Physiological, biochemical, and metabolic responses of abiotic plant stress: salinity and drought

Kiarash Jamshidi GOHARRIZI[1],* , Michael R HAMBLIN[2] , Soraya KARAMI[3],* , Maryam NAZARI[4]

[1]Department of Plant Breeding, Yazd Branch, Islamic Azad University, Yazd, Iran
[2]Laser Research Centre, Faculty of Health Science, University of Johannesburg, Doornfontein, South Africa
[3]Department of Agriculture, Payame Noor University (PNU), Tehran, Iran
[4]Department of Agronomy and Plant Breeding, Faculty of Agriculture, Bu-Ali Sina University, Hamedan, Iran

Abstract: The most important types of abiotic stress that affect agricultural crops throughout the world are drought and salinity. These stresses will continue to worsen as the current climate crisis progresses. Plants have evolved a complex set of mechanisms in order to protect themselves from salt and drought. At the macrobiological level, these include alterations in growth rate, water balance, antioxidant defenses, and photosynthesis. Altered metabolites include proline, carbohydrates, glycine betaine, gamma-aminobutyric acid, and polyamines. It is not surprising, thus, that one of the most important research areas of plant biology is the study of plant responses to abiotic stress and stress tolerance mechanisms. The methods, used in this study, are diverse, including the study of physiological properties, biochemical research, and metabolomics approaches toward abiotic stress. This awareness should lead to the development of (near) future, sustainable and better-adapted agriculture in the sense of global warming and environmental emission scenarios. Also, different information presented in this overview can be regarded by the scientific community to produce tolerant cultivars in response to salinity and drought stresses.

Key words: Salinity and drought stresses, physiological characteristics, biochemical traits, metabolomics

1. Introduction

Salinity and drought are two of the main stressors that affect plants' life throughout the world (Nazari et al., 2019; Jamshidi Goharrizi et al., 2020a). These stresses are able to alter the water distribution within the plant and can disturb the ionic balance in the plant resulting in the generation of reactive oxygen species (ROS) (Wang et al., 2003; Jamshidi Goharrizi et al., 2020b). Moreover, the increased ROS can reduce the overall plant production yield in agriculture (Wang et al., 2003; Jamshidi Goharrizi et al., 2019a).

In the last 25 years, increasing salinity has reduced agricultural land productivity by 30%, and this is expected to reach more than 50% by the year 2050 (Yan et al., 2003; Wang et al., 2008). Moreover, more than 45% of agricultural land around the world suffers from constant or repeated droughts, and this is also increasing every year (Ashraf and Foolad, 2007). Osmotic stress, including salinity and drought, affects different plant pathways including physiology and metabolism, with a severity based on the intensity and time duration of the stress, and finally suppresses crop production yields and plant growth (Munns, 2005; Rahnama et al., 2010; James et al.,

2011; Nazari et al., 2020). Although the region affected by drought and salinity is still expanding, genetic resources with high drought/salinity tolerance must be determined (Ibrahim et al., 2019b; Nazari et al., 2019). Therefore, the task of current and potential agriculture is to increase the availability of food to an ever-growing human population under declining environmental conditions in many parts of the world. It is of general interest to mitigate the impact of different forms of abiotic stresses (Fita et al., 2015; Jamshidi Goharrizi et al., 2018). Given its undoubted academic importance and functional consequences in agriculture, the study of abiotic stress resistance mechanisms is one of the most productive lines of research in plant biology. The various types of abiotic stresses imposed by the environment are typically interconnected and often have an osmotic component, which affects the homeostasis of plant cells (Duque et al., 2013).

This paper presents a detailed summary of the present understanding of the physiological, biochemical, and metabolic mechanisms that govern the adaptation of plants to salinity and drought stresses.

* Correspondence: jamshidi_kiarash@yahoo.com

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2. Physiological Mechanisms of Drought Stress

2.1. Effect on Plant Growth

Drought stress is considered a complex process, which can alter the normal process of plant growth at various stages throughout the life span (Yordanov et al., 2000; Jamshidi Goharrizi et al., 2019a; Pakzad et al., 2019; Pakzad et al., 2021). In response to drought stress and under water deficit conditions, more efficient usage of water by the plants is the most critical factor affecting survival and growth. Also, it is well known that water availability can change the growth pattern in plants. For example, the root system is increased in water deficit conditions (Hamblin et al., 1990); in contrast, under normal growth situations and without any stress, the size of the leaf area and the rate of photosynthesis in plants have a positive correlation together, and, therefore, a bigger leaf area is considered useful to accelerate the growth rate of plants (Poorter and Remkes, 1990). The main disadvantage of having a larger leaf area in plants is the loss of more water by transpiration, even in water deficit conditions. Therefore, although a bigger leaf area can increase the growth rate of plants, it also involves a higher usage of water. In plants, better growth and more efficient water usage together determine not only biomass production but also the loss and absorption of water. Moreover, drought stress reduces the accumulation of both fresh and dry biomasses in plants, but the fresh biomass is decreased more than the dry biomass under water deficit stress (Ramos et al., 1999).

2.2. Changes in Plant Water Distribution

Plant yields are considerably reduced because of drought stress, and overcoming this stressor can be extremely difficult (Jamshidi Goharrizi et al., 2020a). Nevertheless, the process of osmotic adjustment in plants is able to overcome the destructive effects of this stress to some extent (Turner, 1986). For this purpose, several different strategies are used by plants, such as tolerance, escape, and avoidance of cell dehydration in order to survive in drought conditions (Turner, 1986). Plants attempt to resist the damage caused by drought stress by preserving the cell turgor to maintain their metabolism. Resistance to drought stress includes two different mechanisms, which are changes in the elastic attributes of tissues, and osmotic adjustment (Munns, 1988).

