*R*eview Article

Role of inorganic and organic ions in response to salt and drought stresses

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ABSTRACT

Plants have different responses to salt and drought stresses. They transport several ions to balance osmotic potential and stomatal closure and opening. Ions including inorganic and organic cations and anions play a crucial role to alleviate abiotic stresses (salt and drought). Inorganic cations containing Na^+, K^+, Mg^{2+} and Ca^{2+} and inorganic anions comprising Cl^-, PO_4^{2-}, NO_3^-, SO_4^{2-} have a great role in osmotic and ion hemostasis in response to salt and water stresses. Organic anions like acetate, succinate, malate, citrate and oxalate showed vital impacts on alleviating damages of drought and salt stresses that lead to higher yield in severe conditions. In order to recognize the mechanisms that increase tolerance of salt and drought stresses, this review illustrates roles of organic and inorganic anions and cations and their interactions on osmotic adjustment, stomata closure and ion hemostasis. Halophytes will be compared with glycophytes as the proper models to find out differences in stress tolerance mechanisms.

KEYWORDS: Cations, anions, organic anions, drought, salt

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INTRODUCTION

Plants react to salt and drought stresses in nearly the same way. Salinity restricts water ability which results in speedy declines in growth level accompanied by a series of metabolic changes that is similar to drought stress (Munns, 2002). Mechanisms that control osmotic and ionic adjustment are highly vital in response to abiotic stresses. Mechanisms in response to salt are divided into two major types: 1) mechanisms that prevent the entrance of salt into the plant (salt exclusion), and 2) mechanisms that avoid high concentrations of salt in the cytoplasm (salt compartmentalization in vacuole). Osmotic adjustment is different in salt compared with drought stress in terms of metabolic charge. The charge of development and remaining in saline soil excluding salt, of intracellular compartmentation, and of evacuating salt to salt glands, is moderately lower than the production of organic solutes in drought stress (Yeo, 1983). The vacuole of a cell isolates Na^+ and Cl^- follows by an accumulation of K^+ and organic solutes in the cytoplasm and organelles in order to balance the osmotic pressure of the ions (Hasegawa et al., 2000). The most prevalent compounds are proline and glycine betaine along with other molecules in distinct species to adapt to dry or saline soils (Hasegawa et al., 2000). However, their rate of accumulation depends on osmotic stress level (Jones & Storey, 1978).

Climate change leads to drought stress which is a main restrictive factor for crop production (Wang et al., 2018).

Drought restricts mineral nutrient availability which could lead to extensive yield losses (Bi et al., 2021). Several plants are able to control nutrient availability by adjusting their metabolite contents in root exudation flows (Canarini et al., 2019). Moreover, drought affects root volume and length which limits water and mineral access. The positive relationship between root physiological and biochemical processes can efficiently adapt plants to water deficiency. Tolerant species can cope with water stress by increasing root oxidative activity and active absorption area, affecting higher mineral nutrition uptake and finally leads to root growth (Bi et al., 2021).

ROLE OF CATIONS IN SALT STRESS

Salinity can affect growth due to the osmotic effect of the salt in the soil solution, and extreme amounts of salt will lead to toxic levels in the older leaves, producing premature senescence. Therefore, it will decrease photosynthesis and the amount of assimilation conveyed to the growing tissues causing additional growth limitations. Further stress is imposed on plants species that have a high degree of salt uptake, or lack efficient salt compartmentalization in vacuoles that categorized as salt-sensitive. However, salt tolerant plants prevent salt toxicity through the transportation of low rates of Na^+ and Cl^- to leaves, and the compartmentalization of ions in vacuoles to inhibit their accumulation in the cytoplasm or cell walls

