Chapter 1

Quinoa: An Incan Crop to Face Global Changes in Agriculture

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INTRODUCTION

Environmental changes have always occurred in the past but in the last decades these have escalated to critical levels, presenting environmental risk to people, especially in terms of food supply, as it affects crop yield, production, and quality. Rapid population growth leads to increase in demand for land and thus to accelerated degradation and destruction of the environment (Alexandratos 2005; IPCC 2007). Probably the most important change driven by human activity is the increasing accumulation of greenhouse gases such as carbon dioxide (CO_2), among others (Wallington et al. 2004; Montzka et al. 2011). Greenhouse gases can absorb and emit infrared radiation, and thus a global earth warming occurs, otherwise known as the greenhouse effect. Many scientists agree that even a small increase in the global temperature would lead to significant climate and weather changes, affecting cloud cover, precipitation, wind patterns, the frequency and severity of storms, and the duration of seasons (Solomon et al. 2009). This scenario will lead to scarce natural resources and the reduction of food production.

The net consequences of global warming on crop physiology and yield are not yet fully understood, but there are some evidences indicating that decrease in yield may be the main response (Parry et al. 2005). Another deleterious effect of global warming is the increase in diseases, especially those caused by fungi and bacteria, as a consequence of higher humidity (Chakraborty et al. 2000; Hunter 2001). As most crops worldwide are well adapted to previous weather conditions, many of these crops will become less productive and may even disappear in a future of increasing climate change. It is therefore necessary to explore plant species as alternative crops or develop new crops to grow under these changing weather patterns. In this sense, it is very important to take into account plant species that grow in different altitudinal levels or those that have thrived in mountain regions for millennia. Mountain plants, especially those adapted and cultivated in different altitudinal levels, may be very important because of the genetic richness that enabled those adaptations.

Quinoa (*Chenopodium quinoa* Willd.), a native grain to the Andean highlands in South America, could be an excellent alternative crop in many regions of the world. Quinoa has been grown

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in the Andes about 5,000–7,000 years ago and has been cultivated in different ecological zones from sea level in the northwest region of Chile to altitudes over 4,000 m above sea level (masl) in the Bolivian Altiplano (Fuentes et al. 2009). Owing to this plasticity, quinoa has been introduced to higher latitudes as a new or alternative crop, with reports indicating an acceptable adaptation of this species in the United States, Canada, and Europe (Johnson and Ward 1993; Jacobsen 1997) and recently in Morocco (Jellen et al. 2005), India (Bhargava et al. 2006, 2007), and Italy (Pulvento et al. 2010).

A BRIEF HISTORY OF QUINOA CULTIVATION

Archeological studies provide evidence on the consumption of quinoa as human food thousands of years before the first Spanish conquerors arrived in America. Uhle (1919), taking into account evidences from Ayacucho (Perú), said that quinoa domestication began almost 5,000 years BC. According to Nuñez (1974), quinoa was utilized in the north region of Chile at least 3,000 years BC. Many chronicles and archeological studies provide evidence that quinoa was used by indigenous people for centuries in Colombia, Ecuador, Perú, Bolivia, Chile, and the Argentinean northwest. During pre-Columbian times, quinoa seed served as a staple food in the Incan diet, leading the Incas to call it the "mother grain" and considered it as a gift of the sun god, "Inti." It is believed that the Incas considered quinoa to be a sacred plant. Religious festivals including an offering of quinoa in a fountain of gold to the Inti god were held. The Inca Emperor used a special gold tool to make the first furrow of each year's quinoa planting. In Cuzco, ancient Incas worshipped entombed quinoa seeds as the progenitors of the city. The first Spanish conqueror who mentioned quinoa was Pedro de Valdivia. In 1551, he wrote to Carlos I, the Spanish Emperor, about the presence of some crops in the neighboring area of Concepción, Chile and specifically mentioned "… *maize, potatoes and quinuas* …" (Tapia 2009). On the other hand, in the *Comentarios Reales de los Incas*, a book written by Inca Garcilaso de la Vega and published in 1609 in Lisbon, Portugal, Garcilaso mentioned "*quinoa*" as one of the first crops in the Inca Empire (de la Vega 1966). Garcilaso mentioned that there was an intent to export quinoa to Spain but the seeds were nonviable. Other authors had also mentioned the existence of quinoa in Pasto and Quito, Ecuador (Cieza de León 1560), in Collaguas, Bolivia (Ulloa Mogollón 1586), Chiloé island in Chile (Cortés Hogea 1558), and in the Argentinean Northwest and Cordoba province, Argentina (de Sotelo 1583). During the Spanish conquest of South America in the sixteenth century, quinoa was scorned as a "food for Indians" and the conquerors destroyed fields of quinoa, actively suppressing its "non-Christian" production and consumption. The Incan peoples under the yoke of Spanish oppression were forbidden to grow it on pain of death and were forced to grow corn instead. According to Tapia (2009), after the Spanish conquest, the quinoa crop was preserved by Andean peoples in "aynokas" (communal lands) for centuries. This cropping practice also allowed the conservation of quinoa germplasm *in situ* (Tapia 2009). Today, quinoa is cultivated in more than 50 countries beyond the Andes. As a result, the cloud of ambiguity that has enveloped this crop for more than four centuries is beginning to disappear (National Research Council 1989).

NUTRITIONAL VALUE OF QUINOA SEED

There is extensive literature on the chemical composition of quinoa seed (González et al. 1989; Ando et al. 2002; Repo-Carrasco et al. 2003; Abugoch 2009), which cover all nutritional aspects such as chemical characterization of proteins (Brinegar and Goundan 1993; Hevia et al. 2001), fatty acid composition of the seed oil (Wood et al. 1993; Ando et al. 2002), mineral content (Koziol 1992; Konishi et al. 2004; Prado et al. 2010), and nutritional value (Prakash et al. 1993; Ranhotra et al. 1993; Ruales and Nair 1992).