The main response of plants in response to water shortage is osmotic adjustment, which can maintain the cell turgor (Ludlow and Muchow, 1990) and the metabolism of plants and therefore can allow continual plant growth and yield under water deficit stress (Shackel et al., 1982). Moreover, osmotic adjustment in plants leads to dehydration of bulk tissue and reduced cellular osmotic potential, so roots shoots can develop and grow relatively more under water deficit stress (Bray, 1997).

In plants, the balance of both the metabolic process and the water potential is disturbed under drought stress, but water potential is affected in this situation later than the metabolic process, and, therefore, water potential is more tolerant to water deficit stress compared to the metabolic process (Jones and Corlett, 1992). Several studies have confirmed that there is a relationship between the cell volume and the cellular turgor pressure in sunflower (Maury et al., 2000) and common bean (Zlatko Stoyanov, 2005), but, under drought stress conditions, the balance between these two parameters is significantly disturbed (Blake et al., 1991). Another study showed that the leaf water potential had a great effect on plant functions and determined the response of most plant cultivars in response to drought stress (White et al., 2000).

For many years, it was not clear whether the overall proline content could determine the tolerance of plants under drought stress or not, but recently several studies suggested that the content of this amino acid is much higher in drought-tolerant cultivars compared to drought-sensitive ones (Jamshidi Goharrizi et al., 2020d; Jamshidi Goharrizi et al., 2020f). Moreover, in 1992 the relationship of proline content and turgor pressure was discovered, and it was then considered to be an index for drought injury in plants (Irigoyen et al., 1992).

2.3. Effect on Photosynthesis

Under drought stress, several metabolic processes in plants undergo major changes; photosynthesis is one of the most important metabolic processes in plants, which is affected by drought. Under water deficit stress conditions, the fundamental metabolic processes and the basic structures of plants are damaged, which result in reduced carbon assimilation and damage to the photosynthetic apparatus (Ali and Ashraf, 2011; Golldack et al., 2011). Several studies have shown that a reduction in leaf photosynthesis occurs due to stomatal limitations under moderate drought stress and non-stomatal limitations in response to intense drought stress (Degl'Innocenti et al., 2009; Misson et al., 2010).

The reduction in photosynthesis results in the absorption of more light energy by the plants than is strictly required for photosynthesis, and, therefore, this excess energy is able to produce reactive oxygen species, like hydrogen peroxide, H_2O_2 and superoxide $O_2^{\cdot-}$. The reactive oxygen species (ROSs) are able to prevent the synthesis of the photosystem II (PSII) core D1 (Takahashi and Murata, 2008), which can reduce the overall activity of the photosynthetic electron transport chain.

Moreover, CO_2 fixation in the Calvin cycle is highly susceptible to different environmental stresses such as salinity (Al-Taweel et al., 2007), low temperature, and high temperature (Greer et al., 1986). In response to these destructive stresses, the reduction of the photosynthesis

rate most likely occurs due to a decrease in the synthesis of D1 protein, which occurs as a result of an interruption in CO_2 fixation. However, the precise mechanism of how the photosynthetic electron transport chain is affected by droug

3. Physiological Mechanisms of Salinity Stress

3.1. Effect on Plant Growth

The productivity and yield of plants are greatly affected by soil salinity, which is considered to be an important environmental problem. Salinity stress is able to destroy plant growth through the followings: 1) nutritional imbalance, 2) water deficit stress, and 3) excessive uptake of ions such as Na^+ and Cl^-, which can themselves be cytotoxic (Tsugane et al., 1999; Hernández et al., 2001; Isayenkov, 2012).

Numerous studies have confirmed the relationship between the concentration of NaCl in the soil and reduced plant growth. With an increasing concentration of NaCl, the dimensions of the plants are significantly reduced (Beltagi et al., 2006; Mustard and Renault, 2006; Jamil et al., 2007). Moreover, other studies have shown a negative relationship between the total leaf area and high levels of NaCl (López-Aguilar et al., 2003; Netondo et al., 2004; Bohra and Vyas, 2006; Chen et al., 2007; Zhao et al., 2007a; Liu et al., 2009). Furthermore, the harmful effect of salinity stress on leaf number was shown in another study. This study also proved that leaf number was greatly affected by the concentration of salinity stress (López-Aguilar et al., 2003). The negative (and positive) effects of salt stress on the dry and fresh weights of shoots and biomass have also been reported in several studies. These researchers showed that negative or positive effects of salt stress depended on the level and type of salinity stress and on the type of plant species (Bayuelo-Jiménez et al., 2002; Niazi et al., 2005; Saqib et al., 2006; Turan et al., 2007; Taffouo et al., 2009; Taffouo et al., 2010).

3.2. Changes in Plant Water Balance

Under salinity stress, it is known that the osmotic potential and the uptake of water from the soil are decreased, resulting in a disturbance of the water balance in plants (Munns, 2005). The changes in plant water balance in response to salinity stress allow plants to attempt to overcome this stressful condition using osmotic regulation. This is carried out by increasing the negativity of the osmotic (pressure) potential of the leaf sap (Rodriguez et al., 1997; Gama et al., 2009). In salt-stressed plants, stomatal closure frequently occurs, which lessens tissue dehydration by the reduction of water loss (Fricke et al., 2004). Moreover, the toxic effects of ions also decrease because of reduced transport through the xylem as a result of lowered transpiration (Kerstiens et al., 2002). In a previous study, it was found that barley cultivars exposed to salinity stress decreased their stomatal conductivity and transpiration rates, and the reduction in these parameters caused increased growth as well as reduced the concentration of toxic ions (Veselov et al., 2008). Most likely, the triggering of abscisic acid production in salt-treated plants is one reason for stomatal closure (Mulholland et al., 2003; Fricke et al., 2004; Veselov et al., 2008), but it has been shown that the maintenance of water balance in plants can also be affected by hydraulic parameters and chemical substances (Tardieu and Simonneau, 1998). The stomatal variation in water vapor, which confirms the relationship between stomatal and hydraulic conductivity in salt-treated plants, is extremely susceptible to dynamic disturbances in water transport (Cochard et al., 2002; Meinzer, 2002; Bunce, 2006).

