

STATE OF THE ART
REPORT ON QUINOA
AROUND THE WORLD IN 2013



Food and Agriculture
Organization of the
United Nations

International Year of Quinoa Secretariat: Salomón Salcedo (FAO)
General coordination of the International Year of Quinoa: Tania Santivañez (FAO)
Scientific and technical coordination: Didier Bazile (CIRAD)
Scientific publication: Didier Bazile, Daniel Bertero and Carlos Nieto
Original design: Marcia Miranda
Layout of English edition: Art&Design
Collaborators: Sara Granados and Gonzalo Tejada

Recommended citation:

FAO & CIRAD. 2015. *State of the Art Report of Quinoa in the World in 2013*, by D. Bazile, D. Bertero & C. Nieto, eds. Rome.

To cite a chapter:

Authors. 2015. Title of the chapter. Chapter XX. In FAO & CIRAD. *State of the Art Report of Quinoa in the World in 2013*, p. XX-YY. Rome.

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ISBN 978-92-5-108558-5

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Centre de Coopération Internationale en Recherche

Agronomique pour le Développement

Food and Agriculture Organization of the United Nations (FAO)

Santiago, 2014

CHAPTER 2.4.

QUINOA DROUGHT RESPONSES AND ADAPTATION

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Abstract

Quinoa thrives under a wide range of soil and climate conditions, from cold and arid areas to wet tropical regions. The adaptability of quinoa to various levels of drought is due to the differentiation of a diversity of ecotypes originating in contrasting agro-environments. Plants display various adaptive strategies to drought stress, from morphological to physiological adaptations that serve a range of responses to water deficit, from avoidance to resistance and tolerance. Plants cope with drought stress by changing and modifying key physiological processes, such as photosynthesis, respiration, water relations and antioxidant and hormone metabolism. Whole-plant responses to drought involve changes in leaf and root growth, in some cases with strong ontogenetic variation. These drought responses at both physiological and morphological levels show intraspecific variation related to ecotypic differentiation. This chapter explores the responses to this abiotic stress and reviews possible mechanisms

concurring at both whole plant and tissue level, including recent determinations from architectural, morphological, physiological and molecular perspectives. Quinoa thus represents an invaluable opportunity, both as a potential crop in consideration of present and future climate change challenges, and as an important source of genes with biotechnological applications.

Keywords: *Chenopodium quinoa*, drought, ontogeny, physiological responses, morphological traits, plant architecture, molecular responses, intraspecific variation.

1. Introduction

The Andean seed crop, quinoa (*Chenopodium quinoa* Willd.), was domesticated and has been traditionally cultivated in the area for at least 7 000 years. Quinoa diversity is described with five major ecotypes linked to diversity subcentres: Altiplano (Peru and Bolivia), Inter-Andean valleys (Bolivia, Colombia, Ecuador and Peru), Salare (Bolivia, Chile

and Argentina), Yunga (Peru, Bolivia and Argentina) and Coastal (Chile) (Risi and Galwey, 1989a, b; Bertero *et al.*, 2004). Its great diversity is characterized by exceptional adaptation to environmental conditions and edaphoclimatic conditions, including altitudes from sea level to 4 000 m asl, annual precipitation from 2 000 mm to extreme aridity (e.g. Las Quinas-Antofalla in Argentina, where it rarely rains and quinoa is totally dependent on irrigation – Bertero *et al.*, personal communication), significant variability in soil and nutrient availability, and climate conditions ranging from tropical to cold arid. Its adaptability to natural and cultivated ecosystems has made this species an outstanding model for the study of intra- and interspecific variation in growth and development patterns and in the response of shoot and root architecture to water deficit. The physiological adaptability that allows this species to grow under drought and other adverse conditions represents an invaluable opportunity and offers immense potential in the face of present and future climate change challenges.

2. Quinoa Responses to Water Deficit

Plant responses and mechanisms for dealing with low water availability can be divided into two major categories: stress avoidance and stress tolerance (Claeys and Inze, 2013). The aim of stress avoidance mechanisms is to balance water uptake and water loss. Water uptake is enhanced by the accumulation of solutes which lower tissue water potential and by increased root growth. Water loss through evaporation is limited by closing the stomata, resulting in restricted shoot growth and accelerated leaf senescence. Stress tolerance mechanisms are aimed at protecting against cell damage when stress becomes more severe and stress avoidance mechanisms are no longer sufficient. Stress tolerance mechanisms include detoxification by reactive oxygen species (ROS) and the accumulation of protective proteins such as late embryogenesis abundant (LEA) proteins and solutes (e.g. proline, which has a dual role as both osmolyte and osmoprotectant) (Claeys and Inze, 2013). Both avoidance and tolerance responses are mainly orchestrated by abscisic acid (ABA), although ABA-independent mechanisms, such as those involving dehydration responsive element binding (DREB) proteins, also play a role (Nakashima *et al.*, 2009).

