

Abiotic stress in quinoa: A comprehensive review on the impact of salinity and mitigation strategies

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Abstract

Quinoa (*Chenopodium quinoa* wild) is a gluten-free pseudocereal with an exceptionally nutritious, balanced profile of lipids, carbohydrates, proteins, minerals, vitamins, and beneficial secondary metabolites. These nutritional qualities, combined with its capacity to grow successfully under drought, cold, salinity, and heavy metal stress, have earned special attention worldwide and positioned quinoa as a promising future crop for addressing global food security challenges amid climate change. This review highlights the physiological, morphological, and metabolic characteristics of quinoa that enable quinoa to tolerate a variety of abiotic stresses, with a particular emphasis on salinity. Quinoa exhibits various mechanisms under salt stress, including efficient Na⁺ sequestration in leaf vacuoles, controlled xylem Na⁺ loading, accumulation of organic and inorganic osmolytes, enhanced ROS resistance, improved K⁺ retention, and precise stomatal regulation. Quinoa's tolerance to salinity can be significantly enhanced through seed priming, foliar applications of plant growth regulators, organic amendments, and microbial inoculants.

Keywords: Na⁺ sequestration; osmotic adjustment; plant growth regulators; quinoa; reactive oxygen species; tolerance

Introduction

Abiotic stress

Approximately 90% of arable lands globally undergo the influence of various abiotic stressors, such as drought, high temperatures, and salt stress, either alone or in combination (Surekha *et al.*, 2013). These environmental stresses severely suppress plant development, reduce seed quality, and ultimately result in significant yield losses (Surekha *et al.*, 2014; Hussein *et al.*, 2017). Abiotic stresses are major determinants of plant growth and productivity, causing yield reductions exceeding 50% of global crop production. Several research have been conducted on plants under various abiotic stressors, such as drought, waterlogging, salt, heavy metals, excessive heat, and cold (Mittler, 2006; Hasanuzzaman *et al.*, 2013; Suzuki *et al.*, 2014; Pereira, 2016)

Received: 05 Nov 2025. Received in revised form: 04 Dec 2025. Accepted: 07 Dec 2025. Published online: 22 Dec 2025.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

The limited precipitation and high evaporation rates in arid regions intensify freshwater shortage, making the use of saline water for irrigation extremely essential (Li *et al.*, 2019). In arid areas of the world, soil is often excessively irrigated by salty water with limited draining, which results in the accumulation of high salt under the soil surface layer. Thereby, with water evaporation, the salts accumulate around the plants' root zone, causing restricted water absorption, stunting plant growth, and contaminating drinking water (Derbali *et al.*, 2021). Globally, drought and salinity affect approximately 60 million km² and 10.5 million km² of land area annually, respectively (Leng *et al.*, 2018). These stressors collectively contribute to an annual loss in crop yield estimated at roughly 70% (Almodares *et al.*, 2007; Ahmed *et al.*, 2016). The salt-affected areas in North Mediterranean regions will be doubled by 2050 in response to 1 °C increase in the average annual temperature (Hassani *et al.*, 2021).

Salinity

Salinization is considered an environmental threat, particularly in dry regions, affecting global agricultural output (Awadalla *et al.*, 2020). Globally, the total area exposed to soil salinization covers approximately 4.24 million km² of the upper soil surface (0-30 cm) and 8.33 million km² of the lower soil layers (30-100 cm) (FAO, 2024). Conversely, various studies have indicated that over one billion hectares of land have experienced salinization, encompassing roughly 20% of cultivated land (Wicke *et al.*, 2011; Qadir *et al.*, 2014). Ten countries, including Australia, Argentina, China, Russia, the United States, Iran, and Sudan, currently account for around 70% of the world's salt-affected soils (FAO, 2024).

The electrical conductivity (EC) of soil extract is used as an indicator for soil salinity through measuring the dispersion of all salts in the aqueous extract of soil, including both soluble and quickly dissolvable salts. The standard definition of saline soil is an EC > 4 dS m⁻¹ at 25 °C (Rhoades, 1996). However, Nachtergaele *et al.* (2010) highlighted that some crops will suffer at values as low as 2 dS m⁻¹ (e.g., spinach), while others can tolerate up to 16 dS m⁻¹ (e.g., date palm). Therefore, EC 2 dS m⁻¹ is often considered the agronomic starting limit for classifying potential yield losses and implementing salinity management strategies, especially for sensitive species. The salt tolerance of sensitive plants and crops might vary depending on the crop type, climate, and soil-water balance characteristics (Maas and Grattan, 1999). Natural processes like rock weathering or saline groundwater can cause salinity, as can human activity like ineffective irrigation that causes water to evaporate and salt to form (Tarolli *et al.*, 2024).

Elevated salinity is considered one of the land-degrading risks influencing soil fertility and limiting crop yields, as it has numerous negative influences on plants' ability to absorb water, even if water is available in the soil. This occurs due to the high external salt concentration, resulting in a low osmotic potential that hinders water absorption by the roots (Ullah *et al.*, 2021). Furthermore, certain ions, such as sodium (Na⁺) and chloride (Cl⁻), accumulate in high amounts in plant tissues due to salinity, which results in ion toxicity for plant cells. These ions disrupt cell membranes and enzymes, interfering with essential metabolic functions like respiration and photosynthesis, and thereby can cause drying and finally death of the plant (Shani and Ben-Gal, 2005; Chen *et al.*, 2020). In addition, the absorption of excess salt in soil, such as sodium, is responsible for nutrient imbalance by interrupting the plant's absorption of essential nutrients. For example, sodium ions can compete with potassium (K⁺) and calcium (Ca²⁺) ions for absorption sites in the roots, leading to a deficiency of these important elements. Salinity can also retard nitrogen absorption, a vital element for growth (Maksimovic and Ilin, 2012; Ehtaiwesh, 2022). Furthermore, salinity has a negative impact on soil structure; the use of saline water for irrigation, especially in clay soils, leads to the degradation of soil structure. Sodium ions cause soil particles to disperse, reducing their aeration and permeability for water, making them less aerated; that in turn affects root growth and the activity of microorganisms in the soil (El Mouttaqi *et al.*, 2023). All these reasons reduce productivity and quality of crop yield and plants become less capable of producing fruits or flowers, and the nutritional value of the crop may be affected. In some severe cases, salinity can lead to complete crop loss, threatening food security and farmers' livelihoods (Shuyskaya *et al.*, 2023).

To address the challenge, it is necessary to provide the population with the necessary food through increasing the current agricultural production sector. It is essential to increase agricultural output by improving farming practices through optimized growth conditions and suitable crop selection. To do this, new halophytic (salt-loving) crops can be introduced, such as the facultative halophyte quinoa (*Chenopodium quinoa* Willd.) (Santos *et al.*, 2016). Quinoa plants not only can tolerate high levels of saline water but also some quinoa species can be cultivated by seawater directly (Rekaby *et al.*, 2021). Subsequently, this review highlights quinoa's potential as a sustainable crop, primarily due to its high nutritional content and effective resistance to saline stress.

Distribution Pattern of Quinoa

Quinoa (*Chenopodium quinoa* Willd.) is an annual herbaceous species that belongs to the family Amaranthaceae and originates from South America. It was distributed widely in the Bolivian and Peruvian Andean region for 7000 years around Lake Titicaca and continues to be cultivated as a crop in this region today (Ruiz *et al.*, 2013; Bazile *et al.*, 2014). The natural geographical distribution of quinoa was in eastern countries of South America, including Ecuador and Peru in the north expanding in the south, involving northwest Argentina, Chile, and Bolivia, as shown in Figure 1.

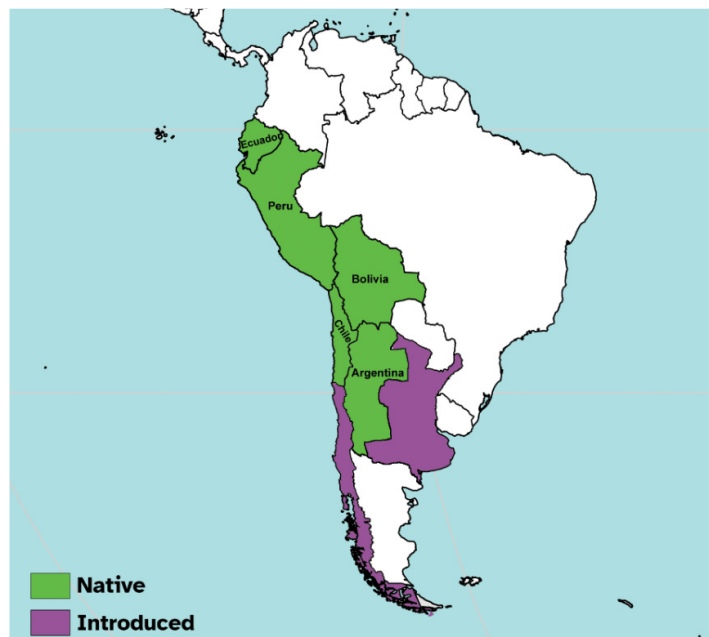


Figure 1. Geographic distribution of quinoa varieties (source: Kew Garden plant list website <https://powo.science.kew.org/>)

Quinoa is a pseudocereal facultative halophyte and has a worldwide grateful reputation as a promising future crop, not only for having remarkable tolerance ability under extreme abiotic stresses but also for having superior nutritional value. Like other halophytes, they can generate economically valuable seeds in a wide variety of salinities when traditional crops cannot (Nowak *et al.*, 2016; Nanduri *et al.*, 2019). According to Ruiz *et al.* (2013, 2016), quinoa's adaptability to diverse agroecological conditions including variations in soil type, temperature, rainfall, frost, salinity and altitude result from the genetic diversity that enables quinoa to tolerate various environmental challenges.

Quinoa seeds are currently produced and exported mostly from Bolivia and Peru. Its cultivation in South America is distributed in diverse climatic regions. For instance, it is mostly grown in the central highland area of Ecuador, although it is also produced on the savannah close to Bogota in Colombia. Quinoa grows in a variety of agroclimatic zones in Peru, such as highlands, inter-Andean valleys, and, more recently, desert mountain zones and coastal locations (Jacobsen and Mujica, 2002).

