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REVIEW

Breeding quinoa (*Chenopodium quinoa* Willd.): potential and perspectives

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Abstract Quinoa (*Chenopodium quinoa* Willd.) originated in the Andean region of South America; this species is associated with exceptional grain nutritional quality and is highly valued for its ability to tolerate abiotic stresses. However, its introduction outside the Andes has yet to take off on a large scale. In the Andes, quinoa has until recently been marginally grown by small-scale Andean farmers, leading to minor interest in the crop from urban consumers and the industry. Quinoa breeding programs were not initiated until the 1960s in the Andes, and elsewhere from the 1970s onwards. New molecular tools available for the existing quinoa breeding programs, which are critically examined in this review, will enable us to tackle the limitations of allotetraploidy and genetic specificities. The recent progress, together with the declaration of "The International Year of the Quinoa" by the Food and Agriculture Organization of the United Nations, anticipates a bright future for this ancient species.

Keywords *Chenopodium quinoa* · Downy mildew · Saponin · Marker-assisted selection · Marginal environments · Stress tolerance

Abbreviations

ABA	Abscisic acid
BAC	Bacterial artificial chromosome
EST	Expressed sequence tag
FAO	Food and Agriculture Organization of the United Nations
GA	Gibberellic acid
IYQ2013	The International Year of the Quinoa

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MAS	Marker-assisted selection
NOR	Nucleolus organizer region
NTS	Non-transcribed spacers
PROINPA	Fundación para la Promoción e Investigación de Productos Andinos
QTL	Quantitative trait loci
RAPD	Random amplified polymorphic DNA
RIL	Recombinant inbred line
SRA	Sequence read archive
SSR	Simple sequence repeat
SNP	Single nucleotide polymorphism

Introduction

Quinoa (*Chenopodium quinoa* Willd.) is a dicotyledonous annual species belonging to the family Amaranthaceae (formerly Chenopodiaceae), which includes other economically important species such as spinach (*Spinacia olereaceae* L.) and sugar beet (*Beta vulgaris* L.). Quinoa, along with its wild relatives (*Chenopodium carnosolum*, *C. petiolare*, *C. pallidicaule*, *C. hircinum*, *C. quinoa* subsp. *melanospermum* and *C. ambrosoides incisum*), has high diversity and variability in uses (Fuentes et al. 2009a, b). These species are known and utilized by the farmers in the Andean highlands (Altiplano) of Colombia, Ecuador, Peru, Bolivia, Chile and Argentina (Mujica and Jacobsen 2006). Quinoa has an exceptional balance between oil (4–9 %), protein (averaging 16 %, with high nutritional relevance due to the ideal balance of its essential amino acid content) and carbohydrates (64 %) (Bhargava et al. 2006; Vega-Gálvez et al. 2010). Due to its high starch content (51–61 %) it can be used in the same way as cereals for flour production (Mastebroek et al. 2000; Repo-Carrasco et al. 2003; Bhargava et al. 2006; Stikic et al. 2012). In addition, quinoa is a good source of vitamins, oil with high linoleate and linolenate content (55–66 % of the lipid fraction), natural antioxidants such as α- and γ-tocopherol, and a wide range of minerals (Repo-Carrasco et al. 2003; Vega-Gálvez et al. 2010; Fuentes and Bhargava 2011; Stikic et al. 2012). Quinoa grain also lacks gluten, which has allowed the development of various foods for consumers with celiac disease (i.e. people allergic to gluten) (Jacobsen 2003). Because of its nutritional importance, the demand for quinoa as a processed product has increased substantially (Mujica and Jacobsen 2006; FAO 2011). In addition, quinoa is an undemanding crop that has remarkable productive advantages of cultivation under adverse environmental conditions (Ward 2000; Jacobsen et al. 2003; Fuentes and Bhargava 2011), resulting in a very good alternative for marginal environments and low-input agriculture.

Despite its clear potential to nourish the developing world, quinoa is under-researched, under-supported and considered a neglected crop (Rojas et al. 2009). Only 101,500 ha of quinoa are grown annually worldwide although annual production has increased about 70 % compared with 12 years ago, to around 80,200 tons (FAO 2011). While most quinoa is still grown in South America, it is also cultivated in the USA (Colorado), Canada and France, and field trials with quinoa are being conducted in China, Europe, India and Africa (Jacobsen et al. 2013).