Quinoa possesses an exceptional innate ability to cope with water shortage based on its intrinsic low water requirement, and the aptitude to resume rapidly its former photosynthetic level and its specific leaf area after a period of drought (Galwey, 1989; Jensen *et al.*, 2000; Jacobsen *et al.*, 2003, 2009). This makes quinoa suitable for growing in arid and semi-arid regions (e.g. India, sub-Saharan African countries), where there is no irrigation and farmers need to rely on seasonal rainfall (Bhargava *et al.*, 2006). Drought tolerance of quinoa has been attributed to its branched and deep root system that penetrates up to 1.5 m in sandy soils (Álvarez-Flores, 2012), and the presence of leaf vesicles containing calcium oxalate, which could reduce transpiration (Jensen *et al.*, 2000; Siener *et al.*, 2006). It has been demonstrated that high instantaneous photosynthetic efficiency (measured either as photochemical efficiency or as radiation use efficiency) is maintained in quinoa despite water deficit (Winkel *et al.*, 2002; Bosque Sanchez *et al.*, 2003). The plant also avoids drought thanks to: reduction of its leaf area by leaf shedding; small and thick-walled cells preserving turgor even after severe water losses; and stomatal regulation (Jensen *et al.*, 2000). In addition, quinoa can escape drought through precocity (i.e. early genotypes), which is important in areas where the risk of drought increases towards the end of the growing season (i.e. terminal drought), and also through low osmotic potential and the ability to maintain positive turgor even at low leaf water potential (Jacobsen and Mujica, 2001; Bhargava *et al.*, 2006). Drought escape manifests itself as a prolongation of the growth cycle in response to drought in the early vegetative stages and as early maturity in response to drought in the later growth stages (Jacobsen *et al.*, 2003; Geerts *et al.*, 2008). Given the vast genetic variability of the different quinoa ecotypes and genotypes for this characteristic, there is no agreement concerning the level of drought resistance of quinoa (Jacobsen and Mujica, 2001).

2.1. Long-distance signals controlling leaf expansion and stomatal conductance

The above-mentioned drought modifications and mechanisms – rapid stomatal closure, increased levels of ABA and increased content of osmoprotectants (i.e. betaine and proline) – are also common and shared with other plants (Jacobsen *et al.*, 2009). However, other mechanisms are still not

completely understood, such as the accumulation of calcium oxalate, increased protein stability and thermostability of chlorophyll, which could be due to mechanisms which are genetically different from those already reported (Morales and Zurita, 2010; Shabala and Mackay, 2011).

The effects of drought on leaf water potential (ψ_l), stomatal conductance (g_s), transpiration (Tr), photosynthesis rate (A_{max}) and crop yields were previously determined under the natural climatic conditions of the southern Bolivian Altiplano (Vacher, 1998). Drought caused large decreases in the parameters measured, and there was a major, rapid stomatal closure with an associated two-thirds reduction in Tr and A_{max} ; and as drought continued, these parameters remained relatively stable, while the minimum potential reached values below -4 MPa. Interestingly, it has also been observed that stomata do not seem to respond to abscisic acid (ABA), except in conditions of extreme drought, and that quinoa plants can photosynthesize for a long period under very low irrigation, even for 3 days after stomata are closed (Jacobsen *et al.*, 2009). When stomata are closed, a phenomenon occurring in many plant species - but not yet demonstrated in quinoa - is that oxalic acid is reconverted to carbon dioxide for photosynthesis, allowing excellent water use efficiency (Sen *et al.*, 1971). In the study of how chemical and hydraulic signalling from the root system controlled gas exchange in plants growing in a drying soil, Jacobsen *et al.* (2009) determined that photosynthesis was maintained after stomata closure and, interestingly, only a slight increment of ABA in the xylem was detected. ABA was also documented when the crop encountered very mild stress, thus demonstrating that chemical signalling can also play an important role in maintaining stomatal conductance under these conditions (Hariadi *et al.*, 2011; Razzaghi *et al.*, 2011). Other mechanisms to maintain turgor under increasing drought could be osmotic adjustment, as suggested in other quinoa cultivars, and antitranspirant compounds other than ABA in the xylem sap (Jacobsen *et al.*, 2009; Hariadi *et al.*, 2011). The authors concluded that during soil drying, quinoa plants present a sensitive stomatal closure, by which the plants are able to maintain ψ_l and A_{max} , resulting in an increase in water use efficiency (WUE). The modest role of root-sourced ABA regulation means that quinoa

must depend also on hydraulic regulation through a change in turgor or other chemical substances yet to be determined (Jacobsen *et al.*, 2009).

Natural candidates for regulatory roles include other hormones which have been shown to play an important role in adjusting growth to water availability. Indeed, transcript analysis of proliferating and expanding leaf tissue from *Arabidopsis* plants exposed to mild osmotic stress revealed a role of ethylene and gibberellic acids (GAs) in acclimation to both short- and long-term mild drought stress (Skirycz *et al.*, 2011; Claeys and Inze, 2013). This important role for GAs in growth regulation was corroborated by other studies that profiled leaf tissue at different developmental stages in *Brachypodium distachyon* and maize subjected to mild drought (Verelst *et al.*, 2013; Claeys and Inze, 2013). The role of the "stress hormone", ABA, is confusing in quinoa and other species, but current consensus suggests that ABA can both directly inhibit growth and indirectly stimulate growth by reducing ethylene biosynthesis, due to signals controlling growth that are organ- and tissue-specific, and finally in severe drought conditions ABA can activate aquaporin expression, thus controlling hydraulic conductance (Tardieu *et al.*, 2010; Wilkinson and Davies, 2010; Claeys and Inze, 2013).

2.2. Turgor maintenance and osmotic adjustment

Recent evidence suggests that quinoa apparently uses a different system for adapting to water-deficient soil than that previously reported in maize, showing interactions between N, ABA and xylem pH to stomatal behaviour during soil drying (Jacobsen *et al.*, 2009). The mechanisms possibly used by quinoa to maintain turgor under increasing drought, in which ABA apparently plays a minor role, may include osmotic adjustment (Jensen *et al.*, 2000). Both high net photosynthesis rate and specific leaf area (SLA) values during early vegetative growth probably result in early vigour of quinoa, supporting early water uptake and thus tolerance to subsequent drought. The leaf water relations were characterized by low osmotic potential and low turgid weight/dry weight (TW/DW) ratio during later growth stages, sustaining a potential gradient for water uptake and turgor maintenance (Jensen *et al.*, 2000). The inherent low osmotic potential in quinoa probably causes drought tolerance, as in the

case of lowering the osmotic potential by osmotic adjustment in other crop species such as wheat.