Quinoa cultivation expanded rapidly from 8 countries in 1980 to 40 in 2010, 75 in 2014, and 123 countries by 2018, with many located in Africa (41%), Asia (32%), and Europe (20%) depending on quinoa for research and primary production. In particular, four countries were identified as medium producers: Belgium, Iran, Switzerland, and Paraguay (Alandia *et al.*, 2020). Breeding projects were started in the 1980s in a number of European countries, including Denmark, the United Kingdom and the Netherlands, focusing on adapting quinoa to European climates and improving traits like early maturity and high yield, using Chilean coastal ecotype varieties as the starting material (Jacobsen, 2017). Chilean varieties as a type of coastal ecotype were the ideal initial seeds for European varieties (Mastebroek *et al.*, 2002; Präger *et al.*, 2018; Craine and Murphy, 2020). Numerous Dutch and Danish variants have been documented in Europe in recent years. The most recent cultivars are nearly entirely day-length neutral and exhibit early maturity (Jacobsen, 2017).

Quinoa's nutritional value

Quinoa seeds were recognized as a main part of the diet of the Inca civilization, alongside maize and potatoes. In the language of the Incas (Quechua), it was known as the "mother of all seeds," reflecting its cultural and nutritional significance. Due to its purported medicinal and nutritional benefits, the Incas regarded quinoa as a vital source of sustenance and health (Andrews, 2017; Mohamed Ahmed *et al.*, 2021).

Quinoa is a nutrient-rich seed supplied with a complete profile of proteins, fats, fiber, vitamins, and minerals (Bruin, 1964; Dini *et al.*, 1992; Koziol, 1992; Wright *et al.*, 2002) (Figure 2). Its exceptional nutritional profile is distinguished by its quality protein content. Quinoa is a complete protein source, containing all nine essential amino acids, with lysine levels notably higher than those in most other plant-based proteins (Figure 3). Furthermore, quinoa grains contain natural compounds with biological and free-radical scavenging properties (Pellegrini *et al.*, 2018). The fat content is higher than in conventional grains, consisting primarily of unsaturated fatty acids (linoleic and linolenic acid) and beneficial phytosterols, while carbohydrates are the main component, they exist primarily as starch with unique functional properties (Mhada *et al.*, 2020). Additionally, quinoa provides valuable dietary fiber and a wealth of essential minerals (iron, magnesium, phosphorus and potassium) and vitamins (B-complex, E, and folic acid) (Romano *et al.*, 2020).

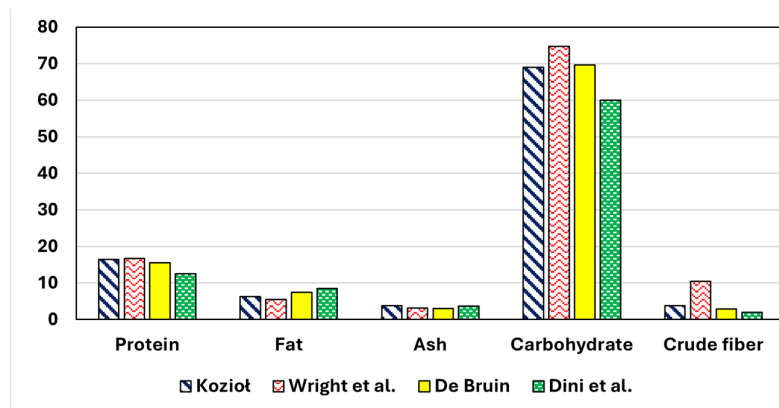


Figure 2. Quinoa seed composition as described by different authors (Bruin, 1964; Dini *et al.*, 1992; Koziol, 1992; Wright *et al.*, 2002). The graph compares the percentage contents of protein, fat, ash, carbohydrate, and crude fiber, illustrating variations in quinoa's nutritional composition among studies

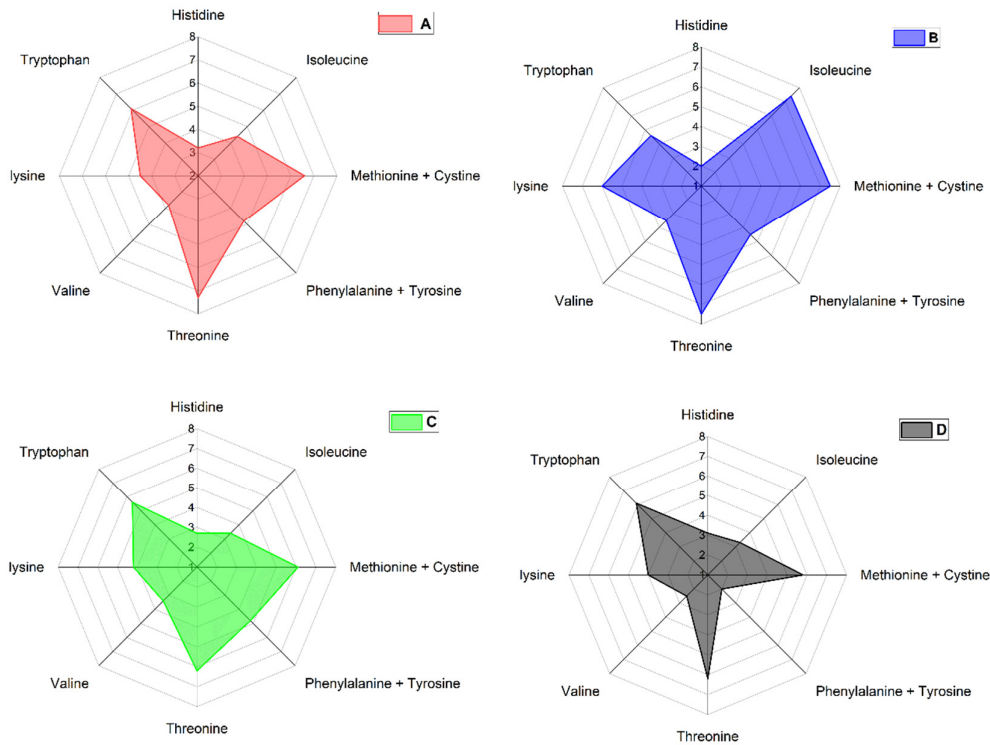


Figure 3. Radar charts illustrating the essential amino acid composition of quinoa seeds based on four different literature sources where (A) represents the composition reported by Koziol, (1992); (B) by Dini *et al.* (1992); (C) by Repo-Carrasco *et al.* (2003); and (D) by Wright *et al.* (2002) Amino acids profiled, including Histidine, Isoleucine, Methionine + Cystine, Phenylalanine + Tyrosine, Threonine, Valine, Lysine, and Tryptophan are plotted on a scale of 0 to 8 (g/100 g protein)

Impact of Salinity on Quinoa

Database and search strategy

Quinoa's response to salinity has been intensively studied over the past two decades. The number of studies increased significantly when the FAO celebrated the International Year of Quinoa after 2013. This event demonstrated the importance of quinoa as a crop resistant to unfavourable environments and a high-quality protein source (Bazile *et al.*, 2016). Since a recent study by Dehghanian *et al.* (2024) comprehensively covers genetic research on quinoa tolerance under salt stress, this review focuses on morphophysiological and agronomic findings on quinoa under salinity stress, highlighting three main points (Figure 4): (i) Comparing salt tolerance across genotypes, (ii) reviewing recent mitigation strategies for salinity stress, focusing on seed priming, soil amendments, and biological approaches, and (iii) highlighting global research trends through bibliometric analysis. The review not only clarifies mechanisms of tolerance but also reveals geographic and institutional drivers focusing on quinoa and salinity research. This approach strengthens the relevance of genotype selection and follows effective management practices for regions most affected by salinity.

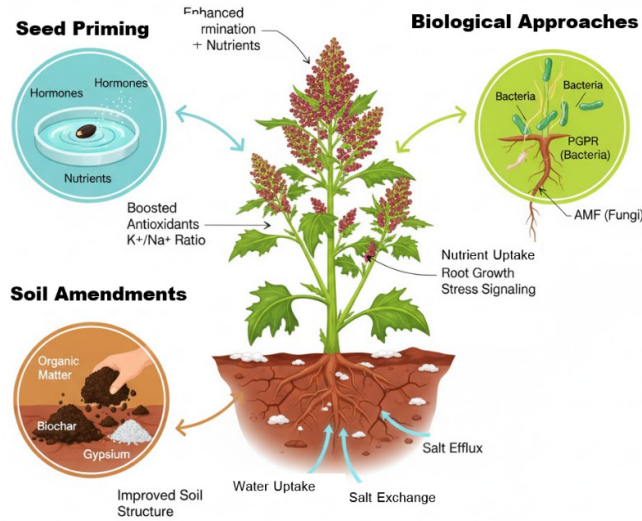


Figure 4. Graphical abstract illustrates the review’s perspective

In this study, the Scopus database and VOS viewer (version 1.6.20) were used to create a comprehensive bibliometric analysis (Figure 5) covering publications from 2000 to 2025. For research on salinity on quinoa, the following search terms were used: “quinoa” AND (salinity OR salt OR NaCl OR salt- affected OR saline). From 650 research records by December 2025, a Bibliometric Collaboration Network Map was generated by VOSviewer, revealing regional hubs and partnerships. In parallel, a literature synthesis extracted genotype tolerance data from recent studies reporting salinity levels (mM NaCl or dS m^{-1}), genotype origin, and quantified growth or yield reductions. These results were compiled into a comparative table (Table 1) to identify promising varieties for saline environments.