Ancestrally, quinoa seeds were used to make flour, soup, cereal and alcohol. It is also grown for animal consumption (i.e., using the whole plant as green foliage), medicinal purposes (anti-inflammatory, analgesic and disinfectant) and as an insect repellent (Vega-Gálvez et al. 2010). Other uses include desaponified powder for animal nutrition and fresh leaves for human consumption. The year 2013 was declared The International Year of the Quinoa (IYQ2013) by the Food and Agriculture Organization of the United Nations (FAO) in recognition of the indigenous peoples of the Andes who have maintained, controlled, protected and preserved quinoa as human food for present and future generations using their traditional knowledge and practices of living in harmony with the earth and nature (FAO 2012). The exceptional nutritional attributes of quinoa, its adaptability to different agro-ecological conditions and its potential contribution in the fight against hunger and malnutrition prompted us to review the current status of the crop and the recent advances in quinoa breeding. Because it is already part of existing high-value agrobiodiversity, quinoa is poised to play an important role in strategies designed to adequately feed the growing world population in a sustainable manner (Jacobsen et al. 2013).

Distribution

Evidence from radiocarbon-dating indicates that *Chenopodium quinoa* has been grown in the Andes of South America, presumably under human cultivation, approximately for 8,000 years (Dillehay et al. 2007), originating near Lake Titicaca on the border of Bolivia and Peru. Quinoa played a prominent role in the Inca Empire, but crops like wheat and barley, which were introduced by the Spaniards, relegated it to more minor uses after the Spanish conquest (Martínez et al. 2009b). This was not a free choice of the original population, but dictated by the conquerors, due to the religious importance of quinoa among the Incas. However, while considerable yield reductions have been reported for the introduced crops due to abiotic stresses, native crops such as quinoa have much lower losses under adverse conditions (Bhargava et al. 2006). The natural distribution of quinoa is from northern Colombia to Southern Chile (from 2°N to 40°S) (Fuentes and Bhargava 2011), and over a wide range of altitudes from sea level up to 4,000 m a.s.l. (González et al. 2011). Annual rainfall ranging between 80 mm (extreme aridity) and 2,000 mm support cultivation of quinoa (Maughan et al. 2004; Martínez et al. 2009b) and it has high potential for cultivation outside its native range (Ward 2000). For example, it can grow on marginal soils over a wide range of pH (Jacobsen et al. 2003). Quinoa is also adaptable to different photoperiods and both short-day and day-neutral cultivars are available (Bertero 2003; Bertero et al. 2004; Christiansen et al. 2010; Bendevis et al. 2013).

Biological and genetic features

Quinoa is a predominantly autogamous (self-pollinated) species with varying rates of natural hybridization (10–17 %) depending upon the coincidence of flowering with the presence of pollen vectors (Mastebroek et al. 2002; Spehar and Santos 2005). It is gynomonoecious (i.e., female and perfect flowers are present on the same individual), possessing large numbers of small (3–4 mm) flowers of three basic types: hermaphrodite, chlamydeous female and achlamydeous female. These flowers are grouped together to form a panicle type of inflorescence which is 15–70 cm long and is usually profusely branched having a principal axis from which secondary and tertiary branches arise. The small flowers make manual emasculation for hybridization difficult (Ward 2000). Some cultivars are male sterile, partially or in all the flowers, and that has been an important tool for hybrid production and breeding of the crop (Ward 1998; Bhargava et al. 2006).

