotic Stress. USA, Iowa: Blackwell
Publishing; 2007. p. 37-70. DOI: 10.1002/9780470988503.ch3

[22] Serrano R, Rios G, Ros R, Marquez JA, Proft M, Mulet JM, Mendrizabal I, de Larrinoa I.F, Ahuir-Pascual A, Montesinos C. A glimpse of the mechanisms of ion homeostasis during salt stress. Journal of Experimental Botany. 1999;50:1023-1036. DOI: 10.1093/jxb/50. Special\_Issue.1023

[23] Hussain S, Bai Z, Huang T, Cao X, Zhu L, Zhu C, Khaskheli MA, Zhang C, Jin Q, Zhang J. 1-Methylcyclopropene modulates physiological,biochemical and antioxidant responses of Rice to different salt stress levels. Journal of Integrative Agriculture. 2019;10(124): 1-18. DOI: 10.3389/fpls.2019.00124

[24] Shah S, director. Morphological, Anatomical and Physiological Responses of Plants to Salinity [Internet]. 2014. Available from: https://www.youtube. com/watch?v=rihGVDoeq8A&t=244s

[25] Suo J, Zhao Q, Chen S, Dai S, David L. Salinity response in chloroplasts: insights from gene characterization. International Journal of Molecular Sciences. 2017;18(5) :1011. DOI: 10.3390/ijms18051011

[26] Koyro HW. Ultrastructural effects of salinity in higher plants. In: A. Lauchli, U. Lüttge,editors. Salinity: Environment-Plants-Molecules. Springer: Dordrecht;2002. p. 139-157. DOI: 10.1007/0-306-48155-3\_7

[27] Tester M, Davenport R.
Na<sup>+</sup> tolerance and Na<sup>+</sup> transport in higher plants. Annals of Botany.
2003;91(5):503-527. DOI: 10.1093/aob/mcg058

[28] Mahajan S, Pandley GK, Tuteja N. Calcium and salt-stress signaling in plants: shedding light on SOS pathway. Archives of Biochemistry and Biophysics. 2008;471(2):146-158. DOI: 10.1016/j.abb.2008.01.010

[29] Demiral T, Türkan İ. Comparative lipid peroxidation, antioxidant defense systems and proline content in roots of two rice cultivars differing in salt tolerance. Environmental and Experimental Botany. 2005;53(3):247-257. DOI: 10.1016/j. envexpbot.2004.03.017

[30] Godfray C, Beddington JR, Crute IR, Haddad L, Muir JF, Lawrence D, Pretty NJ, Robinson S, Thomas SM, Toulmin C. Food security: The challenge of feeding 9 billion people . Science. 2010;327(5967):812-818. DOI: 10.1126/ science.1185383

[31] Kazemi K , Eskandari H. Effects of salt stress on germination and early seedling growth of Rice(*Oryza sativa* L.) cultivars in Iran. African Journal of Biotechnology.

2011;10(77):17789-17792. DOI: 10.5897/ AJB11.2219

[32] Hussain S, Zhong C, Bohr JA, Hu JJ, Jin Q, Cao XC, Zhang JH, Zhu LF. Effects of salt stress on Rice growth and development characteristics and the regulating ways: A review. Journal of Integrative Agriculture. 2017;16(11):2357-2374. DOI: 10.1016/ S2095-3119(16)61608-8

[33] Sheeren A, Mumtaz S, Raza S, Khan A, Solangi S. Salinity effects on seedling growth and yield components of different inbred Rice lines. Pakistan Journal of Botany. 2014;37(1):131-139.