Another possible explanation for drought-induced stomatal closure is that quinoa produces antitranspirant compounds other than ABA in the xylem sap. Cytokinins, the classical antagonists of ABA, may play a role. When cytokinin transport is reduced in the xylem, for instance as a result of limited N supply, stomatal sensitivity to xylem ABA may be increased (Jacobsen *et al.*, 2009). These authors concluded that during soil drying, quinoa plants have sensitive stomatal closure, maintaining leaf water potential and photosynthesis and resulting in increased water use efficiency. The apparent lack of significant root-sourced ABA regulation means that quinoa must depend also on hydraulic regulation through a change in turgor or activity of other biological compounds yet to be determined.

A salt stress-induced increase in the total level of soluble sugars, proline and glycine betaine was reported in quinoa (Jacobsen *et al.*, 2007, 2009; Ruffino *et al.*, 2010). Glycine betaine and other betaine derivatives have long been recognized as major osmolytes in several species. These two compatible solutes may account for around 3% of the total osmolality values measured in experiments on quinoa's responses to salinity (Hariadi *et al.*, 2011), consistent with and suggesting an indirect role for compatible solutes in plant osmotic adjustment.

A very different and surprising form of interplay between tolerance and growth is mediated by proline, which accumulates in response to many abiotic stresses and acts as an osmolyte osmoprotectant regulator of redox balance and signalling molecule. Proline is also considered the only osmolyte able to scavenge free radicals, thereby ensuring membrane stabilization and preventing protein denaturation during severe osmotic stress (Szabados and Savouré, 2010; Shabala *et al.*, 2012). Recently, proline was shown to be transported to growing tissues to act as an energy source to support both root and shoot growth, as proline catabolism directly transfers electrons to the mitochondrial electron transport chain (Sharma *et al.*, 2011).

Since salinity and drought share common osmotic responses, the accumulation of sugars and proline allows plants to maintain the cellular turgor pressure necessary for cell expansion under stress con-

ditions; they also act as osmoprotectants. Indeed, 300 mM NaCl induced an accumulation of proline in all quinoa genotypes evaluated; these could be divided into those that exhibited a moderate increase, and those that accumulated three to five times more of this osmolyte over control levels. Considering that this compatible solute acts as an osmoprotectant with a positive function in mitigating abiotic stress, the highest proline accumulation correlated with the most salt-tolerant quinoa genotype (Ruiz-Carrasco *et al.*, 2011).

2.3 Leaf growth, morphological and anatomical adaptive changes

Inhibition of leaf growth improves water balance and stress tolerance by limiting water loss, and thus ensures plant survival under water deficit. However, if this constraint is not only temporary, limiting growth too extensively (risk avoidance) can lead to a competitive disadvantage and unnecessary yield losses. Conversely, continued growth (taking risks) can threaten survival when water limitation turns out to be long and severe. Therefore, a balance between growth and survival, or in other words a choice between risks, is tightly regulated (Claeys and Inze, 2013).

Thus, growth regulation aimed at limiting shoot growth and thereby transpiration area is an integral part of the drought response of several plants. It has become evident that a very rapid and actively regulated response is not merely a consequence of altered hydraulics, as it cannot be abolished when xylem water potential is maintained, and it occurs in different species even when leaf water potential is not affected. Growth is also much more sensitive to water limitation than photosynthesis, and as a consequence carbohydrates as starch often accumulate in stressed plants, showing that growth reduction is not just the consequence of carbon starvation. There is a rapid and sharp decrease in leaf elongation rate in many species, termed "acute growth inhibition", followed by recovery of a new steady-state growth rate, referred to as "acclimation" (Skiryicz and Inzé, 2010).

Indeed, the leaf expansion rate (LER) determined for well-watered quinoa grown in pots in a controlled environment greenhouse was rather high (up to 500 mm²/day/plant), whereas it decreased

to 0 and was significantly lower than the control from the onset of drought. Drought reduced LER on average to about 50% during the first 10 days compared with well-watered plants. Moreover, plant leaf area was determined by both the area of individual leaves and the number of leaves, and drought may affect both. Nevertheless, the authors observed that reduction in single leaf expansion and whole plant leaf area occurred at a similar soil-water status (Jacobsen *et al.*, 2009).

Other quinoa responses to drought were mentioned earlier in this chapter (Dizès, 1992; Vacher, 1998), for example, massive leaf senescence and the existence of many bladders or glands in the stems and leaves whose volume varies depending on water deficit. Although quinoa leaves wilt under severe drought, thus decreasing leaf transpiration by reducing the leaf surface exposed to direct solar radiation, quinoa has evolved a remarkable ability to resume leaf formation quickly after a major drought stress, and its wilting point is also lower than other Andean crops such as bitter potato (*Solanum juzepczukii*) and sweet potato (*Ipomoea batatas*) (Dizès, 1992). Expanded leaf surfaces are smooth, since trichomes are lost in mature leaves and leaves have a thick cuticular epidermis, whereas young leaves are covered by multiple bladders containing calcium oxalate and silicic anhydride that are hygroscopic in nature and reduce transpiration, as determined by scanning electron microscopy in young leaves and cortical parenchyma, which suggests an indirect role in water economy and turgor maintenance (Dizès, 1992; Shabala and Mackay, 2011). Another anatomical feature likely to confer drought tolerance in quinoa consists of stomata deeply sunken in the leaf epidermis (Dizès, 1992). Similarly, small thick-walled cells may be better adapted to large water losses without loss of turgor (Jensen *et al.*, 2000; Jacobsen *et al.*, 2003), suggesting a biophysical mechanism as well.

2.4 Importance of root morphology and architecture for drought tolerance

The root system is a complex plant organ with multiple critical functions: anchorage and support, soil exploration, water and nutrient acquisition and transport, secondary metabolite synthesis and exudation (Hodge, 2009). When soil water uptake by the roots or xylem water transport becomes insuffi-

cient to satisfy evapotranspiration, or water demand is not satisfied in time by root absorption and transport, as in transient water deficit in irrigated crops, plants enter into a water deficit, which may affect dry matter accumulation (growth) as well as plant phenology (Passioura and Angus, 2010). Growth and development are crucial for plant productivity and, more specifically, for the economic yield of grain crops.