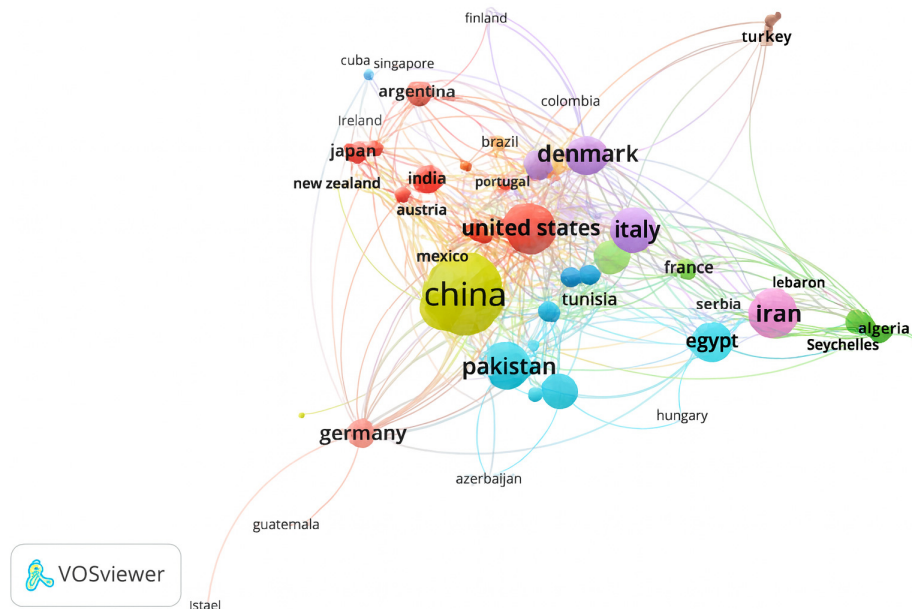


Figure 5. Country co-authorship network on quinoa and salinity research, generated by VOSviewer. Colors cluster of countries with closer research ties; Node size represents the publications number; line thickness indicates collaboration strength. Major contributors include United States, Italy, Denmark, Pakistan, Iran, Egypt, and Germany, with strong collaborations linking Asia, the Middle East, Europe, and South America

Table 1. Overview of the origin and range of salinity levels (expressed in mM NaCl or dS m⁻¹) tested across several quinoa genotypes

Genotype	Origin	Salinity level tested	Salinity tolerance	Reference
Chadmo	Chile	0-400 mM NaCl	Sensitive; Germination reduced ~50% at 300 mM; 0% at 400 mM NaCl	(Causin <i>et al.</i> , 2020)
Villarrica			Moderate tolerance; germination reduced at 300 mM ~27% 0% at 400 mM NaCl	
CICA	Perú		Tolerant up to 300 mM; partial tolerance at 400 mM	
B2	Highland quinoa cultivar (Lake Titicaca region)	0-400 mM NaCl	Tolerant up to 200-300 mM NaCl	(Cai and Gao, 2020)
R1			Tolerant up to 200-300 mM NaCl	
BR2			Germination inhibited at 400 mM NaCl	
W23			Sensitive at ≥300 mM NaCl	
Y2			Sensitive; high Na ⁺ accumulation at 200-400 mM	
CO407D	Lowland Chile	8, 16, 32 25 dS m ⁻¹ (NaCl & Na ₂ SO ₄)	Tolerant up to 32 dS m ⁻¹ NaCl/Na ₂ SO ₄ with high protein, hardest seeds	(Wu <i>et al.</i> , 2016)
Baer			Tolerant up to 32 dS m ⁻¹ with moderate hardness, density	
QQ065			Tolerant up to 32 dS m ⁻¹ with moderate protein, soft seeds	
PRJ	Central Chile	0-300 mM NaCl	Tolerant up to 150-300 mM NaCl with Strong Na ⁺ exclusion	(Ruiz-Carrasco <i>et al.</i> , 2011)
PRP			Moderate tolerance	
UDEc9			Moderate / sensitive, Lower tolerance than PRJ	
Titicaca	Denmark	0, 2, 4, 8, 12, 15, 20, 25 dS·m ⁻¹	Germination sensitive at 200-300 mM NaCl; STV; 8 dS m ⁻¹ (establishment), 20 dS m ⁻¹ (flowering), 15 dS m ⁻¹ (seed filling)	(Maleki <i>et al.</i> , 2019)
Puno	Denmark	0, 50, 100, 200, 300 mM NaCl / Na ₂ SO ₄ / Na ₂ CO ₃	High tolerance; Germination tolerant up to 200 mM NaCl; inhibited at 300 mM Na ₂ CO ₃	(Stoleru <i>et al.</i> , 2019)
Vikinga			High tolerance; Germination unaffected up to 300 mM NaCl; tolerates Na ₂ SO ₄ up to 200 mM, reduced at 300 mM	
Kcoito	USDA / ICBA seedbank	0-300 mM NaCl	Sensitive: Survives 100-300 mM NaCl with Poor recovery after stress	(Derbali <i>et al.</i> , 2021)
UDEC-5	USDA / ICBA seedbank		Salt resistant; survives 300 mM NaCl with significant post-stress growth	
Puno	Denmark	0- 400 mM NaCl	Sensitive at 400 mM NaCl, Biomass collapse at high salinity	(Riaz <i>et al.</i> , 2020)
A1	USA	Survives up to 400 mM NaCl with less reduction		
18 GR	Ecuador	0- 200 mM NaCl	Moderate tolerance; Survives up to 200 mM NaCl; ~54% greenhouse inhibition, ~83% inhibition field	(Slimani <i>et al.</i> , 2023)
R-132	Bolivia		Very sensitive; severe inhibition at 100-200 mM NaCl (up to 89% reduction)	
DE-1	New Mexico, USA		High tolerance; maintains photosynthesis at 200 mM NaCl	
Saponinsiz	Denizli (Turkey)	0, 4, 8, 16, 30 dS m ⁻¹	Optimal growth at 4-8 dS m ⁻¹ ; no growth at 30 dS m ⁻¹	(Koca, 2017)
Q12	USDA / (USA)	0, 10, 20 dS m ⁻¹	Yield stable up to 20 dS m ⁻¹ ; ~2.04 t/ha	(Hussain <i>et al.</i> , 2018)
Q19	USDA / (Chile)		Sensitive; yield drops to ~1.08 t/ha at 20 dS m ⁻¹	
Q26			Poor tolerance; lowest protein content	
Q27			Moderate tolerance	
Q31			Chile	
AMES 22157	USDA / Chile	High tolerance; yield ~2.57 t/ha at 20 dS m ⁻¹		
UAF-Q7 (Q-1)	Pakistan	0- 500 mM NaCl	Tolerates up to 200-300 mM NaCl	(Gul <i>et al.</i> , 2026)
White quinoa (Q-2)	Commercial sources	Tolerates up to 200-300 mM NaCl		
Hybrid quinoa(Q-3)	Pakistan	Sensitive; poor tolerance beyond 200 mM NaCl		

Atlas	European sweet quinoa, France	0-300 mM NaCl	Moderate tolerance: yield reduced 29% at 100 mM, 65% at 300 mM NaCl	(Roman <i>et al.</i> , 2020)
Jessie			Sensitive; lowest yield under salinity	
Pasto			Survival strategy; tolerates 200-300 mM NaCl but low yield	
selRiobamba			Best tolerance; lowest yield reduction at 100-300 mM NaCl	
ICBA-Q1	International Center for Biosaline Agriculture ICBA (Dubai, UAE)	0, 5, 10, 15, 20 dS m ⁻¹	Poor germination; sensitive at 10-20 dS m ⁻¹	(Qureshi and Daba, 2020)
ICBA-Q2			Poor germination; sensitive at 10-20 dS m ⁻¹	
ICBA-Q3			Best tolerance; high yield at 0-10 dS m ⁻¹ : moderate at 15-20 dS m ⁻¹	
ICBA-Q4			High tolerance; stable biomass at 15-20 dS m ⁻¹	
ICBA-Q5			Moderate tolerance; consistent biomass at 10-20 dS m ⁻¹	
Vikinga	Denmark	incremental salinity:	Tolerates up to 400 mM NaCl	(Serrat <i>et al.</i> , 2024)
Regalona	Chile	0 → 100 → 200 → 400 mM NaCl	Sensitive; significant growth reduction at 400 mM NaCl	
Hualhuas	Peru	0-500 mM NaCl	High tolerance; survives up to 500 mM with 80% growth reduction	(Hussin <i>et al.</i> , 2023)
Real	Bolivia		High tolerance; survives up to 500 mM with 87% reduction	

The bibliometric map shows a globally distributed effort, with China, USA, Italy, Denmark, Australia, and Germany as leading contributors. Egypt, Iran, Pakistan and Tunisia represent key Middle Eastern hubs, while South American countries such as Peru, Chile, and Argentina, quinoa's native range remain central players. Countries such as China, Pakistan, Iran, Egypt, and Tunisia have large areas of salt-affected soils that limit the productivity of conventional crops, making quinoa an attractive option for improving food security in vulnerable regions. Countries in Europe and North America, such as Denmark, Italy, Germany, and the United States are investing in quinoa research to diversify cropping systems, explore novel functional foods, and support sustainable agriculture. In South America, where quinoa originated, countries like Argentina, Brazil, and Colombia continue studying the crop to enhance its adaptation and expand its cultivation beyond traditional high-altitude zones. This bibliometric map results are consistent with those of Sellami *et al.* (2020), who generated bibliometric map covers quinoa and abiotic stress articles between 2000-2020 and highlighted that the resistance of quinoa to abiotic stresses and its adaptability to different environments led to increasing studies, especially in countries characterized by a hot, arid climate and water scarcity (Morocco, Egypt, Burkina Faso, and the UAE) and countries at risk of water and salt stress due to climate change (Italy, Greece, Turkey, Pakistan, and USA). Many of the studies in these countries were related to evaluating the effect of deficit irrigation and the use of saline water on quinoa. Much importance has also been bestowed on studying the best sowing date and sowing density, which represents the main agronomic practices for the introduction of a crop in a new environment. This pattern underscores the collaborative nature of quinoa research, linking developed nations with regions facing acute salinity challenges. Data from Table 1 further illustrate the origin and resources of different varieties and the wide variation in tolerance ability, revealing that some genotypes are able to maintain germination and growth at 400-500 mM NaCl (Causin *et al.*, 2020; Hussin *et al.*, 2023).

Germination and plant growth

As a facultative halophyte, quinoa exhibits a significant level of salt tolerance, with EC values 2-4 times higher than those of traditional glycophytic crops such as maize, wheat, and barley (Hinojosa *et al.*, 2018). Quinoa has the ability to tolerate elevated salinity levels, ranging from 150 mM NaCl (EC ~15 dS m⁻¹) up to 750 mM NaCl (EC~75 dS m⁻¹) (Orsini *et al.*, 2011), levels which exceed the salinity of seawater (>45 dS m⁻¹). Conversely, yields of highly sensitive glycophytic crops (e.g., corn, rice, wheat, peas) typically begin to decline when the soil solution surpasses 40 mM NaCl (EC~4 dS m⁻¹) (Peterson and Murphy, 2015; Sun *et al.*, 2017).