The lipid content of quinoa seed is higher than that in common cereals (Repo-Carrasco-Valencia

2011) and is mainly located in the embryo. The oil of quinoa seed is rich in polyunsaturated fatty acids (linoleic and linolenic) and in oleic acid. Its level of unsaturated fatty acids in relation to human nutrition is better than those in other cereals (Alvarez-Jubete et al. 2009). According to the Food and Agricultural Organization (FAO) recommendations on fats and fatty acids in human nutrition (FAO/WHO 2010), infant food should contain 3–4.5% energy in the form of linoleic acid (LA) and 0.4–0.6% in the form of linolenic acid (ALA), which corresponds to LA/ALA ratio (*n*-6/*n*-3 ratio) between 5 (minimum) and 11.2 (maximum). The LA/ALA ratio of quinoa oil is 6.2 (Alvarez-Jubete et al. 2009) and thus falls within the FAO/WHO (2010) recommended values. Furthermore, a diet with a high *n*-6/*n*-3 ratio promotes the pathogenesis of many degenerative diseases such as cardiovascular disease, cancer, osteoporosis, as well as inflammatory and autoimmune diseases (Simopoulos 2001). The main carbohydrate in quinoa seed is the starch where soluble sugars, that is, sucrose, glucose, and fructose are present at low levels (González et al. 1989). Quinoa starch is located mainly in the perisperm and it occurs both as small individual granules and larger compound granules composed of hundreds of individual granules (Prado et al. 1996). The individual granules are polygonal with a diameter of 1.0–2.5 μm and the compound granules are oval, with a diameter of 6.4–32 μm (Atwell et al. 1983). Quinoa starch is rich in amylopectin and gelatinizes at relatively low temperatures (57–71°C). Moreover, it has excellent freeze-thaw stability attributed to its rich amylopectin content (Ahamed et al. 1996). In comparison with common cereals, quinoa is an excellent source of γ-tocopherol (vitamin E), containing about 5 mg/100 g DM (Ruales and Nair 1993). The content of γ-tocopherol is of particular biological relevance because of its potential anticarcinogenic and anti-inflammatory activities (Jiang et al. 2001). Quinoa also contains significant amounts of riboflavin, thiamine, and, especially, vitamin C that is uncommon in cereals (Koziol 1992; Ruales and Nair 1993; Repo-Carrasco et al. 2003). Recently, it has been demonstrated that quinoa seed also contains high levels of folate (Schoenlechner et al. 2010). The folate content found in quinoa is 132.7 mg/100 g DM, about 10-fold higher than that in wheat seed. Quinoa bran contains a higher amount of folate than flour fraction (Repo-Carrasco-Valencia 2011). Furthermore, quinoa seed does not contain allergenic compounds such as gluten or prolamine or enzyme (protease and amylase) inhibitors present in most common cereals (Zuidmeer et al. 2008) or trypsin and chymotrypsin inhibitors present in soybean seeds (Galvez Ranilla et al. 2009).

Despite its healthy nutritional composition, several cultivars of quinoa contain bitter saponins, glycosylated secondary metabolites in the seed coat that act as antinutrients and deterrents of seed predators such as birds and insects (Solíz-Guerrero et al. 2002). Saponins are concentrated in external layers of the seed (Prado et al. 1996) and include a complex mixture of triterpene glycosides that are derivatives of oleanolic acid, hederagenin, phytolaccagenic acid, serjanic acid, and 3β,23,30-trihydroxy olean-12-en-28-oic acid, which bear hydroxyl and carboxylate groups at C-3 and C-28, respectively (Kuljanabhagavad et al. 2008). Presently, at least 16 different saponins have been detected in quinoa seeds (Woldemichael and Wink 2001). Saponins are reported to be toxic for cold-blooded animals and have been used as fish poison by South American inhabitants (Zhu et al. 2002). They have some adverse physiological effects, as they are membranolytic against cells of the small intestine and possess hemolytic activity (Woldemichael and Wink 2001). Moreover, saponins form complexes with iron and may reduce its absorption.

Although saponins have negative effects, they also have positive effects such as reducing serum cholesterol levels, possessing anti-inflammatory, antitumor, and antioxidant activities, and enhancing drug absorption through the mucosal membrane. Saponins also exhibit insecticidal, antibiotic, antiviral, and fungicidal properties (Kuljanabhagavad and Wink 2009). Furthermore, saponins act as immunological and absorption adjuvant to enhance antigen-specific antibody and mucosal response (Estrada et al. 1998).

Saponin content varies among genotypes, ranging between 0.2 and 0.4 g/kg DM (sweet genotypes) and 4.7 and 11.3 g/kg DM (bitter genotypes). Therefore, selection of sweet genotypes with very low saponin content in the seeds is one of the main breeding goals in quinoa. However, selection for sweet genotypes is retarded by cross-pollination (Mastebroek et al. 2000). The tissue containing saponins is of maternal origin, and the saponin content of the seed reflects the genotype of the plant from which the grain is harvested (Ward 2001). According to Gandarillas (1979), the saponin content trait is controlled by two alleles at a single locus, with the bitter allele (high saponin) dominant to the sweet allele (low saponin). More recently, researchers have observed that saponin content in quinoa seed is a continuously distributed variable and is therefore more likely to be polygenically controlled and quantitatively inherited (Galwey et al. 1990; Jacobsen et al. 1996).

Quinoa seeds must be freed of seed coat saponins before consumption. Saponins can be easily eliminated by water washing or abrasive dehulling. There was no difference in the removal of saponins observed between the two methods (Ridout et al. 1991), although the latter method has the advantage of not generating wastewater. However, some nutrients can be lost when the abrasive dehulling method is used (Repo-Carrasco-Valencia 2011).