(Munns, 2002). Streaming Ca^{2+} into the cytosol via the cell membrane and the tonoplast is the primary response to the increase of Na^+ (Zhu, 2003; Wang *et al.*, 2015). The signal transduction pathway of the salt overly sensitive (SOS) plays a major role in salinity tolerance that Ca^{2+} rise triggers SOS3/ SOS2 proteins complexes to motivate SOS1 that is Na^+/H^+ antiporter in the membrane-bound (Zhu, 2002; Chaudhry *et al.*, 2022). Furthermore, SOS1 shows a crucial role in regulating Na^+ efflux at the cellular level along with assistance of Na^+ transport from the root to the shoot. Consequently, the excessive content of the root Na^+ excludes through Na^+/H^+ antiporters of the plasma membrane (Tester & Davenport, 2003). SOS3 is a Ca^{2+}-binding protein that interacts with the SOS2 protein that activate the kinase (Guo *et al.*, 2004). Thus, the kinase activation leads to phosphorylation and transport activity of the SOS1 protein (Quintero *et al.*, 2002). It also controls membrane vesicle transferring, pH homeostasis, and vacuolar functions (Quintero *et al.*, 2011). Therefore, when Na^+ increases, that results in a rapid rise in cytosolic Ca^{2+} content to modulate intracellular Na^+ homeostasis. The SOS3 protein then motivates the SOS2 protein through its inhibitory domain. This complex phosphorylates SOS1 to efflux Na^+ (Figure 1) (Martínez-Atienza *et al.*, 2007). The gene family of HKT has a remarkable impact on Na^+ efflux from leaves to roots. It allows Na^+ loading to phloem from the shoot and Na^+ efflux via unloading it to the roots (Munns & Tester, 2008).

Potassium ion (K^+) has a major role in salinity tolerance that made Na^+ activated net K^+ efflux in salt tolerant barley roots due to a negative relationship between them (Chen *et al.*, 2005). In Arabidopsis, salt damage is mitigated by increasing cytoplasmic K^+ concentrations (Zhu, 2002).

Na^+/K^+ homeostasis has a great impact on plant existence in salt conditions. It was mentioned that NADPH oxidases in Arabidopsis control Na^+/K^+ homeostasis in salt stress (Ma *et al.*, 2012). The content of K^+ was raised to 100 mM in the cytosol to optimize function of cytoplasmic enzymes. Increasing Na^+ concentration in the soil in salt stress leads to reducing K^+ concentration due to the same mechanism for transporting (Schroeder *et al.*, 2013). Na^+ and K^+ have physicochemical resemblances, which Na^+ replaces K^+ in several enzymatic reactions, albeit if Na^+ is available in the soil, it will ultimately be absorbed through plant roots and accumulated in plants (Ghaffari *et al.*, 2014; Huang *et al.*, 2022). Transporter proteins are members of the HKT (histidine kinase transporter) family that regulate Na^+ and K^+ transport (Figure 1) (Yang & Yen, 2002). HKT transporter removes excess Na^+ from the water in tissue, resulting in protecting the leaf tissues from Na^+ toxicity (Schroeder *et al.*, 2013).

ROLE OF CATIONS IN DROUGHT STRESS

Cations play a vital role in response to drought stress. K^+ offers abiotic stress tolerance mechanisms, through enzyme activation, protein synthesis, photosynthesis, stomatal movement, turgor regulation, and osmotic adjustment. It involves in plant signaling systems by motivating antioxidant defense systems.
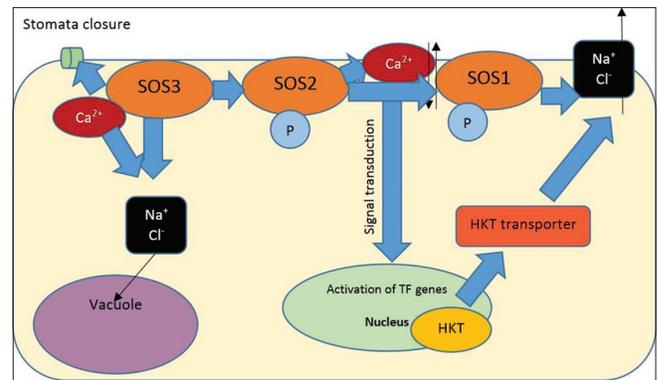
Figure 1: Schematic view of SOS proteins on salt stress tolerance

K^+ provides ideal plant functions by involving in the protein structure and protein activity (Perelman *et al.*, 2022).

