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Allelopathic potential, nutritional qualities, and responses of *Chenopodium quinoa* (Willd.) to abiotic stress conditions—a review

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Abstract: Quinoa (*Chenopodium quinoa* Willd.) is a pseudo cereal crop, which is considered a new alternative crop due to its high nutritional value and tolerance to environmental stresses. Its seeds are rich in proteins and amino acids (e.g., lysine, threonine, and methionine) that are deficient in other pseudo-cereal crops. It also contains essential fatty acids, such as linoleic, and alpha-linolenic acids, and high quantities of vitamins, e.g., riboflavin (B2), and tocopherol (vitamin E), and inorganic nutrients. It has a low glycemic value, is gluten-free, and has high levels of fibre and antioxidants, e.g., alpha- and gamma-tocopherol. In many studies, quinoa is reported to have allelopathic potential in plant growth and development. The aqueous extract from the roots and leaves of quinoa had various stimulatory effects on other plants. On the other hand, the aqueous extract from inflorescences exerted inhibitory activity on other plants. Furthermore, due to its high-stress tolerance, quinoa can be grown in different environments. The response of quinoa to abiotic stresses such as salinity, drought, heat, and frost are reported in the current review. Also, it provides a summary of the literature on allelopathic potential as well as the composition, chemistry, and nutritional properties of quinoa.

Key words: *Chenopodium quinoa*, allelopathic characteristics, nutritional value, stress tolerance

1. Introduction

Chenopodium quinoa has been grown and consumed by humans in the Andean region for almost 7,000 years. It is categorized as a pseudo cereal crop (Bhargava et al., 2006), along with domestic chenopods, amaranths, and buckwheat. Since 1980, quinoa cultivation has generated considerable attention in a number of countries due to its morpho-physiological properties (Hinojosa et al., 2018). It is regarded as a multipurpose crop since it includes a wide range of essential components, including vitamins, protein, fatty acids, carbohydrates, and dietary fiber (Bastidas et al., 2016). Also, a large number of micronutrients, phenolic compounds, minerals, and antioxidant substances are present (Nowak, 2016). However, because of the ever-increasing global population and the severe effects of climate change, this crop is facing various challenges (Fahad et al., 2017). Changes in ecosystems and human activities are generating numerous problems in the form of environmental stresses, which are causing severe concern (Bajwa et al., 2016). Different approaches, such as allelopathy, are used to protect plants from a variety of environmental challenges. Evidence suggests that quinoa has great allelopathic potential, by significantly affecting the biological and physiological functions of other plants (Bajwa et al., 2018). The review's aim is to provide an overview of current knowledge about quinoa's allelopathic potential, chemical composition, and nutritional qualities as well as its tolerance to various abiotic stressors.

2. Morphological characterization of quinoa

Quinoa cultivars differ enormously in morphology, phenology, and chemical composition (Bertero et al., 2004). Seeds are flattened and spherical, with diameters ranging from 1.5 to 4 mm; around 350 seeds weigh 1 g and appear in a range of colors, including white, yellow, purple, and black (Hussain et al., 2021). Inside seeds, a core perisperm is surrounded by a peripheral embryo as shown in Figure 1. One to two cell layers thick endosperm protects the micropyle and the reserve stockpile is divided into many sections (Langlie, 2019). The reserve store is divided into many sections. The core perisperm stores starch, whereas embryonic tissues and endosperm store lipid and protein components (Bobreneva et al., 2018). The pericarp bonds to the seed and contains saponins, which contribute to quinoa's bitter taste. The cylindrical seed is surrounded by a thin layer of episperm. The embryo comprise for up

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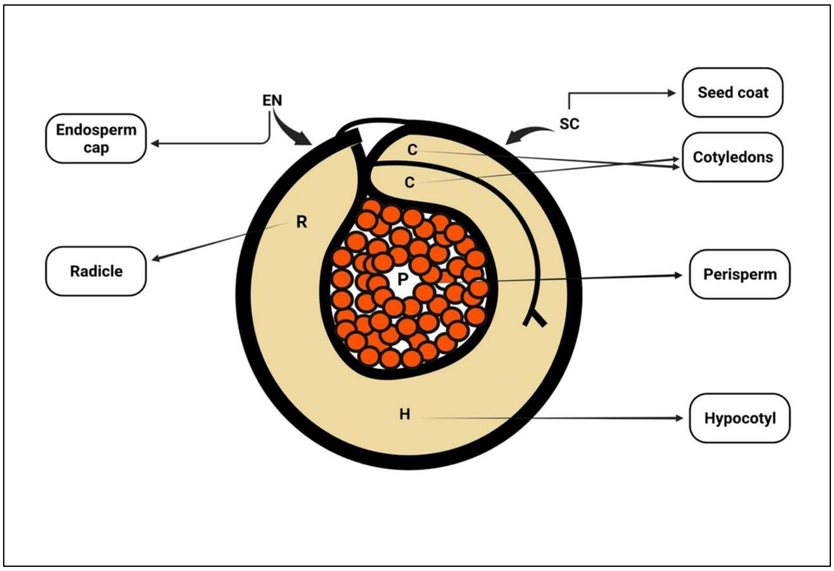

Figure 1. Quinoa seed structure and its parts.