[34] Hasanuzzaman M, Nahar K, Rahman A, Anee TI, Alam MU, Oku H, Fujita M, Bhuiyan TF. Approaches to enhance salt stress on Wheat. In: Wanyera R, Owuoche J,editors. Wheat Improvement,Management and Utilization. IntechOpen: 2017. p. 152-187. DOI: 10.5772/67247

[35] Royo A, Abió D. Salt tolerance in Durum Wheat cultivars. Spanish Journal of Agricultural Research. 2003;1(3):27-35. DOI: 10.5424/sjar/2003013-32

[36] Wahid A, Gelani S, Basra MA, Perveen M. Pretreatment of seed with  $H_2O_2$  improves salt tolerance of Wheat seedlings by alleviation of oxidative damage and expression of stress proteins. Journal of Plant Physiology. 2006;164(3):283-294. DOI: 10.1016/j. jplph.2006.01.005

[37] Zhang X, Li K, Liu S, Zou P, Chen X, Qin Y, Li P, Yu H, Xing R. Relationship between the degree of polymerization of Chitooligomers and their activity affecting the growth of Wheat seedlings under salt stress. Journal of Agricultural and Food Chemistry. 2017;65(2):501-509. DOI: 10.1021/acs.jafc.6b03665

[38] Chinnusamy V, Jagendorf A, Zhu J. Understanding and improving salt tolerance in plants. Crop Science. 2005;45(2):437-448. DOI: 10.2135/ cropsci2005.0437

[39] Menezes-Benavente L, Kernodle SP, Scandalios JG, Margis- Pinheiro M. Salt-induced antioxidant metabolism defenses in maize (*Zea mays* L.) seedlings. Redox Report. 2004;9(1):29-36. DOI: 10.1179/135100004225003888

[40] Khodarahmpour Z, Ifar M, Motamedi M. Effects of NaCl salinity on Maize (*Zea mays* L.) at germination and early seedling stage. African Journal of Biotechnology. 2012;11(2):298-304. DOI: 10.5897/AJB11.2624

[41] Farooq M, Hussain M, Wakeel A, Siddique KHM. Salt stress in Maize: effects, resistance mechanisms, and management.A review. Agronomy for Sustainable Development. 2015;35(2):461-481. DOI: 10.1007/ s13593-015-0287-0

[42] Almodares A, Hadi MR, Ahmadpour *H. sorghum* stem yield and soluble carbohydrates under different salinity levels. African Journal of Biotechnology. 2008;7(22):4051-4055.

[43] Netondo GW, Onyango JC, Beck E. Sorghum and salinity:I.response of growth,water relations,and ion accumulation to NaCl salinity. Crop Science. 2004;44(3):797-805. DOI: 10.2135/cropsci2004.0797

[44] Maas EV, Hoffman GJ. Crop salt tolerance- current assessment. Journal of the Irrigation and Drainage Division, American Society of Civil Engineers. 1977;103(2):115-134.

[45] Almodares A, Hadi MR, Dosti B. Effects of salt stress on germination percentage and seedling growth in sweet sorghum cultivars. Journal of Biological Sciences. 2007;7(8):1492-1495. DOI: 10.3923/jbs.2007.1492.1495 [46] Almodares A, Hadi MR, Kholdebarin B, Samedani B, Kharazian ZA. The response of sweet sorghum cultivars to salt stress and accumulation of Na<sup>+</sup>, Cl<sup>-</sup>, K<sup>+</sup> ions in relation to salinity. Journal of Environmental Biology. 2014;35(4):733-739.

[47] Meyer LA. Cotton and Wool Outlook. United States Department of Agriculture. 2020. 6 pages.

[48] Viglioni Penna JC, Verhalen LM, Kirkham MB, McNew RW. Screening Cotton genotypes for seedling drought tolerance. Genetics and Molecular Biology. 1998;21(4):545-549. DOI: 10.1590/S1415-47571998000400023

[49] Muhammad S, Ditta A, Iqbal MS, Hussain SB, Khan MI, Ramzan M, Malik TH. Effect of salinity stress on Cotton growth and role of marker assisted breeding and agronomic practices (chemical,biological and physical) for salinity tolerance. Scholars Report. 2018;4(1):1-13.