Calcium is one of the crucial cations that have a great impact on drought tolerance. Foliar application of Ca^{2+} in sugar beet plants adjusts some mineral status (Mg^{2+} and Si^+) and sugar metabolism that affects plant metabolism and stable redox conditions that lead to drought stress tolerance. By increasing Mg^{2+} and Si^+, the sugar synthesis rises and regulates the genes involved in sugar transport transcriptionally (BvSUC3 and BvTST3). It was indicated that the foliar application of Ca^{2+} caused effective shoot growth and distributed fairly more sucrose to the beetroots in response to drought stress (Hosseini *et al.*, 2019). Besides, foliar application of calcium, increase considerably maize yield and ionic contents of grains including N, P, K and Fe which decreased water stress due to the decreased transpiration rate, declined active transport and depressed membrane permeability that results in restriction of nutrient uptake under water deficiency conditions (Abbas *et al.*, 2021). Foliar application of calcium is expected to rise intracellular Ca levels that can stimulate Ca dependent protein kinases and leads to regulating the expression levels of stress-responsive genes through phosphorylate or dephosphorylate specific transcription factors (Reddy *et al.*, 2011).

Zinc (Zn^{+2}) is known as a necessary microelement for plant growth that is a main part of the carbonic anhydrase enzymes and exists in all photosynthetic tissues, and chlorophyll biosynthesis (Mousavi, 2011). Besides, Zn^{+2} is associated with several physiological purposes, including protein and carbohydrate synthesis (Yadavi *et al.*, 2014). Thus, the Zn application could affect crop yield and quality under drought situations (Khurana & Chatterjee, 2001). The mutual application of compost and zinc demonstrated an increase in growth factors and seed production of canola under drought stress. Soil application of organic fertilizer led to better water holding capacity in the soil and consequently the water use efficiency, enhancing soil fertility and crop growth, while Zn^{+2} affects the yield (Sayed *et al.*, 2021). Selenium (Se^{4+}) increased the net photosynthetic rate, transpirational rate, stomatal conductance and water use efficiency under water deficit stress. However, Se repressed the surge of malondialdehyde (MDA), soluble sugar and proline levels in tomato leaves leading to less reactive oxygen species (ROS). Furthermore, Se augmented the endogenous salicylic

acid (SA) and methylated SA (MeSA) contents in tomato roots and stimulated the conversion of SA to MeSA in tomato leaves in water deficiency conditions (Fan *et al.*, 2022).

ROLE OF INORGANIC ANIONS IN SALT STRESS

Cl^- toxicity is more intense than Na^+ due to the better Na^+ transport than Cl^- transport. In salinity stress, Cl^- loads to the xylem through anion channels to prevent Cl^- transfer to the shoot that the mechanism is down regulated by ABA (Gilliham & Tester, 2005). Furthermore, plants meet a combination of salts, which mainly contain both sulphate and chloride salts in the field (Tarchoune *et al.*, 2010). Some studies have described that NaCl or Na_2SO_4 salinity stress led to damage to growth, pigments, protein metabolism and redox balance in diverse grades in plants (Tarchoune *et al.*, 2010; Irakoze *et al.*, 2020; Wang *et al.*, 2020; Prodjinoto *et al.*, 2021). The results presented that the reduction in plant biomass was great in chloride-sensitive cultivars than in sulphate-sensitive cultivars in canola. Moreover, the presence of Na^+ along with Cl^-/SO_4^{2-} ions had a great impact the decrease in plant growth (Tavakkoli *et al.*, 2011; Reich *et al.*, 2017). Both chloride and sulphate decreased chlorophyll a and b and the whole leaf area, that finally reduce the light capturing capacity and prevention of photosynthesis in rapeseed (Hussein *et al.*, 2017; Huang *et al.*, 2022). Photosynthetic pigments were decreased because Rubisco was hindered by salt stress (Latef *et al.*, 2017). The presence of chloride/sulphate exacerbated plant growth and chlorophyll degradation in sensitive cultivars along with Na^+ (Tavakkoli *et al.*, 2011; Huang *et al.*, 2022).