Seed germination is the crucial phase in establishing seedlings, especially on salt-affected soils, as it directly influences crop success (Farsiani and Ghobadi, 2009). According to Eisa *et al.* (2017) and Sun *et al.* (2017), quinoa exhibits optimal growth under mild saline stress, with many genotypes showing enhanced growth rates at salinities ranging between 100 and 200 mM NaCl. Moreover, Further studies by Hariadi *et al.* (2011), Ruiz-Carrasco *et al.* (2011), Panuccio *et al.* (2014) and Fischer *et al.* (2017) reported that under salt concentrations ranging from 100 to 250 mM NaCl, most quinoa varieties could maintain consistent germination rates. Nevertheless, between 150 and 250 mM NaCl, the initiation of germination was inhibited, mostly as a result of disruptions in the activity of the invertase enzyme and the metabolism of soluble sugars during the germination phase of quinoa under saline stress (Orsini *et al.*, 2011; Hao *et al.*, 2022). Manaa *et al.* (2019) reported structural damage to chloroplasts, reduced fresh weight, and suppression of photosynthetic efficiency when quinoa was exposed to extreme salinity (300 mM NaCl) conditions.

Field studies have shown that the quinoa variety 'Titicaca' demonstrates high resilience to salinity under Mediterranean conditions. 'Titicaca' genotype was grown under salinity at 22 dS m⁻¹ with limited water, it exhibited no yield reduction (Pulvento *et al.*, 2012; Coccozza *et al.*, 2013). However, at a higher salinity level of 40 dS m⁻¹, 'Titicaca's seed yield declined by 33% compared to control conditions (Razzaghi *et al.*, 2012). On the other hand, under the same Mediterranean conditions (30 dS m⁻¹), the development of the 'Red head' variety of quinoa showed a significant sensitivity to salinity; many physiological processes, including photosynthesis, were affected, showing a reduced tolerance to saline stress (Killi and Haworth, 2017).

Andean cultivars showed remarkable adaptability to NaCl-induced salinity stress due to elevated proline production compared with the control group seeds (Hinojosa *et al.*, 2018). The germination and growth of quinoa under salinity are not affected by only salt concentration but also by the type of salt, where Stoleru *et al.* (2019) found that most detrimental impacts on quinoa seed germination were caused by Na₂CO₃ salts, which reduced the germination rate by 50%. Additionally, when quinoa was grown in salty soil that contained a combination of MgSO₄, Na₂SO₄, Na₂SO₄, and NaCl, and CaCl₂, there was a notable reduction in plant height (3-19 dS m⁻¹) (Wilson *et al.*, 2002).

Furthermore, a previous study by Delatorre-Herrera and Pinto (2009) on four genotypic varieties from Chile that were exposed to a 200 mM NaCl concentration revealed that Hueque varieties were shown to be the most influenced genotype, with a decrease in germinability by 50% while Amarilla varieties showed the least reduction in germination rate. On the other hand, at the highest NaCl level (300 mM), BO78 from southern Chile showed a remarkable decrease in the roots length and the rate at which the quinoa genotype seeds germinated (Ruiz-Carrasco *et al.*, 2011; Bueno and Cordovilla, 2021).

The variation in germination rate of quinoa seeds in saline conditions through different varieties was explained by the presence of specific genes that influence salt stress resilience (Gómez-Pando *et al.*, 2010). Recent Genome-Wide Association Studies (GWAS) have identified key genetic loci responsible for salt tolerance at the germination stage, providing molecular targets for breeding programs (Mizuno *et al.*, 2020). The previous studies have consistently shown that increased salt concentrations reduce germination success and delay seedling emergence (Alam *et al.*, 2021; Bourhim *et al.*, 2022). These results were on the same line with Causin *et al.* (2020) who clarified that high salinity decelerates the rate of seed germination of quinoa, rather than affecting seedling growth.

The influence of salinity on quinoa is not only limited to germination but also plant yield and production. The previous studies on quinoa showed varying effects of salinity on seed yield and biomass. For instance, Rezzouk *et al.* (2020) observed a 12% reduction in the number of inflorescences or panicles per plant under saline conditions compared to non-saline environments. Moreover, another study by Shahid *et al.* (2018) observed a more negative effect of salinity on quinoa growth under saline irrigation (EC = 15 dS m⁻¹) causing a reduction of 22% in plant height, 8% in panicle number, and 12% in panicle length compared to plants irrigated with freshwater (EC = 0.3 dS m⁻¹). Similarly, Koyro and Eisa (2008) found seed yield decreased moderately by about 15-16% under low salinity (10-20 mM NaCl) but reduced drastically by 44-97% at high

salinity levels (300-500 mM NaCl) compared to the control (Figure 6). These results were on the same line with Hussain *et al.* (2020) who reported that the growth and production of quinoa are adversely affected by salinity. Under 10 and 20 dS m⁻¹, seed yield decreased by 44 and 60%, respectively, compared to the control (0 dS m⁻¹), whereas dry biomass was slightly affected, declining by only 2-3%. On the contrary, quinoa demonstrated the optimal growth under moderately saline conditions, specifically at NaCl concentrations of 100-200 mM (approximately 10-20 dS m⁻¹), as reported by Hariadi *et al.* (2011). This optimally aligns with the findings of Jacobsen *et al.* (2003), who demonstrated that quinoa exhibits a positive response to moderate salinity. Specifically, they observed that biomass production, seed yield, and harvest index all peaked at EC of 15 dS m⁻¹, increasing relative to non-saline conditions. However, yields declined at higher salinity levels, reaching their minimum (approximately a 44% reduction from the maximum yield) at seawater salinity (40 dS m⁻¹). Furthermore, Bouras *et al.* (2022) demonstrated that quinoa yield under saline irrigation water increased significantly by 27% and 13%, with EC values up to 12 and 17 dS m⁻¹, respectively, in comparison to the control, indicating some tolerance or positive response to moderate salinity.

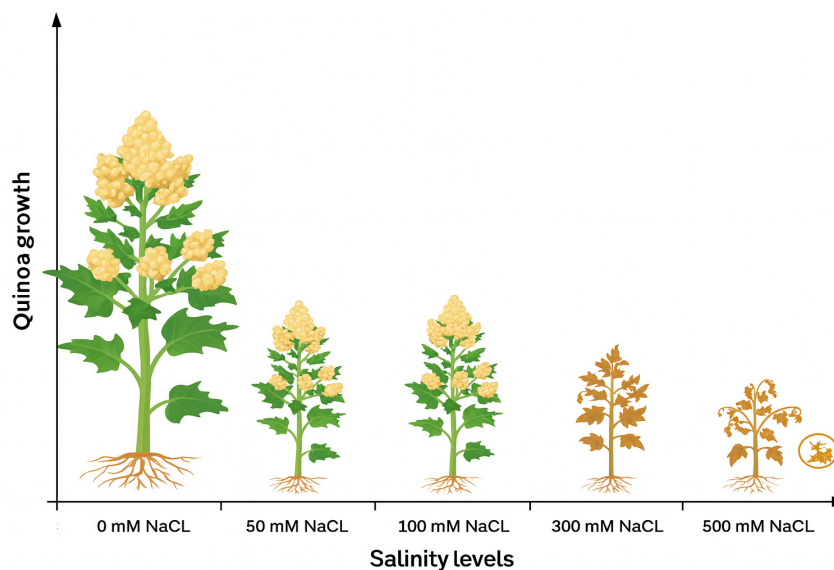


Figure 6. Salinity's effects on quinoa growth according to studies by authors (Koyro and Eisa, 2008)

Mineral uptake and assimilation

Saline soils are characterized by the presence of high concentrations of soluble ions like calcium, chlorides, magnesium, sodium, and sulfates, but lack soluble carbonates (Stavi *et al.*, 2021; Schubert and Qadir 2024). High salt concentrations in the soil solution create a steep osmotic gradient, resulting in a reduction of the water potential difference between the soil and the root cells, which inhibits water absorption by the plant (Choudhary *et al.*, 2023). A previous study by Riccardi *et al.* (2014) demonstrated that irrigating quinoa with saline water affected both plant growth and the concentration of key ions (Na⁺, K⁺ and Ca²⁺) in the tissues. However, quinoa, as a facultative halophyte, primarily adjusts to saline environments by accumulating Na⁺ in various parts except seeds (Choudhary *et al.*, 2023). Furthermore, the absorption of other key ions is also modulated by stress. Wilson *et al.* (2002) mentioned that while there was no significant difference in absorption at low salinity, Mg²⁺ absorption increased specifically with the onset of severe salinity stress. Abo-Kassem (2007) reported that high Na⁺ levels reduced Ca²⁺ absorption in the roots and, consequently, lowered its concentration in the shoots, while Riccardi *et al.* (2014) observed that salinity affects Ca²⁺ concentration differently across quinoa's shoot parts, with no significant change except in leaves. Quinoa can adapt to Ca²⁺ accumulation in the leaves by synthesizing calcium oxalate crystals on the leaf's outer surface, leading to the

extraction of Ca^{2+} from the leaf. This process prevents water loss (dehydration) during salinity stress (De Pascale *et al.*, 2003; Riccardi *et al.*, 2014). On the other hand, Sun *et al.* (2014) stated that rising salinity was associated with a decrease in the Ca^{2+} concentration in the quinoa's xylem. Wilson *et al.* (2002) explained the decrease in the ratio of Ca^{2+} to Mg^{2+} in the shoot by the antagonistic interaction between these two elements under increased salinity levels, as Mg^{2+} absorption in quinoa shoots increases while Ca^{2+} absorption decreases.

Increasing the Na^+ concentration in soil solution leads to a corresponding rise in Na^+ levels in quinoa shoots (Maleki *et al.*, 2019). Hariadi *et al.* (2011) referred that there was an increase in Na^+ concentration in the shoot part of quinoa with elevated salinity levels, highlighting that quinoa absorbs Na^+ through its roots and transports it to shoots under saline conditions for osmotic regulation and cell turgor. In addition, Riccardi *et al.* (2014) observed that quinoa can retain Na^+ ions in its shoot portion, limiting salt transfer to seeds to maintain seed quality. Increasing salinity from 150 to 750 mM NaCl led to obvious accumulation of Na^+ in quinoa tissues. However, the increase in Na^+ content between these two salinity levels was relatively moderate, amounting to only about a 50% increase (Orsini *et al.*, 2011).

In the same way, the concentration of Cl^- increases in plant shoots due to salinity stress. A study by Teakle and Tyerman (2010), and Flowers *et al.* (2015) showed that even in the shoots of halophyte plants, the concentration of Cl^- ions increases with elevating salt levels in the root zone. Moreover, Koyro *et al.* (2008) stated that as salinity levels increased, quinoa plants were able to prevent the accumulation of Na^+ and Cl^- in the seeds due to their defense mechanisms against salinity, even if there was a considerable amount of Cl^- accumulating in the plant's shoot portion.