[50] Munns R. Physiological processes limiting plant growth in saline soils: Some dogmas and hypoteses. Plant Cell and Environment. 1993;16:15-24. DOI: 10.1111/j.1365-3040.1993.tb00840.x

[51] Shahzad B, Fahad S, Tanveer M, Khan BA, Saud S. Plant responses and tolerance to salt stress: profiling and counteraction. In: Hasanuzzaman M, Nahar K, Fujita M, Oku H, Islam T, editors. Approaches for Enhancing Abiotic Stress Tolerance in Plants. 1st ed. CRC Press; 2019. p. 61-78. DOI: 10.1201/9781351104722-3

[52] Katembe WJ, Ungar IA, Mitchell JP. Effect of salinity on germination and seedling growth of two Atriplex species (Chenopodiaceae). Annals of Botany. 1998;82(2):167-175. DOI: 10.1006/ anbo.1998.0663

[53] Lin J, Li X, Zhang Z, Yu X, Gao Z, Wang Y, Li Z, Mu C, Wang J. Salinity- alkalinity tolerance in Wheat, seed germination, early seedling growth,ion relations and solute accumulation. African Journal of Agricultural Research. 2012;7(3): 467-474. DOI: 10.5897/AJAR11.1417

[54] Parida AK, Das AB. Salt tolerance and salinity effects on plants : A review.
Ecotoxicology and Environmental Safety. 2005;60(3):324-349. DOI: 10.1016/j.ecoenv.2004.06.010

[55] Flexas J, Bota J, Galmés J, Medrano H, Ribas- Carbó M. Keeping a positive carbon balance under adverse conditions : Responses of photosynthesis and respiration to water stress . Physiologia Plantarum. 2006;127(3):343-352. DOI: 10.1111/j.1399-3054.2006.00621.x

[56] Zaka AM, Schmeisky H, Hussain N, Rafa H. Utilization of brackish and canal water for reclamation and crop production. In: The International Conference on Water Conservation in Arid Regions; 12-14 October 2009; Jeddah, Saudi Arabia: ICWCAR; 2009. p. 1-16.

[57] Doğan M, Tıpırdamaz R, Demir Y. Salt resistance of Tomato species grown in sand culture. Plant,Soil and Environment. 2010;56(11):499-507. DOI: 10.17221/24/2010-PSE

[58] Jamil M, Jung KY, Lee DB, Ashraf M, Lee SC, Rha ES. Effect of salt (NaCl) stress on germination and early seedling growth of four vegetable species. Journal of Central European Agriculture. 2006;7(2):273-282.

[59] Grattan SR, Grieve CM. Salinity-mineral nutrient relations in Horticultural crops. Scientia Horticulturae. 1998;78(1-4):127-157. DOI: 10.1016/S0304-4238(98)00192-7

[60] Carillo P, Pontecorvo G, Woodrow P, Fuggi A, Annunziata MG. Salinity stress and salt tolerance. In:

Shanker A, Venkateswarlu B, editors. Abiotic Stress in Plants-Mechanisms and Adaptations. 1st ed. Intech; 2011. p. 21-38. DOI: 10.5772/22331

[61] Algül BE, Tekintaş FE, Günver Dalkılıç G. Bitki büyüme düzenleyicilerinin kullanımı ve içsel hormonların biyosentezini arttırıcı uygulamalar. Journal of Adnan Menderes University Agricultural Faculty. 2016;13(2):87-95. DOI: 10.25308/aduziraat.294100

[62] Zeng L, Shannon MC, Grieve CM. Evaluation of salt tolerance in Rice genotypes by multiple agronomic parameters. Euphytica. 2002;127:235-245. DOI: 10.1023/A:1020262932277

[63] Chaudhuri K, Choudhuri MA. Effects of short-term NaCl stress on water relations and gas exchange of two Jute species. Biologia Plantarum. 1997;39:373-380. DOI: 10.1023/A:1001013913773

[64] Abbasi GH, Javaid A, Ul-haq MA, Ali S, Chen ZH, Malik W. Exogenous potassium differentially mitigates salt stress in tolerant and sensitive maize hybrids. Pakistan Journal of Botany. 2014;46(1):135-146.