Among the nutritional attributes of quinoa seed, prominent is its high-quality protein that is gluten-free and has an exceptional amino acid balance. The presence of essential amino acids such as methionine, threonine, lysine, and tryptophan are very important because they are limiting amino acids in most cereal grains (Gorinstein et al. 2002). The high level of tryptophan found in the seed of the Bolivian cultivar "Sajama" is noteworthy (Comai et al. 2007). Protein quality is determined by its biological value (BV), which is an indicator of protein intake by relating nitrogen uptake to nitrogen excretion. The highest values of BV correspond to whole egg (93.7%) and cow milk (84.5%) (Friedman 1996). The protein of quinoa seed has a BV of 83%, which is higher than that of fish (76%), beef (74.3%), soybean (72.8%), wheat (64%), rice (64%), and corn (60%) protein (Abugoch 2009).

According to the FAO/WHO nutritional requirements for 10- to 12-year-old children, quinoa protein possesses adequate levels of phenylalanine, tyrosine, histidine, isoleucine, threonine, and valine (FAO/WHO 1990). Consequently, there is no need to combine quinoa seed with other protein sources to supply human requirements for essential amino acids. This nutritional aspect of quinoa is very significant as it can provide a new protein source for a good diet. Quinoa may also be an important alternative crop for mountainous regions of the world, where many people live. In these regions, there are severe constraints in obtaining good quality food and quinoa will be able to supply the nutrient requirements that other crops cannot, especially for children.

The nutritional composition of quinoa seed is determined by both the genotype and the environment. The metabolism of nitrogen-containing compounds, that is, proteins and amino acids, may be strongly affected by environmental conditions (Triboi et al. 2003). In a recent ecophysiological study carried out on 10 quinoa cultivars from the Bolivian highland region (Patacamaya site, 3,600 masl) and northwest Argentinean lowland region (Encalilla site, 2,000 masl), González et al. (2011) demonstrated that in six cultivars (Amilda, Kancolla, Chucapaka, Ratuqui, Robura, and Sayaña) the protein content showed an increment in the lowland growing site when compared with seeds from the highland site. In contrast, four cultivars (CICA, Kamiri, Sajama, and Samaranti) showed a decreased content (Table 1.1). Similarly, it has also been demonstrated that both the content and the composition of quinoa saponins are affected by environmental conditions. Both drought and salinity decreased the content and profile of saponins of quinoa cultivars (Solíz-Guerrero et al. 2002; Dini et al. 2005; Gómez-Caravaca et al. 2012). In effect, many metabolic and physiological aspects of crops are affected by agroecological conditions (Triboi et al. 2003). Soil type and climatic conditions also play a crucial role in the success of crops. These are important results and should be taken into account when choosing a commercial cultivar.

Table 1.1 Protein content (g/100 g DW) of quinoa seeds cultivated in two agroecological sites (Patacamaya, 3,600 masl and Encalilla, 2,000 masl).

Cultivar	Patacamaya (g/100 g DW)	Encalilla (g/100 g DW)	Difference (%)
Amilda	11.41	12.5	8.7
Kancolla	14.44	15.17	4.8
Chucapaka	11.67	14.34	18.6
CICA	15.46	13.46	−14.9
Kamiri	13.98	13.12	−6.6
Ratuqui	10.38	15.53	33.2
Robura	9.62	10.43	7.8
Sajama	12	9.15	−31.1
Samaranti	12.26	9.34	−31.3
Sayaña	11.36	13.85	18.0

Quinoa may be considered as a potential alternative crop in many regions of the world due to the nutritional quality of its seed and its good potential for adaptation (González et al. 1989, 2012; Dini et al. 2005; Comai et al. 2007; Thanapornpoonpong et al. 2008). Probably all these aspects were taken into account by the FAO when it included quinoa in the list of most promising crops for world food security and human nutrition in the twenty-first century (FAO 2006). The National Aeronautics and Space Administration (NASA) also included quinoa within the Controlled Ecological Life Support System (CELSS) to augment the inadequate protein intake of astronauts in long-duration space travel (Schlick and Bubnehiem 1993).

BOTANICAL AND GENETIC CHARACTERISTICS OF THE QUINOA PLANT

Quinoa is an annual Amaranthaceae. This Andean grain is an important crop of the Andean region in South America from Colombia (2°N) to central Chile (40°S) (Risi and Galwey 1984; Jacobsen 2003). Despite its wide latitudinal distribution, quinoa also has a broad altitudinal distribution. Quinoa may be cultivated at sea level, middle mountain (between 2,000 and 3,000 masl), and high mountain (above 3,000 masl). In relation to this altitudinal and latitudinal distribution pattern, Tapia (2009) distinguished at least five ecotypes of quinoa: (i) *Valley* quinoa, which are late-ripening, with plant heights 150–200 cm or more, and growing at 2,000 and 3,000 masl; (ii) *Altiplano* quinoa, which can withstand severe frost and low precipitation, growing around Titicaca Lake in Bolivia and Perú; (iii) *Salar* quinoa, which can tolerate salty soils with high pH values, growing on the plains of the Bolivian Altiplano such as Uyuni and Coipasa; (iv) *Sea level* quinoa, generally small plants (near 100 cm) with a few stems and bitter grains, found in the south of Chile; and (v) *Subtropical* quinoa, which have small white or yellow grains, growing in the inter-Andean valleys of Bolivia. Royal Quinoa (Quinoa Real) is probably the most recognized quinoa cultivar in the international market. It is a bitter variety and is only produced in Bolivia, particularly in the districts of Oruro and Potosí, around the salt flats of Uyuni and Coipasa. The microclimatic conditions and physicochemical properties of the soil offer the appropriate habitat for the production of this type of quinoa (Rojas et al. 2010). Morphophenological characteristics of quinoa show that there is a huge diversity in varieties or local ecotypes (del Castillo et al. 2007). Therefore, available commercial quinoas exhibit wide genetic diversity, showing great variability in plant color, inflorescence and seeds, inflorescence type, protein, saponin and betacyanine contents, and calcium oxalate crystals in leaves. This extreme variability may reflect wide adaptation to

different agroecological conditions such as soil, rainfall, nutrients, temperature, altitude, drought, salinity, and UV-B radiation.