Carbon fixation and stomatal conductance

The osmotic stress, caused by a high salt concentration, increases ABA production in the roots and the subsequent transport to the leaves via the xylem sap, where it acts as a key signal regulating stomatal closure. The closure of stomata reduces water loss and CO_2 uptake, thereby inhibiting photosynthesis (Dinneny, 2015). Adolf *et al.* (2012) found that in comparison to control conditions with distilled water and no NaCl, the CO_2 assimilation rates of two quinoa types, 'Utusaya' and 'Titicaca', decreased by 25% and 67%, respectively, when treated with 400 mM NaCl. These results were on the same line with Becker *et al.* (2017) who reported that the photosynthesis rate was reduced in quinoa Achachino variety under moderate salinity levels (250 mM NaCl), while the net photosynthetic rate significantly decreased in the 'Hualhuas' valley variety grown under 500 mM NaCl by 70% (Eisa *et al.*, 2012).

Furthermore, a study by Talebnejad and Sepaskhah (2016) on 'Titicaca' variety found that increasing the water salinity from 100 to 400 mM NaCl led to reductions of 48% in net photosynthetic assimilation rate and 72% in seed yield. These findings are consistent with a previous study conducted on 'Titicaca' variety, which revealed that growing in a Mediterranean climate with 22 dS m^{-1} and a drought regimen that consumed 100%, 50%, and 25% of the water needed to restore field capacity did not result in any yield reduction (Pulvento *et al.*, 2012), while under the same environmental conditions, the 'Red Head' variety of quinoa exhibited high sensitivity to salinity (30 dS m^{-1}) by decreasing photosynthesis (Killi and Haworth, 2017). A previous study had shown that the elevation of atmospheric CO_2 levels (540 ppm) lessens the effects of high salinity by lessening the effect of stomatal restriction on photosynthesis, which in turn lowers the probability of oxidative stress (Geissler *et al.*, 2015).

Generally, saline conditions reduce the rate of transpiration by decreasing stomatal conductance. In halophytes, this reduction in stomatal conductance is considered an adaptive mechanism for improving water use efficiency. Orsini *et al.* (2011) reported that exposure to high salinity (600-750 mM NaCl) reduced stomatal density by up to 50% in the relatively salt-sensitive Chilean cultivar BO78, accompanied by a decline in the size of stomata. Similarly, in a previous study conducted to compare the salinity tolerance of 14 quinoa varieties, the results revealed that all variety shows a reduction in stomatal density under saline conditions.

However, the morphological parameters varied through quinoa varieties under salty environments (Shabala *et al.*, 2012).

Seed composition under salinity conditions

Quinoa shows diverse responses to salinity stress, with seed yield and quality often varying across genotypes and environments. Some studies suggest that quinoa can accumulate Na^+ in vegetative tissues to protect seed quality; nevertheless, high salinity still tends to reduce seed quality depending on concentration and exposure duration. For instance, González-Teuber *et al.* (2017) who reported that in ten quinoa varieties grown under saline soil (2 and 7 dS m^{-1}), salinity had a significant effect on essential amino acids than on protein levels or yield, with seven cultivars even showing increased amino acid content. Similarly, Razzaghi *et al.* (2012) found that seed yield and seed number in the 'Titicaca' variety remained stable between 20 and 40 dS m^{-1} , whereas Eisa *et al.* (2017) observed a 61.7% reduction in seed yield under saline soil, along with declines in seed moisture, carbohydrate, and fat content, though protein levels were unaffected. Field trials in Italy with 'Titicaca' and Q52 under 22 dS m^{-1} irrigation also revealed reductions in seed fiber and saponin, while protein remained constant (Gómez-Caravaca *et al.*, 2012; Pulvento *et al.*, 2012). In contrast, Salehi and Dehghany (2023) reported significant increases in protein percentage in the varieties Sadough and NSRCQB at salinity levels of 2, 10, and 17 dS m^{-1} compared to non-saline conditions. These findings are consistent with Wu *et al.* (2016), who showed that four sea-level quinoa varieties (CO407D, UDEC-1, Baer, and QQ065) grown under 32 dS m^{-1} Na_2SO_4 exhibited enhanced seed protein content, suggesting a positive response to certain salt types. However, Wu *et al.* (2016) also noted that under the same concentration of NaCl , seed quality and composition remained unchanged.

Studies on quinoa seed mineral composition under saline conditions reveal significant genotype by-environment ($G \times E$) interactions. Prado *et al.* (2014), for instance, examined seven quinoa cultivars from Argentina and Bolivia and found variations in the tissue distribution and levels of 18 mineral elements, indicating that environmental factors clearly influence mineral uptake. Similarly, Karyotis *et al.* (2003) reported that saline-sodic soils in Larissa, Greece, reduced seed concentrations of calcium (Ca), magnesium (Mg), zinc (Zn), and manganese (Mn). These findings are consistent with Eisa *et al.* (2017), who studied the valley quinoa variety 'Hualhuas' grown in northwest Sinai, Egypt, under field conditions with soil salinity of 17 dS m^{-1} . Using X-ray microanalysis, they showed that Na^+ accumulated heavily in the pericarp and embryo tissues, while the perisperm contained much lower levels; at the same time, iron concentrations increased under high salinity. In contrast, Toderich *et al.* (2020) observed that seeds of the Q5 quinoa variety exposed to mixed salt stress ($\text{NaCl} + \text{Na}_2\text{SO}_4$) exhibited higher levels of essential minerals such as Fe, Zn, and Ca.

Aloisi *et al.* (2016) analyzed the phenolic content, antioxidant activity, and proteomic and amino acid profiles of protein extracts from three different quinoa variety seeds (Salares variety 'R49' and sea-level variants 'VI-1' and 'Villarrica') grown under two salinity levels (100 and 300 mM NaCl). Their findings demonstrated a reduction in all amino acids as a result of protein hydrolysis, particularly in the 'VII' and 'Villarrica' types. However, in "R49," different amino acids either increased or remained the same with higher salinity. Furthermore, all three varieties showed increased levels of polyphenols, flavonoids, and antioxidant activity as salinity increased. In contrast, Fischer *et al.* (2017) reported no change in polyphenol content in variety 'B080' shoot under 150 mM NaCl , although shoot growth was negatively affected.

Mechanisms of Salt Tolerance

Several studies have been conducted on quinoa to identify its salt resistance mechanisms over the last 15 years. As a facultative halophyte, quinoa possesses a variety of adaptive strategies that enable it to tolerate significant salt concentrations (Hinojosa *et al.*, 2018; Ain *et al.*, 2023; Dehghanian *et al.*, 2024). According to

previous studies, quinoa has several mechanisms by which it can resist salt. These encompass efficient osmotic regulation in leaves by buildup inorganic ions like Na^+ , K^+ , and Cl^- ; limiting sodium accumulation in the cytosol by efficiently regulating Na^+ sequestration in leaf vacuoles or salt bladders and Na^+ loading in xylem, moreover, quinoa exhibits higher tolerance strategies with reactive oxygen species (ROS), accomplishing more efficient K^+ retention and reduction in stomatal density and size, resulting in improved water use efficiency (Gómez-Pando *et al.*, 2010; Orsini *et al.*, 2011; Shabala *et al.*, 2013; Aloisi *et al.*, 2016).

Osmotic adjustment

The ability of plants to keep their growth and development under salinity is associated with adjusting to the increased external osmolality through accumulating different types of molecules in their cytoplasm. Plants possess two major adaptive strategies under environmental stresses by synthesizing compatible solutes (organic osmolytes) through creating appropriate dissolved molecules from carbohydrates and proteins, while the other is the accumulation of free inorganic ions (Flowers, 2004; Shabala and Shabala, 2011). However, synthesis of organic osmolytes consumes a significant amount of energy, which leads to a reduction in crop yield (Shabala and Shabala, 2011). For this reason, the majority of halophyte plants keep their cells turgid through pumping Na^+ and Cl^- (free osmolytes) into vacuoles found in shoot cells, while only using compatible solutes to regulate osmotic pressure in the cytosol (Flowers and Colmer, 2008; Shabala and Munns, 2017).

In case of quinoa plants, it was observed that when the quinoa plants exposed to NaCl concentrations between 0 and 500 mM (EC: 0 to 50 dS m^{-1}), a significant amount of osmotic adjustment occurred in leaves, especially in older leaves at 95%, whereas 80-85% of osmotic adjustment occurred in younger leaves depending on buildup some of inorganic ions such as Na^+ , K^+ , and Cl^- (Hariadi *et al.*, 2011). Although this strategy has obvious energetic benefit, it should be avoided because it results in a significant accumulation of Na^+ in the cytosol, which is detrimental to both glycophytes and halophytes. (Flowers and Colmer, 2008). That explains the key strategy is to pump these toxic ions by accumulating Na^+ salt into the leaf vacuoles. However, storing salt in the vacuole creates a water balance problem for the rest of the cell. To compensate, the plant accumulates organic osmolytes, such as compatible solutes like potassium, sugars, and proline, in its cytosol. This dual process of sequestering salt and balancing it with friendly solutes is essential for the plant to maintain turgor pressure and thrive, even during critical stages like seed germination (Jacobsen *et al.*, 2009). Quinoa accumulates a variety of organic osmolytes, including sugars, glycine betaine (GBT), and proline. Specifically, GBT is the primary osmotic adjustment responsible, accounting for up to 67% of the cytoplasmic osmotic adjustment (Olmos *et al.*, 2024). These organic compounds are essential for quinoa development by protecting enzyme activity and cellular structures from the harmful effects of saline conditions, while also maintaining cell turgidity as a requirement for cell expansion under stress (Ain *et al.*, 2023).