The hydrostatic pressure gradient causes water to enter the root xylem from the soil when plants are actively transpiring, but this balance condition is considerably altered when transpiration is limited by salinity stress. In these situations, the cell-to-cell pathway is the main route of water movement (Steudle, 2000), and most of this water is transported by aquaporins or water channels (Morillon and Chrispeels, 2001). Plasma membrane aquaporins, which belong to the phosphatidylinositol 4,5-bisphosphate (PI4,5P2) or PIP2 subfamily, are relatively abundant phospholipids in the root system. An artificially increased expression of this subfamily increased the activity of water channels in plant cells (Chaumont et al., 2000; Javot et al., 2003). In one study, an increase in the expression of PIP2 aquaporins was observed in maize plants subjected to salinity stress (Zhu et al., 2005).

3.3. Effects on Photosynthesis

Decreased productivity in response to salinity stress in plants is common, and this reduction is usually associated with a decreased photosynthesis rate. Although some factors that can restrict or change the photosynthesis rate in salt-treated plants have been identified, the fundamental mechanisms of decreased photosynthesis are still somewhat unclear (Steduto et al., 2000). Several studies have shown that salinity stress can change many biochemical processes in plants. In this regard, the photosynthesis rate, which is measured by the number of photosynthetic pigments, is one of the most important biochemical processes that undergo major alterations. Several studies have shown that salinity stress is able to reduce the quantity of photosynthetic pigments in salt-stressed plants (Sultana et al., 1999; Misra et al., 2006; Taffouo et al., 2010). Following exposure of plants to salt stress, carotenoids, chlorophylls, and various enzymes, which are part of the photosynthetic apparatus, are strongly affected (Chrysargyris et al., 2018).

Stomatal closure is the main reason for the reduced photosynthesis rate in salt-stressed plants. In addition, the toxicity of salt to the photosynthetic apparatus could

be another reason for the reduction of photosynthesis in plants subjected to salinity stress. However, there are conflicting reports on whether stomatal or non-stomatal factors are most responsible for reduced photosynthesis in salt-treated plants. For example, in sunflowers, beans, and cotton, stomatal limitation was the main reason for the reduction of the photosynthesis rate in response to salt stress, while other reports implicated non-stomatal limitation for the reduction of photosynthesis (Steduto et al., 2000).

4. Biochemical Mechanisms of Tolerance to Salinity and Drought

4.1. Production of substances that affect osmotic adjustment

Salinity and drought stress exert deleterious effects on plant metabolism via ion toxicity, osmotic stress, and oxidative stress (Liang et al., 2018). In contrast, plants have evolved a series of biochemical processes to survive in abiotic stress conditions. The initial response to osmotic stress involves osmotic adjustment. Osmotic adjustment is necessary to maintain the cell turgor and to allow plant survival and maintain productivity. In order to promote osmotic adjustment at the cellular level and provide stress tolerance, plants synthesize several osmotic-regulating compounds, such as soluble proline, carbohydrates, glycine betaine, gamma-aminobutyric acid (GABA), polyamines, and others (Ashraf and Foolad, 2007; Chen and Jiang, 2010; Gupta et al., 2014; Slama et al., 2015; Blum, 2017; Rady et al., 2018; Jamshidi Goharrizi et al., 2020f). At the beginning of salinity or drought stress, the accumulation of osmotic regulating substance in the cytoplasm leads to the protection of cellular functions. Also, these compounds increase the activity of antioxidant enzymes and protect the activity of enzymatic systems (Ashraf and Foolad, 2007; Wei et al., 2009; Hossain and Fujita, 2010; Hayat et al., 2012; Kaya et al., 2013; Theerakulpisut and Phongngarm, 2013; Filippou et al., 2014; Najjaa et al., 2018; Khalid et al., 2020). Several studies have looked at the effect of exogenous application of osmoprotectant substances on the growth and tolerance in drought and salinity stressed plants (Mäkelä et al., 2019; Nakhaie et al., 2020).

4.2. Proline

Proline is the main osmotic balancing compound, which exists in plant cells in its free form. Proline has a low molecular weight, high water solubility, and zero net charge at the physiological pH value range (Trovato et al., 2019). The proline content increases in conditions of biotic and abiotic stress (Goharrizi et al., 2021) and is considered to be one of the main physiological indices of plant resistance to stress (Trovato et al., 2008; Kaur and Asthir, 2015; Dar et al., 2016; Furlan et al., 2020; Jamshidi Goharrizi

et al., 2020f; Khalid et al., 2020). In a study from our laboratory, the proline content was significantly increased in response to drought, salinity, and combined drought plus salinity stresses in different pistachio rootstocks (Jamshidi Goharrizi et al., 2020f; Jamshidi Goharrizi et al., 2020c). Two important factors, which determine salt tolerance, are the balance between the K^+/Na^+ ratio and the accumulation of proline (Kim et al., 2002). Results of several studies showed that the content of proline was at its highest level, while the K^+/Na^+ ratio was at its lowest level in tolerant cultivars of different plants (Gharsallah et al., 2016; Jamshidi Goharrizi et al., 2020f).