to 60% of the seed's weight (Hernández et al., 2020). The cultivation period of quinoa is from March 15 to April 15; the germination percentage in late spring, e.g., May, is very low, and the ideal planting density is 25 plants/m^2 or (10 kg per acre) (Dhammu et al., 2019). The root is lengthy up to 30 cm and grow deep. The stem is cylindrical, with a diameter of 3.5 cm, and may be straight or branching, with a range of colors (Jancurová et al., 2009). The leaves are shaped like a goose foot and range in color from white to yellow to light brown to red, depending on the variety. The flowers are incomplete and lacking petals. Quinoa has both male and female flowers that develop at the distal and proximal edges of the inflorescence (Valencia-Chamorro, 2003). Flowers may be grouped into clusters that are glomerulate or amaranthiforme (Jancurová et al., 2009). This structure develops many secondary branches from a central axis, conforming to compact, lax, or mixed inflorescences producing hermaphrodite or unisexual flowers. As a result, hermaphrodite flowers are found at the distal end of the inflorescence's primary, secondary, and tertiary branches (Abdelbar, 2018). Seed harvesting may occur 70–90 days after blossoming, with a total duration from seedling to maturity of eight months (Valencia-Chamorro, 2003). It is likely to give yields ranging from 45 to 500 g/m^2 depending on the species, geographic area, and method of cultivation.

3. Biochemical and nutritional composition of quinoa

Grains are an essential part of the human diet since they provide half of a healthy diet and physical calorie and protein needs (Bobreneva et al., 2018). Quinoa is a perfect example of a "health food" since it may avoid a range of ailments (Singh and Singh, 2016). The functional properties may be linked to the availability of essential elements such as fiber, vitamins, fatty acids, and antioxidants, which are all necessary for human health (Antonio, 2015). Quinoa is gluten-free and has a well-balanced mix of essential amino acids, making it an easy to digest and balanced meal (Abugoch et al., 2009). It also contains more total protein, methionine, and lysine, as well as fatty acids equivalent to those found in soybean oil; it is a healthier alternative to traditional grains like rice, maize, barley, and wheat (Spehar et al., 2007). Quinoa's biological value is comparable to that of milk protein. People with celiac disease may eat a larger variety of more healthy and acceptable meals since quinoa seeds are gluten-free (Calderelli et al., 2016). It also has higher quantities of minerals including potassium, calcium, magnesium, phosphorus, and iron than most other cereals as listed in Table 1. The panicles and leaves are abundant in protein, fiber, minerals, and vitamins, and may be used in soups, cereals, biscuits, and bread in the same way as rice seeds (Spehar et al., 2007). Furthermore, quinoa sprouts and leaves are eaten in salads in the same way as spinach leaves are. Because of its great caloric and nutritional content, it is also fed to cattle, pigs, and chickens (Sezgin and Sanlier, 2019). Some other important nutrients are described in further detail in the following sections.

3.1. Carbohydrates

Quinoa has a high carbohydrate content that gives it the same glycemic index as cereal grains. It is reported that it may now be utilized to generate products that are carbohydrate-based because the seed of quinoa have a perisperm that contains starch, which is different from the

Table 1. Nutritions contained in quinoa plants.

Component	Amount	Plant part	References
Protein[a]	16.5	Grain	(Valencia-Chamorro, 2003)
	14.7	Grain	(Hussain et al., 2021)
	16.5	Grain	(Vega-Gálvez et al., 2010)
	14.1	Grain	(Hernández-Ledesma et al., 2019)
	14.4	Grain	(Repo-Carrasco et al., 2011)
	15.6	Grain	(Usda, 2015)
	16.7	Grain	(Wright et al., 2002)
	12.5	Grain	(Dini et al., 1992)
	3.3	Leaf	(Valencia-Chamorro, 2003)
Carbohydrates[a]	69.0	Grain	(Vega-Gálvez et al., 2010)
	61.6	Grain	(Usda, 2015)
	69.0	Grain	(Valencia-Chamorro, 2003)
	72.6	Grain	(Repo-Carrasco et al., 2011)
	68.1	Grain	(Hussain et al., 2021)
	64.2	Grain	(Hernández-Ledesma et al., 2019)
	4.8	Leaf	(Valencia-Chamorro, 2003)
	74.7	Grain	(Wright et al., 2002)
	60.0	Grain	(Dini et al., 1992)
Fats[a]	5.9	Grain	(Usda, 2015)
	6.3	Grain	(Vega-Gálvez et al., 2010)
	6.0	Grain	(Repo-Carrasco et al., 2011)
	1.8	Leaf	(Valencia-Chamorro, 2003)
	5.3	Grain	(Hussain et al., 2021)
	6.1	Grain	(Hernández-Ledesma et al., 2019)
	6.3	Grain	(Valencia-Chamorro, 2003)
	5.5	Gain	(Wright et al., 2002)
	8.5	Grain	(Dini et al., 1992)
Calcium (Ca)[b]	1274	Grain	(Bhargava et al., 2006)
	153	Leaf	(Vega-Gálvez et al., 2010)
	1213	Grain	(Ando, 2002)
Potassium (K)[b]	9000	Grain	(Chauhan, 1992)
	8257	Grain	(Ando, 2002)
	357	Leaf	(Vega-Gálvez et al., 2010)
Iron (Fe)[b]	92	Grain	(Chauhan, 1992)
	168	Grain	(Repo-Carrasco et al., 2011)
	20	Grain	(Bhargava et al., 2006)
Zinc (Zn)[b]	48	Grain	(Repo-Carrasco et al., 2011)
	48	Grain	(Bhargava et al., 2006)

[a]: g/100g; [b]: mg/kg dry weight; [c]: mg 100 g^{-1}; [d]: g 100 g^{-1} protein; [e]: g 100 g^{-1} of oil extract.