The capacity of plants to explore the soil and exploit water resources depends firstly on the spatial configuration of the root system and its growth dynamics during the vegetative cycle (Malamy, 2005; Hodge, 2009). The general configuration of the root system, or architecture, is described on the basis of dichotomic (without any predominant root axis) or “herringbone” (with a main root axis supporting lateral roots) patterns. With regards to the growth dynamics of the root system, plants with an enhanced capacity for root expansion can reach soil layers with higher resource availability more rapidly than those with slow or spatially limited root growth.

In addition to root system architecture, water acquisition by plants also depends on root morphology and anatomy. Specific root length (SRL: root length/dry matter ratio), for example, is associated with capacity for root elongation (Eissenstat, 1992; Roumet *et al.*, 2006). Similarly, the diameter and order of appearance of the roots may modify the absorption and transport of water to upper plant tissues (Pregitzer *et al.*, 1997; Ito *et al.*, 2006). These traits of root architecture and morphology may vary because of many interacting factors: plant phenology, growth conditions, drought intensity and duration, soil properties (Fitter, 1991; Kranner *et al.*, 2010; Nicotra *et al.*, 2002).

In this context and considering the ephemeral character of soil water resources, root system capacity to adjust itself to these changes appears of fundamental importance (Reader *et al.*, 1993). Several root traits, such as SRL or the root/shoot ratio (R/S: ratio of root dry mass/aerial part dry mass), display some degree of variation, a feature known as root phenotypic plasticity (Fitter, 1991). These traits associated with other anatomical modifications would allow for a higher transport capacity or greater exploration capacity in dry soil layers (Nicotra *et al.*, 2002). However, these root system responses may

also have a high carbon cost (Fitter, 1991) and slow down the development of other basal or adventitious roots (Walk *et al.*, 2006), or may even generate inter-root competition.

As for quinoa's root system, with the exception of short descriptions of some botanical traits (Mujica *et al.*, 2001), and of the chemical composition and R/S ratio (Schlick and Bubenheim, 1996; Bosque Sanchez *et al.*, 2003), interesting studies have recently tended to focus on root hormonal signalling (Jacobsen *et al.*, 2009; Razzaghi *et al.*, 2011), and on the impact of water and environmental factors on the R/S ratio and root length (González *et al.*, 2009a, b). In terms of morphological responses to water deficit, these studies have shown that biomass allocation between roots and shoots is unaffected by water deficit in quinoa (Bosque Sanchez *et al.*, 2003; González *et al.*, 2009a), which suggests the intervention of other adaptive mechanisms in response to drought.

3. Adaptations and traits

Enhanced shoot growth is seen as a contributing factor boosting plant performance under water-limiting conditions, as this reduces evapotranspiration and is also coordinated with enhanced root growth and better water uptake. However, factors controlling growth and tolerance mechanisms are important for continued growth in mild drought conditions, as this allows a plant to de-activate growth inhibition while maintaining a certain level of protection against damage (Claeys and Inzé, 2013). Focusing on particular traits may exacerbate the problems under severe drought, where lack of CO₂ from stomatal closure, photosynthesis inhibition and reduced turgor will passively limit growth (Tardieu *et al.*, 2010). In this case, different strategies need to be adopted to endure the stress as long as it occurs, while limiting plant transpiration and cell damage as much as possible and maximizing water use. Nevertheless, the idea that water use efficiency is synonymous with drought resistance and high yield under drought stress conditions is considered erroneous. Indeed, breeding for maximized soil moisture capture for transpiration is the most important target for yield improvement under drought stress, thus supporting the notion of effective use of water through physiological traits to

minimize yield variations (Blum, 2009; González *et al.*, 2011).

3.1. Gas exchange, stomatal control and water use efficiency

Genotypic variations of leaf gas exchange and seed yield of ten quinoa genotypes adapted to high altitude in northern Argentina were analysed under drought conditions. The results showed that quinoa could produce interesting grain yields (i.e. promising varieties yielding up to 3 855 kg/ha) in arid regions other than the Bolivian Altiplano under reduced irrigation (González *et al.*, 2011). This study raised the possibility that leaf stomatal conductance is a heritable trait associated with heat stress prevention and increased yields. Since biomass production is closely related to the rate of transpiration, the most important breeding objective to optimize yields under drought conditions is to maximize the absorption of soil moisture for transpiration (González *et al.*, 2011). Previous studies revealed that quinoa evolved adaptive mechanisms to cope with drought through high water use efficiency and high root/shoot ratios. The maximum photochemical efficiency of photosystem II (chlorophyll fluorescence Fv/Fm ratio) and quenching analysis (qP and qN) showed that dehydrated quinoa plants were less protected from photo-inhibition than salt-stressed plants (Bosque Sanchez *et al.*, 2003). Similar chlorophyll fluorescence studies demonstrated a fast recovery of photosynthesis in young quinoa plants after a drought stress period, suggesting the maintenance of high photochemical efficiency despite water deficits (Winkel *et al.*, 2002).

Other physiological and biochemical traits have also provided useful information about plant adaptations to arid and semi-arid conditions using yield and chlorophyll concentration, since chlorophyll degradation under stress is an adjustment to reduce the electron flow between photosystem I (PSI) and PSII that could prevent photo-oxidative damage. Thus high carotenoid and chlorophyll content are desirable characteristics, as they indicate low levels of photoinhibition (González *et al.*, 2011). Moreover, stomatal conductance was relatively stable with low gas exchange, but steady under very dry conditions and low leaf water potential. Quinoa maintained high water use efficiency to compensate for the decreased leaf stomatal conductance

and carbon gain by minimizing water loss (Vacher, 1998).

