Physiology of Quinoa in Saline Conditions

10

Hugo Bosque and Juan Pablo Rodríguez

Abstract

Salinity is affecting many regions in the world, and common crop plants are not capable of growing under these conditions. First, to introduce new plants to other ecosystems, it is necessary to understand how they perform under salinity conditions. Some plants can grow under high salinity conditions as halophytes. Quinoa, an Andean native crop, is known as a facultative halophyte because can grow up to 18 d S m^{-1}, a high level of salinity, but can tolerate and perform without having a decrease in seed yield and biomass with salinity up to 6 d S m^{-1}.

Quinoa is compared with other plants due to its capacity to withstand saline conditions. Throughout this chapter, the physiological aspects under salinity conditions are depicted and how salinity can affect the absorption of macro- and microelements and high salinity can increase the availability of some elements such as Fe and decrease the availability of microelements. Content of Fe is important in seeds, and that is why quinoa is recommended for marginal, semiarid, and arid regions with soils affected by salinity to grow.

Another advantage of why Quinoa can tolerate salinity is due to particular cells found in the leaves. Roles and functions of epidermal bladder cells (EBCs) located in the leaves are important in quinoa for tolerance to salinity. The EBCs play an important function to quinoa and its environment to regulate tolerance to salinity and high temperature.

H. Bosque (✉)
Faculty of Agronomy, Universidad Mayor de San Andrés, La Paz, Bolivia
e-mail: hdbosque@umsa.bo

J. P. Rodríguez
Crop Diversification and Genetics Program, International Center for Biosaline Agriculture, Dubai, United Arab Emirates
e-mail: jprodriguezcalle@yahoo.fr

A. Varma (ed.), *Biology and Biotechnology of Quinoa*,
https://doi.org/10.1007/978-981-16-3832-9_10

At molecular and genetic level, it is discussed the recent genes discovered in quinoa genotypes that make up to quinoa ready to tolerate salinity. The main advantages of quinoa tolerating salinity are due to the huge quinoa gene pool with many genotypes, particularly "Salares" genotypes tolerant to salinity.

Keywords

Andean grain · Facultative halophyte · Biosaline solution · Sustainable saline plant solution · Saline tolerance

10.1 Introduction

Saline conditions, both soil and water, have always been a significant problem in crop production, because they directly influence the dynamics of water and nutrients in the plant organism, the physiological and metabolic behavior, and indirectly the physical and chemical and even biological properties of the soil, which results in the negative effect on the growth and development of plants in general.

As this situation significantly affects food production, a number of investigations have been generated in all around the world, particularly in those regions with soil salinity problems. Indeed, this aspect is not only limited to traditional, arid, semiarid, and coastal areas but also to those areas that, having adequate conditions in their soils, may suffer salinization phenomena, due to poor management of irrigation and fertilizers or to the use of water with high levels of salinity.

Due to the high economic and social costs of attempts for reclaiming saline soils, many investigations have focused on the use of plant species considered tolerant to salinity. These researches show that this strategy is the most appropriate from the economic point of view, also, with the understanding that global climate change will expend millions of hectares with this problem.

In this way, a race against time is faced, so that humanity has plant genetic resources specially adapted to the new production conditions, mainly salinity and droughts, which will take place in many parts of the world, where particularly glycophytes will no longer have opportunity to contribute to the provision of food.

Moreover, halophytes and facultative halophytes, with food production potential, have a particular interest for many countries and their scientists, giving global importance to this group of plants, which many of them are already considered the food of the future for the humankind.

In this way, the *Chenopodium quinoa* Wild, which is available, and because of its exceptional nutritional quality (Rodríguez et al. 2020), versatility to be adapted to extreme environments such as droughts, frosts, high temperatures, wide latitudinal and altitudinal distribution, have made to this crop, native from Los Andes, and it has captured worldwide interest in the last 20 years. In consequence, facing research its unique treatment in the world of science and technology implies a unique opportunity for those of us who are dedicated to research and academia.

This chapter deals with the plant physiology in saline conditions, understanding that this discipline is of particular interest, when we treat the behavior of an organism under stress conditions, mainly referring to salinity and its consequences on the general metabolism of this crop and others under these conditions.

10.1.1 Saline Conditions

A salt-affected soil is defined as one that has been adversely affected, to the extent that it is no longer suitable for the growth of most crops, by the presence or action of soluble salts. This group of soils includes both saline and sodic soils (Sparks 2003; Evangelou 1994). In general, saline soil is considered with a specific electrical conductance of saturated extract (EC_e) greater than 4 d S cm^{-1} at 25 °C and percentage of Na^+ ions less than 15 concerning the total exchange bases and the pH generally less than 8.5 (O'geen 2018; Ibañez 2008), which is equivalent to approximately 40 mM NaCl, and generates an osmotic potential of approximately 0.2 MPa (Razzaghi et al. 2011), while a saline-sodic soil has CE_e higher than 4 d S cm^{-1} at 25 °C, exchangeable sodium more significant than 15%, sodium index higher than 13, and pH less than 8.5 due to the high electrolyte concentration causing flocculation of soil particles.

Usually, the presence of salts in agricultural soils comes from different sources, like native, irrigation water, fertilizers, groundwater, and others. However, the primary source of salts in soil and waters is the ever-continuing geochemical weathering of rocks that form the upper strata of the earth's continental crust (Tanji 1990). When we refer to saline conditions, we indirectly refer to the reduction of the soil water potential, that is, the higher concentration of salts in the soil solution will be a factor of water deficit due to osmotic effect for plants. The effect on the physical, chemical, and biological properties of the soil is highly significant, due to the ionic composition that occurs when this situation is reached or when the process occurs naturally.

It is well known that saline soils generally have standard physical properties, but as it is mentioned by Warrence et al. (2003), the soil solution salinity can have a flocculating effect on soils, causing fine particles to bind together into aggregates. Elevated salt concentration in the soil solution will promote clay particle aggregation. The net result of this aggregation is that voids between the soil aggregates will be relatively more significant than in non-flocculated soil, the soil will remain more permeable, and the soil will be less likely to become or remain waterlogged upon wetting. The same authors remark that the relationship between soil salinity and its flocculating effects, and soil ESP (exchangeable sodium percentage) and its dispersive effects, dictates whether or not a soil will stay aggregated or become dispersed under various salinity and sodicity combinations.

The excess of sodium in the soil is harmful because it promotes the soil particle dispersion, which at the same time causes the aggregate destruction. This phenomenon causes the clays to close the soil pores and crusting problems, which means that when the soil is moisturized, the particles swell and block the water infiltration. As mentioned by Evangelou (1994), many processes and conditions in the soil environment are highly dependent on colloid dispersion or flocculation. Such processes or conditions include erosion, water suspension of solids, soil structure, and hydraulic conductivity, among many others.

Related to the chemistry of salt-affected soils, Tanji (1990) mentions that the essential cations are Na^+, $Ca2^+$, $Mg2^+$, and, to a lesser extent, K^+. The significant anions are Cl^-, $SO_4{}^{2-}$, $HCO_3{}^-$, $NO_3{}^-$, and, at high pH, $CO_3{}^{2-}$. These interactions occur rapidly enough that we can neglect kinetics and assume chemical equilibrium conditions to prevail in soil chemistry. In some instances, K^+ and $NO_3{}^-$ may contribute to salinity, and when the pH is greater than 9, $CO_3{}^{2-}$ becomes an important anion (Dudley 1994).

As Orsag (2020) summarizes, each of these salts has specific characteristics in their properties when they are present in saline soils. The most soluble salt is NaCl, and it is the most frequent in saline soils by this property. It affects the solubility of other salts by the effect of a common ion. The $MgCl_2$ also has high solubility and is very hygroscopic and can absorb water from the air that dissolves the crystals of these salts. The KCl is a salt with properties analogous to those of NaCl, and it is scarce in saline soils because K^+ can form internal sphere complexes on the surface of some clays, where it is retained. The Na_2SO_4 is frequent in saline soils and presents notable characteristics, its molecular composition varies with humidity, and its solubility varies significantly with temperature, which affects precipitates from other salts. The $MgSO_4$ is a frequent constituent and highly soluble and never accumulates in soils in pure form but in combination with other soluble salts. The presence of Na_2CO_3 and $NaHCO_3$ indicates special physicochemical conditions, linked to alkalinization processes, which leads to soils with very high pH.

On the other hand, $CaCO_3$ is a very poorly soluble salt, and they form firmly cemented, waterproof, and impenetrable soil horizons, while $MgCO_3$ is much more soluble than $CaCO_3$; however, accumulations of this salt rarely occur in soils, due to the adsorption of Mg by clays. In most cases, $CaCO_3$ and $MgCO_3$ are present together. $CaSO_4.2H_2O$ has very low solubility, and nitrates ($NaNO_3$ and KNO_3) are highly soluble salts. However, they do not accumulate in large amounts in soils, where they rarely exceed 0.05%.

Regarding the biological properties of the soils, it should be noted that every organism has specific requirements on temperature, moisture, pH, aeration, and organic matter content as an energy source for its proliferation, among the other factors. On the other hand, it is well known that the microorganisms play a significant role in the dynamics of nutrients and other aspects to give natural fertility to soils. In this way, salinity precisely does not provide these appropriate conditions, so the effects will be more negative as the salt concentrations increase steadily.

In saline conditions, the loss of biological activity of soils is associated with the decline of food supplies for soil microflora necessary for ecosystem functioning (Pankova et al. 2018). High concentrations of soluble salts affect microbes via two primary mechanisms: osmotic effect and specific ion effects. Soluble salts increase the osmotic potential (more negative) of the soil water, drawing water out of cells which may kill microbes and roots through plasmolysis (Yan et al. 2015). Then come biological degradations in saline conditions, mainly because of the reduction of the contents of organic matter and humus and the population of its living organisms. The reason for organic matter reduction is because of the increase in soil pH above 8.5 which promotes the increase in the solubility of organic matter and consequently its washing (Orsag 2010).