ROLE OF INORGANIC ANIONS IN DROUGHT STRESS

It was reported that Cl^- along with Na^+ and K^+ is involved in the osmotic adjustment of *J. curcas* plants, in both leaves and roots under control and drought stress. Besides, Cl^- and NO_3^- increased in leaves in response to water stress. It was observed that Cl^- concentration increased in leaves in the plants under drought conditions, whereas it reduced in roots slightly (Silva *et al.*, 2010). The plant species that are cultivated in arid and semi-arid areas have a high attraction to these ions (Silva *et al.*, 2009). NO_3^- contribution to the osmotic potential can be important in leaves and roots, but its impact on the osmotic adjustment is less than Na^+ and Cl^- (Silva *et al.*, 2010). Increasing NO_3^- concentration has been reported in several species to prevent reductase activity (Kameli & Lösel, 1995). On the other hand, chloride (Cl^-) has recently been demonstrated as an advantageous macronutrient that leads to improvement in water use efficiency (WUE), nitrogen use efficiency (NUE), and CO_2 in irrigated plants. If Cl^- is supplied in a range of 1–5 mM, it will expand leaf cell size, improves leaf osmoregulation, and diminishes water consumption with no damaging photosynthetic efficiency. Application of 0.5-5 mM Cl^- in tobacco indicated that application of Cl^- decreased stress symptoms and improved plant growth under drought. Drought resistance stimulated by Cl^- originated from the coincident incidence of drought avoidance and tolerance

mechanisms that results in enhancing leaf turgor, water balance, photosynthesis performance, and WUE. Consequently, it is concluded that advantageous Cl^- levels (1–5 mM) improve the crop's capabilities to stimulate more sustainable and resilient agriculture (Franco-Navarro *et al.*, 2021).

Phosphorus (P) has two anion forms that are taken up by plants ($H_2PO_4^-$ and HPO_4^{2-}) known as essential soil macronutrients (Bindraban *et al.*, 2020) to transport and storing of photosynthesis products in various plant growth and development steps that low P uptake leads to diminishing crop growth and yields (Huguenin-Elie *et al.*, 2009). It was pointed out that cytoplasmic P (metabolic pool) is preserved at a steady level, while great content of the P is deposited in vacuoles as phytate (the salt type of phytic acid; PA) (Shane *et al.*, 2004). Therefore, when cellular phosphate decreases in stress conditions, vacuolar P is unloaded and buffering to the cytoplasm, keeping inorganic P homeostasis in the cytoplasm, but phytate inhibits the absorption of Zn (Bindraban *et al.*, 2020). Foliar application of Pi may not be absorbed in severe drought stress, whereas, there was a regaining of growth and photo assimilation in leaves under mild water deficit at the rehydration step (Santos *et al.*, 2004).

ROLE OF STOMATA IN ION HEMOSTASIS UNDER ABIOTIC STRESS

Abiotic stress hinders photosynthesis by stomatal restriction (Bose *et al.*, 2017). Stomata characterize the microscopic sphincters placed in the shoot epidermis that balance photosynthetic CO_2 gain and water loss. Plants lose 95% of water content by stomata transpiration (Ache *et al.*, 2010). Stomata comprise sets of guard cells to regulate the size of the stomatal pore through changes in their turgor and volume. Abiotic stress accumulates extreme amounts of sodium and chloride in chloroplasts, and potassium homeostasis was interrupted in the chloroplast (Bose *et al.*, 2017). Water influx is achieved by the uptake of K^+ and inorganic anions (Cl^- and NO_3^-), along with the biosynthesis of organic complexes (malate) (Zhu, 2003).

Stomatal closure is a reverse of the opening program when K^+ and inorganic anions (Cl^- and NO_3^-) are released from guard cells and organic anions (malate) are decomposed that resulting in
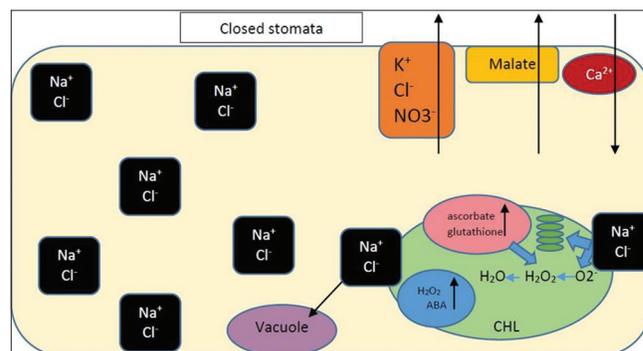
**Figure 2:** Schematic view of a plant cell in stress condition in glycophyte plants