Drought effects on stomatal conductance, photosynthesis and leaf water relationships at different phenological stages have been determined (Jacobsen and Mujica, 2001; Razzaghi *et al.*, 2011), concluding that some quinoa varieties exhibit gas exchange parameters within the normal C3 plant range, and water relations are characterized by low osmotic potential that can be a major trait associated with drought tolerance. In general, measurements are expensive and difficult to implement, and also have generally limited spatial significance. A different approach to evaluate the effect of drought stress on quinoa development was assessed with three different indicators in field experiments: the number of days that the soil water content of the root zone was above a threshold, average relative transpiration and the standardized sum of daily actual transpiration, $\Sigma(T_a/ET_0)$ (Geerts *et al.*, 2008a). The best indicator to quantify the effect of pre-anthesis drought stress on phenological development was $\Sigma(T_a/ET_0)$ accumulated until 60 days after sowing (Geerts *et al.*, 2008a). Recently, the use of stable carbon isotopes provided reliable measurements, which were positively correlated with grain yields and negatively with intrinsic water use efficiency (González *et al.*, 2011). This study indicated that genotypes with higher yield under stress had higher stomatal conductance and increased transpiration, consistent with reports for other crops (Blum, 2009).

A recent evaluation assessed grain yield and environment interaction of nine quinoa genotypes of different origins, which were exposed to two watering regimes (dry and irrigated) over two seasons in a Mediterranean environment in central Chile (Garrido *et al.*, 2013). Genotype yields were reduced to less than 50% when irrigated at 44% and 80% reference evapotranspiration. The authors determined significant interactions between genotype and environment for yield, harvest index and grains/m².

Interestingly, a principal component analysis (PCA) showed a strong and significant association among yield, harvest index and grain number/m², low variability among genotypes when stressed, and much higher variability when the stress was not present (Garrido *et al.*, 2013). Low yields resulted from the effect of drought on the key stages of pre-flowering, flowering and pasty grain, which were previously determined as the most sensitive stages to water stress in quinoa, with a negative effect both on total grain yield and WUE (García, 1991; Geerts *et al.*, 2008a).

3.2. Root morphology and architecture of quinoa ecotypes

Recent studies open new perspectives on the morphology and architecture of the quinoa root system, its intraspecific diversity and plasticity in response to drought (Álvarez-Flores, 2012). For this reason, it is helpful to consider the contrasts existing among quinoa ecotypes, such as the Salare ecotype from the southern dry Altiplano of Bolivia and the Coastal ecotype from the humid coastal lowlands of Chile, two ecotypes that differ in their morphophysiological traits (Risi and Galwey, 1989a), as well as in the pedoclimatic conditions of their native habitats (Table 1). The southern Altiplano is characterized by altitudes near 3 700 m asl, sandy or rocky soils, a cold and arid climate with more than 250 days of frost per year in the most extreme areas, and mean annual precipitation of 150–300 mm (Aroni *et al.*, 2009). The low and infrequent precipitation, high evaporation rate and low soil water retention capacity are extremely adverse factors for crop growth and development (García *et al.*, 2007). The crop environment is quite different 2 000 km further south in the high latitudes and rainy environments of Chile's Pacific coastal lowlands. The temperate and humid habitat creates much more favourable conditions for agriculture, with more than 1 200 mm of precipitation distributed throughout the year and soils with a high water retention capacity (Tosso, 1985).

Table 1. Origin of the two studied ecotypes of quinoa

Ecotype	Locality	Latitude	Longitude	Altitude
Salares	Jirira, Bolivia	19°51'S	67°34'W	3 700 m
Lowlands	Cunco, Chile	38°56'S	72°03'W	200 m

Rhizotron studies under controlled conditions allowed to compare the root growth of quinoa plants grown in sandy soil with non-limiting (12% volumetric humidity) or restricted (7% volumetric humidity) water availability, during 2 months beginning after seed germination (Álvarez-Flores, 2012). This period corresponded to the critical phase of crop establishment and plant vegetative growth, representing nearly half of the complete crop cycle. Under non-limiting water conditions, both quinoa ecotypes revealed a herringbone pattern in the root system architecture. In general, this topology reduces competition among roots of the same plant, as well as among roots of neighbouring plants, thus optimizing the exploitation of soil resources, even more so when these resources are limited (Fitter, 1991; León *et al.*, 2011). Furthermore, the presence of a strong main root axis allows to explore deep soil layers more rapidly and efficiently, a critical feature in early stages of plant development (Glimskär, 2000; Paula and Pausas, 2011).

In spite of their similarity in root topology, the quinoa ecotypes studied differed with regard to their growth dynamics and the features of their root system architectures. Under non-limiting conditions, primary root elongation was rapid during the first 6 weeks of crop growth, and slowed down thereafter. In the 6th week, when shoots of both ecotypes hardly reached 6–8 cm above the soil surface, the primary root of the Salare ecotype reached a depth of 1 m. The Coastal ecotype reached the same length a week later, a delay that reflects early vigour differences between the seedlings in relation to average seed size in the studied ecotypes (4.9 vs 2.1 mg per seed for the Salare and Coastal ecotypes, respectively – Álvarez-Flores, 2012). From the sixth week onwards, when primary root elongation began to slow down, growth of the rest of the root system began to accelerate due to ramification and elongation of the lateral roots. Consequently, total root system length reached up to 650 m/plant without significant differences between ecotypes at week 9 under non-limiting water conditions (Álvarez-Flores, 2012).