endosperm of cereal grains (Satheesh and Fanta, 2018). Based on analyses, starch accounts for 58.1%–64.2% of the dry weight of quinoa, with amylose contributing for around 11% (Repo-Carrasco et al., 2003). Similarly, the seed of quinoa has 26% higher lignin content than other pseudo cereal crop even the size of quinoa's seed is lower than maize and wheat (Asher et al., 2020). Besides, monosaccharides, disaccharides, crude fiber, and pentosanes were found about 3%, 2%, 3%, and 2.9%, respectively (Valencia-Chamorro, 2003). Some other carbohydrates including maltose (1.4 2.9 mg/100 gm), saccharide (2.9 mg/100 gm, D-galactose, D-ribose, fructose (0.2 mg/100 gm) and glucose (1.7 mg/100 gm) can be also found in quinoa's seed (Saturni et al., 2010). The starch of quinoa's seed has higher viscosity compere to other cereals crops such as wheat and barley (Tang et al., 2002). It is one of two key starches that are well-known across the world having average molar mass of 11.3, less dense than waxy maize starch and healthier (Park et al., 2007). Furthermore, it has a maximum polymerization degree of 161,000 glucose units and a weighted average polymerization degree of 70,000; it is also depending on the plant origin (Yao and Shi, 2014). The length of the chain may range from 500 to 6,000 glucose units; however this is the most common range (Satheesh and Fanta, 2018).

3.2. Protein

Proteins and amino acids serve as structural building blocks, catalysts, energy sources, and protein synthesis supplies in biological processes (Morrison and Laeger, 2015). Quinoa is a good source of protein for vegetarians and vegans alike, since it contains all essential amino acids and excludes casein, a protein found in milk (Repo-Carrasco et al., 2003). Its protein content ranges from 12.9 to 16.5%, and it includes all the necessary amino acids. The embryo of quinoa is the primary protein source (Meneguetti et al., 2011). Also have a higher concentration of the first essential amino acid, lysine, than wheat or maize seeds, which improves amino acid balance (Vilche et al., 2003). In a recent study, it was shown that bolivian sweet and bitter quinoa provide 14.8% and 15.7% of the daily recommended protein intake, respectively (Wright et al., 2002). Besides, quinoa contains isoleucine, lysine, methionine, cysteine, phenylalanine, tyrosine, tryptophan and valine which could be used in different purposes. It has been discovered that a high-quality edible vegetable oil made from the lipids of quinoa seeds has an acid-fatty acid composition similar to soybean oil, meaning that the oil is of greater quality for cooking and other purposes than soybean oil (Comai et al., 2007). Quinoa, being one of the most concentrated leaf protein sources available, has the potential to be used as a protein alternative in food and feed, medicine, and other applications (Bhargava et al., 2005). However, more discoveries are being made all the time, and more research is required to fully understand the protein and amino acid profiles of quinoa.

3.3. Fats

Essential fatty acids must be obtained from the diet since humans are unable to produce all the fatty acids they need. In this context, quinoa has been considered for the high quality and quantity of its lipid content in their seed oil. Lipid bodies are storage components found in endosperm and embryo tissue cells (Varma and Jain, 2021). The oil content varies from 2.0% to 9.5% and it contains important fatty acids like linoleic acid, oleic acid, and alpha-linolenic acid, as well as high levels of antioxidants, such as α and γ-tocopherol (Maradini et al., 2015). Tocopherols exist in four isomers, each with antioxidant properties. The obtained oils have a slightly higher concentration of γ-tocopherol than corn germ oil, which has 251 ppm of α-tocopherol and 558 ppm of γ-tocopherol. Thus, quinoa has a long shelf-life due to its high oil content and the antioxidant properties of γ-tocopherol (Repo-Carrasco et al., 2003). Furthermore, quinoa oil contains unsaponifiable matter (5.2%), lecithins (1.8%), and sterols (1.5%), and has a specific gravity of 0.8910 at 20°C, a refractive index of 1.4637 at 25°C, an acid number of 16.5, a saponification number of 190, and an iodine value (Wijs) of 129 (Filho et al., 2017). Moreover, the oil contains 85% unsaturated fats, making it comparable in terms of total fats. The most essential lipids are triglycerides found in quinoa seed around 50%, which is identified in significant amounts throughout the seed (Valencia-Chamorro, 2003). All of the fatty acids in quinoa are protected by vitamin E, which is a natural antioxidant (Gordillo-Bastidas et al., 2016).

3.4. Minerals and vitamins

Quinoa is rich in micronutrients, vitamins, and minerals, which make it a great source of food (Nascimento et al., 2014). The embryo contains potassium and magnesium, while the pericarp cell wall contains calcium and phosphorus (Schoenlechner, 2017). Compered to maize, wheat and barley, quinoa has higher calcium, magnesium, iron, and zinc levels in their grains (Vega-Gálvez et al., 2010). It is estimated that 100 g of quinoa seed will provide adequate magnesium, copper, and iron for both neonates and adults to fulfill their daily needs. However, phosphorus and zinc levels only meet 40%–60% of adult daily needs (González et al., 2014). Furthermore, quinoa has folic acid (78.1 mg/100 gm), vitamin C (1.4 mg/100 gm), vitamin B6 (0.20 mg/100 gm) and pantothenic acid (0.61 gm/100 gm) (Vega-Gálvez et al., 2010). Quinoa contains vitamin B1, vitamin B2, vitamin E, and α-carotene which are not available in other pseudo cereal crops (Li et al., 2012). In addition, other vitamins such as vitamins A, B2, E, K2, γ, β-carotene, tocopherols, tocotrienols, and niacin can also be found in quinoa seed. Compared to other pseudo cereals, quinoa has a higher concentration of niacin, riboflavin, vitamin B6, and total folate in their grains (Usda, 2005). According to another study, the riboflavin, which is found in quinoa, can fulfil 85% of the children's daily requirements in a single 100 g meal (National Academy of Sciences, 2004). Quinoa is also high in betaine and its metabolic precursor choline, which is a vitamin-like nutrient that helps the body produce phospholipids (e.g., phosphatidylcholine and sphingomyelin).