10.1.2 Halophytes and Facultative Halophytes

Through the scientific literature, when referring to quinoa, it was indiscriminately referred to as a halophyte (Cai and Gao 2020; Eisa Sayed et al. 2017; Panuccio et al. 2014; Hirich et al. 2014; Koyro and Eisa 2008) or facultative halophyte (Causin et al. 2020; Pitzschke 2016). However, it should be clarified that it is a facultative halophyte, mainly in its place of origin, the Andean region of South America, since there are quinoa crops in saline and non-saline soils. However, some ecotypes have better performance in saline conditions and vice versa.

The halophytes correspond to a group of plants that occupy a famous line within the plant taxonomy. Rozema (1995) refers that the halophytes are plant species with a set of ecological and physiological characteristics allowing growth and reproduction in a saline environment. The occurrence of halophytes on saline soils has often led to the assumption that these halophytic plant species have a (physiological) requirement for salt, sodium, and chloride. In niches of halophytic species, high levels of salt in soil and water often play an essential role. For halophytes, functional traits, those plant attributes that significantly influence establishment and survival, include any mechanisms that contribute to their tolerance of high soil or water salinity as well as other abiotic stresses of their habitats, such as drought or flooding (Flowers and Muscolo 2015).

The definition of halophytes has had significant historical development, and they are manifold. In this regard, Grigore et al. (2014) recount the evolution of this definition since 1892, referring to Grazier who indicates that a halophyte is a plant containing a large quantity of common salt in its composition and which thrives best in salty places, until 2009, referring to Quinn, who says that the halophytes are plants that are tolerant of excess salt.

Nikalje et al. (2019) say that halophytes grow in saline soils and are suitable for saline agriculture. Most of the halophyte plants respond similarly to biochemical and physicochemical stress by salinity. Halophytes are more prepared to tolerate salinity than glycophytes. Halophytes could have stress memory to salinity when pretreatment/priming is used in seeds.

Halophytes can survive under harsh conditions because of their developed adaptation mechanisms, not only toward salinity but also to other abiotic stresses. These tolerance mechanisms help plants to tolerate a wide range of abiotic stresses. Tolerance mechanism involved in abiotic stress includes ion toxicity, water stress, oxidative burst, osmotic adjustment, and homeostasis. Interaction between salinity and other abiotic stresses leads to physiological and biochemical amplification of specific traits, which are usually associated with salinity, such as proline accumulation and antioxidant capability (Nikalje et al. 2019).

While we still have much to learn about these salt-tolerant plants, more than one mechanism operates to generate tolerance—hence the difficulties in engineering tolerance in more salt-sensitive species. Consequently, it is crucial to understand tolerance mechanisms operating at various levels, molecular, physiological, and ecological, to develop an understanding of what is involved in being a halophyte. The long-term aim of such research is to be able to utilize knowledge of halophytes for improvement of the performance of crops in salt-affected soils. However, halophytes are not only valuable as scientific models but also have potential as crops in saline agriculture (Flowers and Muscolo 2015).

10.2 Water Relations in Saline Conditions

Since the last century, dynamics and nature of water-soil and the plant-atmosphere have received much attention, mainly for the development of several concepts to explain the movement of water throughout this complex system. As Kramer and Boyer (1995) summarize, in the twentieth century, emphasis has been placed on osmosis, water potential, water balance, relative water content, plant water potential, and soil-plant-atmosphere continuum, and then research emphasis has had shifted from the whole plant to the cellular and molecular level.

Under saline conditions, the primary importance is related to the influence of electrical conductivity (EC_e) of the soil, as a consequence of the concentration of salts, on the behavior of plants in the uptake of water and specific ions, which will have in its physiological and biochemical effects. In this way, quinoa has been a plant widely investigated to test these effects.

Aly et al. (2018) have found that this plant was able to complete its life cycle and produced economic yield at the salinity of 6.3 d S m^{-1} (EC_e) with 100% of field capacity, while the use of saline water of 38.1 d S m^{-1} and higher caused the quinoa plant's permanent wilting. Nguyen (2016) also confirmed that at a high salt concentration as much as 8 d S m^{-1} NaCl, most of the studied quinoa still produced acceptable yield. Ebrahim et al. (2018) reported that their results showed that the tested cultivars were successfully grown and produced seed yield under high salinity in soil equal to 44% of that present in seawater level. Peterson and Murphy (2015) mentioned that quinoa cultivars decline 73.7% in growth at 32 d S m^{-1} compared with the no-salt control. Eisa Sayed et al. (2017) say that these plants can be grown and yielded successfully in salt-affected soils (17.9 d S m^{-1}), where most if not all of the traditional crops cannot grow, although the yield was reduced. Derbali et al. (2020) mentioned that the tested varieties were able to survive under high salt level (500 mM NaCl) more than seawater salinity (with electrical conductivity of 35 d S m^{-1} as 400 mM NaCl).

In the same way, Yan et al. (2020) have found that at less than 200 mM NaCl, the electrical conductivity reached 18.6 d S m^{-1}, and the water potential of the treatment solutions ranged from -0.22 to -0.89 MPa. Talebnejad and Sepaskhah (2016) reported that the mean value of water potential decrease from -1.53 to -3.09 MPa by increasing water salinity from 10 to 40 d S m^{-1}. With these results, we can conclude that quinoa can still give some yield at high salinity levels and can survive at maximum salinity levels as 35 and 40 d S m^{-1}.

This behavior is related to the water uptake rate. In this sense, Hirich et al. (2014) showed that the increasing levels of irrigation water salinity significantly depressed the water uptake, in which, in terms of total water uptake, there was 25% reduction by using saline water with 10 d S m^{-1} and 52% when irrigating with 30 d S m^{-1} compared to the irrigation with freshwater. Razzaghi et al. (2011) showed that the continuous addition of the salt solutions decreased the soil water osmotic potential and then inhibited plant water uptake, causing the reduction of the total soil water potential. It means that increasing salinity stress and decreasing water availability for plants will have direct effects on physiological behavior. To test water relations in plants and plant water status have been used mainly the leaf water potential, stomatal conductance (or resistance), and transpiration rate, and some findings in these topics are presented in the following paragraphs.

Cocozza et al. (2012) reported that the plant water relations were relatively more sensitive to salt stress concerning water limitation, showing lower values of potential water components. Stomatal conductance decreased as leaf water potential became more negative with a steep drop at leaf water potential between -0.8 and -1.2 MPa, and stomatal conductance decreased with diminishing turgor pressure, with a steep drop between 0.6 and 0.3 MPa. Razzaghi et al. (2011) mentioned that the variation in stomatal conductance in saline-stressed quinoa declined steadily, and Causin et al. (2020) found that in environments with moderate to high salinity, both the decrease in water potential and the accumulation of Na^+ and Cl^- ions can constitute stress factors.

In the same way, Bosque Sanchez et al. (2003) indicate that *Chenopodium quinoa* has amphistomatous leaves and anomocytic stomata with randomly orientated pore, and there is a general tendency in saline-stressed plants to have higher stomatal resistances because they experience a reduction of transpiration rate, which helps the plants to survive the water deficit. Morales (2009) reported that the stomatal conductance measurement of salt-treated plants was also significantly lower than their corresponding controls. Related to these parameters, Saleem et al. (2017) showed that the transpiration rates were found to be decreased in plants with increasing salinity up to 200 mM salinity level. These results suggest high plasticity of quinoa for tolerance to increasing salinity stress, which means increasing soil water deficit. Saleem et al. (2017) also reported that transpiration rates were found to be decreased in two ecotypes of quinoa plants with increasing salinity, up to 200 mM salinity level. Killi and Haworth (2017) also found that supplied saline water (300 mmol NaCl equivalent to 60% of the salinity of seawater) induced reductions in stomatal and mesophyll conductance. Talebnejad and Sepaskhah (2016) concluded that a decrease in transpiration rates accompanied salt-induced photosynthesis inhibition, but also with improved intrinsic water use efficiency. Derbali et al. (2020) mentioned that the maintenance of shoot and root hydration under moderate salinity was undoubtedly due to the control of transpiration rate which remained almost constant, even at high salinity (300 and 500 mM NaCl). These results allow us to conclude that quinoa, with salinity levels as high as 500 mM (50 d S m^{-1}), reduces its transpiration rate but still maintains its metabolic functions.

The stomatal resistance and water potential on quinoa plants are related to some other features. Bosque Sanchez et al. (2003) found out that the salt is not active in the metabolism of the leaves and it is "compartmentalized" in the tissues and organelles. The most elaborated adaptation to salinity is the formation of salt-excreting structures or the salt glands (bladders) on both leaf surfaces and in the stem, inflorescences, and panicles. Ruiz et al. (2015), say that its essential influence in plant water retention and they may also be useful for reducing water loss and UV-induced damage to the photosynthetic apparatus by acting as a "secondary epidermis." Hinojosa et al. (2018) refer that the epidermal bladder cells are modified epidermal hairs and classified as trichomes, along with glandular hairs, thorns, and surface glands. These glands are shaped like gigantic balloons, with a diameter around 10 times bigger than epidermal cells, and can sequester 1000-fold more Na^+ compared with regular leaf cell vacuoles. Talebnejad and Sepaskhah (2016) say that these structures are involved in compartmentalizing salt, thereby excluding it from the other leaf tissues from the underlying photosynthetically active mesophyll. Kiani-Pouya et al. (2019) emphasize on the presence of epidermal bladder cells (EBCs) in halophytes that allows a considerable amount of Na^+ being accumulated, away from the metabolically active mesophyll cells.

Further salinity stress significantly increases bladder density in all the quinoa plants, and at a maximum amount, it increased by more than 3.5-fold, complementing that bladder diameter remained unchanged under saline condition. Shabala et al. (2012) remark that the EBC density differs dramatically with leafage, being most dense in young juvenile leaves; hence, it can be envisaged that it may be attributed not only to the differential amounts of accumulated organic osmolytes but also to the difference in epidermal bladder cell densities. Kiani-Pouya et al. (2017) found the direct evidence for a role of epidermal bladder cells in salt tolerance in halophytes and attribute this to (1) a vital role of these cells as a salt dump for external sequestration of sodium, (2) improved K^+ retention in leaf mesophyll, and (3) the bladders as a storage space for several metabolites known to modulate plant ionic relations. Complementing these assumptions, Orsini et al. (2011) say that the density of epidermal bladder cells on the leaf surface remained unaffected up to 600 mM NaCl. Derbali et al. (2020) reported that the high ability to maintain shoot water content and biomass production under moderate salinity (100 mM NaCl) together with Na^+ accumulation offers quinoa a new character as "salt-includer halophyte."