The differences in root architecture determined among ecotypes only appeared when two components of total root length were considered, namely number and length of root segments (i.e. root elements situated between two ramifications or be-

tween a ramification and a root meristem). During the first week, the Salare ecotype produced a primary root with longer segments than the Coastal ecotype (7.3 vs 2.5 cm average). This allowed the Salare ecotype to explore deep soil layers rapidly (Figure 1, 28 DAS [days after sowing]) and a major part of the lateral roots were formed at depth in the subsequent stage of root ramification (Figure 1, 42 DAS). These lateral roots displayed segments with 50% greater average length compared to those of the Coastal ecotype, which allowed to compensate for the equal or similar number of segments of the Salare ecotype. The final result was that the Salare ecotype did not produce a greater total root length than the Coastal ecotype, but it displayed a much faster colonization rate and dense in-depth root system (Álvarez-Flores, 2012).

3.3. *Ecotype responses to water deficit in the quinoa root system*

Root systems of Salare and Coastal ecotypes presented a more “herringbone” topology under water deficit, which implied greater reduction in lateral root growth than in primary roots. In fact, when drought occurs at early plant growth stages, the elongation of the primary root is considered beneficial for the acquisition of deeper, more reliable water resources, while a dense root ramification could result in rapid exhaustion of an unreliable water resource in the shallow soil layers (Padilla and Pugnaire, 2007). Indeed, differences between the ecotypes studied were that the root system of the Salare ecotype presented faster elongation and denser in-depth colonization. The architectural traits of the root system of the Salare ecotype may be the reason for a common practice in the driest areas of the Altiplano: cultivating quinoa fields every other year, so that water can accumulate in the deep soil layers during the crop-free year.

Water deficit also reduced the total length of root systems, although to a lesser extent in the Salare ecotype (-38% vs -57% in Coastal). These growth reductions were greater in the aerial plant parts than in the underground plant parts, since the root/shoot ratio of both ecotypes increased in water-stressed plants. In general, water deficit did not affect the **mean** length of the root segments. On the other hand, there was a significant reduction in the **total** length of the root system as the actual number of

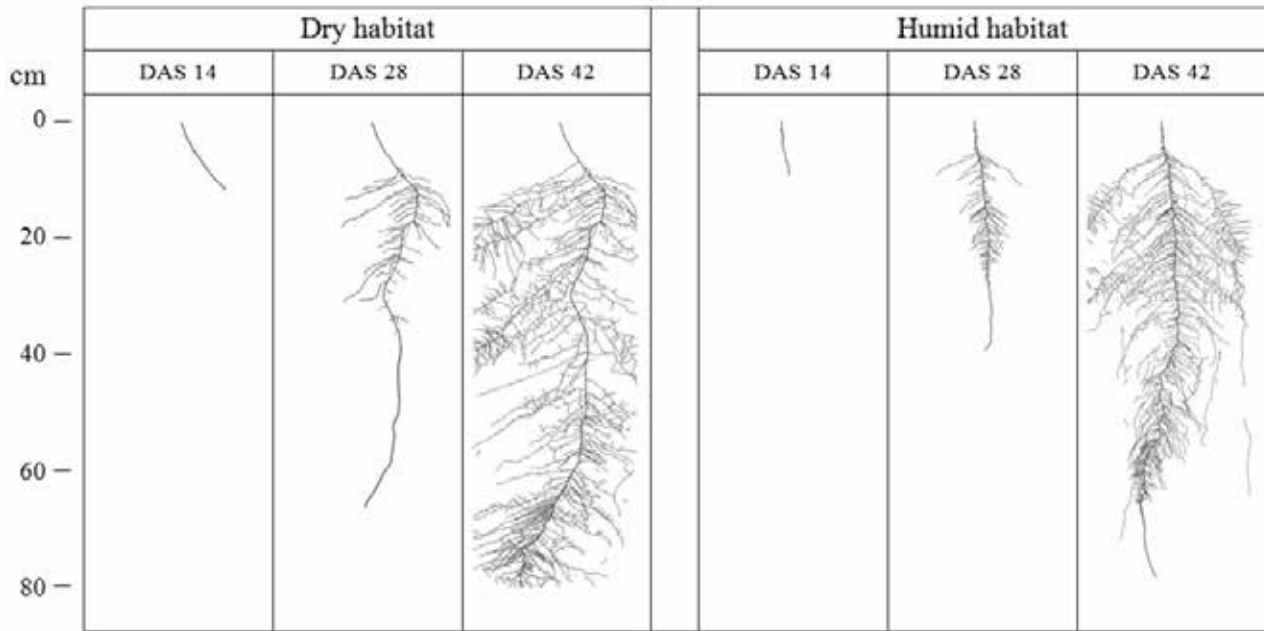


Figure 1: Time-course of root growth in two quinoa ecotypes from contrasted habitats at 14, 28 and 42 DAS (days after sowing).

root segments was reduced, with a difference between ecotypes (-8% in Salare vs -23% in Coastal). This could imply a significant ecotypic difference in root systems with regards to water absorption and sensitivity to water deficits (Álvarez-Flores, 2012).

It should be noted that water deficit – compared with non-limiting availability of water – stimulated primary root elongation in both ecotypes. In the Salare ecotype under non-limiting conditions, primary roots grew up to 50 cm during the first four weeks of the plant cycle, whereas they reached 75 cm in the same time interval under water deficit. In the Coastal ecotype, they grew to 35 and 40 cm, respectively (Figure 2). The rapid elongation of the primary root allowed the Salare ecotype to produce lateral roots distributed evenly throughout the entire soil profile, with a root density similar to that of plants growing with higher water availability. In contrast, the Coastal ecotype concentrated its lateral roots in soil layers between 5 and 50 cm, and exhibited very low root density in deeper soil layers (Álvarez-Flores, 2012).