4. Tolerance against abiotic stress

Abiotic stress is one of the most intractable problems that agriculture faces today. Abiotic stress causes morphological, physiological, biochemical, and molecular changes in plants that have a negative influence on their development and productivity (Chaudhry and Sidhu, 2021). Abiotic stress, which reduces yields by more than 50% worldwide, is the main cause of crop losses. Quinoa can adapt to a variety of stresses due to its natural variability in traits such as inflorescence type, seed size, life-cycle duration, and chemical composition as shown in Table 2 (Bertero et al., 2004). Quinoa selected by the United Nations Food and Agriculture Organization (FAO) as the plant species that can ensure food security in the twenty-first century due to its nutritional properties and significant tolerance to abiotic stresses (Orsini et al., 2011). Tolerance to many stressors has been reported for quinoa, including salt, drought, cold, frost, and heat, which are reviewed in the following sections.

4.1. Salt stress

Salt stress is one of the abiotic stresses which most strongly impacts crop quality and productivity. The Amaranthaceae family comprises the highest number of halophytic genera, accounting for 44% of all halophytic genera and 321 species (Adolf et al., 2013). Quinoa is the most commercially significant species in this family because it produces highly nutritious seeds. It can survive salinities as high as 750 mM NaCl without losing nutritional value (Jacobsen and Mujica, 2001). However, even at 500 mM NaCl, some varieties can complete their life cycle (Adolf et al., 2013). Quinoa may store salt ions inside its tissues to manage and maintain the water potential of its leaves in order to prevent dehydration and possibly death (Jacobsen et al., 2000). Leaf area, biomass output, seed yield, and harvest index all increased when grown in moderately salty conditions, demonstrating that quinoa is an adaptive plant that thrives in saline situations (Jacobsen, 2003). Quinoa reduces salt toxicity in salt bladders by excluding salt from leaf tissues and compartmentalising Na^+ into vacuoles (Jaikishun et al., 2019). Epidermal bladder cells (EBCs) are modified epidermal hairs found in quinoa leaves, stems, and inflorescences that have a diameter about 10 times bigger than epidermal cells and can sequester 1000-fold more Na^+ than regular leaf cell vacuoles (Hinojosa et al., 2018). EBCs are thought to be storage cells for excess Na^+, Cl^-, and K^+ (Agarie et al., 2007). Plant germination stages are sensitive to salinity; salt concentrations ranging from 100 to 250 mM NaCl have no effect on quinoa germination rates in most genotypes, whereas the optimum salinity for quinoa growth ranges from 100 to 200 mM NaCl (Gul et al., 2013). However, NaCl concentrations ranging from 150 to 250 mM cause germination to be delayed (Orsini et al., 2011) and seed germination is inhibited above 400 mM NaCl (Hariadi et al., 2011). The number of stomata per leaf area and density have been shown to be affected by salinity in different parts of the world. In young, middle, and old leaves, a saline concentration of 400 mg/NaCl was shown to have an effect on the stomatal area (Orsini et al., 2011). The opposite effect was reported in 'Achachino', with stomatal density increasing by 18% when the plants were grown at 250 mM NaCl; however, salinity reduced stomatal size (Becker et al., 2017). High salt concentrations in the soil cause hyperosmotic stress in the roots, reducing the plant's ability to absorb water efficiently and lowering photosynthetic efficiency (Zhao et al., 2020). When quinoa plants were cultivated at a salt level of 500 mM NaCl, the net photosynthetic rate was reduced by 70%, while CO_2 assimilation was reduced by 25% and 67%, respectively, when quinoa plants were grown at 400 mM NaCl (Dinneny, 2015). Other studies showed that halotolerant bacteria (*Enterobacter* sp. and *Bacillus* sp.) reduced the negative effects of salinity in quinoa when grown in 300 mM NaCl (Yang et al., 2016). Due to their ability to produce phytohormones and solubilize phosphate, halotolerant rhizobacteria have been used to reduce the damage caused by salt stress in plants (Li et al., 2017). In addition paclobutrazol, a gibberellic acid synthesis inhibitor, has been used to increase yield in quinoa under high salinity conditions (Gómez et al., 2011).

4.2. Drought stress

Drought is an extreme environmental condition that is increasing as a result of climate change and has a negative impact on agricultural yields globally (Barrera-Figueroa et al., 2011). Quinoa is drought-tolerant, with the capacity to resume photosynthetic activity, and growth (leaf area) after a period of drought (Jacobsen et al., 2009). Quinoa has drought escape, tolerance, and avoidance mechanisms; other preventive methods include tissue flexibility, low osmotic potential, decreased leaf area through dehiscence, the presence of vesicular calcium oxalate, and small and thin-walled cells (Abugoch et al., 2009). According to Alvarez-Flores (2012) quinoa's drought resistance is due to its branched and deep root system, which can reach 1.5 m in sandy soils, as well as the presence of calcium oxalate-containing leaf vesicles, which may reduce transpiration. Quinoa also avoids drought by shedding leaves, having small, thick-walled cells that maintain turgor even after

Table 2. Involvement of different compounds in stress responses of quinoa.