Regarding the behavior of the stomata, Kiani-Pouya et al. (2019) mentioned that salinity stress significantly affected stomata characteristics, saying that a large genetic variability was found for the stomata density among accessions, ranging from 67 to 159% in relative terms. The relative length of stomata declined by 3–43% in salt-grown plants, which implies that quinoa plants manage to reduce stomatal gas exchange under saline condition by minimizing the size of the pores. Salt-tolerant plants had a negative correlation between salinity tolerance index and stomatal length under saline condition. In this way, Orsini et al. (2011) mentioned that transpiration and stomatal conductance were decreased at the highest salinity levels tested, consistent with reduced stomatal density and size. Talebnejad and Sepaskhah (2016) indicated that salt-induced closure of stomata resulted in photosynthesis rate reduction and, consequently, reduced dry matter accumulation, concluding that stomatal closure in quinoa occurred when the leaf water potential fell below about -1.0 MPa. Increasing water salinity from 30 to 40 d S m^{-1} resulted in a significant decrease in transpiration rate.

Waqas et al. (2017) reported that salinity stress induced a significant reduction in leaf stomata characteristics on adaxial and abaxial leaf surfaces of quinoa plants. The exposure to salinity stresses markedly reduced stomata density by 33 and 35% on adaxial and abaxial surfaces of the leaf, respectively, relative to the untreated control. The stomata aperture also diminished when quinoa plants were exposed, and nonetheless, stomata aperture was reduced by 35.61 and 36.21% on both surfaces of the leaf under salinity stress. Morales (2009) mentioned that the stress response commonly observed in green plants decreases stomatal apertures to limit water loss. Becker et al. (2017) reported that plants increased their number of stomata in response to salt stress but reduced their size on both sides of the leaf, which gives to a hypothesis that this morphological plasticity improves the partition of water and CO_2 resulting in maintenance of photosynthesis in quinoa under adverse environmental conditions. Cocozza et al. (2012) said that the salt-irrigated plants showed a severe drop in leaf water potential, resulting in stomatal closure through interactive effects of soil water availability and salt excess to control the loss of turgor in leaves. Ruiz et al. (2015) said that the observed reduction in stomatal conductance in halophyte leaves is assumed to be essential for better water use efficiency. It may originate from both physiological, e.g., control over stomatal aperture, and morphological, e.g., stomatal density and size, adaptive responses to salinity. Decreased stomatal conductance under saline conditions is regulated by reversible and rapid regulation of the opening and closing of the stomatal pore via ion fluxes in and out of guard cells. Furthermore, Hinojosa et al. (2018) said that their study found a strong positive correlation between stomatal density and plant salinity tolerance and determine that the stomatal density and size could be a key mechanism for optimizing water use efficiency under saline conditions.

Another feature in these aspects is the osmotic adjustment, which is regarded as a critical adaptation of plants to salinity because it helps to maintain turgor and cell volume, and there is a wealth of evidence linking exclusion of salt from the leaf with salt tolerance (Volkmar et al. 1997). Related to this statement, Cocozza et al. (2012) mention that the ability of leaves to adjust osmotically and thereby decrease the value of turgor pressure at full turgor did not appear to be present in different trends between plants experiencing water deficits and salinity conditions, probably because the concurrent increase in tissue elasticity resulted in a larger symplast volume at full turgor. Muscolo et al. (2016) narrated that in most plants, especially halophytes, the solute content of cells at high salinity is higher than in non-saline conditions, mainly due to the accumulation of ions (e.g., Na^+ and Cl^-) and organic solutes, showing that the Cl^- concentration was more than enough to contribute to osmotic adjustment.

Complementarily, Hariadi et al. (2011) observed that quinoa possesses a very efficient system to adjust osmotically for abrupt increases in NaCl stress. Up to 95% of osmotic adjustment in old leaves and between 80 and 85% of osmotic adjustment in young leaves were achieved employing an accumulation of inorganic ions (Na^+, K^+, and Cl^-) at these NaCl levels. Also, Ruiz et al. (2015) reported that the accumulated ions, mainly Na^+, Cl^-, and K^+, are supposedly used for osmotic adjustment, thus facilitating water uptake and transport and presumably lowering the metabolic cost required for the production of organic osmolytes, and this appears to be the case also for quinoa. In the same way, Shabala et al. (2012) found that plant's ability to maintain positive growth under extreme saline condition was indicative of the fact that a full osmotic adjustment in the shoot tissues was achieved by the accumulation of Na^+, Cl^-, and K^+ in old leaves. Moreno et al. (2017) have found that the seed hydropriming and osmopriming caused significant improvements in germination velocity and uniformity with solutions of low water potential of *C. quinoa.*

Furthermore, Orsini et al. (2011) reported the importance of inorganic ions for osmotic adjustment, the plant's ability to maintain K^+ levels, and the involvement of putrescine efflux in maintaining ionic balance under high salinity conditions. Conversely, ion excretion and proline appear to play a minor role. This physiological mechanism is significant for quinoa crops, mainly in saline environments. Complementarily, related to other organic compounds, Delatorre-Herrera et al. (2019) found the osmotic stimulus increased the concentrations of proline, glycine betaine, sucrose, fructose, glucose, and trehalose two- to sevenfold compared to a low salinity conditions.

Regarding the relative water content, Cocozza et al. (2012) observed that the effects of salinity and drought resulted in strict dependencies between relative water content and potential water components, showing that regulating cellular water deficit and volume is a powerful mechanism for conserving cellular hydration under stress. Riaz et al. (2019) mention that the relative water content was significantly decreased at higher salinity levels. Complementarily, Parvez et al. (2020) reported that the relative water contents of leaves were negatively influenced by increasing levels of salinity (300 mM NaCl). Riaz et al. (2019) found that the relative water content was not decreased at lower salt level (100 mM) and was somewhat increased. Stefanov et al. (2020) complemented that large amounts of Na^+ limit the uptake of K^+ from the plants, which is a reason for the disruption of the stomatal regulation and results in irreversible changes in the transpiration flow and a loss of cellular water content. Higher accumulation of Cl^- in plants leads to a significant reduction in the growth and the efficient use of water in plants.

In the end, when we are talking about plant water relations, we focus on water use efficiency. Saleem et al. (2017) said that the intrinsic water use efficiency ($_i$WUE) significantly increased following salinity treatment, showing that their results revealed that $_i$WUE was increased to 58.45% and 37.85% at 20 and 10 $d\ S\ m^{-1}$ NaCl treatments, respectively, as compared to non-saline condition. Related to this statement, Shabala et al. (2012) reported the changes in stomatal density as a mechanism contributing to the improved WUE. Saleem et al. (2017) showed that another interesting observation was the phenomenon of salinity-induced reduction in stomatal density observed in quinoa leaves. It is in contrast to the consensus that, as the cell growth rate is reduced under saline conditions, cells become smaller in size, and this resulted in the more significant number of cells per surface area (i.e., increased cell density).

On the contrary, they believe that such changes may represent a fundamental mechanism by which plant may optimize the WUE under saline conditions. A substantial amount of water evaporated from the leaf surface may bypass stomata and occur through the cuticle. The decrease in stomata density may be a direct result of leaf succulence and an increase in the size of pavement cells. It could be suggested that, by doing this, plants not only improve WUE for the reasons discussed above but also provide additional space for efficient Na^+ sequestration in the leaf epidermis.

As a conclusion for this topic, we refer to Iqbal et al. (2017) who observed that the large quinoa genetic variability in salinity tolerance opened new avenues to explore it further in different salt-affected field conditions. Also, Bonales-Alatorre et al. (2013a, b) from their results suggested that multiple mechanisms contribute toward genotypic differences in salinity tolerance. These include (1) a higher rate of Na^+ exclusion from leaf mesophyll; (2) maintenance of low cytosolic Na^+ levels; (3) better K^+ retention in the leaf mesophyll; (4) a high rate of H^+ pumping, which increases the ability of mesophyll cells to restore their membrane potential; and (5) the ability to reduce the activity of slow tonoplast and fast tonoplast channels under saline conditions. These mechanisms appear to be highly orchestrated, thus enabling the remarkable overall salinity tolerance of quinoa species.

10.3 Nutrient Dynamics on Saline Conditions

Whether in the soil or the plant, due to salinity, the dynamics of mineral nutrients are positively or negatively affected, what is called synergism and ionic antagonism between the different nutrients, since they are assimilated in ionic form from the soil, and also into the plant itself, there will be some interactions. Under this consideration, the most conspicuous in saline conditions is the accumulation of Na^+ and Cl^- in plants, above normal levels, and that indirectly affects the relative concentration of other nutrients. It should also be remembered that sodium is not an essential nutrient. However, most of the research carried out has focused on the dynamics of these two ions and the effect they have on the other nutrients and on the plants.

In regard to this consideration, Aly et al. (2018) observed that salinity induced a significant increase of Na^+ and Cl^- concentrations, while it reduced the ${Mg_2}^+$ and ${Ca_2}^+$ in stems, leaves, seed's coating, and seeds. Kiani-Pouya et al. (2019) have found that under saline condition showed higher K^+, indicating that the uptake of this ion was stimulated under this condition. Also, Koyro and Eisa (2008) found that there were high concentrations of the potential cations K, Ca, and Mg in the pericarp and additionally of the potential anions S and P in the seed interior (perisperm, cotyledons, and hypocotyl). Besides this apparent gradient between potentially toxic (Na and Cl) and primarily needed elements (K, Mg, Ca, P, and S) across the seed coat, there was also a visible change in the distribution of elements in the embryo.

The concentrations of all essential nutrients decreased NaCl-related in the hypocotyl, whereas they were stable (Mg and Ca) or significantly elevated (K, P, S) in the cotyledons. In this way, Cai and Gao (2020) indicated that leaf osmoregulation, K^+ retention, Na^+ exclusion, and ion homeostasis are the main physiological mechanisms conferring salinity tolerance. Complementarily, Eisa Sayed et al. (2017) observed that soil salinity led to a significant decrease of Ca^{++} and Zn^{++} contents in the seed. The higher ash content in seeds under saline conditions was due to the increase of Na^+, K^+, $P_3{}^-$, and Fe^{++} concentrations. Iron increases in quinoa seeds produced under high saline conditions given quinoa a distinctive value for human consumption. This assumption is complemented by Guarino et al. (2020) who also mentioned that the treatment with NaCl alone enhanced the Fe accumulation.