Quinoa is a dicotyledonous annual herbaceous plant usually erect, with a height of about 100–300 cm, depending on environmental conditions and genotype. Leaves are generally lobed, pubescent, powdery, rarely smooth, and alternatively inserted on a woody central stem. The plant may be branched or unbranched, depending on variety and sowing density. Stem color may be green, red, or purple. The leafy flower cluster (a panicle with groups of flowers in glomerulus) arises predominantly from the top of the plant and may also arise from the leaf junction (axil) on the stem. Flowers are sessile, of the same color as the sepals, and may be hermaphrodite, pistillate, or male sterile. The stamens have short filaments bearing basifixed anthers; the style has two or three feathery stigma. The fruit occurs in an indehiscent achene, protected by the perigonium. The seeds are usually somewhat flat, measure 1–2.6 mm, and approximately 250–500 seeds comprise 1 g. The seeds also exhibit a great variety of colors – white, yellow, red, purple, brown, and black, among others. Seed embryo can be up to 60% of the seed weight and forms a ring around the endosperm. The taproot (20–50 cm long) is profusely branched and forms a dense web of rootlets that penetrate to about the same depth as the plant height (National Research Council 1989).

The vegetative period of quinoa is related to photoperiod sensitivity and varies between 120 and 240 days. Some varieties, such as CO-407 from Chile, have a vegetative period between 110 and 120 days, but others, such as the CICA variety, have more than 200 days. On the other hand, *C. quinoa* is a C_3 species confirmed by anatomical studies and carbon isotope discrimination (González et al. 2011). The $\delta^{13}C$ values of leaves of 10 varieties of quinoa ranged from a minimum of −27.3‰ to a maximum of −25.2‰ (Table 1.2). Typical values of $\delta^{13}C$ in C3 species can ranges from −35 to −20‰ (Ehleringer and Osmond 1989).

C. quinoa is an allotetraploid ($2n = 4x = 36$) and exhibits disomic inheritance for most qualitative traits (Simmonds 1971; Risi and Galwey 1989; Ward 2001; Maughan et al. 2004). The species closest to cultivated quinoa are *Chenopodium hircinum* and *Chenopodium berlandieri*, whose basic chromosome number ($2n = 4x = 36$) is the same as that of the cultivated types, and *Chenopodium petiolare* and *Chenopodium pallidicaule*, which have $2n = 2x = 18$ chromosomes (Fuentes et al. 2009). Quinoa species includes both domesticated cultivars (subsp. *quinoa*) and free-living, weedy forms (subsp. *milleanum* or *melanospermum*) (Wilson 1981, 1988). Domesticated and weedy quinoa populations are sympatric, and share a fundamentally autogamous reproductive system as well as a wide range of variation in leaf and grain size and color (del Castillo et al. 2007). Wild and domesticated populations of quinoa exist under cultivation, which indicates that domesticated quinoas are generally accompanied by wild populations in their various distribution areas. Thus, natural hybridization between wild and domesticated populations probably occurs easily (Fuentes et al. 2009). The highest variation in cultivated quinoa is found near Titicaca Lake, between Cuzco (Peru) and Lake Poopó (Bolivia), and this is where scientists believe the crop was first domesticated (Heiser and Nelson 1974). The main varieties known in this region are Kancolla, Cheweca, Witulla, Tahuaco, Camacani, Yocara, Wilacayuni, Blanca de Juli, Amarilla de Maranganí, Pacus, Rosada de Junín, Blanca de Junín, Hualhuas, Huancayo, Mantaro, Huacariz, Huacataz, Acostambo, Blanca Ayacuchana, and Nariño in Peru and Sajama,

Table 1.2 Carbon isotope composition $\delta^{13}C$ of 10 varieties of quinoa.

Cultivar	$\delta^{13}C$
Amilda	−25.6
Chucapaca	−26.3
CICA	−26.6
Kancolla	−27.3
Kamiri	−26.7
Ratuqui	−26.4
Sayaña	−26.3
Robura	−25.7
Sajama	−25.2
Samaranti	−25.6

Real Blanca, Chucapaca, Kamiri, Huaranga, Pasancalla, Pandela, Tupiza. Jachapucu, Wila Coymini, Kellu, Uthusaya, Chullpi, Kaslali, and Chillpi in Bolivia (Hernández Bermejo and León 1994). Throughout the Andean region, there are several genebanks where over 2,500 quinoa accessions are preserved in cold-storage rooms: in Peru, at the experimental stations of Camacani and Illpa (Puno), K'ayra and Andenes (Cuzco), Canaan (Ayacucho), Mantaro y Santa Ana (Huancayo), Baños del Inca (Cajamarca); in Bolivia, at the Patacamaya station of the IBTA; and in Ecuador, at the Santa Catalina station of INIAP.