Chemical	Function	Stress type	References
Saponin	Reducing Na+ uptake and improving water relations	Salinity	(Yang et al., 2018)
Polyethylene glycol	Improved germination in salinity conditions	Salinity	(Moreno et al., 2018)
Paclobutrazol	Improved chlorophyll and carotenoid content, increased accumulation of osmoprotectants and antioxidants in leaf and root tissues	Salinity	(Waqas et al., 2017)
Proline and phenolics	They reduce the accumulation of H_2O_2 and MDA in association with the activation of antioxidant enzymes under salinity and play an important role in reducing the detrimental effects of salinity	Salinity	(Ruffino et al., 2010; Ruiz-Carrasco et al., 2011)
Choline	Play an important role in the osmotic adjustment to salinity stress	Salinity	(Pottosin et al., 2014)
Betalains	Salt stress tolerance due to their antioxidant activity	Salinity	(Jain et al., 2015)
Gene *CqCYP76AD1-1*	Involved in betalain biosynthesis during the hypocotyl pigmentation process	Salinity	(Imamura et al., 2018)
Proline and soluble sugars (fructose, sucrose)	They facilitate the avoidance of ice formation and lower the freezing and mean lethal temperatures (T_L50)	Cold	(Sanchez, 2018)
CO2/H_2O gas	Key determinant for plant growth and biomass production	Salinity	(González et al., 2015)
Heat-shock proteins (HSPs)	Play a central role in the heat stress response (HSR) when plants suffer from either an abrupt or gradual increase in temperature	Heat	(Hinojosa et al., 2018)
Proteins (dehydrins)	Osmoprotective function	Salinity	(Grenfell and Tester, 2021)
Abscisic acid (ABA)	Induced a decreased turgor of stomata guard cells	Drought	(Jacobsen et al., 2009)
Ammonium nitrate (NH_4NO_3)	Improve plant performance	Drought	(Alandia et al., 2016)
Acidified biochar	Improve quinoa plant growth, yield, physiological, and antioxidant activity	Drought	(Aziz et al., 2018)
Synthetic ascorbic acid and orange juice (natural ascorbic acid)	Increase plant growth, total carotenoids, free amino acids, and several antioxidant enzymes	Drought	(Aziz et al., 2018)
Heat shock protein (HSP70s)	Play an important role in stress response	Drought	(Liu et al., 2018)
Amino acids, proline, betains	Plants respond to stress by accumulating them	Drought	(Sadak et al., 2019)

severe water losses, and regulating its stomata (Zurita et al., 2015). Quinoa has a high ability to quickly resume leaf formation after severe drought stress, and its wilting point is lower than other crops; the anatomical features that may confer drought tolerance are stomata deeply sunken in the leaf epidermis (Andrés et al., 2015). Quinoa resists drought for up to three months at the start of its growth cycle (González et al., 2015). Jensen (2000) reported high net photosynthesis and specific leaf area in the early vegetative stage, and low osmotic potential and turgid/dry weight ratios in the later growth stage, during the desiccating soil effect on quinoa leaf conductance, photosynthetic rate, and water relations. Quinoa had higher levels of glucose and total soluble sugars under drought conditions, whereas other carbohydrates like fructose, sucrose, and starch differed slightly but not significantly (Gonzalez et al., 2012). Mild soil drying increased xylem abscisic acid (ABA) levels, however ABA produced in the root influenced stomatal function, and soil drying promoted stomatal closure, which reduced photosynthesis (Jacobsen et al., 2009). Stomata do not appear to respond to ABA unless they are exposed to extreme dryness, and quinoa plants may photosynthesize for a long period with low irrigation, even three days after stomata close (Jacobsen et al., 2009). Quinoa's physiological responses to stress are shown in Figure 2. Other studies suggested that adding compost and acidified biochar to drought-affected soils can enhance quinoa plant growth, yield, and antioxidant activities, as well as improve the chemical and biochemical characteristics of quinoa seeds (Aziz et al., 2018). Synthetic ascorbic acid and natural ascorbic acid (orange juice) increased plant growth, total carotenoids, free amino acids, and several antioxidant enzymes in drought conditions (Hinojosa et al., 2018). Drought tolerance of quinoa was increased by using exogenous H_2O_2 as a seed primer and 15 mM as a foliar spray, resulting in higher photosynthetic rates, stomatal conductance, chlorophyll content indices, sugar, ABA, and proline levels (Iqbal et al., 2018). Proline accumulation can improve growth parameters, relative water content, yield components, and nutritional quality in drought conditions (Elewa et al., 2017).

4.3. Cold stress

Quinoa is an important grain crop that is less damaged by cold than most other crop species, although little is known about its frost resistance mechanisms (Jacobsen et al., 2005). Cold weather affects germination and other developmental stages such as leaf appearance, water relations, biochemical changes, biomass, and portioning (Bois et al., 2006). Germination of quinoa occurs in a wide range of temperatures, from extremely cold (1.9 °C) to very hot (>48.0 °C) (Hinojosa et al., 2018). The base germination temperature is 3 °C, the optimal germination temperature is from 30 to 35 °C, and the maximum germination temperature is 50 °C (González et al., 2017). The base temperature (T_b) is a variable threshold for quinoa development; e.g., T_b is 1°C for the flowering period and leaf appearance, whereas 6 °C for leaf width (Bois et al., 2006). Furthermore, it has also been shown to have super cooling properties, protecting it from damage caused by intense cold, andcan tolerate temperatures as low as 16 °C during the vegetative stage and grows well at temperatures as low as –5 °C (Bois et al., 2006). Strong antioxidant activities enable it to tolerate ice formation in its cell walls without causing irreversible damage to the structure and components of the cell (Vera-Hernández et al., 2018). Proline and soluble sugars, such as fructans, sucrose, and dehydrins, are used to facilitate the avoidance of ice formation and could also be used as an indicator of frost resistance and lower the freezing and mean lethal temperatures (T_L50) (Jacobsen et al., 2007). During anthesis, frost was more detrimental than during the vegetative stage, and frost later in the growing season is more detrimental to the crop than frost earlier in the season (Jacobsen et al., 2005). The flowering stage is more susceptible to frost, with yield decreases of 56% in the research when plants were exposed to 4 °C for 4 h (Hinojosa et al., 2018). A strong frost (–4.4°C) during flowering caused yield losses of more than 70% (Murphy et al., 2018). Temperatures below –2 °C during flowering resulted in significant quinoa losses; however, frost tolerance developed once the seed reached the soft dough stage, and plants could tolerate temperatures as low as –7 °C (Alvar-Beltrán et al., 2020). When plants in anthesis were exposed to –4 °C, they reduced 66% of their yield, whereas seedlings at the two-leaf growth stage reduced