Talebnejad and Sepaskhah (2016) pointed out that increasing water salinity from the lowest value (10 d S m^{-1}) to the highest value (40 d S m^{-1}) resulted in about 4.6-fold increases in plant Na^+ concentration that is almost proportional to an increase in salinity level. At the highest salinity (40 d S m^{-1}), foliar injury symptoms were observed on quinoa leaves that occurred due to the toxic effect of excess Na^+ and Cl^- accumulation in plant. Related to C^{2+}, their results showed that plant $Ca_2{}^+$ concentration variation was in line with plant Na^+ concentration, saying that increasing water salinity from the lowest value (10 d S m^{-1}) to the highest value (40 d S m^{-1}) resulted in about 2.1-fold increases in plant $Ca_2{}^+$ concentration. Increasing water salinity resulted in a significant increase in plant Cl^- concentration, finalizing that the increasing water salinity resulted in a significant decrease in K^+/Na^+ ratio. In regard to these results, Hariadi et al. (2011) found a robust correlation between $NaCl^-$-induced K^+ and $NaCl^-$-induced H^+ fluxes that was observed in quinoa root, suggesting that rapid $NaCl^-$-induced activation of H^+-ATPase is needed to restore otherwise depolarized membrane potential and prevent further K^+ leak from the cytosol. Muscolo et al. (2016) have observed a significant accumulation of Na^+ and no Cl^- in shoots. Orsini et al. (2011) also have observed that the tissue contents of Na^+ and Cl^- increased dramatically with salt treatment but resulted in only a 50% increase in Na^+ from 150 to 750 mM NaCl. Internal K^+ was unaffected up to 450 mM NaCl but increased at the highest salinity levels tested. Sun et al. (2017) suggested that salinity tolerance in quinoa is achieved by a faster removal of Na^+ from the cytosol and a high K^+ concentration in roots and shoots under salinity, resulting in a high K^+/Na^+ ratio, and that a higher proton pump activity drives this mechanism. Parvez et al. (2020) found that the concentration of Na^+ in the shoot and root of quinoa increased with increasing levels of salinity. The lowest amount of K^+ was noted in plants that received an elevated amount of Na^+. Intriguingly, Na^+ and K^+ ions have a very similar ionic radius and hydration energy. Resultant concentration of Na^+ ions is increased, which decreases the concentration of essential nutrients such as K^+. Due to these essential physiological roles of K^+ in plant cells, the maintenance of the proper amount of K^+ under salt stress is very crucial.

Derbali et al. (2020) suggested that some varieties of quinoa possess a high capacity to limit the sodium accumulation in shoot via the control of Na^+ uptake from the medium. Generally, excessive accumulation of Na^+ leads to a nutritional imbalance, usually associated with the restriction of nutrient (K^+, Mg^{2+}, and Ca^{2+}) uptake. It is also the same in the case of quinoa which showed a significant decrease in leaf K^+, Mg^{2+}, and Ca^{2+} under salt treatment. Their data also showed a high K^+ and Mg^{2+} efficiency under high salinity (300 and 500 mM NaCl). A decrease in K^+ content under high salinity can be related to its replacement by Na^+ for a function in osmoregulation. In addition to this statement, Derbali et al. (2020) have shown that low level of sodium toxicity was accompanied by high K^+ and Na^+ selectivity and high K^+ and Mg^{2+} efficiency under high salinity. Complementarily, Muscolo et al. (2016) stated that the significant amount of $SO_4{}^{2-}$ and $NH_4{}^+$ could be the result of accelerated protein catabolism generally activated in high-stress conditions. The deleterious effects of the accumulation of sulfate in seedlings were sufficient to cause metabolic disorders such as chlorophyll decrease and consequent seedling growth depression. Ruffino et al. (2010) mentioned that salt stress considers exerting both osmotic and ionic effects. The content of Na^+ and Cl^- in cotyledons of *C. quinoa* significantly increased in the presence of 250 mM NaCl, whereas K^+ content showed a slighter decrease. As expected, the endogenous Na^+ concentration in cotyledons of *C. quinoa* was significantly higher in the presence of salt. By contrast, K+ concentration decreased slightly under salinity. They conclude that the results confirm the hypothesis that the high adaptability to soil salinity that was growing quinoa seedlings exhibit, is a consequence of better metabolic control than non-halophytic species, based on cotyledon's functionality, of ion absorption, osmolyte accumulation, and osmotic adjustment.

On the other hand, Panuccio et al. (2014) showed that in the presence of KCl and $CaCl_2$, the total ionic concentration gradually decreased with increasing concentrations of salts. Different salts caused a different distribution of cations and anions between the root and shoot. The highest accumulation of anions was observed with $CaCl_2$ and KCl but with a different trend. In $CaCl_2$, the anions increased in a concentration-dependent manner; in contrast, increasing KCl concentrations lowered the anion percentage. El Sebai et al. (2016) showed that all salinity levels resulted in a gradual reduction in N, P, and K percentage. Isobe et al. (2019) showed that increasing the exchangeable K content in soil by the application of KCl has contributed to the increased accumulation of K. Thus, the lower exchangeable K content in the soil led to lower plant K content. Kaya and Aydemir (2020) mentioned that the highest Ca and K nutritional element values were found, respectively, as 12.73 and 33.43 g kg^{-1} dry matter in Heloud cultivar. Peterson and Murphy (2015) say that at 32 d S m^{-1}, quinoa exhibited higher tolerance to Na_2SO_4 applications than to NaCl. Substantial variation was found in salinity tolerance among the quinoa cultivars. Wilson et al. (2002), in the examination of ion ratios, indicated that K^+/Na^+ ratio decreased with increasing salinity. A similar observation was also made for the Ca^{2+}/Na^+ ratios. In quinoa, leaf K^+ levels measured at 19 d S m^{-1} had decreased by only 7% compared with controls. Stem K^+ levels were not significantly affected. Adolf et al. (2012) say that in quinoa the key traits seem to be an efficient control of Na^+ sequestration in leaf vacuoles, xylem Na^+ loading, higher tolerance, better K^+ retention, and efficient control over stomatal development and aperture.

Related to the overall K^+/Na^+ ratio, Aly et al. (2018) say that this was also reduced in plant shoots with salinity stress. Although Na^+ increase was very high, the K^+/Na^+ ratio never fell below 1. P, Zn, Mn, and Cu increased in plant tissue even at high salinity. The seed coat limited the passage of possibly toxic Na^+ and Cl^- to the seed interior, as high Na^+ and Cl^- concentrations were found in the seed coat. Riaz et al. (2019) reported that the Na^+ concentrations in shoot and root were increased with an increase in salinity levels, whereas the K^+ concentrations of plants (shoot and root) decreased as a result of increasing NaCl, giving the ratios of K^+/Na^+ in plants decreased considerably with an increase in the salt stress. Saleem et al. (2017) stated that the highest salinity level is linked to salt stress, which might be due to more absorption of K^+ by the roots at increased Na^+ level. As the salinity level increased, the selective transport of K^+ decreased significantly from root to leaves.

Related to the carbon dynamics, Hussain et al. (2018) showed that salinity decreased the C concentration at both levels (10 and 20 $d\ S\ m^{-1}$) as compared to control. The Na concentration increased more (and was higher), and the C concentration decreased more (and was lower) as in any other part of the seed interior. They concluded that quinoa genotypes differ in foliar $\delta^{13}C$ and $\delta^{15}N$ isotope composition, which reflected complex interactions of salinity and plant carbon and nitrogen metabolisms; then this result can be interpreted as an evidence for the substitution of carbohydrates with NaCl. Koyro and Eisa (2008) say that the change in C concentration mirrored the one of oxygen independent of the salinity treatment.

As a summary of all the research results described in this section, we must point out that, when it is related to mineral nutrients as macronutrients N, P, and K, and secondary Ca, Mg, and S, and micronutrients Fe, Zn, Cu, B, Cl, Mn, and Mo. From this set, in saline conditions, we observed a significant accumulation of Na^+ and Cl^- ions, which will directly or indirectly influence the absorption of all these nutrients. If Na^+ or Cl^- is absorbed, composition of elements such as N, P, K, Ca, Mg, and S can decrease. There are stability or balanced concentration and excellent absorption of Na^+ that would favor the absorption of these elements because the Na^+ ion is excluded as a mechanism of tolerance to salinity. In any case, it is observed that the quinoa plant has the capacity for homeostasis, which makes this species an exceptional plant crop of adapting to extreme saline conditions and salinity itself. Something interesting about this analysis is that, at higher salinity, there is more significant absorption of Fe, a very positive aspect when it comes to the nutritional quality of quinoa, apart from its already known qualities regarding the content of proteins and antioxidants. Undoubtedly, more research will continue to be carried out in this subject, which in the long run will allow us to have a clearer picture of the dynamics of nutrients, mainly under stress conditions, not only saline but others, mainly droughts.

10.4 Photosynthesis in Saline Conditions

Everything we have seen so far will result in the metabolic process itself, that is, both photosynthesis and the respiratory process will be affected differently; it is understood that in general salinity is considered a stress condition. One of the essential factors for the photosynthetic process is water, and salinity causes a deficit of this essential element. On the other hand, the gas exchange in the leaves is considered necessary, which is sometimes affected because the plant, as a preventive way against salinity, causes stomata to close or at least increases the stomatal resistance, and also affects the chlorophyll content. In general, it will be observed that salinity will negatively affect cellular metabolism, which we briefly describe in some research results on quinoa in saline conditions. Stefanov et al. (2020) emphasized it must be borne in mind that salt-induced changes in photosynthesis are directly related to total plant yield, and it is essential to understand how this process is affected by high salt concentrations. Thus, we summarize some research results in saline stress effects in the photosynthetic process.