QUINOA AND ENVIRONMENTAL STRESSES: DROUGHT AND SALINITY

Soil salinization is one of the major environmental issue affecting crop production, especially in marginal landscapes or areas with limited resources (Munns and Tester 2008; Rengasamy 2010; Munns 2011; Hussin et al. 2013). The intensive use of valuable natural resources such as land and water, along with high soil evapotranspiration and inefficient irrigation systems associated with poor water and soil management, inevitably accelerate secondary salinization that usually results in the loss of productive areas (Munns 2005; Hussin et al. 2013). Nearly 20% of the world's cultivated areas and about half of the world's irrigated lands are salt affected (FAO 2008). Out of the current 230 Mha of irrigated land, 45 Mha are salt-affected soils (19.5%), and of the almost 1,500 Mha dry agricultural land, 32 Mha are salt affected to varying degrees by human-induced processes (Munns and Tester 2008). Salinization of irrigated lands causes a loss of US$12 billion of the annual global income (Ghassemi et al. 1995).

In this context, enhancing salt tolerance of the conventional crops has proved to be somewhat elusive in terms of genetic manipulation to allow greater yields in salt-affected soils and marginal areas (Flowers 2004). The results, although promising, remain insignificant so far (Läuchli and Grattan 2007). An alternative approach is the use of naturally occurring xero-halophyte for crop production, "cash crop halophytes," as they already have the required level of salt tolerance (Lieth et al. 1999). The sustainable utilization of halophytes as cash crops may significantly contribute toward food, feed, fuel, wood, fiber, chemical production, and environmental quality (dune stabilization, combating desertification, bioremediation, or CO_2 sequestration) in many countries (Geissler et al. 2010; Hussin et al. 2013). Hence, research has focused more and more on the identification and selection of plant species such as *C. quinoa* that are naturally tolerant to drought and salinity.

Quinoa is one of the few crops, if not the only crop, able to grow in the most extreme environmental conditions (Jacobsen et al. 2003). In effect, quinoa can be cultivated from sea level to 4,000 masl, even in the Bolivian Altiplano with an extreme altitude of 4,200 masl. Quinoa is also remarkably adaptable to different agroecological zones. It adapts to hot, dry climates, can grow in areas of varying relative humidity, ranging from 40% to 88%, and can withstand temperatures from −4 to 38°C. Quinoa can grow in marginal soils lacking in nutrients, in soils with a wide range of pH from acid to basic (Boero et al. 1999), and even tolerates soil infertility (Sanchez et al. 2003). It also has excellent tolerance to extreme frost (Halloy and González 1993; Jacobsen et al. 2005, 2007), long drought periods (Vacher 1998; González et al. 2009a; Jacobsen et al. 2009), salinity (González and Prado 1992; Prado et al. 2000; Rosa et al. 2009; Ruffino et al. 2010; Hariadi et al. 2011), and high solar radiation (Palenque et al. 1997; Sircelj et al. 2002; Hilal et al. 2004; González et al. 2009b). It has high water use efficiency (WUE) shown by its tolerance or resistance to lack of soil moisture and produces acceptable yields with rainfall of 100–200 mm (Garcia et al. 2003, 2007; Bertero et al. 2004). Quinoa resists up to 3 months of drought at the beginning of its growth cycle. To make up for this part of its growth cycle, the stalk becomes fibrous and roots strengthen. When rains come, it recovers physiological activity (National Research Council 1989). Some varieties can grow in salt concentrations similar to those found in seawater

(40 dS/m) and even higher, well above the threshold for any known crop species (Hariadi et al. 2011; Razzaghi et al. 2011).

Salt tolerance is a complex trait and attributed to a plethora of interconnected morphological, physiological, biochemical, and molecular mechanisms. These mechanisms are linked to the major constraints of salinity on plant growth (i.e., osmotic effects, restriction of CO_2 gas exchange, ion toxicity, and nutritional imbalance) and operate in coordination to alleviate both the cellular hyperosmolarity and ion disequilibrium (Koyro 2006; Flowers and Colmer 2008; Geissler et al. 2009). The primary deleterious effect of soil salinity on plant growth is due to an osmotic effect, resulting from the lower soil water potential (Ψ), defined as the work water can do as it moves from its present state to the reference state. The reference state is the energy of a pool of pure water at an elevation defined to be zero (Munns 2002; Koyro et al. 2012). A low value of (Ψ) interferes with plant ability to take up water from the soil and, hence, causes a growth reduction, along with a range of physiological and biochemical changes similar to those caused by water deficit (Larcher 2001; Schulze et al. 2002; Munns 2005). To endure osmotic constraint, salt-tolerant plants are more restrictive with water loss via transpiration by a sensitive stomatal closure response. Inevitably, this leads to a decrease in the apparent photosynthetic rate due to a restricted availability of CO_2 for the carboxylation reaction (stomatal limitation of photosynthesis) (Huchzermeyer and Koyro 2005; Flexas et al. 2007; Dasgupta et al. 2011; Benzarti et al. 2012), thereby suppressing plant growth and productivity (D'Souza and Devaraj 2010; Gorai et al. 2011; Tarchoune et al. 2012; Yan et al. 2013).

According to several studies, quinoa tolerance to drought and salinity stresses is dependent on its vegetative stage (Bosque Sanchez et al. 2003; Garcia et al. 2003; Jacobsen et al. 2003). At the cotyledonary stage, the high adaptability of quinoa to soil salinity is related to metabolic adjustment. In studies carried out with seedlings of the Sajama cultivar, it was demonstrated that salinity tolerance depends on improved metabolic control of ion absorption and osmotic adjustment through osmolyte accumulation derived from a salt-induced altered carbohydrate metabolism (Rosa et al. 2009; Ruffino et al. 2010), whereas in early maturing stage, it is also related to structural and physiological adaptations. In this way, quinoa avoids the negative effects of drought through the development of a deep and dense root system, reduction of the leaf area, leaf dropping, special vesicular glands (salt bladders), small and thick-walled cells adapted to losses of water without loss of turgor even at severe water losses, and stomatal closure (Jensen et al. 2000; Adolf et al. 2013).