Many reports have shown that the harmful effects of salt stress on plant growth could be reduced by proline (Khedr et al., 2003; Szabados and Savoure, 2010; Aqsa et al., 2013; Butt et al., 2016; Ami et al., 2020). Also, the accumulation of proline improved the root capacity for water uptake in drought conditions, protected chloroplast structures by suppressing ROS generation in drought-stressed plants, and is also involved in the tolerance towards photoinhibition (Chimenti et al., 2006; Moustakas et al., 2011; Semida et al., 2020). The findings of Semida et al. (2020) demonstrated that exogenous application of proline could rescue drought-stressed onion (*Allium cepa*) plants and increase plant growth. Supplementation with proline could reduce the irrigation frequency and increase the crop yield in drought-stressed fennel (*Foeniculum vulgare*) plants (Zali and Ehsanzadeh, 2018). Proline pretreatment protected *Aloe. vera* plants against salt stress by modifying the K/Na ratio and water balance, and increasing the antioxidant systems (Nakhaie et al., 2020). Moreover, exogenous application of proline to drought-stressed *Arabidopsis thaliana* plants led to a notable increase in the accumulation of proline and soluble sugars (Moustakas et al., 2011).

4.3. Accumulations of carbohydrates

Under salt and drought stress, the accumulation of sugars and carbohydrates e.g., glucose, fructose, fructans, trehalose, and starch are changed in plants (Anjum et al., 2017; Bianco and Scalisi, 2017). These carbohydrates can reduce the effects of stress by osmotic regulation, improving carbon and energy storage, and scavenging reactive oxygen species (Chen and Jiang, 2010; Nguyen et al., 2010; Yin et al., 2010; Bianco and Scalisi, 2017; Woodrow et al., 2017; Traversari et al., 2020). The studies showed that sucrose accumulation in the leaves in response to drought stress provides the necessary energy for the protection of cells during high respiration rates (Burke, 2007) and promotes plant tolerance to osmotic stresses (salinity and drought) (Van den Ende and Valluru, 2009; Al Hassan et al., 2016; Sami et al., 2016; Kumar et al., 2017a). Indeed, soluble sugars (sucrose, glucose, and fructose) are main energy sources and carry out osmoregulation

in plant cells (Rosa et al., 2009; Bolouri-Moghaddam et al., 2010; Sami et al., 2016; Du et al., 2020b). The sugars are also involved in the regulation of biological processes (Rosa et al., 2009), stability of membranes and protoplasts (Keunen et al., 2013), and the protection of enzymes from high intracellular concentrations of inorganic ions in both normal and stress conditions. Many studies have reported an increased accumulation of sugars in response to drought and salinity stress (Singh et al., 2015). For instance, Tang et al. (2013) showed that the water-soluble carbohydrate concentration increased under salt stress in *Lolium perenne* L. Palma et al. (2013) reported that salt stress caused the content of total soluble sugars and proline to increase in *Medicago sativa*. Zaher-Ara et al. (2016) showed that the accumulation of soluble sugars was involved in drought tolerance in citrus plants. Najjaa et al. (2018) reported that soluble sugars increased in *Allium roseum* in both salt and drought stress conditions. On the other hand, Abdallah et al. (2016) demonstrated that the exogenous application of trehalose reduced the adverse effects of salinity stress in rice plants. Li et al. (2020) reported that the glucose contents increased in *Lilium davidii* var. *unicolor* under drought stress conditions. Fructan can also protect plants against ROS damage, as reducing oxidative stress can increase drought stress tolerance (Rigui et al., 2019). Fructan accumulation under salinity stress could protect a tolerant wheat cultivar and avoid any yield loss under salt stress (Sharbatkhari et al., 2016). Also, it has been reported that fructan could protect sprouting *Helianthus tuberosus L* plants subjected to salt stress (Luo et al., 2018).

4.4. Glycine betaine

Glycine betaine (GB, trimethylglycine) is an amphoteric quaternized amino acid, which is present in plants, animals, and some microorganisms (Rhodes and Hanson, 1993; Chen and Murata, 2008). Glycine betaine has an overall neutral and is stable at a wide range of pH values. Numerous studies have demonstrated that GB accumulation is involved in the tolerance to salinity and drought stress conditions in many plants such as potato (You et al., 2019), *Phasoulis vulgaris* (Desoky et al., 2019; Sofy et al., 2020), stevia (Rameeh et al., 2017), tomato (De la Torre-González et al., 2018), cucumber (Youssef et al., 2018), pigeonpea (Kumar et al., 2017b), sugar beet (Li et al., 2016a), cowpea (Manaf, 2016), wheat (Gupta and Thind, 2019), and lettuce (Shams et al., 2016). Glycine betaine mainly exists in the chloroplasts where it protects the thylakoid membrane and maintains the efficiency of photochemical reactions (Tian et al., 2017). In addition, it promotes plant defensive responses such as osmotic homestasis, protection of enzyme activity, and the expression of genes related to resistance (Chen and Murata, 2011; Giri, 2011; Ahmad et al., 2013; He et al.,

2013; Karabudak et al., 2014; Xu et al., 2018; Annunziata et al., 2019; Kahraman et al., 2019; Mäkelä et al., 2019; Sun et al., 2020). Under drought or salinity stress, GB protects the biological membranes from oxidative damage (Gupta et al., 2014; Wutipraditkul et al., 2015; Kumar et al., 2017c; Wei et al., 2017; Rady et al., 2018; Ahmad et al., 2020), modifies the cell water balance through osmotic adjustment (Gupta et al., 2014; Lai et al., 2014; Yildiztugay et al., 2014), and improves photosynthesis (Zhao et al., 2007b; Wang et al., 2010; Nusrat et al., 2014; Athar et al., 2015; Tian et al., 2017; Wei et al., 2017; Wang et al., 2019b; You et al., 2019; Nawaz and Wang, 2020), resulting in increased plant tolerance.