puncture of the guard cells by osmotic water efflux (Figure 2). The stomata aperture is controlled by several environmental and internal signals. In salinity (Sah *et al.*, 2016) and drought (Pazirandeh *et al.*, 2013) conditions, soil water potential reduces that induces abscisic acid (ABA) biosynthesis and hydrogen peroxide (H_2O_2) accumulation in the leaf. ABA induces stomatal closure to reduce transpiration (Sah *et al.*, 2016). However, in halophytes, the ABA content of the leaf is greatly lower than in glycophytic species in both control and stress conditions (Figures 2 & 3) (Hedrich & Shabala, 2018). Accumulation of H_2O_2 in shoots can regulate stomata aperture to adapt to changed soil conditions. H_2O_2 hinders K^+ influx channels (Zhang *et al.*, 2001). Besides, H_2O_2 triggers Ca^{2+} influx channels to an increase in the cytosolic free Ca^{2+} level that leads to activating guard cell anion channels (Pei *et al.*, 2000).

Mg-chelatase H subunit (CHLH), which is known to bring about chlorophyll biosynthesis, controls stomatal closure by dephosphorylating of guard cell H^+-ATPase (Zhao *et al.*, 2018). Thus, stomata close in salt stress condition by ABA and H_2O_2 motivation of potassium and anion efflux in guard cells. Halophytes are abundant in the antioxidant system of ascorbate and glutathione (Bose *et al.*, 2017) and higher levels of antioxidants could affect stomata. Polyphenol accumulation and antioxidant effectiveness are higher in halophytes than in glycophytes (Ozgur *et al.*, 2013). Polyphenols including flavonols accumulate in guard cells to control ROS-induced channel actions and ABA reaction (Watkins *et al.*, 2017). Halophytes concentrate CO_2 and enhance the number of chloroplasts per cell to control stomatal restraint in salt stress. Furthermore, salt influx may be critical for grana formation (thylakoid stacks) in the chloroplast stroma and the activity of photosystem II in halophytes (Figure 3).

A minor amount of fructose-1, 6-bisphosphatase (FruP$_2$ase) and Phosphoenolpyruvate carboxylase (PEPC) enzymes decreased in halophytes in stress conditions than glycophytes (Figure 3). Halophytes use sodium in functional roles and gather further chloride in chloroplasts compared to glycophytes. It is assumed that halophytes have a vital feature that makes halophyte chloroplasts capable of adjusting Na^+, Cl^-, and K^+ transport in different ways than glycophytes which leads to salt
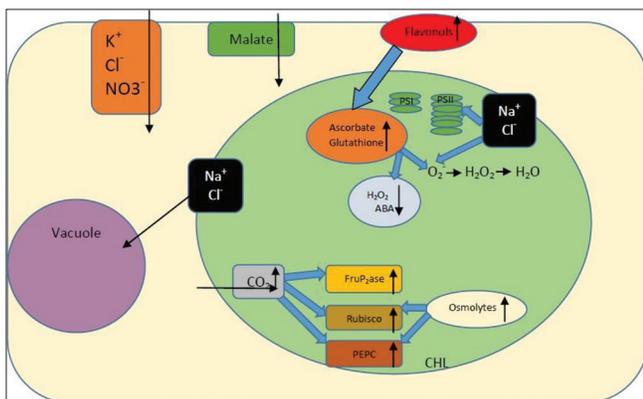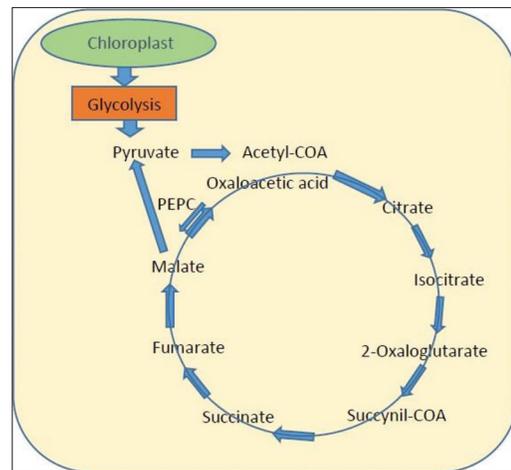
Figure 4: Schematic view of TCA cycle that illustrates Phosphoenolpyruvate carboxylase (PEPC) is a main enzyme creates oxaloacetate and converts it to malic acid in salt-alkali condition

tolerance (Bose *et al.*, 2017). Besides, the Na^+ ion transports pyruvate (Zhao *et al.*, 2016), ascorbate (Miyaji *et al.*, 2015), and phosphate (Guo *et al.*, 2008) into chloroplasts.