Cytological evidence has shown that quinoa is an allotetraploid species ($2n = 4x = 36$, with basic chromosome number of $x = 9$), mainly possessing a diploid type of chromosomal segregation (Palomino et al. 2008), but some tetrasomic inheritance occurs as well (Ward 2000). The incidence of both disomic and tetrasomic segregations at the same locus is rare but could be explained by mutual exchange of fragments between homeologous chromosomes. Although quinoa displays disomic inheritance for most qualitative traits (Ward 2000; Maughan et al. 2004; Fuentes and Bhargava 2011), combined modes of segregation could complicate analyses and mapping of the quinoa genome (Ward 2000). Based on morphology, quinoa has been classified as *Chenopodium*, subsection *Cellulata* (alveolate-fruited), together with the *C. berlandieri* complex (commonly known as C. *berlandieri* var. *nuttaliae*), the South American tetraploid weed *C. hircinum*, the Andean wild diploid *C. philippianum*, and the North American diploids *C. neomexicanum* Standl. and *C. watsonii* A. Nels. (Aellen and Just 1929; Wilson 1980; Jellen et al. 2011). Quinoa origins presumably occurred from diploid descendants such as *C. pallidicaule* Aellen (Kañawa), *C. petiolare* Kunth and *C. carnasolum* Moq., and from tetraploid weed species such as *C. hircinum* Schard and *C. quinoa* var. *melanospermum* (Mujica and Jacobsen 2006). Conversely, it has also been proposed that quinoa descended from a North American ancestor similar to *C. berlandieri* var. *zschackei*, which might have traveled to South America via human migration or by bird dispersals, and was subsequently domesticated as quinoa (Wilson 1990). The latter hypothesis is in agreement with molecular cytogenetic analysis studying the organization and genomic distribution of 45S nucleolus organizer region (NOR) and 5S ribosomal RNA (rRNA) genes in quinoa. DNA sequence analysis of NOR intergenic spacers (IGS) confirmed the close relationship between *C. quinoa* and tetraploid *C. berlandieri* var. *zschackei*. Likewise, the characterization of a 5S rDNA spacer region revealed the existence of two different non-transcribed spacer

(NTS) sequence classes that presumably originated from the two subgenomes of allopolyploid *C. quinoa* (Kolano et al. 2008). Interestingly, one of these was very similar in sequence to the NTS present in *C. berlandieri*, suggesting that these two allotetraploid species have at least one common diploid ancestor (Maughan et al. 2006).

Quinoa diversity has been associated with five main ecotypes associated with diversity sub-centers (Table 1). Each of these sub-centers is associated with sub-centers of diversity that originated near Lake Titicaca (Risi and Galwey 1984). Initially, Gandarillas (1979) and Wilson (1988a) identified the southern highlands of Bolivia as the genetic diversity center for quinoa. Subsequently, Christensen et al. (2007) identified the genetic diversity center at the Altiplano area between Peru and Bolivia (central Andean highlands) using molecular data. Furthermore, germplasm from Ecuador and Argentina has revealed limited diversity, indicating the Altiplano (Peru–Bolivia) as the most probable point of introduction for Ecuadorian accessions, whereas for Argentina the original introduction of genotypes could have occurred from the Chilean highland and lowland zones (Southern Chile). In this context, Christensen et al. (2007) highlighted the differences between coastal lowland accessions from Chile and those from the northern highlands of Peru, confirming the hypothesis proposed by Wilson (1988a) that the Chilean quinoas show more similarity with those from the southern Altiplano of Bolivia. Nevertheless, Fuentes et al. (2009a) reported that the Chilean coastal lowland germplasm was much more genetically diverse than previously postulated, suggesting that the observed diversity at molecular level could be explained by promiscuous outcrossing involving abundant weed populations of *C. album* and *C. hircinum* in lowland quinoa fields of Chile. This explanation agrees well with the difficulties experienced by coastal lowland quinoa breeders to obtain inbreds in Southern Chile (I. von Baer, personal communication). Taken together, recent genetic-based analyses consistently confirmed that quinoa itself has existed until now as two distinct germplasm pools: Andean highland quinoa with its associated weedy complex (ajara or ashpa quinoa, *C. quinoa* ssp. *milleanum* Aellen, also referred to as *C. quinoa* var. *melanospermum* Hunziker), and quinoa among the Mapuche people of the central and southern Chilean coastal lowlands, constituting a second center of major quinoa diversity (Jellen et al. 2011). A possible third distinct germplasm pool involves the weedy *C. hircinum* from lowland Argentina, which may represent a remnant of archaic quinoa cultivation in that part of South America (Wilson 1990).