4.5. Gamma-aminobutyric acid

Gamma-aminobutyric acid (GABA) is an important component of the free amino acid storage system in plants, which provides a substrate for carbon and nitrogen metabolism, and is necessary for plant growth (Ansari et al., 2014). The accumulation of GABA in plants is rapidly increased in various biotic and abiotic stress conditions (Kanwal et al., 2014; Malekzadeh et al., 2014; Nayyar et al., 2014; Wang et al., 2014; Boonburapong et al., 2016; Mei et al., 2016; Vijayakumari and Puthur, 2016; Xiang et al., 2016; Otto et al., 2017; Yoon et al., 2017; Rezaei-Chiyaneh et al., 2018). Also, under salinity stress, GABA acts as an active osmolyte and also has ROS scavenging activity, suggesting that GABA may be associated with plant tolerance (Sheteiwy et al., 2019; Jalil and Ansari, 2020). Under salinity stress, the administration of exogenous GABA protected seedling growth and maintained the normal function of plants by lowering the transport of salt ions into the leaves (Wang et al., 2017b). Moreover, GABA can mitigate the harmful effects of salinity stress by improving photosynthesis and promoting the activity of antioxidant enzymes (Li et al., 2016b; Xiang et al., 2016). GABA can prevent oxidative and osmotic damage (Al-Quraan and Al-Omari, 2017), maintain cell morphology, improve cell function, and stabilize the intracellular PH value (Wang et al., 2017a). Mekonnen et al. (2016) reported that, under drought stress, the accumulation of GABA regulated stomatal opening in *Arabidopsis thaliana.* Vijayakumari and Puthur (2016) reported that the accumulation of proline and total sugars occurred earlier in plants that had been primed with GABA compared with control plants, and the activity of the antioxidant enzymes was enhanced in response to drought stress.

4.6. Polyamines

Polyamines (PAs), which include spermidine, spermine, and the diamine obligate precursor putrescine, are organic nitrogen-containing polycations of low molecular weight. They are involved in the regulation of plant growth and development and govern the defensive responses to abiotic stresses, such as drought and salinity (Takahashi and Kakehi, 2010; Hussain et al., 2011; Hu et al., 2014;

Sobieszczuk-Nowicka and Legocka, 2014; Sun et al., 2016). Hu et al. (2014) reported that exogenously applied spermidine could maintain the structure of chloroplasts and protect the photosynthetic capacity in tomato plants under salinity and alkalinity stress. Li et al. (2018a) showed that exogenous spermidine application could reduce the harmful effects of drought stress in maize plants and improved the growth, photosynthetic pigment content, photosynthesis rate, and photochemical quenching parameters. On the other hand, exogenous spermidine application altered the level of phytohormones, osmolytes, and photosynthetic pigments. It also regulated the redox balance, enhanced antioxidant enzymes, regulated endogenous PA production, and preserved the vacuole structure, which all improved the tolerance of the plants to drought and salinity (Baniasadi et al., 2018; Hassan et al., 2018; Li et al., 2018b; Li et al., 2018a; Mohammadi et al., 2018; Mostafaei et al., 2018; Zhang et al., 2018; Liu et al., 2019; Du et al., 2020a; Hassan et al., 2020; Semida et al., 2020; Zhong et al., 2020).

4.7. Antioxidant Defenses

One of the biochemical changes that occur under drought and salinity stress is the generation of ROS such as hydrogen peroxide (H_2O_2), hydroxyl radicals (•HO), superoxide radical anion (O2•−), and singlet oxygen ($^1O2$). One of the target areas of ROS is the cell membrane, so that ROS with a negative effect on membrane integrity may impair its motility and morphology and possibly lead to cell death (Wang et al., 2019a). In addition to membrane integrity, ROS can damage important cellular components, such as nucleic acids, proteins, carbohydrates, lipids, and enzymes, if not correctly regulated (Miller et al., 2010; Jamshidi Goharrizi et al., 2019b; Jamshidi Goharrizi et al., 2020e). To restore the normal balance of ROS under drought stress, plants increase the expression of different enzymes that can scavenge ROS leading to increased tolerance of salinity and drought stress (Miller et al., 2010; Dar et al., 2017). In addition to antioxidant enzymes, various antioxidant compounds can chemically quench the ROS, thus protecting plants/tissues against oxidative stress. These enzymatic and non-enzymatic ROS scavenging systems can also protect plants against the adverse effects of drought stress (Zhang et al., 2016; Dar et al., 2017; Schneider et al., 2019). The enzymatic antioxidant systems include superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX) and peroxiredoxin (PRDX). Non-enzymatic antioxidants include ascorbic acid (AsA) and glutathione (GS). Antioxidants are required for ROS detoxification during normal plant growth, and especially in stress conditions (Ahmad et al., 2014; Das and Roychoudhury, 2014; Ahmed et al., 2015). Kumar et al. (2017a) reported that the increased activity of SOD and CAT, as well as

soluble carbohydrates, increased the tolerance of *Nerium oleander* to drought and salt stress. Jamshidi Goharrizi et al. (2020f) reported that the activity of antioxidants such as ascorbate peroxidase, catalase, and guaiacol peroxidase (GP) was enhanced in pistachio rootstocks under drought or salinity stress or a combination of the two stresses. Numerous studies have shown that the increased activity of enzymatic and non-enzymatic antioxidant systems are associated with tolerance to drought and salinity in a variety of plants, including wheat (Ahanger and Agarwal, 2017; Ahmadi et al., 2018; Dugasa et al., 2019), maize (AbdElgawad et al., 2016), rice (Islam et al., 2016; Basu et al., 2017; Vighi et al., 2017), *Amaranthus tricolor* (Sarker et al., 2018), soybeans (Liu et al., 2017b), *Chenopodium quinoa* (Fischer et al., 2017), *Thymus vulgaris* & *T. daenensis* (Bistgani et al., 2019), citrus (Hussain et al., 2018), cotton (Ibrahim et al., 2019a), *Nicotiana tabacum* (Da Silva et al., 2017), *Fargesia rufa* (Liu et al., 2017a), cabbage (Sahin et al., 2018), *Anacardium occidentale* (Lima et al., 2018), *Cucumis sativus* (Ouzounidou et al., 2016), sweet basil (Jakovljević et al., 2017), *Carthamus tinctorius* (Golkar and Taghizadeh, 2018), and *Tagetes minuta* (Moghaddam et al., 2019). The results of a study by Sheikh-Mohamadi et al. (2017) showed that high levels of diamine oxidase (histaminase: DAO) and polyamine oxidase were associated with increased tolerance to drought and salinity.