However, glycophytes and halophytes may be unlike in their transport processes through Na^+. Most C4 halophytes are NAD-dependent malic enzyme (NAD-ME) to bring in pyruvate to the chloroplast by Na^+, though C4 glycophytes are NADP-dependent malic enzyme (NADP-ME) to introduce pyruvate via H^+ (Aoki *et al.*, 1992; Rao & Dixon, 2019).

C. spinosa is a xerophyte plant that has evolved an extremely effective structure in scarce water conditions. Stomata stay open during the day and season causing a high transpiration rate resulting in a robust cooling effect on leaf temperature and an extraordinarily high net photosynthetic rate compared to other species. This outstanding photosynthetic performance throughout the most stressful period of the year represented that *C. spinosa* has a reasonable benefit than other species (Levizou *et al.*, 2004).

ROLE OF ORGANIC ANIONS IN SALT STRESS

Organic acids are known as the low-molecular-weight complex through the carboxyl group with the role of buffering. Several organic acids containing malic acid, succinic acid, oxalic acid and citric acid can be found in plants (Ma *et al.*, 2015). Though, the amount of organic acid accumulation depends on species, developmental stages and tissue types that indicate the interconversion enzymes of metabolic intermediates are under strong regulatory control (Fernie & Martinoia, 2009). Organic acids play a crucial role in adapting to diverse stresses of plants including heavy metal, drought, and saline-alkali stresses (Chen *et al.*, 2009; Li *et al.*, 2017; Fu *et al.*, 2019). In the tricarboxylic acid cycle, Phosphoenolpyruvate carboxylase (PEPC) is the main enzyme that creates oxaloacetate through phosphoenolpyruvate and CO2, then oxaloacetate was converted to malic acid, and other organic acids will be produced (Figure 4) (Zhang & Fernie, 2018). Consequently, PEPC plays a significant role in organic

Figure 3: Schematic view of a plant cell in halophyte plants under salinity condition

acid synthesis in plant adaption to salt-alkali stress. Plants can conserve pH neutrality by synthesizing the organic acid via the higher activity of PEPC (Ma *et al.*, 2016). PEPC activity was significantly higher in the roots of two sugar beet cultivars in response to salt–alkali stress (Zou *et al.*, 2021). This may indicate that PEPC is one of the major enzymes in organic acid synthesis (Jiang *et al.*, 2019). Tartaric acid and succinic acid were the two main organic acids that accumulated in sugar beet roots in alkali stress (Zou *et al.*, 2021).

However, in other halophytes, including Kochia sieversiana (Yang *et al.*, 2007) and Suaeda glauca (Yang *et al.*, 2008), the oxalate contents were around 90% of organic acids under alkali stress. These results demonstrated that changes in the organic acids metabolism in halophytes signify the critical aim of research under alkali-salt stress in the prospect (Zou *et al.*, 2021).

ROLE OF ORGANIC ANIONS IN DROUGHT STRESS

Organic anions have a great impact on mineral absorption in drought stress through acidification, chelation, and exchange reactions (Oburger *et al.*, 2011; Wang *et al.*, 2016). For example, phosphorus (P) has a main role in numerous biological and biochemical mechanisms including gene duplication, root system development and photosynthesis that are vital to crop production (Raghothama, 2005). Nevertheless, the main challenge in P uptake is that only a small quantity of P is accessible (Holford, 1997).