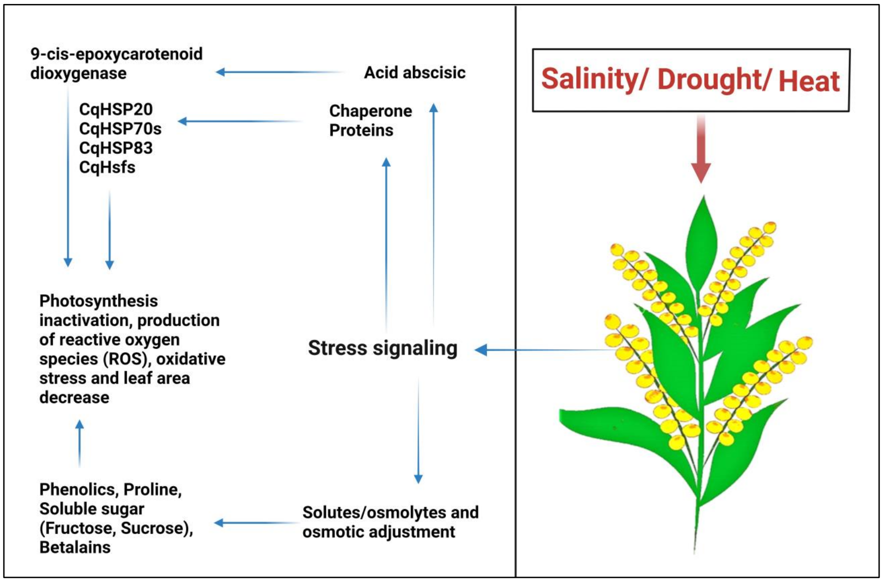

Figure 2. The physiological response of quinoa to drought, heat, and salinity.

only 9% (Jacobsen et al., 2005). Quinoa can withstand freezing temperatures before flowerbud formation as well as temperatures as low as –8 °C for up to 2 h during flowering (Gómez et al., 2022).

4.4. Heat stress

Excessive high temperatures during plant growth are one of the major abiotic stresses, and they are becoming more common as a result of current climate change. The average annual global air temperature is expected to rise from 0.3 to 0.7 °C per decade, with a maximum temperature rise of 4.8 °C predicted by the end of the century (IPCC et al., 2014). Heat stress, defined as an increase in air temperature above the optimal growth temperature for a period of time long enough to harm plant growth and development, occurs often in tandem with drought in plants and causes severe agricultural losses all across the globe (Sehgal et al., 2017). The response of plants to heat stress is different among different varieties (Driedonks et al., 2016). Heat stress directly affects plants through several mechanisms, including protein denaturation, increased membrane fluidity, photosynthesis, and carbon metabolism enzyme activity. It also causes dramatic changes in phytohormones, such as ABA, salicylic acid, and ethylene, as well as increased production of secondary metabolites (Wahid et al., 2007). The heat stress responses of the quinoa plant are shown in Figure 3. Quinoa can tolerate a wide range of temperatures, i.e. –8 to 35 °C, and relative humidity conditions i.e. 40%–88%, depending on genetic characteristics and phenological stage (Jacobsen et al., 2005). Heat-shock proteins (HSPs) play an important role in heat tolerance, and HSP70 and HSP90 are required to induce heat tolerance (Ohama et al., 2017). Temperatures above 35 °C during the flowering and seed filling stages reduce yield by producing inflorescences that are seedless or contain empty seeds, as well as the reabsorption of seed endosperm and inhibition of anther dehiscence (Walters et al., 2016). At 28 °C, heat had no effect on plant dry mass or yield, but the plants had more and longer branches (Becker et al., 2017). The increase in day/night temperature from 25/6 °C to 40/25 °C during phenological development in quinoa had no effect on seed size, but there were differences in seed weights. When the temperature varied between 21 °C and 28 °C, the size of the seeds can change by up to 14% (Hinojosa et al., 2019). Seed production at high temperatures also depends on quinoa varieties, e.g., day/night temperature from 20/14 °C to 35/29 °C decreased seed yield of the variety ‘Cherry Vanilla’, whereas in the variety ‘Salcedo’ it