5. Metabolomics profiling in the response to drought and salinity stress

Metabolomics is a fundamental technology to study aspects of functional genomics and systems biology. Metabolomics looks at the final products of gene expression and protein activity and provides a wide overview of the biochemical status of plant tissue under different stresses (Bowne et al., 2018). The regulation of metabolic pathways is a strategy used by plants to increase tolerance under drought and salt stresses. The metabolic profile of plants under drought stress is somewhat similar to plants exposed to salt stress (Table 1). In other words, the signaling pathways of drought and salt stress exhibit some degree of overlap because both of them can lead to cell dehydration, osmotic imbalance, and oxidative stress (Golldack et al., 2014). On the other hand, there are differences in how the metabolic pathways in different species respond to drought, and understanding these differences can help to improve crop productivity (Parida et al., 2018). The TCA (tricarboxylic acid) cycle and metabolism pathways of galactose, starch, sucrose, nitrogen, and antioxidant as well as oxylipin were all important pathways that responded to drought stress (Rangani et al., 2020; Catola et al., 2016).

5.1. Carbohydrates.

The results of metabolomics analysis have shown that the accumulation of several carbohydrates, such as sucrose,

Table 1. Important metabolites, which are altered in both drought and salinity stress.

Metabolite Class	Metabolites	Reference
Sugars	Glucose	(Shi et al., 2015; Nam et al., 2016; Li et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020)
	Sucrose	(Shi et al., 2015; Gupta and De, 2017; Li et al., 2017; Rangani et al., 2020; Xiong et al., 2021)
	Galactose	(Li et al., 2017; Kumari and Parida, 2018; 2019a; Rangani et al., 2020)
	Mannose	(Shi et al., 2015; Li et al., 2017; Mibei et al., 2018; Rangani et al., 2020)
	Myo-inositol	(Li et al., 2017; Mibei et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021)
	Glycerol	(Nam et al., 2016; Gupta and De, 2017; Guo et al., 2018; Kumari and Parida, 2018; Rangani et al., 2020)
	Fructose	(Shi et al., 2015; Gupta and De, 2017; Li et al., 2017; Guo et al., 2018; Kumari and Parida, 2018)
	Trehalose	(Shi et al., 2015; Nam et al., 2016; Mibei et al., 2018; Xiong et al., 2021)
Amino acids	Aspartic acid	(Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Guo et al., 2018; Kumari and Parida, 2018; Rangani et al., 2020)
	Glutamic acid	(Shi et al., 2015; Gupta and De, 2017; Li et al., 2017; Guo et al., 2018; Kumari and Parida, 2018; Mibei et al., 2018; Nawaz and Wang, 2020; Rangani et al., 2020)
	Serine	(Alla et al., 2012; Shi et al., 2015; Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021)
	Glycine	(Alla et al., 2012; Shi et al., 2015; Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020)
	Histidine	(Alla et al., 2012; Gupta and De, 2017; Kumari and Parida, 2018; Xiong et al., 2021)
	Arginine	(Kumari and Parida, 2018; Rangani et al., 2020)
	Threonine	(Shi et al., 2015; Nam et al., 2016; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2020)
	Alanine	(Alla et al., 2012; Shi et al., 2015; Nam et al., 2016; Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021)
	Proline	(Alla et al., 2012; Shi et al., 2015; Nam et al., 2016; Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020)
	Valine	(Alla et al., 2012; Shi et al., 2015; Nam et al., 2016; Li et al., 2017; Guo et al., 2018; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021)
	Methionine	(Alla et al., 2012; Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020)
	Isoleucine	(Shi et al., 2015; Nam et al., 2016; Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021)
	Leucine	(Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020)
	Phenylalanine	(Gupta and De, 2017; Li et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020)
	Lysine	(Shi et al., 2015; Nam et al., 2016; Kumari and Parida, 2018; Rangani et al., 2020)
	Asparagin	(Shi et al., 2015; Nam et al., 2016; Li et al., 2017)
	Tryptophan	(Gupta and De, 2017; Mostafaei et al., 2018; Kang et al., 2019)
Organic acids	Glyceric acid	(Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Guo et al., 2018; Rangani et al., 2020)
	GABA	(Guo et al., 2018; Xiong et al., 2021)
	Shikimic acid	(Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020)
TCA cycle	Oxalic acid	(Nam et al., 2016; Gupta and De, 2017; Guo et al., 2018; Kumari and Parida, 2018; Rangani et al., 2020)
	Malic acid	(Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Guo et al., 2018 Kumari and Parida, 2018; Kang et al., 2019; Rangani et al., 2020)
	Citric acid	(Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021)
	Fumaric acid	(Xiong et al., 2021)
	Succinic acid	(Nam et al., 2016; Gupta and De, 2017; Li et al., 2017; Guo et al., 2018)

glucose, mannose, galactose, erythrose, sorbose, glycerol, galactose, rhamnose, and xylose were significantly changed under water deficit and salinity stress (Kanani et al., 2010; Sanchez et al., 2012; Marček et al., 2019; Rangani et al., 2020; Kumari and Parida, 2018). Besides, Kanani et al. (2010) reported that the concentrations of glycine, N-acetylglutamate, and allantoin were increased in salt stress in *Arabidopsis thaliana*. On the other hand, metabolomics profiling showed a positive relationship between concentrations of sugars and resistance to drought stress in drought-tolerant varieties of *Brachypodium distachyon* (Shi et al., 2015). Marček et al. (2019) showed that the accumulation of sugars such as sucrose, glucose, fructose, and several disaccharides were enhanced in different genotypes of winter wheat under drought stress.