Salt bladders

Quinoa's exceptional morphological traits have been a focal point of studies exploring plant reactions to salinity stress. Specifically, the existence of epidermal bladder cells (EBCs) is considered the primary morphological trait enhancing salt tolerance, with stomatal density being a contributing factor (Orsini *et al.*, 2011; Becker *et al.*, 2017; Kiani-Pouya *et al.*, 2017; Shabala and Munns, 2017). Quinoa's epidermal bladder cells (EBCs) are believed to be critical for the plant's environmental stress tolerance, these cells store betacyanins and flavonoids, which provide UV protection and water-regulating qualities (Freitas and Breckle, 1992; Barkla *et al.*, 2012). Additionally, by storing K^+ and Na^+ ions, EBCs help with salinity tolerance by reducing water loss and maintaining ionic balance under environmental stresses (Freitas and Breckle, 1992). Since EBCs have been known as leaf protectors from UV-B rays, several studies have demonstrated that they are an important defense against environmental stress, particularly in regions with high levels of intense light (Imamura *et al.*, 2020). In addition, it has been demonstrated that EBCs have been shown to perform roles other than salt buildup (Moog *et al.*, 2023).

In *Chenopodium* species such as quinoa, epidermal bladder cells (EBCs) play a key role in plant defense against herbivorous pests through their unique structural and chemical properties (LoPresti, 2014). EBCs are localized mainly in the leaves, stems, and inflorescences of quinoa (Kiani-Pouya *et al.*, 2017) and are responsible principally for storing some metabolic products such as gamma-aminobutyric acid (GABA). EBCs play an important role in improving potassium (K^+) retention, as well as helping in salt sequestration, contributing to the plant's resilience under stress conditions. EBCs have been demonstrated to contribute to salt stress resistance by accumulating potassium (K^+), which is the primary cation in saline soil and is far more abundant than sodium (Moog *et al.*, 2022). When quinoa plants were exposed to saline (400 mM NaCl), Bonales-Alatorre *et al.* (2013) observed considerable Na^+ concentrations within the EBCs of young quinoa leaves compared to older leaves, indicating that young leaves have a greater quantity of EBCs, confirming its importance in Na^+ sequestering (Bonales-Alatorre *et al.*, 2013). Nonetheless, EBCs' structure on quinoa leaves remains largely unaffected by elevated salinity levels (Orsini *et al.*, 2011; Becker *et al.*, 2017).

Osmo protection

High salt concentration reduced water absorption directly, thereby impacting stomatal closure and CO_2 uptake, resulting in limited CO_2 fixation (Munns *et al.*, 2006). Limited CO_2 fixation causes production of excessive reactive oxygen species (ROS) through reduction in NADPH oxidation by the Calvin cycle. Consequently, the NADPH electron that reduces $NADP^+$ moves to O_2 , resulting in the formation of ROS. Lipid peroxidation, DNA mutations, and protein denaturation are the results of reactive oxygen species reactions with various macromolecules (Gill and Tuteja, 2010).

Different antioxidant responses are displayed by plants to reduce the impact of ROS-induced tissue damage. The antioxidant defense mechanism is more active when quinoa plants produce more antioxidant enzymes, including catalase (CAT) and superoxide dismutase (SOD) (Khalofah *et al.*, 2021). SOD catalyzes the transformation of O_2^- into H_2O_2 and O_2 whereas CAT breaks down H_2O_2 into H_2O and O_2 (Gill and Tuteja, 2010). A previous study by Shabala *et al.*, (2012) showed that the betacyanin levels in quinoa tissue increased with elevated salinity from 0 to 150 mM of NaCl. However, the dry weight of roots and shoots of quinoa seedlings was unaffected under salinity levels. Additionally, early seedlings exposed to 150-200 mM sodium chloride concentrations showed enhanced activity of antioxidant enzymes, including CAT and SOD in each root and shoot, as well as greater levels of ascorbate in shoots at 100-200 mM sodium chloride compared to root tissues. On the other hand, under 200 mM of sodium chloride, shoots showed an increase in lipid peroxidation, while roots showed no change between treatments. In addition, only at 150-200 mM of sodium chloride, the levels of H_2O_2 showed a significant increase in shoots. However, there were not observed differences in roots at different NaCl levels (Shabala *et al.*, 2013).

Superoxide dismutase (SOD) production is considered the first line of the antioxidant defense system (Gill and Tuteja, 2010). However, excessive production of SOD causes overproduction of H_2O_2 , which is a toxic molecule (oxidative stress), thereby resulting in increased CAT and ascorbate peroxidase (APX) activities for breakdown of ROS (Tang *et al.*, 2015). Depending on the concentration of H_2O_2 , these antioxidant enzymes react with it in different ways. For instance, APX has a high affinity for H_2O_2 and can break down H_2O_2 even at low substrate concentrations, while CAT has a low affinity for H_2O_2 and requires a high concentration of its substrate (Pooja and Munjal, 2019). These results were on the same line with Sharma *et al.* (2012) who observed that quinoa tissue produced a high amount of ascorbate peroxidase (APX) at lower sodium chloride concentrations, indicating that APX is active even at lower H_2O_2 concentrations. In addition, Sharma and his group found that with the presence of high SOD activity under 150-200 mM of sodium chloride concentration, the early quinoa seedling needed more CAT activity to break down the produced H_2O_2 . These findings demonstrate the important role of CAT in the antioxidant defense system, which mainly shows greater activity under higher H_2O_2 concentrations.

Additionally, quinoa produces betalains as protective secondary metabolites in the leaves and stems, which exhibit antioxidant properties and act as osmolytes helping in the protection of various physiological processes under environmental stresses. Quinoa accumulates various free amino acids at high salinity levels, such as phenylalanine, which serves as a precursor for the production of betalains (Tanaka *et al.*, 2008; Wang *et al.*, 2021). In addition, during salt stress, certain proteins, including dehydrins, have an Osmo protective effect on plant stress tolerance (Saavedra *et al.*, 2006; Brini *et al.*, 2007). Dehydrins, stress-related proteins found in various plant tissues, including roots, stems, and leaves, play a crucial role in helping plants adapt to water deficits caused by salt conditions (Rorat, 2006). In quinoa, there were at least four dehydrins detected in seeds from plants under salt stress, with one, a 30 KDa dehydrin, exhibiting accumulation in quinoa seeds subjected to high salinity. Burrieza *et al.* (2012) suggested the significant role of this protein (30 KDa) in protecting DNA from damage during dehydration stress due to its localization in the nucleus and association with chromatin in embryo tissue.

Potassium and sodium retention

Quinoa's exceptional salinity tolerance mechanism is linked to its higher ability to retain cellular potassium (K^+). Under saline conditions, most plants experience a massive leak of K^+ from the cytosol, which reduces essential K^+ pools and can trigger destructive processes like protein catabolism and programmed cell death (Shabala *et al.*, 2005; Shabala *et al.*, 2006).

Quinoa exhibits a high capacity for K^+ retention under saline stress, effectively limiting the detrimental K^+ efflux often seen in glycophytes, where it was reported that relatively high K^+ content was found to be preserved in the cotyledons of quinoa seedlings (Ruffino *et al.*, 2010), and also in leaf and xylem sap in quinoa under high salinity levels at developmental stage (Adolf *et al.*, 2012). Previous research by Hariadi *et al.* (2011) indicated that potassium leakage in quinoa roots is minimized by blocking specific depolarization-activated K^+ outward-rectifying (KOR) channels. Furthermore, the plant maintains cytosolic K^+ homeostasis by efficiently compartmentalizing K^+ within the vacuole using tonoplast-localized NHX proteins, a process that also helps regulate cell turgor and overall water balance (Barragán *et al.*, 2012).

Quinoa's strategy does not depend only on excluding sodium (Na^+). Instead, the plant appears to use Na^+ as a "cheap osmoticum" to help maintain osmotic pressure and absorb water from the saline environment. Quinoa uptakes a lot of Na^+ with a corresponding increase in the transport of K^+ to the shoots, thereby preserving a healthy K^+/Na^+ ratio in its leaves and preventing sodium toxicity (Cuin *et al.*, 2009). Similar to other species, quinoa roots uptake a significant amount of Na^+ through non-selective channels (NSCC), to maintain low internal Na^+ levels by actively pumping it out via the SOS1 transporter using the NHX exchanger. For transport, Na^+ must be actively loaded into the xylem (transport tubes) by SOS1 to travel to the shoots (Shabala and Shabala, 2011). Meanwhile, the roots prevent K^+ leakage via voltage-gated channels (KOR), which are carefully controlled by a plasma membrane pump to maintain a negative charge that keeps the K^+ inside. Significantly, when salt appears, the plant rapidly loads both Na^+ and K^+ into the shoots to achieve a quick water balance (osmotic adjustment), with a significant Na^+ increase observed in the shoot within just six hours (Shabala and Shabala, 2011; Adolf *et al.*, 2013).

Stomatal regulation, gas exchange, and water use efficiency

Plants' photosynthetic activity decreases in saline environments mostly due to decreased stomatal conductance, which lowers CO_2 uptake and transpiration rate (Okon, 2019). A previous study by Hussin *et al.* (2023) demonstrated that the transpiration rate and gas exchange in quinoa have a significant decrease under saline conditions. Additionally, Razzaghi *et al.* (2011) further showed that quinoa under salt stress and combined salinity and drought stress, both completely irrigated plants and plants receiving drought treatment had decreased soil water potential, which in turn affected leaf water potential and stomatal conductance. Furthermore, Razzaghi and his group found that when there was a soil water deficit, quinoa's shoots and roots

produced more abscisic acid (ABA), showing that ABA plays a role as a signal dynamic regulating stomatal conductance. These results were on the same line with Jacobsen *et al.* (2009), who reported that the hydraulic signal represents an early signal towards drought stress. Under salinity conditions, soil water potential decreases, and abscisic acid (ABA) levels increase in the leaves, roots, and shoots. This response is attributed mainly to osmotic stress resulting from water deficit, rather than to a specific ion-toxicity effect (Zhang *et al.*, 2006).

Adolf *et al.* (2012) investigated how salinity affected two quinoa varieties, 'Utusaya' and 'Titicaca', focusing on their photosynthetic CO₂ uptake and stomatal conductance. The result revealed that 'Utusaya' was less affected than 'Titicaca'. The origin of quinoa variety 'Utusaya' from Bolivia's saline salar region exhibited greater tolerance to salinity than 'Titicaca', which was developed in Denmark. 'Utusaya' showed only a 25% reduction in CO₂ assimilation under salt stress, compared to a 67% reduction in 'Titicaca'. This difference is primarily due to 'Utusaya's ability to maintain higher stomatal conductance and more effective osmoregulation, allowing continued gas exchange and photosynthesis even under saline conditions. Nevertheless, the overall lower stomatal conductance and, consequently, the photosynthesis rate in 'Utusaya' indicates that 'Utusaya' cannot take much advantage of non-saline growth conditions. In addition, salinity had no effect on PSII's photochemical efficiency in either of the two varieties, indicating that PSII is not the main target of salinity stress (Hariadi *et al.*, 2011; Adolf *et al.*, 2012).