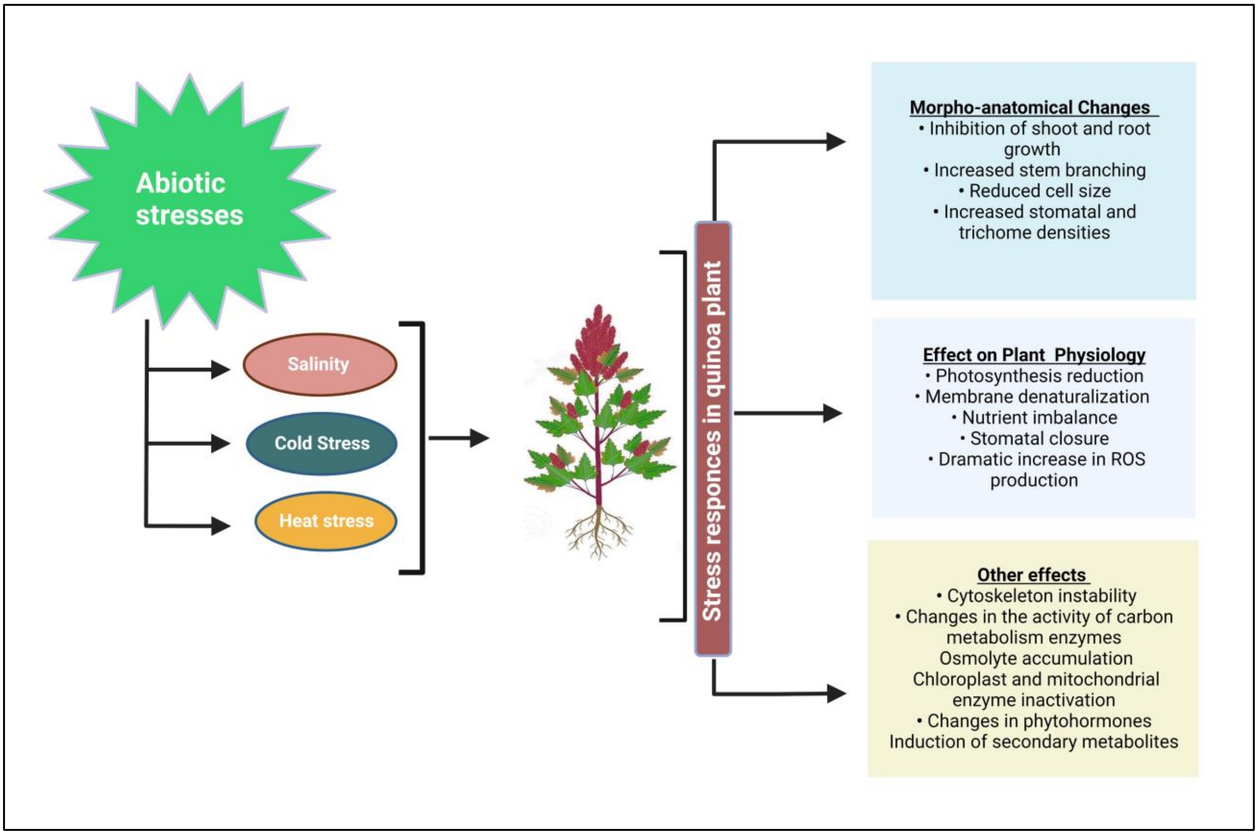

Figure 3. Stress responses in quinoa plant.

increased by 70% (Bunce, 2017). Quinoa is a heat-tolerant plant that can maintain a high stomatal conductance at high temperatures, allowing for heat to be dissipated through transpiration (Kaushal et al., 2016). When quinoa plants were exposed to high temperatures (40/24 °C), they improved maximum photosynthetic rate (A_{max}), stomatal conductance (g_s), as well as secondary axis elongation, and branching (Hinojosa et al., 2019). Quinoa pollen viability decreased at high temperatures (40/24 °C); however, there was no effect on seed set and no morphological changes in the pollen surface (Hinojosa et al., 2019). When quinoa plants were exposed to high temperatures of 40–24 °C, they improved maximum photosynthetic rate (A_{max}), stomatal conductance (g_s), as well as secondary axis elongation, and branching stimulation (Hinojosa et al., 2019). Quinoa pollen viability decreased at high temperatures (40–24 °C); however, there was no effect on seed set and no morphological changes in the pollen surface (Hinojosa et al., 2019). Thus, quinoa plants may maintain evaporative cooling under heat stress if there is enough water available (Becker et al., 2017). Quinoa exposed to various water treatments and temperatures showed greater values of stomatal conductance, leaf photosynthetic rate, photosynthetic system efficiency (PSII), and water use efficiency under high temperature conditions (Yang et al., 2016). By reducing the effects of heat stress, irrigation may be an important tool in quinoa cultivation. Under heat-stressed growth conditions, irrigation significantly increased yields (Walters et al., 2016).

5. Allelopathic potential of quinoa

Allelochemicals are produced naturally, and they are responsible for the development of allelopathic reactions (Cheng and Cheng, 2015). These allelochemicals are released into the environment through a variety of mechanisms as shown in Figure 4. Many of these chemical compounds may have an influence on the physiology and ecosystems of nearby plants and animals (Cheng and Cheng, 2015). Quinoa showed various effects (negative and positive) on other plants. Aqueous extracts from the inflorescences of quinoa were shown to suppress growth of oat, bean, and duckweed plants, whereas extracts from the leaves and roots had less negative effects on the abovementioned plants (Bilalis et al., 2013). Due to its growth suppressive properties, quinoa is an allelopathic crop that may be used to control weeds and crops without the use of pesticides (Bianchini et al., 2019). The phytotoxicity of quinoa plant extracts was assessed using three bioassay approaches. Exposure to the inflorescence extract caused a greater phytotoxic response than exposure to other quinoa tissue components, i.e. leaves, stems, and roots (Bilalis et al., 2013). Quinoa extract had a negative effect on wheat plantlet length, germination percentage, dry weight, and relative water content at low concentrations (5 and 25%), but it also improved it; however, at high concentrations, the extract had a negative effect on morphological traits, and the negative effects of leaf and inflorescence extracts were greater than those of stem and root extracts (Amraie et al., 2021). According to another study, the quinoa varieties KVL-