Sugar alcohols are one type of important osmotic adjustment substances. Metabolic profiling has shown that sugar alcohols and metabolites, such as mannitol, inositol, tagatose, d-arabitol, galactose, 1-kestose, myo-inositol, and galactinol were increased when plants were exposed to salt or drought stress (Li et al., 2017; Kumari and Parida, 2018; Rangani et al., 2020; Xiong et al., 2021).

5.2. Amino acids

Amino acid metabolism results in the accumulation of osmoprotectant amino acids, such as proline, glutamate, aspartate, isoleucine, glycine, GABA and phenylalanine, tryptophan, and alanine (Shi et al., 2015; Li et al., 2017; Marček et al., 2019; Xiong et al., 2021). The results showed that high concentrations of amino acids such as isoleucine and phenylalanine may increase glycolysis in order to reduce salt stress and can also act as an osmotic regulator (Kumari and Parida, 2018; Rangani et al., 2020). It has been reported that the levels of alanine, phenylalanine, and tyrosine were enhanced in drought stress, while levels of serine, methionine, glycine, glutamate, and arginine were decreased (Rangani et al., 2020). On the other hand, Xiong et al. (2021) reported that levels of valine, leucine, fumarate, citrulline, and isoleucine were increased in *Phlox subulata* under drought stress, while the levels of alanine and tryptophan were decreased. The results of a study by Marček et al. (2019) showed that amino acids such as proline, threonine, GABA, and glutamine were associated with tolerance to drought stress in wheat genotypes. It was reported that the concentrations of proline, methionine, arginine, lysine, were changed in drought-tolerant wheat genotypes (Michaletti et al., 2018).

5.3. Metabolites involved in ROS scavenging

Results of metabolomics profiling in different species of plants have shown how various metabolites involved in ROS scavenging are altered in response to drought and salinity stress. Some osmoprotectant substances play a simultaneous role as ROS scavenging agents. For example, the results of a metabolomic analysis by Jia et

al. (2020) showed that some soluble carbohydrates, such as glucose, sucrose, fructose, galactose, lactose, trehalose, and myo-inositol were significantly increased in tolerant and susceptible species of poplar (*Populus* spp.) trees in response to drought stress. The accumulation of these metabolites protects cells from damage through osmotic adjustment and by ROS scavenging in drought conditions. The results of this study showed that various non-enzymatic antioxidants, including ascorbate, α-tocopherol, zeaxanthin, and β-carotene, were increased in tolerant species. α-Tocopherol prevented lipid peroxidation by translocating to the lipid membranes and quenching ROS free radicals (Kim et al., 2017).

The carotenoids, β-carotene and zeaxanthin, are involved in photosynthesis and photoprotection, are precursors to phytohormones such as ABA and strigolactone, and are also antioxidants and robustly scavenge free radicals (Cazzonelli, 2011; Mibei et al., 2017). Flavonoids are also secondary metabolites that can quench free radicals and mediate the activation of ROS-induced signaling cascades. Metabolic profiling has shown that many flavonoids are increased in plants subjected to salinity and drought stress (Nakabayashi et al., 2014; Pandey et al., 2015; Goufo et al., 2017; Li et al., 2017; Biswas et al., 2018; Gai et al., 2020). Increased levels of several polyphenols, such as sorbitol (Biswas et al., 2018) and gallic acid (Li et al., 2017) were observed in various plant species subjected to salinity stress.

A raised concentration of isoleucine and phenylalanine can help to scavenge oxygen free radicals. Phenylalanine production via the shikimate pathway is increased under salinity and drought stress. On the other hand, phenylalanine is involved in the production of secondary metabolites that act as ROS scavengers (Kumari and Parida, 2018; Rangani et al., 2020). It was reported that antioxidants such as hydroxylamine and putrescine were increased under neutral salt stress in soybeans (Li et al., 2017).

5.4. Organic acids

Metabolic profiling has shown that various organic acids are involved in plant tolerance to drought and salinity stress. Rangani et al. (2020) reported that galactaric acid, oxalic acid, malic acid, and tartaric acid were all increased in *Salvadora persica* leaves in response to drought stress, while the levels of myristic acid, ribonic acid, tartaric acid, stearic acid, lactic acid, and 2-oxoglutaric acid were all decreased. The accumulation of organic acids, such as 3-hydroxybutyric acid, galacturonic acid, 15-alkyl oleic acid, linoleic acid, and glycuronic acid was also reported to occur after salt stress in soybean plants (Li et al., 2017). It was reported that the accumulation of malic and oxalic acids was increased in several wheat genotypes under drought stress (Marček et al., 2019). On the other hand,

fatty acids and their derivatives play an important role in plant resistance and the storage of energy under abiotic stress. Elevated levels of fatty acids, such as palmitic acid, lauric acid, myristic acid, and sterol acids have been reported to mediate resistance to salinity and drought stress (Kanani et al., 2010; Biswas et al., 2018). The increased accumulation of citric and benzoic acids was also reported in *Phlox subulata* under drought stress (Xiong et al., 2021). Moreover, other organic acids such as pyruvic acid, aminoadipic acid (Michaletti et al., 2018), O-acetyl salicylic acid (Biswas et al., 2018) have been reported to be involved in plant tolerance to drought and salinity stress (Marček et al., 2019). The 16-hydroxypalmitic acid pathway, which is involved in cuticular wax biosynthesis was reported to increase tolerance to drought (Jia et al., 2020).