As is reported by Saleem et al. (2017), they found a severe decline in photosynthesis activity, and it was correlated with a significant reduction in stomatal conductance and high levels of Na^+ accumulation in leaf tissues, which also sharply decrease the photosynthetic capacity of plants. Hussain et al. (2018) have found that the ratio of intercellular to ambient CO_2 concentration was significantly less after treatment with 20 and 10 $d\,S\,m^{-1}$ as compared to control, indicating the closing of stomata and inhibition of CO_2. Killi and Haworth (2017) found that quinoa may not be a suitable crop for areas subject to intense salt stress or irrigation with a concentration of saline water equivalent to a 300 mmol NaCl solution. Talebnejad and Sepaskhah (2016) found that increasing water salinity from 10 to 40 $d\,S\,m^{-1}$ resulted in 12% and 45% decrease of photosynthetic rate, respectively. Zelm et al. (2020) say that there is also an ionic effect or at least a stomatal closure-independent effect of sodium on photosynthesis, and the Na^+ influences photosynthesis by disrupting the proton motive force and chloroplast function and by interfering with CO_2-fixing enzymes. Bonales-Alatorre et al. (2013a, b) concluded that the negative control of tonoplast channel activity in old leaves reduces Na^+ leak, thus enabling efficient sequestration of Na^+ to their vacuoles, which enables optimal photosynthetic performance, conferring salinity tolerance in quinoa species. Derbali et al. (2020) demonstrated that under high salt treatment (500 mM NaCl), the most resistant variety achieved a high stomatal conductance, leading thus to high levels of both intercellular CO_2 concentration and net photosynthesis. Killi and Haworth (2017) showed that salt stress-induced short-term diffusive but also longer-term metabolic limitations to CO_2 assimilation in quinoa. The deleterious effect of salinity was apparent in impaired Rubisco carboxylase activity, RuBP regeneration, and PSII performance.

Regarding the photosynthetic pigments, the chlorophylls (a and b) and carotenoids are the primary photosynthetic pigments because they directly play mainly in the photosynthetic process. Changes in their content will affect the photosynthetic rate directly. El Sebai et al. (2016) reported that quinoa plants irrigated with saline water (4000 and 8000 mg L^{-1}) caused significant gradual decreases in chlorophyll a, chlorophyll b, carotenoid, and total pigment contents. In this way, Riaz et al. (2019) also found that at lower salinities, 100–200 mM NaCl, the chlorophyll content was higher compared with control treatment but decreased at 400 mM NaCl. Waqas et al. (2017) mentioned that salinity affects decreasing chlorophyll a and b and carotenoid content. Rangani et al. (2016) also reported that the reduction in chlorophyll contents at higher salinity level might be due to the degradation of chlorophyll structure. Parvez et al. (2020) observed that chlorophyll contents, chlorophyll a, chlorophyll b, and total chlorophyll decreased with increasing levels of salinity (300 mM NaCl). Ruffino et al. (2010) reported that the total chlorophyll, chlorophyll a, chlorophyll b, and carotenoid concentrations on a dry weight basis were significantly lower in salt-treated samples than in control cotyledons. Under salinity, the content of chlorophyll b was reduced faster than in control cotyledons. Chlorophyll a/b ratio in salt-treated cotyledons showed a progressive increase until the end of the experiment, whereas in control cotyledons, the chlorophyll a/b ratio did not show significant variations during the experimental period. Qureshi and Worku (2020) reported that the chlorophyll content of five genotypes of quinoa tolerated salinity stress up to 10 d S m^{-1} but decreased significantly at higher salinity levels. The highest chlorophyll content was recorded at salinity levels of 0–5 d S m^{-1}. The results indicate a decreasing trend of chlorophyll content with increasing salinity stress. In the same way, Ruiz et al. (2016) found that their data support the inherent potential of the salares landrace R49 to tolerate salinity insofar as it was the only one of the three genotypes analyzed not to exhibit decreased photosynthetic pigment concentrations.

On the other hand, the advent of "stress meters" has allowed the rapid determination of some stress conditions on plants, the fluorescence quenching parameters, especially the ratio of variable to maximal fluorescence, Fv/Fm (Hovenden and Seppelt 1995). Bosque Sanchez et al. (2003) have shown that the salt-treated plants, in general, had slightly higher Fv/Fm ratios than the control. It indicated that salt-stressed plants have better protection to photoinhibition at the level of the reaction center of PSII. Killi and Haworth (2017) reported that analysis of the chlorophyll fluorescence transient suggests that electron transport was impaired throughout PSII in salt-stressed quinoa. Salt stress degraded and damaged the pigment-protein complexes of the thylakoid membrane, likely inducing oxidative stress. Manaa et al. (2019), say that a high resistance of quinoa photosynthetic machinery under moderate salinity as assessed by the high stability of PSI and PSII functions, and by maintenance of functional chloroplast ultrastructure. Indeed, the high PSII efficiency largely maintained under moderate salinity could be associated with the following features: (1) high PSII connectivity and donor side intactness (maintained the fluorescence at K and J step of the induction curve (Fk/Fj) ratio and energy transfer between PSII and antennae) and (2) maintenance of maximal photochemical efficiency (Fv/Fm) and whole primary photochemical reactions. However, under high salinity, both PSI and PSII activities were impaired differentially, and the swelling of thylakoids and disappearance of grana observed under 300 mM NaCl may cause the marginal decrease of maximal fluorescence (Fm) and the decrease in the maximal photochemical efficiency (Fv/Fm), leading to the downregulation of PSII activity.

In this topic, given the scope of the chapter, many other aspects that determine the photosynthetic process have not been explored, that is, the structure and physiology of the photosynthetic apparatus, as well as other factors such as lipid metabolism, proteins, and other organic compounds such as sugars that play a fundamental role in this process. It has focused on the photosynthetic rate and the content of photosynthetic pigments, considering that these are the most significant and that they are directly affected by the salinity of soils and water. It is well known that the essential factors for photosynthesis to take place are the quantity and quality of light, the concentration of CO_2, the content of photosynthetic pigments, the ambient temperature, and even the natural state of the plant organism.

This clarification indicated that in conditions of saline stress, quinoa plants tend to close the stomata to minimize the rate of transpiration and reduce gas exchange, that is, absorption of CO_2, which affects negatively on the capture of light energy by the photosynthetic apparatus, which results in a negative effect on the entire photosynthetic process and therefore on the final yield of the crop. The reduction in the absorption of water by salinity is the determining factor, as this element is crucial for all metabolic processes at the cellular level. It is also worth mentioning that the behavior of the content of photosynthetic pigments is essential since, in most cases, at high salinity levels, there is a degradation of these molecules.

With this conclusion, the question is what happens with quinoa in saline conditions and why so many researchers around the world are looking for salinity tolerance in quinoa these last years? Taking this into account, Shabala et al. (2012) reported that a lack of any detrimental effects of salinity on chlorophyll content it is reasonable to suggest that all accumulated Na^+ was safely sequestered in vacuoles, regardless of the leaf position. These changes include preferential accumulation of Na^+ in old versus young leaves; better osmoprotection of young developing leaves against associated oxidative stress; a significant reduction in the number of stomata per leaf area, as well as a concomitant decrease in the number of pavement cells; and a reduction in measured stomatal conductance that was less pronounced in salt-tolerant varieties. Collectively, these traits contribute to the remarkable salinity tolerance of quinoa, a species that can complete its life cycle in NaCl concentrations equivalent to seawater.

It was concluded that the vast diversity of quinoa is an incredible pool to be able to have appropriate genetic material for extreme conditions of stress, in this case, the stress of salinity.

10.5 Abscisic Acid: The Plant Stress Hormone

Plant hormones play vital roles in the ability of plants to acclimatize to varying environments by mediating growth, development, and nutrient allocation. Hormones move through specific pathways to regulatory sites where they respond to stress at the deficient concentration (Fahad et al. 2014). In several plant species are observed marked and often rapid changes at the hormonal levels in response to stresses, including osmotic and water stress, anaerobiosis, nutrients, and temperature extremes (Naqvi 1994).

In this feature of saline stress conditions, the role of abscisic acid (ABA) is well known; as Taiz and Zeiger (2002) mention, it inhibits growth and stomatal opening, mainly when the plant is under environmental stress. Hartung and Davies (1994) referring to this hormone mention that when abscisic acid is applied externally to plants, their water relations are improved. ABA reduces water loss and promotes water uptake into roots and helps plants to cope with a range of environmental stresses. Examples of such changes are the restricted growth of shoots, reduction in leaf surface area, stimulation of root extents, lateral root growth, and root hair development. Thus, under these remarks, there are research on ABA and its role in quinoa.

Askari-Khorasgani and Pessarakli (2020), when dealing with this hormone, in their recently published work entitled "Phytohormone Homeostasis and Crosstalk Effects in Response to Osmotic Stress, In Passarakli M. (Ed.) Handbook and Crop Stress," extensively explained the role of ABA, whose content was summarized as follows: ABA induces stomatal closure and, therein, activates guard cell anion channels in a calcium-dependent as well as calcium-independent manner. ABA triggers the release of anions and K^+ from guard cells. The decrease in guard cell osmotic pressure and volume results in stomatal closure, reducing the transpirational loss of water from the leaf. The role of ABA on stomatal closure in stress conditions could be originated either from its biosynthesis in the roots or directly from guard cells. Throughout, the ABA contents of the guard cell apoplast, but not the guard cell symplast, were convincingly correlated with stomatal aperture size, identifying an external locus for ABA perception under stress conditions. ABA accumulates in the guard cell apoplast by evaporation from the guard cell wall, so the ABA signal in the xylem is amplified maximally at high transpiration rates. Leaf ABA and ABA in the xylem stream entering the leaf account for changes in the stomatal conductance. On receiving a stress signal, ABA formation starts in vascular tissues and is released from the biosynthesis site into other cells through ATP-dependent transporters. The pH of the xylem sap and water relations can modify the leaf ABA signal.

Additionally, the limitations in stomatal opening imposed by high concentrations of ABA can rapidly and completely reverse by lowering the leaf temperature, and there are also precise interactions between the effect of ABA and CO_2 on stomata (apoplast of the guard cells), intercellular CO_2, and also evaporative demand. ABA, both endogenous synthesized and exogenous application, affect plant water status, water uptake, and growth in different ways such as hydraulic water conductivity both in roots and leaves, root system architecture, and aquaporin (AQP) activity. Despite contradictions, the central tendency is toward a positive effect of ABA on hydraulic conductivity, AQP activity, maintenance of primary root growth with less lateral roots, and plant recovery after rehydration, resulting in higher productivity. ABA can be removed from or released into the transpiration stream before reaching guard cells, depending on the membrane pH gradients around the ABA transport pathway. Changes in transpiration rate can influence the local accumulation of ABA in guard cell walls, while the metabolism of ABA can prevent its buildup.