There are two forms of P soil, inorganic and organic forms (Hedley *et al.*, 1982). Inorganic P is surrounded and absorbed by iron (Fe), aluminium (Al), and calcium (Ca) cations, along with soil positively charged elements (Hinsinger, 2001) that make inorganic P available for plant uptake. On the other hand, organic P makes up to 65% of total P and needs a mineralization process to transform accessible for plant uptake (Richardson *et al.*, 2011). In P deficiencies, plants require to employ several chemical, biological, and biochemical mechanisms to increase P uptake (Yang & Post, 2011). The most significant developments include rhizosphere acidification and the secretion of organic anions and phosphatase enzymes in the rhizosphere in response to poor P conditions (Hinsinger *et al.*, 2009). The releasing of protons from plant roots makes soil acidic which results in solubilizing inorganic P (Nannipieri *et al.*, 2011). Furthermore,
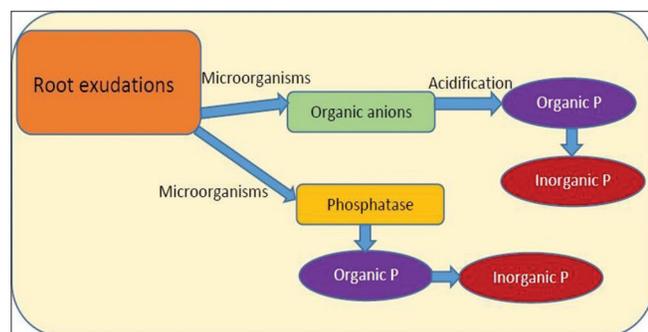
Figure 5: Schematic diagram showing the effects of organic anions and phosphatase on soil phosphorus (P) mobilization

organic P was divided by phosphatase enzymes exudated by plants and microorganisms to make P available to the soil (Figure 5) (Oburger *et al.*, 2011; Gianfreda, 2015).

Microbes can accelerate several mechanisms of P mobilization (Gianfreda, 2015; Zhou *et al.*, 2018). It was demonstrated that organic acids produced by the drought-resistant rice cultivar roots led to higher P uptake and sustain higher yields under drought situations. It was emphasized that the richness of organic acids resulted in solubilizing soil P in moderate and low irrigation conditions. The organic acids comprised 3-hydroxy propionic acid, 5-methoxytryptamine, glutamic acid, aminomalonate, nicotinic acid, proline, ornithine, methionine, succinic acid, citric acid, glutaric acid, malate, and fumaric acid. By exudation of these organic acids, rice resistant cultivar changed the root oxidation and active absorption area of its root system to increase the absorption of P under moderate irrigation, while under low irrigation, the resistant cultivar altered its root length and volume, and increases its root oxidation activity (Bi *et al.*, 2021). On the other hand, research showed that plant biomass and total P content increased by phosphorus addition in blue lupin, white clover, perennial ryegrass, and wheat, along with an increase in microbial biomass P in white clover and ryegrass. Legumes showed higher contents of organic anions in comparison with grasses. After adding P, alkaline phosphatase activity showed a higher concentration in blue lupin. They proposed that organic anions were not associated with the achievement of inorganic P in legumes and grasses. However, alkaline phosphatase activity was associated with the mobilization of stable organic P in blue lupin (Touhami *et al.*, 2020). Another scholar indicated that the application of microbial bio inoculants including trichoderma, mycorrhiza, rhizobium, and organic compounds like cycocel and benzyl adenine are able to mitigate the negative effects of salt and drought stresses on Mustard plant production (Bhardwaj & Kumar, 2020). In conclusion, several root attributes (root hairs and exudation) should be investigated in breeding programs to create P-efficient cultivars (Wang & Lambers, 2019).

INTERACTION BETWEEN ANIONS AND CATIONS IN SALT STRESS

Interactions between anions and cations have a great impact on ion hemostasis in response to salt stress. The cations including Na^+, Ca^{2+} and Mg^{2+} showed a vital impact on salinity, while the main anions are Cl^-, sulphate (SO_4^{2-}) and bicarbonate (HCO_3^-) which contribute to soil salinity. Nevertheless, Na^+ and Cl^- ions are known as the most significant ions due to their toxicity to plants in high concentrations (Hasegawa *et al.*, 2000; Tavakkoli *et al.*, 2010b). Data presented that plants were more sensitive to high Cl^- concentration than Na^+. It was indicated that if leaf Cl^- concentrations are great, the attendance of the Na^+ ions, as the main cation worsens the damage of salt stress that caused chlorophyll degradation and biomass reduction in barley and faba bean (Tavakkoli *et al.*, 2010a, 2010b). In salt stress, plants challenge to preserve a high K^+ to Na^+ ratio in the cytosol (optimal K^+ content is ~80 mM). Thus, regulating the expression and activity of K^+ and Na^+ transporters and H^+ pumps is vital to