5.5. Tricarboxylic acid cycle
The tricarboxylic acid (TCA) cycle is one of the main pathways in energy metabolism in all living cells. This cycle involves the oxidation of respiratory substrates to finally produce ATP. Kanani et al. (2010) reported that the levels of all the TCA cycle intermediates ranging from citrate to fumarate were increased in salt stress. The role of the TCA cycle in different plant species has been investigated in both drought and salinity stress conditions (Nam et al., 2016; Gupta and De, 2017; Kumari and Parida, 2018; Rangani et al., 2020).

5.6. Phytohormones
Phytohormones are the key regulators in many plant responses to abiotic stresses (Wani et al., 2016). Plants must be able to modulate their growth and development in response to different internal and external stimuli (Wolters and Jürgens, 2009). Phytohormones are signaling molecules that exist in only small amounts in plant cells but are designed to regulate these responses. Their crucial role in plant adaptation to ever-changing conditions, by regulating growth, sink-source transition in leaves, overall development, and nutrient distribution is well understood (Fahad et al., 2015). Although the response of plants to abiotic stress depends on many different factors, phytohormones are the most significant endogenous agents that regulate physiological and molecular responses, which is important for the survival of plants as sessile organisms (Fahad et al., 2015). Phytohormones can function either at their site of biosynthesis or elsewhere in the plant after their transport (Peleg and Blumwald, 2011). Phytohormones are of major importance in the development of plants and in growth plasticity. Phytohormones are formed from auxins such as indole-3-acetic acid (IAA), cytokinins (CKs), abscisic acid (ABA), ethylene (ET), gibberellins (GAs), salicylic acid (SA), brassinosteroids (BRs), and jasmonates (JAs); it has recently been discovered that strigolactones (SL) are new phytohormones. According to the results obtained,

the levels and activities of phytohormones, such as ABA, SA, and JA increase under drought and salinity conditions (Rangani et al., 2020), so they can act as signaling molecules to promote plant survival under these stress (Kumari and Parida, 2018). Moreover, there is increasing evidence that IAA plays an integral role in the adaptation of plants to salinity stress (Iqbal et al., 2014; Fahad et al., 2015). In plants under water stress, CK levels decreases, and on the other hand, increasing the level of ABA leads to an increase in the ABA/CK ratio. Indeed, the decreased CK levels function to increase apical dominance, and along with ABA acts to modulate the stomatal aperture, which helps in the adaptation to drought stress (O'Brien and Benková, 2013).

6. Conclusion
In summary, as mentioned above, salinity (in water and soil) and drought are important factors that hinder the crop production in areas affected by water scarcity and salt. Regarding the effects of salinity stress, it was found that the metabolic activities of plants could be limited due to the accumulation of salt. Hence, the occurrence of salt stress can be the cause of severe changes in the development and growth of plants, which ultimately reduces plant survival. In contrast, against various ionic and osmotic components of the stress of salinity, several complicated physiological and biochemical reactions (single or combined) are activated at the whole, organ, or cell plant level to overcome or adapt to these harsh conditions. These reactions can occur in the form of various strategies in plants including avoidance, exclusion, ion compartmentalization, extrusion, and so on (single or combined). Therefore, a correct understanding of the mechanisms related to salt tolerance in tissue/organ/cell of plants can provide a new opportunity to integrate biochemical and physiological knowledge to amend and improve salinity tolerance in order to improve economic productivity and facilitate cultivation, especially in salt-affected areas. In addition to salinity, another usual event in many areas is drought. Hence, various mechanisms have been developed by many plant species to deal with this limitation (water supply). Briefly, plant species can prevent stress of drought via maximizing water uptake (e.g., tapping groundwater by longitudinal growth of roots) and/or minimizing water loss (e.g., reducing transpiration by small leaves and closing stomata), etc. However, these strategies can also affect other fundamental plant processes or systems such as the photosynthetic apparatus and related processes (RuBisCo activity, energy balance, and contents and components of chlorophyll) as well as metabolic activities. Despite significant advances in identifying and elucidating drought tolerance mechanisms, significant challenges remain.

In general, the points that should not be overlooked is the fact that, in selection and breeding programs, various indices related to drought and salinity resistance/tolerance/adaptation can be used; however, the interaction between the different indices in the environment and the plant complicates breeding programs for osmotic stresses. On the other hand, variable levels of multiple stresses affect plants under field conditions, but many researchers evaluate the response of plants to specific stress alone under controlled conditions (in laboratory or field conditions). Therefore, there occurs a significant gap between the knowledge obtained under controlled conditions and the knowledge needed to breed plants with the goal of enhancing tolerance/resistance/adaptation to osmotic stresses in field conditions. This is because; the plants' response to specific stress (alone) may not be a true and clear reflection of their behavior in the natural conditions, where several multiple stresses happen simultaneously. In addition, in many cases, the effects of salinity and drought stresses are indistinguishable from each other, because many of the physiological and biochemical mechanisms of osmotic stresses tolerance/resistance are common to many plant species when plants are exposed to the stress of salinity or drought, such as proline, which is an extremely important biochemical mechanism of tolerance to salinity and drought stresses in plants, whereas some mechanisms are specifically amplified under a combination of stresses or vice versa. As a final point, since the response of plants to multiple stresses could not be deduced from the response to individual stress, one of the scopes of study that should be considered is the response of plants to a combination of stresses to develop stress-tolerant/resistant plants in field conditions. On the other hand, the plant's response to multiple stresses may not reflect the incremental impact of these restrictions, but rather, a specific response to a new situation in which many constraints operate simultaneously. Therefore, to accurately describe the actual response of plants to multiple stresses, the stresses must be imposed sequentially or simultaneously, and each set of environmental conditions must be considered as a completely new stress.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Data availability statement

The data that support this study will be shared upon reasonable request to the corresponding authors.

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