Crop potential and breeding challenges

Adaptation and abiotic tolerance

Efforts to introduce quinoa as an alternative crop have been made in numerous countries, and successful adaptation of this species has been reported in Europe, North America, Africa and India (Jacobsen 2003; Fuentes et al. 2009b). It has been grown for commercial purposes in Colorado (USA) since the early 1980s (Ward 2000), and has been considered a promising new crop for northern Europe (Galwey 1993; Jacobsen 2003; Jacobsen et al. 1994, 2010). Jacobsen (1997, 1998) also studied the developmental patterns and stability of quinoa lines of different maturity classes and concluded that Chilean lines were well adapted to the conditions of northern Europe (Denmark), although they could also be grown at more southerly latitudes. Under high latitude regions, a genotype for production ought to be uniform, to mature early, to have a short stem, to be unbranched, and to have a consistently high seed yield and low saponin content (Jacobsen 1997, 1998). Early maturity is one of the most important traits considered in breeding programs since the short growing season is a major obstacle to growing crops in high latitude regions, and quinoa requires at least 150 days to develop maximally and assure a proper seed harvest (Jacobsen 2003; Table 1).

The extreme climatic conditions where quinoa evolved appear to have contributed to the crop's high levels of tolerance to frost, soil salinity, drought and other adverse conditions (Bosque et al. 2003; Trognitz 2003). Tolerance to abiotic stresses is determined by complex mechanisms and polygenically inherited traits. For example, quinoa can tolerate soils with pH ranging between 4.8 and 9.5 due to its mycorrhizal associations, which also maximize the acquisition of scarce nutrients (Urcelay et al. 2010). The effect of temperature on germination, phenology and growth have also been the focus of several studies, since frosts are common in the Andes (Jacobsen et al. 2005, 2007), and several genotypes and cultivars from the Andean

Table 1 General attributes of some quinoa varieties from different agro-ecological areas in the Andean region of South America (Bertero et al. 2004; Fuentes 2008)

Variety	Ecotype	Origin[a]	Grain color	Grain diameter (mm)	Grain yield (ton/ha)	Saponin level	Elevation (m.a.s.l)	Maturity days	Tolerance[b]
Blanca de Nariño	IAV	Colombia	White	1.9–2.2	3.5–4.5	Low	2,800–3,250	185–205	DM-SR
Huancayo	IAV	Rosada de Junin (Peru) × Real purpura (Bolivia)	White/pink	1.8–2.1	3.0–4.0	Low	2,400–3,000	150–160	DM-SR
Hualhuas	IAV	Pink segregant (Junin × Real Purpura)	White	1.9–2.2	3.5–4.0	Low	3,000–3,800	150–160	SH-DM-SR
Mantaro	IAV	Huancayo × Sajama	White	1.6–1.9	3.5–4.5	High	3,000–4,000	135–145	n/a
Amarilla de Marangani	IAV	Massal selection from Cuzco (Peru)	Yellow	2.0–2.2	n/a	High	3,500–3,800	200–210	DM-LD
Blanca y Rosada de Junin	IAV	Selection from Huancayo variety	White	1.6–1.9	3.5–4.0	Low	3,000–3,400	180–200	DM
INIAP Tunkahuan	IAV	Ecuador	White	1.8–2.0	2.0	Low	2,600–3,200	170–190	n/a
INIAP Pata de venado	IAV	Ecuador	White opaque	1.7–1.9	1.4	Low	3,000–3,600	140–160	DM
Cheweca	HL	Massal selection from Orurillo	White	1.2	1.6–1.9	Low	3,800–3,900	180–210	SH
Sajama	HL	547 real × 559 illimani	White	2.0–2.2	2.5–3.5	Sweet	3,800–3,900	140–160	FR-HA
Kancolla	HL	Massal selection from Cabanillas	White	1.6–1.9	1.5–2.0	High	3,800–3,900	160–180	DM-NA
Witulla	HL	Puno (Peru)	White	1.5–1.8	1.2–1.8	Medium/high	3,800–3,900	160–180	DM
Camacani	HL	Bolivia	White	1.5–1.7	3.2–3.6	High	3,800–3,900	160–180	DM
Tahuaco	HL	Peru	White	1.5–1.7	2.5–3.0	High	3,800–3,900	160–180	DM
Chupaca	HL	Bolivia	White	2.0–2.2	3.3–3.4	n/a	3,800–3,900	150–170	DM-FR
Kurmi	HL	Bolivia	White	2.3–2.5	1.2–1.8	Sweet	3,800–3,900	155–165	DM
Blanca de Juli	HL	Peru	White	1.4–1.8	1.2–2.5	Medium	3,800–3,900	160–170	n/a
Real	SA	Bolivia	White	1.9–2.2	1.5–3.5	High	3,800–4,000	180–210	n/a
Amarilla Ancovinto (elite line)	SA	Ancovinto massal selection (Chile)	White	2.0–2.4	0.4–1.5	Medium	3,500–3,900	150–180	n/a
Roja Ancovinto (elite line)	SA	Ancovinto massal selection (Chile)	White/pink	2.2–2.5	0.5–2.0	High	3,500–3,900	150–180	FR
Regalona Baer	C/L	Chile	White opaque	1.8–2.0	2.5–6.0	Medium	200–800	170–190	LD