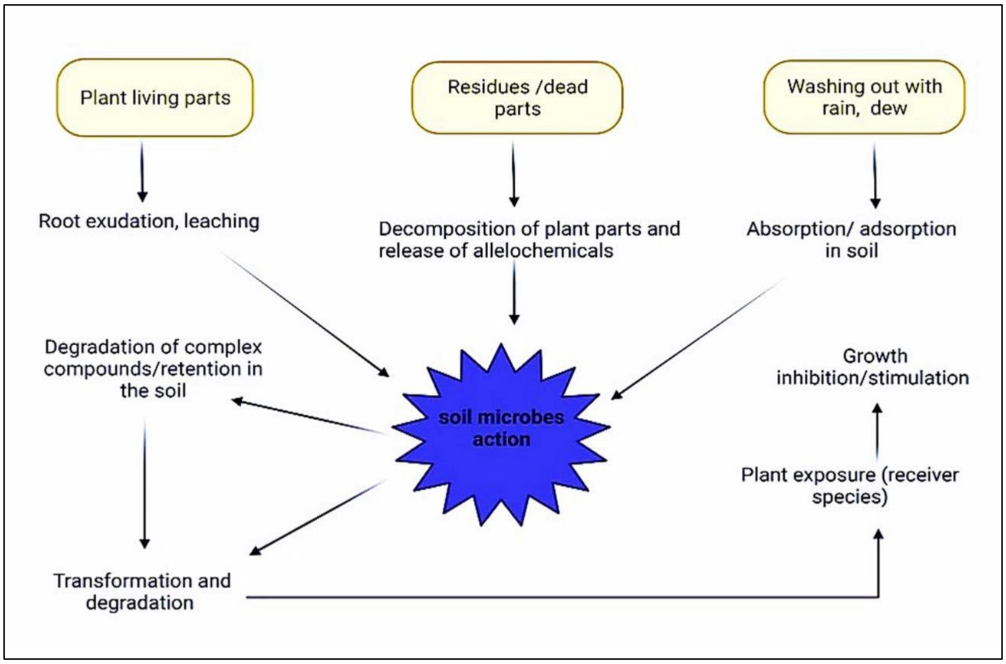

Figure 4. Release of allelochemicals into the environment through different mechanisms.

SRA2, Regalona, Q-37 and Q-52 have a positive allelopathic effect on the content of primary (sugar and carbohydrates) and secondary metabolites (flavonoids, hydroxicinnamic acids, phenolic acid) of barley (*Hordeum vulgare*) and onion (*Allium cepa*) (Valencia et al., 2017). Extracts from quinoa containing secondary metabolits, such as saponin, have proven to have a minor influence on wheat growth as well as on the plant defence system (Oleszek, 1993). Phenolic compounds, such as flavonoids, found in different varieties of quinoa seeds, have allelopathic potential on some weeds and cultivated plants (Valencia et al., 2017; Bianchini et al., 2019). Furthermore, aqueous extracts from quinoa have shown positive effects on the germination of fire plant (*Euphorbia heterophylla),* buckwheat *(Fagopyrum esculentum),* chicory *(Cichorium intbus)* and bristle oats *(Avena strigosa)* (Bianchini et al., 2019). The use of high concentrations of different quinoa organ extracts reduced germination percentage, germination rate, and the number of normal seedlings. The effects of inflorescence extract on wheat seeds were the most negative, yet low concentrations of shoot and root extract were found to have positive effects on some of the studied traits (Mansouri and Heshmat, 2020). Similarly, the extract of quinoa flowers, leaves, stems, and roots has been found to have a significant effect on wheat seedlings. High concentrations of different organ extracts increased electrolyte leakage, and antioxidant content; after being exposed to the quinoa organ extract, the concentration of chlorophylls *a* and *b* and that of carotenoids decreased (Mansouri and Heshmat, 2020). Quinoa is well known for its antifungal properties against fungal pathogens (Ali et al., 2017). Compounds such as 1-butanol, 3-methyl-sitosterol, and stigmasterol found in the n-butanol extract of quinoa leaves have an antifungal activity against *Macrophomina phaseolina* (Khan and Iqra, 2020). Furthermore, quinoa extracts of various parts inhibit mycelial growth and sporulation of a variety of phytopathogenic fungi, such as *Sclerotinia sclerotiorum, Rhizoctonia solani*, and *Botrytis cinerea,* and the antifungal effects are due to phenolics, flavonoids, and saponins (Glen-Karolczyk et al., 2016).

6. Conclusion

Quinoa is one of the main pseudo-grain crop with high nutritional value and a variety of allelopathic effects on other plants. Quinoa can exert allelopathic effects on herbs, shrubs, and trees by affecting the physiological and defense mechanisms of many plants. It has the potential to be a beneficial crop for both humans and animals due to the high concentration of health-promoting compounds that it contains. Quinoa is an easy-to-grow plant with a wide range of qualities that may be useful to people and the environment. The morphological and biochemical responses of different quinoa varieties to abiotic stresses show that quinoa has a wide tolerance to those stresses and that it can tolerate salt, cold/frost, and heat stress better than other plants. Quinoa provides a significant portion of human nutritional needs, yet there has been relatively limited genetic research to improve the plant's growth, yield, and productivity. Furthermore, new varieties of quinoa with better flavor and other qualities ought to be introduced, so the use of quinoa in human and animal nutrition may increase. Similarly, knowledge about the allelopathic potential of quinoa is insufficient and requires more research.

Contribution of authors

SS combined all literature and data, and wrote the first draft of the manuscript; YK revised and approved the final draft of the manuscript. All authors agreed to submit the final version of the manuscript.

Conflict of intrest

The authors declare that they have no conflict of interest.

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