Although quinoa was classified as a highly salt-tolerant species (Jacobsen 2003; Hariadi et al. 2011; Razzaghi et al. 2011; Eisa et al. 2012; Adolf et al. 2013), many quinoa cultivars show distinct variability in their germination and growth responses to salinity. More than 200 quinoa accessions have been tested under saline conditions and found to be different in their responses to salinity. Differences were observed at germination stage and also later during the vegetative growth stage (Adolf et al. 2012). Moreover, salt tolerance at germination is not necessarily correlated with the degree of tolerance at later developmental stages. Eisa et al. (2012) found that the growth of the Peruvian quinoa cultivar "Hualhuas" was slightly stimulated in response to a low salinity level (20% seawater salinity). The same trend of salt-induced growth stimulation has been recently observed for the cultivar "CICA" (Fig. 1.1). The overall growth of CICA plants based on fresh weight (FW) gain was significantly increased ~85% compared with control plants grown under non-saline conditions. This increase was mainly a result of increased shoot FW rather than root FW (Fig. 1.1). Similar salt-induced stimulation of growth has also been reported for other Peruvian and Bolivian quinoa cultivars (Wilson et al. 2002; Koyro and Eisa 2008; Hariadi et al. 2011). Furthermore, the Andean hybrid grown at salinity level of 11 dS/m showed increases in both leaf area and dry mass when comparing with plants grow at control salinity level of 3 dS/m. As shown in Fig. 1.1, salinity tolerance threshold for CICA variety was at 200 mM NaCl, whereas

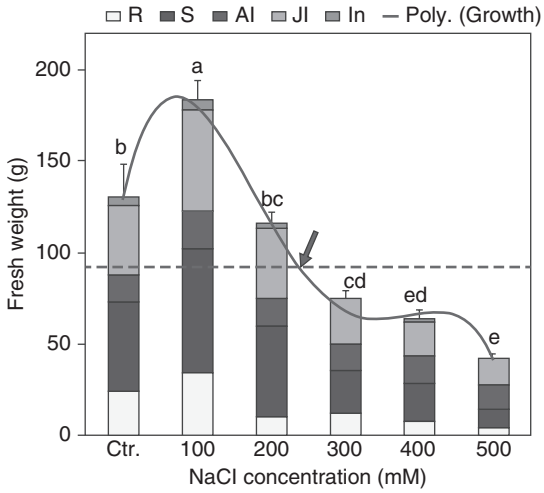

Fig. 1.1 Development and growth responses of different organs (expressed as fresh weights) of *C. quinoa* cv. CICA grown at different NaCl concentrations. The dotted line marks the C_{50} value. Each column represents the mean value of three replicates and the bars represent standard deviations. Columns with the same letter are not significantly different at $P \leq 0.05$, Duncan test. (R) root, (S) stem, (Al) adult leaf, (Jl) juvenile leaf, and (In) inflorescence.

C_{50} was slightly above 40% seawater salinity. The salinity tolerance threshold is the salt level that leads to the initial significant reduction in the maximum expected yield (Shannon and Grieve 1999), whereas C_{50} is the water salinity leading to 50% growth reduction in the maximum expected yield. In contrast, salinity levels above threshold value (supraoptimal condition) severely inhibit plant growth in many quinoa cultivars (Hariadi et al. 2011; Eisa et al. 2012). Seawater salinity level (500 mM NaCl) led to a significant reduction (~66%) in the FW of CICA plants relative to the control (Fig. 1.1). Inhibition of the initiation of new leaves and the formation of small leaves, some with symptoms of nutrient disorders, might contribute to the low FW observed at this salinity level. Interestingly, the plants displayed conspicuous growth and continued to grow even at seawater salinity levels (Fig. 1.1). Together, these results indicate that the CICA cultivar is highly salt tolerant and productive, capable of growing even under sea water salinity levels.

Salinity stress results in a decrease of photosynthesis in a wide variety of plant species (Sudhir and Murthy 2004). However, many halophyte species show higher level of photosynthesis under conditions of elevated salinity (Andersone et al. 2012), depending on the level of salt tolerance of the species and/or genotypes (Brock et al. 2007). Quinoa cultivars also show different photosynthetic responses, depending on parental origin. Recently, Adolf et al. (2012) found significant differences in both photosynthetic CO_2 assimilation and stomatal conductance when two varieties of quinoa when grown under saline conditions. "Utusaya," originating from the salar region of Bolivia, maintained a relatively high stomatal conductance, with only 25% reduction in net CO_2 assimilation when compared with the untreated control plants. In contrast, the cultivar "Titicaca" that has been bred in Denmark showed a higher decrease in stomatal conductance and also a 67% reduction in CO_2 assimilation. Interestingly, in the Utusaya variety, both the stomatal conductance and the photosynthesis rate were generally low under non-saline conditions, whereas these did not decrease in the Titicaca variety. Thus, it may be assumed that in saline environments, the Utusaya variety has a genetically improved osmoregulator mechanism to counteract the deleterious osmotic effects of salt and has less need to reduce water loss by transpiration (Adolf et al. 2013). A similar trait was observed between the CICA (less salt tolerant) and the Hualhuas (more salt tolerant) cultivars grown under increasing saline levels. The CO_2 assimilation (net photosynthetic rate, P_N) of the CICA cultivar steadily and significantly declined with increasing water salinity, reaching only 1.5% of the control values at seawater salinity treatment (Table 1.3). This result was consistent with observations on the effect of salinity on photosynthesis in many salt-tolerant species (Ashraf 1999; Bayuelo-Jiménez et al., 2003; Qiu et al. 2003; Koyro 2006). In a previous study, however, Eisa et al. (2012) showed that the photosynthetic activity of the Hualhuas cultivar was less affected with salt-induced reduction of about 72% at seawater salinity level. Furthermore, the photosynthetic responses of the cultivars CICA and Hualhuas correspond with the assumptions of Kao et al. (2006) and Moradi and Ismail (2007), who assume

that relatively higher salt-tolerant species would have less reduced net photosynthesis. On the other hand, the reduction of P_N observed in CICA coincided with the progressive decrease of stomatal conductance (C_S), suggesting that salinity impacted the photosynthesis of CICA plants, at least partly, by an enhanced stomatal closure. Positive correlations between P_N and C_S have been found in *C. quinoa*, Hualhaus cultivar (Eisa et al. 2012), *Atriplex prostrata* (Wang et al. 1997), *Atriplex nummularia* and *Atriplex hastata* (Dunn and Neales 1993), *Atriplex centralasiatica* (Qiu et al. 2003), and *Avicennia marina* (Ball and Farquhar 1984).