[a] Ecotype: *IAV* inter-Andean valley, *HL* highlands, *SA* salares, *C/L* coastal/lowland

[b] Tolerance: *DM* Downy mildew (*Peronospora farinosa*), *SR* Stalk rot (*Phoma exigua* var. *foveata*), *NA Nacobus* (nematode), *SH* shelling, *LD* lodging, *FR* frost, *HA* hail

n/a not available

highlands of Bolivia that exhibit differential responses to low temperatures have been identified (Table 1). Interestingly, the absence of consistent associations between frost sensitivity and the geographical origin of genotypes has reinforced the idea that Andean growers manage frost risk by relying on a diversity of functionally distinct cultivars and landraces rather than a single adapted and frost-hardy type (Bois et al. 2006). Quinoa can also tolerate freezing prior to the formation of flower buds (Bhargava et al. 2006). It grows properly at temperatures down to −5 °C, and tolerates temperatures as low as −16 °C during the vegetative stage (Bois et al. 2006). In flowering it tolerates −8 °C up to 2 h (Jacobsen et al. 2007). Details of the physiological and the genetic mechanisms responsible for the observed frost resistance remain unknown (Jacobsen et al. 2007). One distinctive feature of this species is that the epidermal vesicles of cells form a sort of blanket mainly in young leaves and shoots, but the specific role of these vesicles in the tolerance of quinoa to low temperatures remains unclear (Bois et al. 2006). Measurements of median lethal temperature of leaf tissue (LT_{50}) based on ion leakage and supercooling activity have been undertaken by thermal analysis using thermocouples (Jacobsen et al. 2007). The ice nucleating temperature was always lower than LT_{50}, suggesting that the main mechanism of frost survival in quinoa is the avoidance of ice formation during moderate supercooling. Quinoa has relatively high soluble sugar content, which can cause a decrease in the freezing point, and consequently help to reduce LT_{50} (Jacobsen et al. 2007). Thus, proline content and levels of soluble sugars such as sucrose might also serve as indicators of frost tolerance in quinoa breeding lines (Jacobsen et al. 2007).

Quinoa can grow under harsh soil conditions, developing seeds in salt concentrations as high as those encountered in seawater (Adolf et al. 2012). Indeed, this important attribute has been thoroughly studied, particularly the physiological and the molecular mechanisms involved in thriving the crop in saline soils, and those specifically related to salt ion accumulation in specialized tissues and the adjustment of leaf water potential (Adolf et al. 2013). The species accumulates salt ions in its tissues by adjusting the water potential in leaves, which allows the plant to maintain cell turgor and limit plant transpiration under saline conditions (Hariadi et al. 2011; Shabala et al. 2012). Other studies suggest that dehydrin accumulation, subcellular localization and phosphorylation state of seed mature embryos are related to high salt stress tolerance (Koyro and Eisa 2008; Burrieza et al. 2012).