After having this explanation regarding ABA on stress conditions, we will outline some research results on quinoa on this topic. According to Razzaghi et al. (2011), the xylem ABA concentration in the shoot was two to nine times higher than in the root in saline conditions, while Cocozza et al. (2012) reported that in 2-year experiment, the ABA concentration in leaves was significantly higher in 2010 than in 2009, and marked differences have been observed between days of monitoring in both years. Ruiz et al. (2015) reported that the decreased stomatal conductance under saline conditions is regulated by a reversible and rapid regulation of the opening and closing of the stomatal pore via ion fluxes in and out of guard cells. The process in the stomata is under the control of abscisic acid (ABA), concluding that the first increases in ABA and decreased leaf and soil water potential are indicative of osmotic stress caused by salinity.

As salinity is synonymous with water deficit, we can compare with studies in drought stress, where Jacobsen et al. (2009) reported that root-originated ABA plays a role in stomata performance during soil drying. ABA regulation seems to be one of the mechanisms utilized by quinoa when facing drought inducing a decrease of turgor of stomata guard cells. Gamez et al. (2019) reported that the lower stomatal opening and transpiration rates were also associated with higher leaf ABA concentration values detected in Rainbow cultivar. They have found negative logarithmic relationships between stomatal conductance and leaf ABA concentration in two quinoa varieties (Rainbow and Illpa). These moderate-to-medium values suggest that, in addition to ABA signaling, other causes for stomatal closure under drought such as hydraulic regulation may play a role. Fahad et al. (2014) found that ABA acts as a mediator in plant responses to many stresses, including salt stress, and the functional analysis of cytokinin receptor mutants shows that cytokinin receptors of *Arabidopsis* act as negative regulators in ABA signaling and osmotic stress response.

10.6 Molecular and Cellular Response in Saline Conditions

Salinity in soil and water presents constraints when the resources of freshwater are reducing in the world. Many crop plants that we consume are glycophytes, which grow with freshwater. However, some plants can grow under saline irrigation known as halophytes (Volkmar et al. 1997). The reaction at the cellular and molecular level is different between them. Amaranthaceae (botanical family) has many plant species that can grow under saline conditions such as *Swaeda foliosa*, *Suaeda fruticosa*, *Salicornia europaea*, *Atriplex cordobensis*, *A. nummularia*, and the facultative *Chenopodium quinoa*. Recently, quinoa is a well-promoted Andean crop and introduced in many parts of the world due to its capacity to tolerate salinity in irrigation and soil content.

Salinity effect in plants affects principally at the cellular level; however, quinoa tolerates salinity due to specific cells located in the epidermis of leaves. These cells are the epidermal bladder cells (EBCs) that help quinoa to balance salt between the environment and the plant.

Salinity is a significant factor that can affect strongly the productivity in crops (Shabala et al. 2016; Bohm et al. 2018). However, some plants can tolerate salinity from low to high concentration of salt. This type of salinity-tolerant plants can become an alternative to produce food, seed, and biomass. Several studies confirmed the potential of quinoa to grow from emergence stage to grain setting under saline conditions. *Arabidopsis* plant has been used as a model plant to understand salinity adaptation at the cellular and molecular level (Hasegawa et al. 2000; Yun 2005). Quinoa due to its high genetic variability can offer many genotypes to grow under saline conditions, low water requirement, seed size, and growth type. However, *Chenopodium quinoa* at the cellular and molecular level becomes an extraordinary Andean plant model to salinity tolerance. Quinoa is a facultative halophyte that can tolerate high levels of salinity up to 50 Mm (50 d S m^{-1}) (Adolf et al. 2012; Becker et al. 2017).

At the molecular level, epidermal bladder cells (EBCs) are external structures that are of interest of quinoa due to capacity to tolerate salt. Kiani-Pouya et al. (2017) gave direct evidence on the role of EBC to salt tolerance and salt dump for external sequestration of sodium in quinoa. Besides, quinoa becomes a good model plant to explain salt mechanisms at the cellular and molecular levels (Ruiz et al. 2017; Bohm et al. 2018). When salt enters and is accumulated in the vacuole, the Na^+ and Cl^- are required to cross the membranes and be transported to bladder cytoplasm (Bohm et al. 2018).

Bohm et al. (2018) demonstrated by RNA-seq analysis of leaf and bladder samples a small number (83) of genes showing responses to salt. It is suggested that bladder cells are responsible for salt sequestration. Quinoa has two genes expressed in the root CqHKT1.1 and the leaves CqHKT1.2. The bladder in quinoa leaves has a specific function to allow Na^+ inside salt dumpers. This gene in quinoa allows to supervise enough amount of Na^+ and to avoid overloading the cytoplasm (Bohm et al. 2018).

Quinoa bladders in the leaves contain CIC-type proteins as an ortholog of AtC1C-c, which has the function to accumulate chloride in EBC vacuoles (Bohm et al. 2018). At the cellular level, the osmolytes have a role in protecting the cytosolic metabolism from the toxic effect of NaCl. Proline an essential amino acid produced in the leaves has a role in supporting the leaves to tolerate salt stress conditions (Bohm et al. 2018). Bohm et al. (2018) demonstrated with their study that bladder in quinoa leaves functions as salt dumper which helps tolerate salt.

Morales et al. (2017) used a Chilean “Salares” quinoa ecotype. RNA-seq analysis of R49 genotype compared drought and control irrigation conditions. 104.8 million reads were obtained with 54 M reads for the control and 51 M reads for drought condition. Expression pattern for canonical drought responses such as ABA biosynthesis and other genes induced by qPCR was assessed, and it suggests the novelty of R49 drought responses. R49 genotype had the best performance on physiological parameters and the highest tolerance to drought.

Zou et al. (2017) generated a high-quality genome draft using an inbred line of the quinoa cultivar “Real.” The genome was highly repetitive (64.5% repeat content) and contained 54,438 protein-coding genes and 192 microRNA genes, with more than 99.3% having orthologous genes from glycophylic species. Stress tolerance in quinoa is associated with genes involved in ion and nutrient transport, ABA homeostasis and signaling, and enhanced basal-level ABA responses.

Ruiz et al. (2019) used quinoa to clear up on salt tolerance mechanisms at the transcriptomic level. RNA-seq analysis of genotype R49 at an early vegetative stage compared high salinity (300 mM NaCl) and control (freshwater) conditions in a time-course pot experiment. A total of 2416 differentially expressed genes (DEGs) were identified based on the treatment and time of sampling. A total number of upregulated and downregulated genes were 945 for salt-treated and 1471 for control plant. Besides, the genes are involved in biological processes like oxidation-reduction, response to stress and response to ABA, and cell wall organization. These genes in this quinoa genotype have the role of “stress-anticipatory preparedness” to salinity tolerance.

Shi and Gu (2020) performed a reference-guided assembly and compared gene expression in quinoa roots treated with 300 mM NaCl for 0, 0.5, 2, and 24 h of two contrasting genotypes, salt-tolerant (ST) and salt-sensitive (SS), under salt stress. One hundred seventeen DEGs were common of both genotypes, identified as core salt-responsive genes, including some transcription factor members, like MYB, WRKY, and NAC, and some plant hormone signal transduction-related genes, like PYL, PP2C, and TIFY10A, that play a role in the adaptation to salt conditions. Twenty-one DEGs by quantitative real-time PCR (qRT-PCR) were detected and confirmed the reliability of the RNA-seq results—candidate genes involved in salt tolerance as DEGs in ST genotype.

Quinoa is a facultative halophyte plant and is considered halophyte at laboratory perspective for its tolerance to salinity and other metals in the soils. Guarino et al. (2020) demonstrated with real-time RT-qPCR analysis on gene transporters for sulfate, iron, and phosphate and phytochelatin, metallothionein, glutathione synthetase, dehydrin, Hsp70, and enzymes responsible for the biosynthesis of proline (P5CS), glycine betaine (BADH), tocopherols (TAT), and phenolic compounds (PAL). The analysis showed that genes were affected by Cr(III), Cr(III)+, and NaCl. Changes in sulfur and phosphorus allocation are related to quinoa and its ability to tolerate Cr through the activation of stress-protective molecules. With this study, Guarino et al. (2020) demonstrated that quinoa could be an essential alternative to grow in soils affected by chromium and moderate saline conditions.

10.7 Conclusions

In conclusion, there is a shred of clear evidence that quinoa has high adaptability to salinity. Halophyte plant species grow in extreme salinity conditions. Nevertheless, many of them do not have the same profile as the quinoa. *Chenopodium quinoa* is a facultative halophyte that can grow and produce an adequate seed yield at 6 d S m^{-1}

without the effect of salinity; however, salinity irrigation up to 18 d S m^{-1} decreases seed yield.

Chlorophyll content in leaves is affected when saline conditions are high and environmental temperature is warm. However, quinoa can withstand these conditions. Therefore, quinoa is recommended for cultivation in semi-arid to arid ecosystems, when precipitation is lower and soils are affected by salinity.

High salinity affects the absorption of macro- and microelements essential for the nutrition of the quinoa plant but can increase the mobilization of Fe, an important element, particularly in the seed.