According to Moradi and Ismail (2007) and Centritto et al. (2003), reduction of stomatal conductance is a significant way to decrease water loss from the leaves via transpiration and could be considered as an adaptive feature for salt tolerance. In CICA plants, the salt-induced reduction of C_S gives a strong inhibition of the transpiration rate (E), which reaches a minimum value at the highest salinity treatment (Table 1.3). This would contribute to conservation of water and also maintain a positive water balance. In fact, lower values of E represent an additional adaptive mechanism for coping with high salinity levels, as it could reduce salt loading into leaves and hence prolong the leaf lifespan by maintaining a subtoxic level of salt (Everard et al. 1994; Koyro 2006).

The coordinated regulation of CO_2/H_2O gas exchange is considered a key determinant for plant growth and biomass production under saline conditions (Romero-Aranda et al. 2001; Lu et al. 2002; Gulzar et al. 2003, 2005). In Hualhuas, Eisa et al. (2012) found that salt-induced reduction of transpiration rate was proportionally larger than the photosynthetic rate, leading to improved photosynthetic water use efficiency (PWUE). However, this is not the case for CICA, as the salt-induced reduction of photosynthetic rate was proportionally larger than that of the transpiration rate, resulting in a marked decline of PWUE (Table 1.3). According to Naidoo and Mundree (1993) and Koyro (2000), increasing PWUE is an important adaptive feature for long-term survival of plants and would be an advantage in saline environments. This may explain the relatively lower salt tolerance of CICA compared to Hualhaus. Interestingly, salt-induced reduction of P_N in CICA showed a positive correlation with C_S, but not with intercellular CO_2 concentration (C_i) (Table 1.3), suggesting that C_i is not the limiting factor for photosynthesis reduction in CICA under saline conditions.

Non-stomatal inhibition of photosynthesis in salt-stressed plants, particularly under severe stress conditions, has also been reported for several other crop species such as *Gossypium hirsutum* and *Phaseolus vulgaris* (Brugnoli and Lauteri 1991), *Oryza sativa* (Dionisio-Sese and Tobita 2000), *Helianthus annuus* (Steduto et al. 2000), and *Beta vulgaris* (Dadkhah 2011), among others. This inhibition of photosynthetic capacity has been attributed to an inhibited coupling factor activity (Tezara et al. 2008), reduced carboxylation efficiency (Wise et al. 1992; Jia and Gray 2004), reduced amount and/or activity of crucial photosynthetic enzymes such as Rubisco (Parry

Table 1.3 Effect of elevated water salinity on the net photosynthesis rate (P_N), transpiration rate (E), Stomatal conductance (C_s), ratio of the internal to the external CO_2 concentration (C_i/C_a), and photosynthetic water use efficiency (PWUE) of *C. quinoa* cv. CICA. All of these values are at the light saturation point of photosynthesis.

Treatments	P_N (μmol m^{-2} s^{-1})	E (mmol/m^2s)	C_s (mmol H_2O/m^2s)	C_i/C_a	PWUE (%)
Control	$16.615^a \pm 1.011$	$2.733^a \pm 0.234$	$0.164^a \pm 0.018$	$0.491^a \pm 0.022$	$0.625^a \pm 0.019$
100 mM	$12.310^b \pm 0.122$	$2.417^a \pm 0.045$	$0.140^b \pm 0.003$	$0.588^b \pm 0.006$	$0.510^{bc} \pm 0.006$
200 mM	$10.907^c \pm 0.119$	$1.998^b \pm 0.019$	$0.111^c \pm 0.002$	$0.550^b \pm 0.010$	$0.546^b \pm 0.007$
300 mM	$8.088^d \pm 0.398$	$1.232^c \pm 0.148$	$0.064^d \pm 0.008$	$0.577^b \pm 0.018$	$0.446^c \pm 0.034$
400 mM	$1.105^e \pm 0.240$	$0.357^d \pm 0.032$	$0.017^e \pm 0.002$	$0.747^c \pm 0.029$	$0.256^d \pm 0.034$
500 mM	$0.237^e \pm 0.048$	$0.280^d \pm 0.009$	$0.012^e \pm 0.000$	$0.882^e \pm 0.015$	$0.171^e \pm 0.018$

Means within a column followed by the same letter are not significantly different at $P \leq 0.05$, as determined by Duncan test. Each mean represents three replicates.

et al. 2002), reduced ribulose-1,5-bisphosphate (RuBP) regeneration (Giménez et al. 1992; Gunasekera and Berkowitz 1993), and reduction of the contents of photosynthetic pigments (Seemann and Critchley 1985; Hajar et al. 1996; Koyro 2006).