[65] Apel K, Hirt H. Reactive oxygen species : metabolism, oxidative stress, and signal transduction.
Annual Review of Plant Biology.
2004;55:373-399. DOI: 10.1146/annurev. arplant.55.031903.141701

[66] Büyük İ, Aydın Soydam S, Aras S. Bitkilerin stres koşullarına verdiği moleküler cevaplar. Türk Hijyen ve Deneysel Biyoloji Dergisi. 2012;69(2):97-110. DOI: 10.5505/ TurkHijyen.2012.40316

[67] Sairam RK, Tyagi A. Physiology and molecular biology of salinity stress tolerance in plants. Current Science. 2004;86(3):407-421. DOI: 10.1007/1-4020-4225-6 [68] Blumwald E. Sodium transport and salt tolerance in plants. Current Opinion in Cell Biology. 2000;12(4):431-434. DOI: 10.1016/S0955-0674(00)00112-5

[69] Dietz KJ, Tavakoli N, Kluge C, Mimura T, Sharma SS, Harris GC, ChardonnensAN,GolldackD.Significance of the V-Type ATPase for the adaptation to stressful growth conditions and its regulation on the molecular and biochemical level. Journal of Experimental Botany. 2001;52(363):1969-1980. DOI: 10.1093/ jexbot/52.363.1969

[70] Chakraborty K, Sairam RK,
Bhaduri D. Effects of different levels of soil salinity on yield attributes,
accumulation of nitrogen, and
micronutrients in Brassica spp.
Journal of Plant Nutrition.
2016;39(7):1026-1037. DOI:
10.1080/01904167.2015.1109105

[71] McNeil SD, Nuccio ML, Hanson AD.
Betaines and related osmoprotectants.
Targets for metabolic engineering of stress resistance. Plant Physiology.
1999;120(4):945-949. DOI: 10.1104/ pp.120.4.945

[72] Hanson AD, Rathinasabapathi B, Rivoal J, Burnet M, Dillon MO,
Gage DA. Osmoprotective compounds in the Plumbaginaceae: A natural experiment in metabolic engineering of stress tolerance. Plant Biology.
1994;91(1):306-310. DOI: 10.1073/ pnas.91.1.306

[73] Jantaro S, Mulo P, Incharoensakdi A, Mäenpää P. Content and biosynthesis of polyamines in salt and osmotically stressed cells of Synechocystis sp. PCC 6803. FEMS Microbiology Letters. 2003;228(1):129-135. DOI: 10.1016/ S0378-1097(03)00747-X

[74] Ashrafijou M, Izadi A, Sadat-Noori SA, Saghafi S. Effect of salinity and radiation on proline accumulation in seeds of Canola (*Brassica napus* L.). Plant, Soil and Environment. 2010;56(7):312-317. DOI: 10.17221/2/2010-PSE

[75] Mansour MMF. Nitrogen containing compounds and adaptation of plants to salinity stress. Biologia Plantarum. 2000;43:491-500. DOI: 10.1023/A:1002873531707

[76] Saxena SC, Kaur H, Verma P, Prakash B, Rao V, Majee M. Osmoprotectants: potential for crop improvement under adverse conditions. In: Tuteja N, Gill SS,editors. Plant Accimilation to Environmental Stress. 1st ed. Springer; 2013. p . 197-232. DOI: 10.1007/978-1-4614-5001-6\_9

[77] Ahmed CB, Rouina BB, Sensoy S, Boukhriss M, Abdullah FB. Exogenous proline effects on photosynthetic performance and antioxidant defense system of young olive tree. Journal of Agricultural and Food Chemistry.
2010;58(7):4216-4222. DOI: 10.1021/ jf9041479

[78] Rhodes D, Hanson AD. Quaternary ammonium and tertiary sulfonium compounds in higher plants. Annual Reviews of Plant Physiology and Plant Molecular Biology. 1993;44:357-384. DOI: 10.1146/annurev.
pp.44.060193.002041

[79] Sakamoto A, Murata AN. Metabolic engineering of Rice leading to biosynthesis of glycinebetaine and tolerance to salt and cold. Plant Molecular Biology. 1998;38:1011-1019. DOI: 10.1023/A:1006095015717

[80] Rahman, S, Miyake H,Takeoka Y. Effects of exogenous glycinebetaine on growth and ultrastructure of saltstressed Rice seedlings (*Oryza sativa* L.). Plant Production Science. 2002;5(1): 33-44. DOI: 10.1626/pps.5.33