4. Molecular Studies and Gene Discovery

Efforts to improve the crop have led to an increased focus on genetic research. The first study was published in 2005 by Maughan's group (Coles *et al.*,

2005): an EST database for quinoa using immature seed and floral tissue. These sequences were analysed for homology with known gene sequences and also for the identification of single nucleotide polymorphisms (SNPs) for quinoa. They compared 424 cDNA sequences of quinoa with sequences in the publicly available databases. Two-thirds (67%) of the quinoa proteins showed homology to *Arabidopsis* proteins with putative function, 18% had no significant matches, 9% had significant homology to *Arabidopsis* proteins with no known function and 6% shared significant homology with plant proteins of species other than *Arabidopsis*. Fragments of 34 ESTs were amplified and sequenced in five quinoa accessions and one related weedy species, *C. berlandieri*. Analysis of the quinoa EST sequences revealed a total of 51 SNPs in 20 EST sequences.

A recent paper from the same group (Maughan *et al.*, 2012) reported the identification of 14 178 putative SNPs; a diversity screen of 113 quinoa accessions was used for comparison with the five accessions used in the former study. The study also recovered the two major subgroups corresponding to Andean and Coastal quinoa ecotypes. Therefore the SNPs identified represent a valuable genomic tool that will be very useful for emerging plant breeding programmes looking for important agronomic

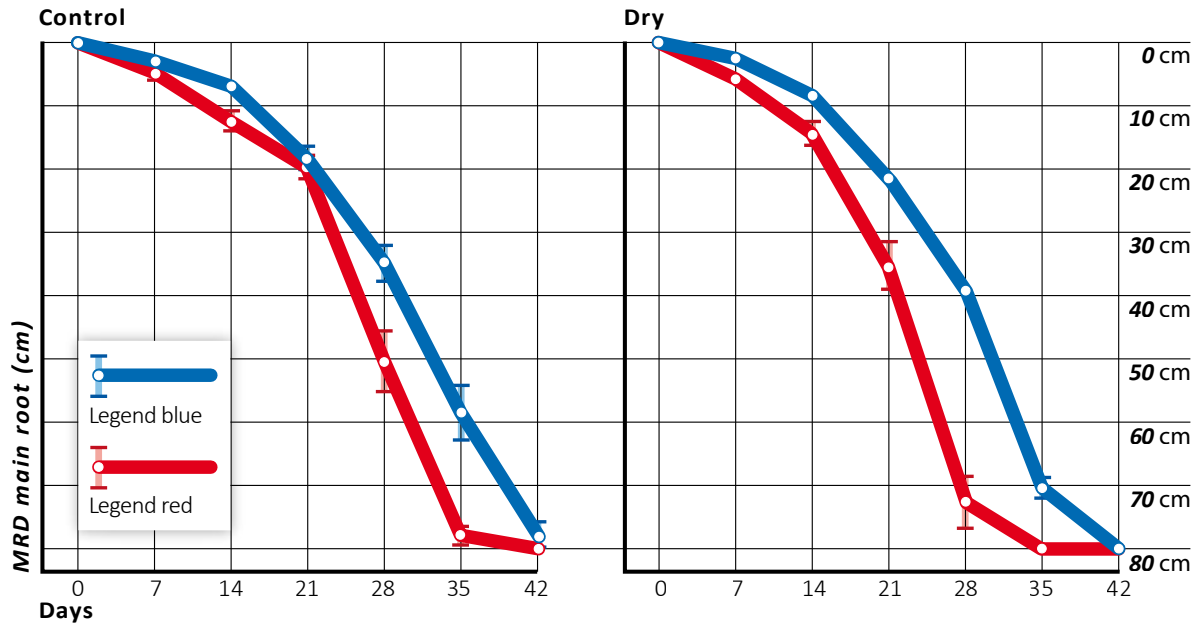


Figure 2: Dynamics of the maximal root depth (MRD) in two ecotypes of quinoa from Salares (Δ) and Lowlands (\blacktriangle) ($n = 5$, the vertical bars show the standard errors, the gray areas show the water content in the soil: dark gray = 12% vol., light gray = 7% vol.).

traits in quinoa. Furthermore, a linkage mapping of the SNPs in two recombinant inbred line populations produced an integrated 29 linkage group map, spanning 1 404 cM with a marker density of 3.1 cM per SNP marker.

Unfortunately, quinoa EST generation based on Sanger sequencing is still very limited compared to other species. At present, only 424 ESTs can be found in the public domain (<http://www.ncbi.nlm.nih.gov/nucest/?term=chenopodium+quinoa>). Most of the work done on quinoa has been based on response to salt stress and some important genes have been characterized. Maughan *et al.* (2009) cloned and characterized two *SOS1* gene homologs (*CqSOS1A* and *CqSOS1B*) of quinoa and found a high level of homology of these gene sequences to orthologous *SOS1* of other species. The expression of *CqSOS1* upon application of NaCl was investigated in a cultivar originating from the Salare region in the Bolivian Altiplano. Gene expression analyses showed greater expression in roots than in leaf tissue in the absence of salinity. However, the presence of 450 mM NaCl caused an up-regulation of both genes in leaf but not in root tissue (Maughan *et al.*, 2009). Ruiz-Carrasco *et al.* (2011) confirmed the different responses of sodium antiporters to NaCl in shoots and roots, and also cloned and ana-

lysed the expression of *CqNHX*. Interestingly, genes were differentially regulated in different genotypes. Different studies related to this abiotic stress have been used to study a salt tolerance mechanism in quinoa (Adolf *et al.*, 2012). However, more studies and discovery of new genes are needed, as reviewed by Jellen *et al.* (2013).

Studies have also been conducted on early drought stress effects (up to 9 days after sowing – Morales *et al.*, 2011a). These authors used an Altiplano Chilean quinoa genotype and performed a transcriptome sequencing analysis under dry and normal irrigation conditions. The transcriptome was sequenced by Illumina paired ends. The results were 53 million reads under control conditions and 50 million reads under drought conditions, which were assembled into 18 000 contigs measuring > 1 kb. In this study, a digital expression gene analysis was performed, resulting in 529 genes induced and 201 genes repressed under drought conditions (Morales *et al.*, 2011b; Zurita-Silva *et al.*, 2013, unpublished data). This drought RNA-seq database is being used to discover/identify transcription factors in response to salt stress, given that these two stresses share similar molecular/physiological mechanisms for dealing with osmotic stress and ion toxicity (Ruiz and Silva, personal communication).