Salinity and drought may also impair photosynthesis by disturbing the photochemical reactions in the chloroplast (Tezara et al. 2005; Hura et al. 2007). Furthermore, as an indirect consequence of stomatal closure induced by salt and/or drought stress, restriction in intercellular CO_2 concentration should increase susceptibility to photochemical damages as excessive light energy at PSII level increases when CO_2 assimilation rates are low (Silva et al. 2010). This effect, however, seems to be species specific. For example, sorghum (*Sorghum bicolor*) plants subjected to salt stress showed a strong disturbance of photochemical activity (Netondo et al. 2004), whereas cowpea (*Vigna unguiculata*) plants subjected to progressive drought displayed slight changes in the PSII activity (Souza et al. 2004). Moreover, it has been demonstrated that stomatal closure reduces the CO_2/O_2 ratio in leaves and inhibits the fixation of CO_2, which induces an increased ROS generation via enhanced leakage of electrons to oxygen (Foyer and Noctor 2000). Therefore, in salt-treated plants, a low rate of CO_2 assimilation can result in oxidative stress.

Salt-induced leaf succulence and reduction in chlorophyll content has also been observed in quinoa plants in response to high water salinity (Eisa et al. unpublished results). With quinoa being a salt-tolerant species, it is conceivable that in salt-stressed plants the stomatal closure allows the leaves to either develop an additional scavenging mechanism in their light reaction centers or utilize the excessive energy for ion excretion or sequestration. This condition may lead to a reduction of the flow of electrons through the photosystems (reduction of the apparent quantum efficiency) (Table 1.3). Furthermore, the presence of a dense layer of bladder hairs filled with salt on the surface of leaves can form a strong reflective light (Fig. 1.2). Thus, this light-reflecting layer is thought to protect the photosystems from overreduction and photoinhibition under stress

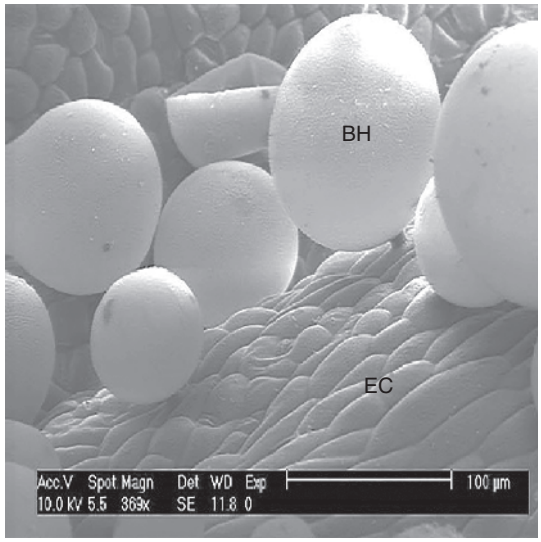

Fig. 1.2 Representative SEM micrographs of the juvenile leaf surface showing the various stages of bladder hairs development. BH, bladder hair and EC, epidermal cells.

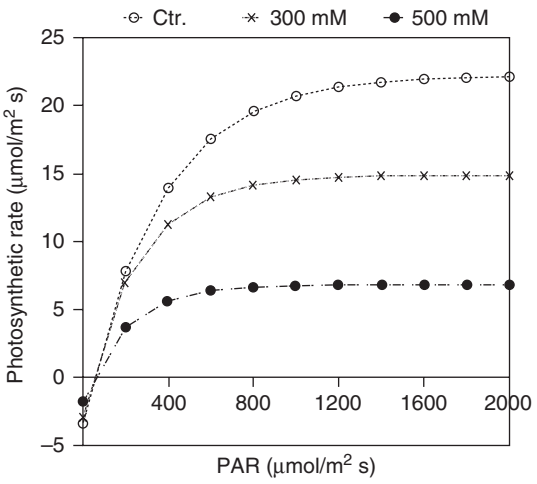

Fig. 1.3 Light response curves of *C. quinoa*, CICA cultivar, at different NaCl concentrations. Values are the mean of three independent measurements.

conditions (Freitas and Breckle 1992; Agarie et al. 2007; Orsini et al. 2011).

Light saturation point (L_s) gradually decreased with increasing water salinity, as shown in the cultivar CICA, commensurate with the reduction in photosynthetic capacity (Fig. 1.3). This might partially be due to salt-induced reduction in chlorophyll concentration per unit area

Table 1.4 Calculated photosynthetic efficiency (Φ_c), dark respiration (D_r), light compensation point (L_c), and light saturation point (L_s) of *C. quinoa* cv. CICA plants grown under various NaCl salinities.

Treatments	Φ_c[μmol CO_2 μmol^{-1} Quantum]	D_r[μmol m^{-2} s^{-1}]	L_c[μmol m^{-2} s^{-1}]	L_s[μmol m^{-2} s^{-1}]
Control 300 mM	0.062 0.052	−3.343 −2.627	49.945 46.172	872.297 652.115
500 mM	0.034	−1.756	45.722	506.239

The calculation was done using SigmaPlot software.

(Eisa et al. 2012). As a consequence, the calculated CO_2 compensation point (L_c) decreased in response to water salinity. Furthermore, the calculated dark respiration (D_r) decreased markedly with elevated water salinity, being minimal at 500 mM NaCl (Table 1.4). Salt-induced reduction in respiration rates might be due to the fact that the maintenance respiration of rapidly growing control plants is generally much higher than that of the more slowly growing plants grown under high saline stress (Koyro and Huchzermeyer 1999).

CONCLUSION

New goals and insights into food production and market development are needed in light of dwindling fresh water resources and the rapid loss of arable land due to soil salinization. Domestication of native halophytes and increasing the salt tolerance of glycophytic crops through the genetic engineering could achieve these goals, but research on these processes is still in the early stages. Realistically, success in both approaches will require considerable investment of time and resources (Rozema and Schat 2013). Given this scenario, *C. quinoa* appears to be a reliable new crop option to sustain the food supply for a rapidly growing world population. Its high tolerance to salinity and drought, together with its excellent nutritional quality, makes it an ideal crop to contribute to food security for the twenty-first century.

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