create the dynamic force to transport (Shabala & Pottosin, 2014). Specific Ca^{2+} signals have been identified in some regions of the roots in response to K^+ reduction ((Xu *et al.*, 2006). On the other hand, when NO_3^- concentration increases, it activates Ca^{2+} signals to regulate NO_3^- uptake in roots in salt stress (Liu *et al.*, 2017). Ca^{2+} is a cation that has a major role in adjusting anion fluxes for guaranteeing plant nutrition (Manishankar *et al.*, 2018). The same adjustments occur in roots through Ca^{2+} signaling and its interactions with ABA signaling. Anion-conducting ion channel SLAC1 controls the guard cell aperture (Negi *et al.*, 2008). This channel is used for studying and explaining the regulation of ion transfer processes (Hedrich & Geiger, 2017).

One of the main factors for phosphorus availability in soil is the presence of cations including Ca^{2+}, Fe^{2+}, and Al^{+3} (Penn & Camberato, 2019; Dey *et al.*, 2021). Most P fertilizers are fixed in soils with cations in the formula of calcium phosphate, aluminium phosphate, and ferric phosphate which leads to immobilizing P into an inorganic P, and not directly available to plants (Walpola & Yoon, 2012). Besides, the decline of P availability is also increased by salinity (Hu & Schmidhalter, 2005). Applying salt-tolerant phosphate solubilizing bacteria (ST-PSB) that could solubilize and mobilize bio-unavailable P and causes P available for plants in saline soils (Zhu *et al.*, 2011).

INTERACTION BETWEEN ANIONS AND CATIONS IN DROUGHT STRESS

There are some interactions between phosphate anion and nitrate cation on soil in water deficit conditions. It was shown that the application of N fertilizers could surge microbial activity along with an augmentation of phosphatase activity and rhizodeposition in an N-scarce situation (Zang *et al.*, 2017; Chen *et al.*, 2018). However, the addition of N changes to P restriction in P-deficient soil. Thus, it is vital to make P available through triggering mechanisms. But, it has been demonstrated that adding inorganic P hinders phosphatase activity in P-deficient soils (Vitousek *et al.*, 2010). On the other hand, it was described that adding N and P did not show positive consequences on phosphatase activity and microbial biomass (Deng *et al.*, 2017). On the contrary, some scholars described that adding P rise alkaline phosphatase activity, whereas adding N had a reverse effect (Liu *et al.*, 2010; Yang *et al.*, 2015). Furthermore, some data showed that quinoa which is tolerant to drought stress had significant changes in anions including fluoride, phosphate and cations containing potassium, calcium, and ammonium, in response to temperature changes. Both anions and cations increased at higher temperatures (Yang *et al.*, 2016). Increasing concentration of anions and cations at higher temperatures in the xylem illustrated that quinoa could have an osmotic adjustment to compensate transpirational water injury through the accumulation of inorganic ions than organic osmolytes (Shabala & Shabala, 2011). Irrigation and temperature showed significant changes for anions: chloride, sulphate and cation: magnesium. On the other hand, irrigation had a remarkable effect on Cl^- content, but no significant effect on other ionic concentrations. The concentration of both cations and anions was higher under alternate root-zone drying (ARD) and full irrigation (FI) compared to deficit irrigation (DI),

representing improved nutritional grade. It was proved that in FI and ARD conditions, plants could reasonably uptake higher anions and cations than DI (Yang *et al.*, 2016). Besides, the rise in ionic concentration in ARD over DI could be described through the 'birth effect' that leads to alternate wetting and drying cycles of ARD to increase nutrient availability in the rhizosphere (Wang *et al.*, 2012).

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

In this review, we discussed role of inorganic and organic anions and cations on osmotic adjustment, stomata closure and ion hemostasis in response to drought and salt stresses. Besides, we illustrated interaction between anions and cations in both salt and water deficit stresses. We demonstrated schematic views of glycophytes that are sensitive to salt stress and halophytes that are naturally salt-tolerant plants, as success stories in response to salt stress. This review highlights some significant questions that need to be addressed. How Organic acids have a major role in alleviating salt and drought stresses? How do plants establish the interactions between anions and cations in response to salt and water deficit stresses? Investigating the main components of salt and drought stress responses and the development of effective biotechnological approaches between the ionomic and molecular background of stress tolerance that could lead to improve crops efficiently to water and salt stresses.

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