4.1 *The Future of Molecular Studies and Gene Discovery in Quinoa*

Most molecular studies in quinoa have been developed under salt stress conditions and gene identification has not kept the pace required to understand the genetic basis of differential physiological responses. The genome has still not been sequenced. An RNA-seq transcriptome analysis in different tissues of *Chenopodium quinoa* using four water treatments (from field capacity to drought) on an Inter-Andean valley ecotype ('Ingapirca') and a Salare ecotype ('Ollague') was recently released (<http://www.ncbi.nlm.nih.gov/bioproject/195391>). It is important to mention that a transcriptomic analysis of amaranth, a pseudocereal like quinoa, has been published and could serve as a reference for annotation and gene discovery (Délano-Frier *et al.*, 2011). Other strategies include the study of different genotypes of quinoa in search of genes induced by drought conditions. A full-length cDNA library was generated for transforming *Arabidopsis*, and transgenic lines obtained were assessed for their tolerance to drought conditions. Consequently, the genes that suggest tolerance in *Arabidopsis* were sequenced and identified, resulting in candidates corresponding both to orthologous and unknown genes, which may help to identify novel drought-tolerance genes (Zurita-Silva *et al.*, 2013, unpublished data).

5. Conclusions and Perspectives

Quinoa endures harsh climate conditions in various regions of its distribution area, particularly in the southern Altiplano of Bolivia, northern Chile and northwestern Argentina. In southern Bolivia, the world leader in quinoa production for export, the crop faces frequent drought events due to low and irregular precipitation and high evaporative demand (Vacher *et al.*, 1994; Geerts *et al.*, 2006; Jacobsen, 2011), and there is also high probability of frost (Jacobsen *et al.*, 2005, 2007; Winkel *et al.*, 2009; Pouteau *et al.*, 2011), as well as extreme solar radiation due to high altitude (Vacher *et al.*, 1994).

Although the causes of the variability in the physiological responses of quinoa to the environment remain largely unknown, it is often considered that the diversity of local quinoa varieties reflects selection and adaptation to the local soil and climate conditions of different habitats. However, a clear mor-

phophysiological adaptation of these genotypes to local ecological conditions had not previously been demonstrated (Del Castillo *et al.*, 2007; Winkel *et al.*, 2009; Garcia *et al.*, 2007). The diversity of the five major quinoa ecotypes and their tolerance features makes quinoa an interesting plant model (Fuentes and Zurita-Silva, 2013), mostly for studies of the functioning of shoot components related to photosynthesis (Bertero, 2001; Winkel *et al.*, 2002; Jacobsen *et al.*, 2005, 2007; Ruiz and Bertero, 2008), hormonal regulation (Jacobsen *et al.*, 2009; Gómez *et al.*, 2011), nutrient absorption (Razzaghi *et al.*, 2012a) and deficit irrigation responses (Geerts *et al.*, 2008a, b, c) – just some of the features included in other chapters in this volume.

As for other crop species, the responses and mechanisms of quinoa for coping with low water availability are included in two major strategies: stress avoidance and stress tolerance. However, this species has shown an outstanding ability to balance water uptake and water loss, and thus avoid water deficit. Quinoa enhances water uptake in various ways: by accumulating solutes (e.g. proline) which lower tissue water potential; by modulating root architecture; and through tight stomata control, which restricts shoot growth and accelerates leaf senescence, limiting water loss through evaporation. These mechanisms require fine regulation through, for example: hormonal signalling; balancing leaf growth and stomatal conductance; turgor maintenance; and dynamic osmotic adjustment. Indeed, Geerts *et al.* (2008a) demonstrated the high phenotypic plasticity of quinoa as a drought escape mechanism. Although they did not present a complete drought stress-thermal time interaction model, quinoa plasticity in response to pre-anthesis droughts was quantified for field conditions; the proposed model should be validated for other quinoa varieties and regions, and also improved by considering post-anthesis drought (Geerts *et al.*, 2008a). Reported values of seed yield per unit of water consumed (WP_{VET}) are rather low (0.3–0.6 kg/m³) as a result of the generally prevailing low fertility conditions (Geerts *et al.*, 2009). Quinoa plants have also evolved morphological and anatomical features that allow adaptive changes in response to drought, for example: leaf senescence control, vesicles containing calcium oxalate in the stems and leaves, thick cuticular epidermis and more sunken stomata than other Andean crops.

Variations in root architecture among quinoa ecotypes under water-limiting conditions, such as primary root elongation rate and root density in deep soil layers, point to a genotypic differentiation possibly associated with the selection of habitats with different resource availability, combined with selection by local growers. These root system traits could be of crucial significance in the dry conditions of the Altiplano, where the average annual precipitation does not satisfy water requirements for a complete crop cycle. They could also be useful for breeding new cultivars for agroecosystems with reduced input requirements (Lynch and Brown, 2012). Breeding for maximized soil moisture capture for transpiration is the most important target for yield improvement under drought stress (Blum, 2009).

With the incorporation of new technologies and approaches, such as the integration of genomic, transcriptomic and reverse genetic studies, the full potential of quinoa genetic variability could be exploited in order to generate new cultivars; this also represents a novel source for gene discovery that might serve in other crops of agronomic importance. These considerations are made in the face of current challenges, such as climate change and oscillations that constrain food production in the world, and quinoa is therefore an outstanding crop model for stress tolerance studies. Considering also its superior nutritional attributes (covered in Chapter 3.4), quinoa represents both a challenge and an opportunity to contribute to food security and sovereignty, not only in the Andes, but also in Africa, Asia and other parts of the world.

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