Genetic constituents related to salt tolerance exhibit additive effects, recessive or dominant relationships and heterosis. Fewer than 25 % of the salt-regulated genes that have been identified are salt-stress-specific (Ma et al. 2006). A genetic linkage map that lays the groundwork for fine mapping quantitative trait loci (QTL) for salt tolerance in quinoa has been published (Maughan et al. 2004). Mechanisms contributing to salt tolerance in quinoa include efficient control of xylem Na^{+} loading and Na^{+} compartmentalization in leaf vacuoles, higher tolerance to reactive oxygen species (ROS), better K^{+} retention, and an efficient control over stomatal development and aperture, as recently reviewed by Adolf et al. (2012). Salinity tolerance may also be improved by pyramiding key genes regulating the most essential physiological traits (Shabala and Mackay 2011) and quinoa might serve as a valuable donor of salt tolerance genes to other crops. The large genetic variability in quinoa salinity tolerance is a huge resource for the selection and breeding for higher tolerance, and this poses challenges and opportunities for the future (Maughan et al. 2009; Gómez-Pando et al. 2010; Ruiz-Carrasco et al. 2011; Adolf et al. 2012) .

Quinoa has intrinsically low water requirements and therefore displays a strong natural ability to cope with drought. There are genotypic differences in drought tolerance among quinoa cultivars, and most of the known mechanisms of drought tolerance are encountered in this species (Jacobsen et al. 2003). Physiological characteristics contributing to drought tolerance in quinoa include low osmotic potential, low turgid weight/dry weight ratio, low elasticity and an ability to maintain positive turgor even at low leaf water potentials (Andersen et al. 1996). Quinoa lines also exhibit gas exchange parameters within the range of C_3 plants and water relationships in quinoa are characterized by low osmotic potentials, a major trait that has been associated with drought tolerance (Hariadi et al. 2011; Razzaghi et al. 2011, 2012). Quinoa maintains high water use efficiency to offset its decreased leaf stomatal conductance, and optimizes carbon gain thus minimizing water loss (Bhargava et al. 2006). When studying how signalling from the

root system to the aerial controlled gas exchange in a drying soil, it was found that photosynthesis was maintained after stomata closure and, interestingly, an increment of abscisic acid (ABA) in the xylem was detected, indicating that there was an effect of a mild soil water deficit on the production of ABA (Jacobsen et al. 2009). Other suggested mechanisms that maintain turgor under increasing drought could be osmotic adjustment and anti-transpirant compounds other than ABA in the xylem sap (Jacobsen et al. 2009). In this context, quinoa could also depend on hydraulic regulation through changes in turgor or other chemical substances yet to be studied (Jacobsen et al. 2009; Bendevis et al. 2013). Other natural candidates for regulatory roles in quinoa could include cytokinins, which are the classical antagonists of ABA, and ethylene which is known as an early drought-induced signal influencing leaf and shoot growth. There is wide genetic diversity of drought tolerance in different quinoa genotypes grown under dry conditions based on seed yield, suggesting that quinoa could be bred for the very dry conditions of certain regions of Argentina, Brazil and Chile, as well as revealing new opportunities for production of biomass and forage (Spehar and Santos 2005; Fuentes and Bhargava 2011; González et al. 2011; Costa-Tártara et al. 2012).

Other studies of drought tolerance in quinoa include the use of next-generation sequencing approaches and biological validation through reverse-transcription quantitative PCR expression analysis. This methodology, in which RNA-Seq samples isolated from control and drought-treated seedlings are sequenced using the Illumina paired-end method and the acquired data is assembled and analyzed using bioinformatics tools, allowed analysis of a tolerant quinoa genotype in contrasting conditions, including identification of genes that were induced or repressed in response to drought conditions, such as *HSP20* (hsp20-putative chaperones superfamily protein), *LEA* (late embryogenesis abundant protein family), *AP2/ERF* (integrase-type DNA-binding superfamily protein), *PP2C* (protein phosphatase 2C family protein), *HSP83* (chaperone protein, HTPG family protein) and *P5CS* (delta-1-pyrroline-5-carboxylate synthase 2), among others (A. Zurita-Silva et al. in preparation). RNAseq data related to drought tolerance from tissues of the quinoa cultivars Ingapirca and Ollague was recently submitted to the Sequence Read Archive (SRA) (NCBI) by Dr Maughan's group from Brigham Young University (Utah, USA). SRA stores raw sequencing data from next-generation sequencing platforms and this group's submission represents an important wealth of public data. The use of these new technologies should reveal insights into gene regulation at the whole plant level and also point out possible mechanisms and metabolic pathways involved in the complex drought-tolerance response.