Mitigation Strategies for Salinity Stress in Quinoa

Quinoa is a crop with high nutritional value and well salt resistance, making it a viable option for cultivation in saline environments, particularly in arid regions. However, the salinity reduces quinoa yield and affects physio- morphological characteristics. Several strategies have been applied to further enhance its resilience and productivity under salt stress conditions, for instance, Seed Priming, Application of Plant Growth Regulators (PGRs), Organic Amendments, and the use of Arbuscular Mycorrhizal Fungi (AMF) and Plant Growth-Promoting Rhizobacteria (PGPR) (Table 2, 3).

Table 2. Role of seed priming reclaims the salt tolerance in quinoa

Priming techniques	Priming agents	Improvement	References
Hydropriming	Water	Germination	(Daur, 2018)
			(Moreno <i>et al.</i> , 2018)
Halopriming	NaCl	Germination rate & Antioxidants	(Cifuentes <i>et al.</i> , 2023)
Osmopriming	CaCl ₂	Germination & Seedling Vigor	(Mamedi and Sharifzadeh, 2023)
	CaCl ₂	Antioxidant enzymes & Osmolytes	(Mamedi <i>et al.</i> , 2022)
	KNO ₃		
	Polyethylene glycol PEG (6,000 MW)	Germination under salinity; broadened salinity threshold for germination	(Moreno <i>et al.</i> , 2018)
Hormonal priming	Gibberellic acid	Germination	(Daur, 2018)
	Kinetin	Seedling growth & reduced abnormal germination percentage	

Table 3. Comprehensive overview of mitigation strategies for alleviating salt stress in quinoa

Mitigation method	Mitigation agents	Improvement	References
Soil amendment	Biochar	Plant growth, relative water content, plant biomass and grain yield and	(Abbas <i>et al.</i> , 2022)
		Soil organic matter, nutrient use efficiency and dry biomass of quinoa	(Rekaby <i>et al.</i> , 2021)
		Soil quality, nutrient availability, and plant physiological parameters	(Naveed <i>et al.</i> , 2020)
		Soil properties (EC, SAR, ESP reduction), plant growth and seed quality	(Alcivar <i>et al.</i> , 2018)
		Fresh matter production, chlorophyll content and photosynthetic CO ₂ assimilation	(Derbali <i>et al.</i> , 2024)
		Chlorophyll content, stomatal conductance, transpiration rate, net photosynthesis, antioxidant enzyme activities, ascorbate, and glutathione	(Abdulmajeed, 2023)
	Humic Substances	Soil fertility & protein and polyphenol content in seeds	(Alcivar <i>et al.</i> , 2018)
	Gypsum	Soil structure, salinity tolerance and decreased exchangeable sodium percentage (ESP)	
	Green compost	Soil fertility	(Salma <i>et al.</i> , 2023)
Superabsorbent polymer	Fresh matter production & ROS scavenging	(Derbali <i>et al.</i> , 2024)	
Biochemical mitigation	Osmolytes (proline, glycine betaine, soluble sugars)	Antioxidant enzymes & Osmotic regulation under salinity stress	(Choudhary <i>et al.</i> , 2023)
	Polyamines	Stabilization membranes, neutralized acids, suppressed ROS synthesis, enhanced adaptation to salt stress	
	Polyamines	Quinoa tolerance to salt stress; enhanced physiological and biochemical responses	(Biondi <i>et al.</i> , 2022)
	Glycine betaine	K ⁺ /Na ⁺ ratio & Osmolytes, Photosynthetic rate	(Vali <i>et al.</i> , 2024)
Biological mitigation	Siderophore-producing endophytic bacteria (<i>Burkholderia phytofirmans</i>)	Plant growth, grain yield, and grain nutrient contents	(Naveed <i>et al.</i> , 2020)
	Plant growth-promoting rhizobacteria (PGPR)	Plant growth and physiology	(Toubali and Meddich, 2023)
	Arbuscular mycorrhizal fungi (AMF)	Tolerance to salinity stress; improved growth and physiological traits	
		Soil physicochemical parameters	(Salma <i>et al.</i> , 2023)
	Trichoderma	Alleviation salinity effects on Na ⁺ and K ⁺ content & improved K ⁺ /Na ⁺ ratio under stress	(Karimi <i>et al.</i> , 2022)
	N biofertilizer	Quino growth and development	
	P biofertilizer	Phenolic and flavonoid compounds	
	<i>Halomonas</i> sp. (SFS)	Nitrogen fixation & phosphate solubilization	(Yañez-Yazlle <i>et al.</i> , 2021)
	<i>Micrococcus luteus</i> (SA211)	Indole acetic acid production	
<i>Bacillus</i> sp. (HX11)	Growth parameters & Quinoa tolerance to saline stress		

Seed priming and nutrient management

Seed priming is a cost-effective and simple method, recognized as one of the most efficient methods to alleviate the adverse effects of salt stress and maintain plant metabolic activities (Yang *et al.*, 2016; Devika *et al.*, 2021). By treating the seeds with certain solutions that improve their capacity to adjust to environmental factors, such as excessive salts. According to Sen *et al.* (2021), the priming technique improves metabolic activity and enhances resistance to high salinity through soaking seeds in water, nutrient-rich solutions, or growth regulators for a certain amount of time, followed by drying them before planting. Contrary to previous assertions, the mechanism by which seed priming reduces salt stress is now well-understood, even in halophytes like quinoa (Bourhim *et al.*, 2025) (Table 2).

A study by Yang *et al.* (2018) investigated utilizing saponin as a seed primer bio-stimulator on quinoa variety 'Titicaca' germination under 400 mM NaCl. Whereas, seeds were treated with varying saponin concentrations 10%, 15%, and 25% saponin solutions, and exposed to 0 and 400 mM NaCl conditions. The results revealed that saponin priming significantly improved germination rates, reduced mean germination time, exhibited better growth, physiological traits, and yield compared to non-primed controls under salt stress. Moreover, priming reduced abscisic acid levels, enhanced water and gas exchange, and favorable ion balance (low Na⁺, high K⁺). Another study on 'Titicaca' showed that both hydropriming and osmo-priming enhanced germination under salinity conditions (Moreno *et al.*, 2018).

Lallouche and Kouider (2024) demonstrated that application of hydropriming with distilled water at 25 °C for 12 hours, halopriming including 75 mM CaCl₂, KNO₃, and MgSO₄ at 25 °C for 12 hours, as well as hormone priming, significantly improved salinity tolerance in quinoa varieties ('Giza 02' and 'Q102'). The best results were recorded in the halopriming technique with KNO₃, then hormone priming with gibberellic acid (GAs), followed by halopriming with MgSO₄, effectively alleviating the negative impacts of salt conditions. Chauhan *et al.* (2019) explained the role of hormone priming, such as GAs in modifying biochemical processes, enabling plants to become more resistant under stressful environments. Additionally, this process enhances plant growth, function, and chemical pathways, ultimately helping to mitigate the effects of salt stress (Jiang *et al.*, 2020). On the other hand, Halopriming promotes ions like Na⁺, K⁺, and Ca²⁺ accumulation, protein response, and antioxidant activity, helping plants in coping with salinity and drought (Mamedji *et al.*, 2022; Paul *et al.*, 2024).

A field experiment in Egypt conducted by Wakeda *et al.* (2023) investigated the effect of pre-soaking quinoa seeds in different chemical substances like hydrogen peroxide, salicylic acid (SA), and potassium chloride. Overall, soaking with all three solutions significantly improved quinoa's morphological traits. SA and KCl treatment yielded the highest fresh and dry weights, grain yield, as well as SA at 10⁻² mol/L maximized chlorophyll and proline content, followed closely by KCl and H₂O₂. Additionally, potassium chloride enhanced quinoa's nitrogen, phosphorus, potassium, and sodium contents. However, hydrogen peroxide showed comparatively fewer effects.

Exogenous application of growth regulators and osmo protectants

In saline environments, the application of exogenous plant-growth regulators (PGRs) greatly balances the hormones in plants, enhancing their resistance to salt stress (Arif *et al.*, 2020). The effect of foliar applications of GAS at 50 ppm, jasmonic acid (JA at 20 ppm), and ascorbic acid (Asc. at 50 ppm) on the growth parameters and yield of quinoa plants grown in natural loamy clay soil has been studied by Sofy *et al.* (2016). The treatments significantly enhanced growth and yield parameters, including shoot and root lengths, branch and leaf numbers, overall biomass, and seed weight. Additionally, these applications enhanced photosynthetic pigments' structure, proteins, soluble carbohydrates, and total phenols throughout the experiment. On the other hand, Sun *et al.* (2022) demonstrated that auxins play a vital role in helping quinoa adapt to salt stress by promoting photosynthetic pigment accumulation, supporting both enzymatic and nonenzymatic antioxidant defenses, and effectively scavenging harmful reactive oxygen species (ROS).

Another type of growth regulator is SA, which is considered a vital plant growth regulator that controls the processes of flowering, glycolysis, yield, and germination, besides promoting plant tolerance and improving overall growth and yield (Azooz *et al.*, 2011). In addition, previous studies show that SA regulates the unilateral internal K⁺ channel inactivation, which promotes ionic balance, stomatal closure, photosynthesis, enzymatic activity, and proteins and carbohydrates synthesis, thereby improving product quality (Pirasteh-Anosheh *et al.*, 2019). However, because SA also affects redox regulation, excessive concentrations can impair stress tolerance and reduce plant growth and yield (Pirasteh-Anosheh *et al.*, 2019; Pirasteh-Anosheh and Emam, 2020). The optimal concentration of SA is a very crucial point, because it can reduce the growth and yield of different plants at high concentrations (Pirasteh-Anosheh and Emam, 2020).