References

Adolf VI, Jacobsen S-E, Shabala S (2012) Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). Environ Exp Bot 92:43–54. https://doi.org/10.1016/j.envexpbot.2012.07.004

Aly AA, Al-Barakah FN, El-Mahrouky MA (2018) Salinity stress promote drought tolerance of *Chenopodium quinoa* Willd. Commun Soil Sci Plant Anal 49:1331–1343. https://doi.org/10.1080/00103624.2018.1457160

Askari-Khorasgani O, Pessarakli M (2020) Chapter 19: Phytohormone homeostasis and crosstalk effects in response to osmotic stress. In: Pessarakli M (ed) Handbook of plant and crop stress, 4th edn. CRC Press, Taylor and Francis Group, Boca Raton, pp 361–384. https://doi.org/10.1201/9781351104609

Becker VI, Goessling JW, Duarte B et al (2017) Combined effects of soil salinity and high temperatures on photosynthesis and growth of quinoa plants (*Chenopodium quinoa*). Funct Plant Biol 44(7):665–678. https://doi.org/10.1071/FP16370

Bohm J, Messerer M, Muller HM et al (2018) Understanding the molecular basis of salt sequestration in epidermal bladder cells of *Chenopodium quinoa*. Curr Biol 28:3075–3085. https://doi.org/10.1016/j.cub.2018.08.004

Bonales-Alatorre E, Pottosin I, Shabala L et al (2013a) Differential activity of plasma and vacuolar membrane transporters contributes to genotypic differences in salinity tolerance in a halophyte species, *Chenopodium quinoa*. Int J Mol Sci 14:9267–9285. https://doi.org/10.3390/ijms14059267

Bonales-Alatorre E, Shabala S, Chen Z-H et al (2013b) Reduced tonoplast FV and SV channels activity is essential for conferring salinity tolerance in a facultative halophyte, *Chenopodium quinoa*. Plant Physiol Preview. https://doi.org/10.1104/pp.113.216572

Bosque Sanchez H, Lemeur R, Van Damme P (2003) Ecophysiological analysis of drought and salinity stress of quinoa (*Chenopodium quinoa* Willd.). Food Rev Intl 19:111–119. https://doi.org/10.1081/FRI-120018874

Cai ZQ, Gao Q (2020) Comparative physiological and biochemical mechanisms of salt tolerance in five contrasting Highland quinoa cultivars. BMC Plant Biol 20:1–15. https://doi.org/10.1186/S12870-020-2279-8

Causin HF, Bordon DAE, Burrieza H (2020) Salinity tolerance mechanisms during germination and early seedling growth in *Chenopodium quinoa* Wild. genotypes with different sensitivity to saline stress. Environ Exp Bot 172:103995. https://doi.org/10.1016/j.envexpbot.2020.103995

Cocozza C, Pulvento C, Lavini A (2012) Effects of increasing salinity stress and decreasing water availability on ecophysiological traits of quinoa (*Chenopodium quinoa* Willd.) grown in a Mediterranean-type agroecosystem. J Agron Crop Sci 199:229–240. https://doi.org/10.1111/jac.12012

Delatorre-Herrera J, Rojas-Urrutia J, Rojo LE et al (2019) Osmotic stress in *Chenopodium quinoa* Willd.: variations in osmoprotectants at different phenological stages. Afr J Agric Res 14:361–368. https://doi.org/10.5897/AJAR2018.13484

Derbali W, Goussi R, Koyro H-W et al (2020) Physiological and biochemical markers for screening salt tolerant quinoa genotypes at early seedling stage. J Plant Interact 15(1):27–38. https://doi.org/10.1080/17429145.2020.1722266

Dudley LM (1994) Salinity in the soil environment. In: Pessarakli M (ed) Handbook of plant and crop stress. Marcel Dekker, Inc., New York, pp 13–30

Ebrahim MEA, Hussin SA, Abdel-Ati AA et al (2018) Evaluation of some *Chenopodium quinoa* cultivars under saline soil conditions in Egypt. Arab Univ J Agric Sci 26:337–347

Eisa Sayed S, Eid MA, Abd El-Samad EH (2017) *Chenopodium quinoa* Willd. A new cash crop halophyte for saline regions of Egypt. Aust J Crop Sci 11:343–351. https://doi.org/10.21475/ajcs.17.11.03.pne316

El Sebai TN, AbdAllah MMS, El-Bassiouny HMS (2016) Amelioration of the adverse effects of salinity stress by using compost, Nigella Sativa extract or ascorbic acid in quinoa plants. Int J PharmTech Res 9:127–144

Evangelou VP (1994) Influence of sodium on soils of humid regions. In: Pessarakli M (ed) Handbook of plant and crop stress. Marcel Dekker, Inc., New York, pp 31–86

Fahad S, Nie L, Chen Y et al (2014) Crop plant hormones and environmental stress. In: Lichtfouse E (ed) Sustainable agriculture reviews, vol 15. Springer, Cham. https://doi.org/10.1007/978-3-319-09132-7_10

Flowers TJ, Muscolo A (2015) Introduction to the Special Issue: halophytes in a changing world. AoB Plants 7:plv020. https://doi.org/10.1093/aobpla/plv020

Gamez AL, Soba D, Zamarreño AM et al (2019) Effect of water stress during grain filling on yield, quality and physiological traits of Illpa and rainbow quinoa (*Chenopodium quinoa* Willd.) cultivars. Plants (Basel) 8(6):173. https://doi.org/10.3390/plants8060173

Grigore MN, Ivanescu L, Toma C (2014) Halophytes: an integrative anatomical study. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-05729-3

Guarino F, Ruiz KB, Castiglione S et al (2020) The combined effect of Cr(III) and NaCl determines changes in metal uptake nutrient content, and gene expression in quinoa (*Chenopodium quinoa* Willd.). Ecotoxicol Environ Saf 193(110345):1–12. https://doi.org/10.1016/j.ecoenv.2020.110345

Hariadi Y, Marandon K, Tian Y et al (2011) Ionic and osmotic relations in quinoa (*Chenopodium quinoa* Willd.) plants grown at various salinity levels. J Exp Bot 62:185–193. https://doi.org/10.1093/jxb/erq257

Hartung W, Davies WJ (1994) Abscisic acid under drought and salt stress. In: Passarakli M (ed) Handbook of plant and crop stress, 1st edn. Marcel Dekker, Inc., New York, pp 401–411

Hasegawa PM, Bressan RA, Zhu J-K et al (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 54:463–499. https://doi.org/10.1146/annurev.arplant.51.1.463

Hinojosa H, González JA, Barrios-Masias FH et al (2018) Quinoa abiotic stress responses: a review. Plants 7:106, 1–32. https://doi.org/10.3390/plants7040106

Hirich A, Choukr-Allah R, Jelloul A (2014) Quinoa (*Chenopodium quinoa* Willd.) seedling, water uptake and yield responses to irrigation water salinity. Acta Hortic 1054:145–152. https://doi.org/10.17660/ActaHortic.2014.1054.16

Hovenden MJ, Seppelt RD (1995) Utility of modulated fluorescence in measuring photosynthetic activity of Antarctic plants: field and laboratory studies. Aust J Plant Physiol 22:321–330. https://doi.org/10.1071/PP9950321

Hussain MI, Al-Dakheel AJ, Reigosa MJ (2018) Genotypic differences in agro-physiological, biochemical and isotopic responses to salinity stress in quinoa (*Chenopodium quinoa* Willd.) plants: prospects for salinity tolerance and yield stability. Plant Physiol Biochem 129:411–420. https://doi.org/10.1016/j.plaphy.2018.06.023

Ibañez JJ (2008) Tipos de Suelos Salinos. Available via Madrid Blogs. https://www.madrimasd.org/blogs/universo/2008/01/04/81822. Accessed 11 July 2020

Iqbal S, Basra SMA, Afzal I et al (2017) Exploring potential of well adapted quinoa lines for salt tolerance. Int J Agric Biol 19:933–940. https://doi.org/10.17957/IJAB/15.0399

Isobe K, Nakajima M, Morita N et al (2019) Effects of NaCl on growth and cesium absorption in quinoa (*Chenopodium quinoa* Willd.). Water Air Soil Pollut 230:66. https://doi.org/10.1007/s11270-019-4120-2

Jacobsen S-E, Liu F, Jensen CR (2009) Does root-sourced ABA play a role for regulation of stomata under drought in quinoa (*Chenopodium quinoa* Willd.). Sci Hortic 122(2):281–287. https://doi.org/10.1016/j.scienta.2009.05.019

Kaya E, Aydemir SK (2020) Determining the forage yield, quality and nutritional element contents of quinoa cultivars and correlation analysis on these parameters. Pak J Agric Sci 57:311–317. https://doi.org/10.21162/PAKJAS/20.7229

Kiani-Pouya A, Roessner U, Jayasinghe NS et al (2017) Epidermal bladder cells confer salinity stress tolerance in the halophyte quinoa and atriplex species. Plant Cell Environ 40 (9):1900–1915. https://doi.org/10.1111/pce.12995

Kiani-Pouya A, Rasouli F, Bazihizina N (2019) A large-scale screening of quinoa accessions reveals an important role of epidermal bladder cells and stomatal patterning in salinity tolerance. Environ Exp Bot 168:1–10. https://doi.org/10.1016/j.envexpbot.2019.103885

Killi D, Haworth M (2017) Diffusive and metabolic constraints to photosynthesis in quinoa during drought and salt stress. Plants 6:1–15. https://doi.org/10.3390/plants6040049

Koyro HW, Eisa SS (2008) Effect of salinity on composition, viability and germination of seeds of *Chenopodium quinoa* Willd. Plant Soil 302:79–90. https://doi.org/10.1007/s11104-007-9457-4

Kramer PJ, Boyer JS (1995) Water relations of plant and soils. Academic, San Diego

Manaa A, Goussi R, Derbali W et al (2019) Salinity tolerance of quinoa (*Chenopodium quinoa* Willd) as assessed by chloroplast ultrastructure and photosynthetic performance. Environ Exp Bot 162:103–114. https://doi.org/10.1016/j.envexpbot.2019.02.012

Morales AJ (2009) Physiological assessment of *Chenopodium quinoa* to salt stress. All theses and dissertations. 2205. Brigham Young University—Provo. Life Sciences; Plant and Wildlife Sciences. 2205. 64 p. https://scholarsarchive.byu.edu/etd/2205

Morales A, Zurita-Silva A, Maldonado et al (2017) Transcriptional responses of Chilean quinoa (*Chenopodium quinoa* Willd.) under water deficit conditions uncovers ABA-independent expression patterns. Front Plant Sci 8:216. https://doi.org/10.3389/fpls.2017.00216

Moreno C, Seal CE, Papenbrock J (2017) Seed priming improves germination in saline conditions for *Chenopodium quinoa* and *Amaranthus caudatus*. J Agron Crops Sci 204:40–48. https://doi.org/10.1111/jac.12242