A study by Mohammadi *et al.* (2022) tested the impact of SA as a phytohormone in different concentrations (0, 0.75, and 1.5 mM) on two quinoa genotypes, 'Titicaca' and 'Giza1', under various salinity levels (0, 7, 14, and 21 dS m⁻¹). The result revealed that SA at 0.75 mM improved growth and ion balance, while 1.5 mM had minimal effects thereby SA foliar application reduced Cl⁻ accumulation, and improved the uptake of beneficial ions like Ca²⁺ and Mg²⁺ and increasing shoot K⁺ and reducing root Na⁺ levels with transferring fewer toxic ions (Na⁺, Cl⁻) and more beneficial ones (K⁺, Ca²⁺, Mg²⁺) to shoots. On the other hand, Reisizadeh *et al.* (2024) explored the impact of the combination of SA and spermidine treatments on quinoa's growth and physiology under salt stress in field and greenhouse settings. Applying 1.5 mM of SA and spermidine improved the plant's stress tolerance by boosting water content, root volume, and antioxidant enzyme levels, while reducing ion leakage and harmful hydrogen peroxide.

Abbas *et al.* (2022) found that applying exogenous mineral nutrients and organic amendments to plants has a significant and promising effect for enhancing plant resilience under challenging environmental conditions. For instance, Alghamdi *et al.* (2023) demonstrated that SA and K supplementation can enhance quinoa's tolerance under combined stress of soil salinity and cadmium (Cd) contamination. Quinoa experienced over 50% reductions in growth, chlorophyll levels, and stomatal conductance, along with increased oxidative stress and compromised membrane stability under soil salinity and cadmium (Cd) contamination. However, applying 0.1 mM SA and 10 mM K, either alone or together, significantly mitigated these effects by reducing Na and Cd accumulation and limiting biomass loss.

Awadalla *et al.* (2020) examined the impact of different concentrations of proline (0, 25, 50, and 75 ppm) in foliar application on quinoa growth, yield, and quality under saline soil conditions. Results showed that the highest concentration (75 ppm) significantly enhanced quinoa's growth, yield, and quality traits compared to lower doses. Another study revealed that combining soil compost with foliar applications of proline or trehalose significantly benefits quinoa plants under salinity stress, where the treatment with proline, especially when combined with compost-enhanced free amino acids, proline, and total soluble sugars (Abdallah *et al.*, 2020)

Organic and mineral amendments

Organic amendments have a highly valuable and beneficial role in crop production, particularly under environmental stresses (Leogrande and Vitti, 2019). Enriching the soil with organic matter improves the plant's uptake of nutrients, retains more water, and enhances soil biological activity. Furthermore, organic additions, particularly farmyard manure, enhance the structure and chemical properties of saline soils. Addition of organic matter improves the leaching process, thereby alleviating the detrimental effects of salinity on soil properties and plant growth (Ding *et al.*, 2020). In the Sahara Desert, particularly in southern Morocco, where drought, salinity, and poor soil fertility limit crop options, quinoa has emerged as a viable alternative crop. A study was conducted by Maksimovic and Ilin (2012) to investigate the effects of nine organic soil amendments on quinoa (var. ICBA-Q5) under varying saline irrigation levels (4, 12, and 20 dS m⁻¹). They found that these treatments significantly improved growth, yield, and biochemical responses. Although biomass and seed yield declined with increasing salinity, organic amendments mitigated these effects and enhanced productivity compared to

untreated controls. Furthermore, Abdrabou *et al.* (2022) examined adding farmyard manure to soil cultivated by quinoa under eleven salinity levels (0.4 to 34 dS m⁻¹). Results showed that while quinoa seeds could germinate under high salinity, germination stopped at 26 dS m⁻¹ and dropped to 50% at 24 dS m⁻¹, as well as yield declined with rising salinity; however, applying organic manure significantly mitigated salt stress, raising the salinity tolerance to 34 dS m⁻¹.

Another study on quinoa grown under salinity stress and treated with compost combined with foliar sprays of *Nigella sativa* extract or ascorbic acid. The result showed significant improvements in growth, yield, photosynthesis, and carbohydrate content. The treatments also enhanced the accumulation of Osmo protectants and antioxidant enzymes, enhancing nutritional quality better with 25% compared to non-treated quinoa under saline conditions (El Sebai *et al.*, 2016). Furthermore, Derbali *et al.* (2024) explored the impact of soil amendments, specifically biochar (BC) and a superabsorbent polymer (SAP), on quinoa variety (ICBA-5) under salt stress and treated with 3% BC or 0.2% SAP. The result showed improved physiological and biochemical responses during 27 days of hypersaline stress (300 mM NaCl), including enhanced photosynthetic CO₂ assimilation, increased chlorophyll content, and greater fresh matter production. In contrast, untreated plants suffered significant reductions in growth and photosynthesis, along with elevated oxidative stress markers like malondialdehyde (MDA) and proline.

Yang *et al.* (2020) studied how biochar could improve quinoa tolerance under the combined impacts of salt stress and drought. They discovered that quinoa plants were less affected by drought and salinity stress when biochar was added to the soil. On the other hand, a study by Salama *et al.* (2021) on the response of quinoa grown under drought stress and sprayed by SA as a growth regulator, revealed that comparing the exogenous application of SA to the untreated treatment, the growth parameters, inflorescence length, number of inflorescences per plant, and seed yield were all significantly improved. In addition, a study of differential effects of heat stress on the drought and salt tolerance potentials of different quinoa genotypes clarified that the combined effects of high temperatures, salinity, and drought had a greater influence on plant development and production than individual stresses according to Abbas *et al.* (2023). Moreover, Turcios *et al.* (2021) examined the impact of varying potassium concentrations (0.5, 2, and 6 mM) on quinoa growth under different salinity levels (0, 100, and 200 mM NaCl). The findings revealed that providing an adequate potassium supply, especially under moderate salinity, enhanced plant growth and increased potassium uptake despite the salt stress. Additionally, Jafari *et al.* (2024) investigated foliar application of nitric oxide on quinoa seedlings under low and high salinity conditions (1.5 and 8 dS m⁻¹ EC). Nitric oxide application enhanced shoot biomass and leaf production under low salinity and helped mitigate stress under high salinity. It increased proline levels in both roots and leaves, especially when combined with salinity, and reduced saponin content is a beneficial trait for food quality.

Arbuscular mycorrhizal fungi and plant-growth-promoting rhizobacteria

Plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) are essential for reducing salt stress in plants by enhancing soil fertility and boosting nutrient availability (Scotti *et al.*, 2016). AMF improves phosphorus mobilization by expanding the root's uptake area through their extensive hyphal networks and releasing phosphatases that convert immobile phosphorus into forms plants can absorb. Additionally, AMF also supports nitrogen nutrition by facilitating the use of ammonium and nitrate. Moreover, these symbiotic fungi help plants increase uptake of essential minerals such as potassium, calcium, magnesium, zinc, sulfur, and copper, collectively strengthening plant growth and resilience under challenging saline conditions (Meddich *et al.*, 2015). A previous study by Salma *et al.* (2023) evaluated the impact of bio-stimulants such as AMF and organic amendment green compost (Comp), individually and combined, on the growth of two quinoa varieties ('Titicaca' and 'Puno') under varying levels of salt stress. The experiment revealed that salt stress negatively affected plant growth and physiology, but the combined AMF + Comp treatment significantly enhanced growth parameters, including stomatal conductance, photosystem II

efficiency, and photosynthetic pigment levels. Notably, dry weight increased by up to 337% in 'Titicaca' and 275% in 'Puno', depending on salinity levels.

Yang *et al.* (2016) explored how quinoa and halotolerant bacteria strains (*Bacillus* and *Enterobacter* species) that promote plant growth interact in saline environments. Their results showed that when the plants were grown at 300 mM NaCl, both bacterial strains effectively reduced the detrimental impacts of salinity by improving water relations and reducing Na⁺ absorption.

The dry biomass of the 'Titicaca' quinoa variety has increased by 930%, by the addition of biofertilizers containing AMF and PGPR in both saline and non-saline environments (0, 200, and 400 mM NaCl), while leaf water potential rose by 38%, stomatal conductance by 266%, and chlorophyll fluorescence by 7% compared to non-applied by biofertilizers in saline conditions (Toubali and Meddich, 2023). Moreover, Slatni *et al.* (2024) showed improvement in growth and physiological traits, including biomass, root length, secondary root number, proline content, and photosynthetic activity of quinoa seedlings exposed to high salinity (300 mM NaCl) and inoculated with plant growth-promoting rhizobacteria (*Bacillus* strains such as *Bacillus inaquosorum*, *Bacillus thuringiensis*, and *Bacillus proteolyticus*).

Conclusion

This review demonstrates that quinoa is a promising crop with immense potential to contribute to global food security, especially in the face of increasing environmental challenges such as salinity. Although abiotic factors, particularly salinity, can negatively affect quinoa growth and germination, this crop has developed a complex set of physiological and molecular adaptation mechanisms that enable it to thrive in harsh environments. The adaptation mechanisms include osmotic adjustment (via compatible solutes like glycine betaine and proline), precise control of ion uptake and transport, efficient K⁺ retention, the excretion of excess salts via Epidermal Bladder Cells (EBCs), and significant antioxidant defense mechanisms. The significant genetic diversity within quinoa species also offers promising opportunities for developing more salt-tolerant cultivars.

Mitigation strategies against salinity stress in quinoa can be broadly categorized into three approaches that enhance growth and productivity: Physiological/Chemical pre-treatments (e.g., seed priming and growth regulators), biological interventions (e.g., application of AMF and PGPR), and soil/structural amendments (e.g., organic additions). The effectiveness of these methods can vary depending on the genotype, environmental conditions, and application methods. Integrating growth regulators with other salinity management strategies, such as soil amendments and the selection of salt-tolerant genotypes, can provide a comprehensive approach to enhancing quinoa production in saline environments. Several agronomic practices should be explored, such as weed control, use of wastewater, soil processing, etc.

This systematic review can be used by researchers to identify previous studies on various quinoa varieties and evaluate the mitigation methods against salt stress in quinoa and the best practices in research methodology, foster collaboration, especially among researchers in arid countries, increase the field research, and exploit research results to the maximum extent. It would make a significant contribution to the expansion of quinoa cultivation in different environments.

Authors' Contributions

Conceptualization: MAM and OB; Methodology: MAM and OB; Software: MAM; Validation: MAM and OB; Formal analysis: MAM; Investigation: MAM; Resources: MAM and OB; Data curation: SV and OB; Writing - original draft: MAM; Writing - review and editing: OB and SV; Visualization: MAM, SV and OB; Supervision: OB; Project administration: SV and OB; Funding acquisition: MAM and OB.

All authors read and approved of the final manuscript.

Acknowledgements

This publication was funded by the Open Access Support Program of the University of Debrecen.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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