Muscolo A, Panuccio MR, Gioffre AM et al (2016) Chapter 19: drought and salinity differently affect growth and secondary metabolites of “*Chenopodium quinoa* Willd” seedlings. In: Khan MA, Ozturk M, Gul B, Ahmed MZ (eds) Halophytes for food security in dry lands, pp 259–275. https://doi.org/10.1016/B978-0-12-801854-5.00016-9

Naqvi SSM (1994) Plant hormone and stress phenomena. In: Pessarakli M (ed) Handbook of plant and crop stress, 1st edn. Marcel Dekker, Inc., New York, pp 383–400

Nguyen LV (2016) Genetic variation in response to salt stress of quinoa grown under controlled and field conditions. Int J Adv Sci Eng Inf Technol 6:233–238

Nikalje GC, Yadav K, Penna S (2019) Halophyte responses and tolerance to abiotic stresses. In: Hasamuzzaman M, Nahar K, Östürk M (eds) Ecophysiology, abiotic stress responses and utilization of halophytes. Springer, Singapore

O’Geen A (2018) Consejos sobre la Sequía: Recuperar los Suelos Salinos, Sódicos y Salino—Sódicos. Agricultura y Recursos Naturales. Universidad de California. ANR Publicación 8629 https://anrcatalog.ucanr.edu/pdf/8629.pdf. Accessed 11 July 2020

Orsag V (2010) El Recurso Suelo: Principios para su Manejo y Conservación. Editorial Zeus, La Paz, p 489

Orsag V (2020) Salinización y Sodificación: Suelos de Regadío. Lecture Notes. Faculty of Agronomy, Universidad Mayor de San Andrés, La Paz, Bolivia

Orsini F, Accorsi M, Gianquinto G et al (2011) Beyond the ionic and osmotic response to salinity in *Chenopodium quinoa*: functional elements of successful halophytism. Funct Plant Biol 38:818–831

Pankova EI, Vorobieva LA, Balyuk SA (2018) Chapter 1: Salt-affected soils of the Eurasian region: diagnostics, criteria and distribution. In: Vargas V, Pankova EI, Balyuk SA (eds) Handbook for saline soil management. Food and Agriculture Organization of the United Nations and Lomonosov Moscow State University, pp 3–15

Panuccio MR, Jacobsen S-E, Akhtar SS (2014) Effect of saline water on seed germination and early seedling growth of the halophyte quinoa. AoB Plants 6:plu047. https://doi.org/10.1093/aobpla/plu047

Parvez S, Abbas G, Shahid M et al (2020) Effect of salinity on physiological, biochemical and photostabilizing attributes of two genotypes of quinoa (*Chenopodium quinoa* Willd.) exposed to arsenic stress. Ecotoxicol Environ Saf 187:109814. https://doi.org/10.1016/j.ecoenv.2019.109814

Peterson A, Murphy K (2015) Tolerance of lowland quinoa cultivars to sodium chloride and sodium sulfate salinity. Crop Sci 55:331–338

Pitzschke A (2016) Developmental peculiarities and seed-borne endophytes in quinoa: omnipresent, robust bacilli contribute to plant fitness. Front Microbiol 7:2. https://doi.org/10.3389/fmicb.2016.00002

Qureshi AS, Worku DA (2020) Evaluating growth and yield parameters of five quinoa (*Chenopodium quinoa* Willd.) genotypes under different salt stress conditions. J Agric Sci 12:128–140. https://doi.org/10.5539/jas.v12n3p128

Rangani J, Parida AK, Panda A et al (2016) Coordinated changes in antioxidative enzymes protect the photosynthetic machinery from salinity induced oxidative damage and confer salt tolerance in an extreme halophyte Salvadora persica L. Front Plant Sci 7:50. https://doi.org/10.3389/fpls.2016.00050

Razzaghi F, Ahmadi SH, Adolf VI (2011) Water relations and transpiration of quinoa (*Chenopodium quinoa* Willd.) under salinity and soil drying. J Agron Crop Sci 197:348–360. https://doi.org/10.1111/j.1439-037X.2011.00473.x

Riaz F, Abbas G, Saqib M (2019) Comparative effect of salinity on growth, ionic and physiological attributes of two quinoa genotypes. Pak J Agric Sci 57:115–122. https://doi.org/10.21162/PAKJAS/20.9018

Rodríguez JP, Rahman H, Thushar S et al (2020) Healthy and resilient cereals and pseudo-cereals for marginal agriculture: molecular advances for improving nutrient bioavailability. Front Genet 11:49. https://doi.org/10.3389/fgene.2020.00049

Rozema J (1995) Biology of halophytes. In: Choukr-Allah R, Malcolm Clive V, Hamdy A (eds) Halophytes and biosaline agriculture. Marcel Dekker, pp 17–30

Ruffino AMC, Rosa M, Hilal M et al (2010) The role of cotyledon metabolism in the establishment of quinoa (*Chenopodium quinoa*) seedlings growing under salinity. Plant Soil 326:213–224. https://doi.org/10.1007/s11104-009-9999-8

Ruiz KB, Biondi S, Martínez EA, Orsini F, Antognoni F, Jacobsen S-E (2015) Quinoa—a model crop for understanding salt tolerance mechanisms in halophytes. Plant Biosyst 150:357–371. https://doi.org/10.1080/11263504.2015.1027317

Ruiz KB, Aloisi I, Del Duca S (2016) Salares versus coastal ecotypes of quinoa: salinity responses in Chilean landraces from contrasting habitats. Plant Physiol Biochem 101:1–13. https://doi.org/10.1016/j.plaphy.2016.01.010

Ruiz KB, Rapparini F, Bertazza G et al (2017) Comparing salt-induced responses at the transcript level in a *Salares* and coastal-lowlands landrace of quinoa (*Chenopodium quinoa* Willd.). Environ Exp Bot 139:127–142. https://doi.org/10.1016/j.envexpbot.2017.05.003

Ruiz KB, Maldonado J, Biondi S et al (2019) RNA-seq analysis of salt-stressed versus non salt-stressed transcriptomes of *Chenopodium quinoa* landrace R49. Genes 10:1042

Saleem MA, Basra SMA, Afzal I (2017) Exploring the potential of quinoa accessions for salt tolerance in soilless culture. Int J Agric Biol 19(2):233–240. https://doi.org/10.17957/IJAB/15.0267

Shabala L, Mackay A, Tian Y et al (2012) Oxidative stress protection and stomatal patterning as components of salinity tolerance mechanism in quinoa (*Chenopodium quinoa*). Physiol Plant 146:26–38. https://doi.org/10.1111/j.1399-3054.2012.01599.x

Shabala S, Bose J, Fuglasang AT (2016) On a quest for stress tolerance genes: membrane transporters in sensing and adapting to hostile soils. J Exp Bot 67:1015–1031. https://doi.org/10.1093/jxb/erv465

Shi P, Gu M (2020) Transcriptome analysis and differential gene expression profiling of two contrasting quinoa genotypes in response to salt stress, 14 July 2020, PREPRINT (Version 1) available at Research Square. https://doi.org/10.21203/rs.3.rs-35255/v1

Sparks DL (2003) Chapter 10: The chemistry of saline and sodic soils. In: Sparks DL (ed) Environmental soil chemistry, 2nd edn. Academic, pp 285–300. https://doi.org/10.1016/B978-012656446-4/50010-4

Stefanov M, Biswal AK, Misra M et al (2020) Chapter 13: Responses of photosynthetic apparatus to salt stress, structure, function and protection. In: Pessarakli M (ed) Handbook of plant and crop stress, 4th edn. CRC Press, Taylor and Francis Group, Boca Raton, pp 233–250

Sun Y, Lindberg S, Shabala L et al (2017) A comparative analysis of cytosolic Na+ changes under salinity between halophyte quinoa (*Chenopodium quinoa*) and glycophyte pea (*Pisum sativum*). Environ Exp Bot 141:154–160. https://doi.org/10.1016/j.envexpbot.2017.07.003

Taiz L, Zeiger E (2002) Plant physiology, 3rd edn. Sinauer Associates, Inc., Publishers, Sunderland

Talebnejad R, Sepaskhah AR (2016) Physiological characteristics, gas exchange and plant ion relations of quinoa to different saline groundwater depths and water salinity. Arch Agron Soil Sci 62:1347–1367. https://doi.org/10.1080/03650340.2016.1144925

Tanji KK (1990) Agricultural salinity assessment and management. The American Society of Civil Engineers, New York

Volkmar KM, Hu Y, Steppuhn H (1997) Physiological responses of plants to salinity: a review. Can J Plant Sci 78:19–27

Waqas M, Yaning C, Iqbal H (2017) Paclobutrazol improves salt tolerance in quinoa: beyond the stomatal and biochemical interventions. J Agron Crop Sci 203:315–322. https://doi.org/10.1111/jac.12217

Warrence NJ, Pearson KE, Bauder JW (2003) Basics of salinity and sodicity effects on soil physical properties, land resources and environmental sciences Department, Montana State University. http://waterquality.montana.edu/energy/cbm/background/soil-prop.html

Wilson C, Read JJ, Abo-Kassem E (2002) Effect of mixed-salt salinity on growth and ion relations of a quinoa and wheat variety. J Plant Nutr 25:2689–2704. https://doi.org/10.1081/PLN-120015532

Yan N, Marschner P, Cao W (2015) Influence of salinity and water content on soil microorganisms. Int Soil Water Conserv Res 3:316–323. https://doi.org/10.1016/j.iswcr.2015.11.003

Yan H, Shah SS, Shao W (2020) Variation in water relations, stomatal characteristics, and plant growth between quinoa and pea under salt-stress conditions. Pak J Bot 52:1–7. https://doi.org/10.30848/PJB2020-1(8)

Yun D-J (2005) Molecular mechanism of plant adaptation to high salinity. Korean J Plant Biotechnol 32:1–14

Zelm EV, Zhang Y, Testerink C (2020) Salt tolerance mechanisms of plants. Annu Rev Plant Biol 71:24.1–24.31. https://doi.org/10.1146/annurev-arplant-050718-100005

Zou C, Chen A, Xiao L et al (2017) A high-quality genome assembly of quinoa provides insights into the molecular basis of salt bladder-based salinity tolerance and the exceptional nutritional value. Cell Res 27:1327–1340. https://doi.org/10.1038/cr.2017.124