Downy mildew

Downy mildew (*Peronospora farinosa* f. sp. *chenopodii*) has been recognized as a key limiting factor in quinoa, causing yield reductions of up to 99 % in susceptible cultivars (Danielsen and Munk 2004; Kumar et al. 2006). This fungal disease was initially reported to be endemic in Bolivia, Chile, Colombia, Ecuador and Peru (Alandia et al. 1979; Aragón and Gutiérrez 1992), but reports from Canada (Tewari and Boyetchko 1990) and Europe (Danielsen et al. 2002), and the first report of downy mildew in quinoa caused by *Peronospora variabilis* at research plots in Pennsylvania (USA), were recently published (Testen et al. 2012), demonstrating wide occurrence in the world. Downey mildew has been also reported to occur on *Chenopodium murale* L., a wild amaranthaceous species in India (Verma et al. 1964), but has not yet been reported on cultivated *C. quinoa* in India (Kumar et al. 2006).

Downy mildew is influenced by temperature (maximum around 23 °C) and relative humidity (over 90 %) (Kumar et al. 2006), and the disease can be seed-transmitted (Danielsen et al. 2004). This pathogen reduces photosynthetic area due to the development of chlorotic and necrotic spots in the leaves and premature leaf fall (Danielsen and Munk 2004). Different studies have suggested that downy mildew resistance in quinoa is a complex trait regulated by multiple resistance genes (Kumar et al. 2006; Kitz et al. 2009), and that resistant cultivars traditionally developed by artificial crosses and/or mass selection (Table 1) can be effectively assisted by marker-assisted selection (MAS) for introgressing the major disease resistance genes and QTL into more susceptible lines (Maughan et al. 2004; Kitz et al. 2009). Nevertheless, further research is required to identify the specific chromosomal regions associated with downy mildew resistance.

Saponins

Saponins are the major anti-nutritional compounds of quinoa and, when present in the integuments of mature achenes, they confer bitterness. These glucosidic triterpenoids vary from 0.2 g/kg in sweet to 11.3 g/kg in bitter genotypes based on dry matter (Mastebroek et al. 2000). Twenty different saponins have been isolated from quinoa seed coats, seeds, fruits and flowers, and their structures were chemically identified through spectroscopy (Kuljanabhagavad et al. 2008). Saponins possess wide industrial importance in the production of soaps, detergents, shampoos, beer, fire extinguishers, and in the cosmetic and pharmaceutical industries (Jacobsen 2003; Kumar et al. 2006). These saponin derivatives could broaden quinoa production globally in a more economically sustainable manner (Martínez et al. 2009a). Saponin content can be determined using several methods, the simplest being the foam test (Koziol 1992), in which total saponin content and saponin composition (i.e., amounts of the three main groups of saponins found in quinoa: oleanolic acid, hederagenin and phytolaccagenic acid) are quantified (McElhinny et al. 2007).

Saponin content depends on the developmental stage of the crop, being low during branching and high during flowering (Bhargava et al. 2006). Drought reduces by 45 % the accumulation of sapogenins in quinoa seeds, based on one study of severe water deficit conducted in Southern Europe (Gómez-Caravaca et al. 2012), whereas salinity has the opposite effect (Solíz-Guerrero et al. 2002; Pulvento et al. 2012). More recently, a significant increase of saponins and other seed components has been reported in an arid location (irrigated) as opposed to a cold-temperate climate (rainfed) site (Miranda et al. 2012; Miranda et al. 2013). Thus, the above data suggest that additional studies must be conducted to elucidate how the environmental and the genotypic effects influence the seed saponin levels.

Farmers prefer in general sweet quinoa cultivars because they skip the tedious process of grain washing to remove bitterness, whereas other growers prefer bitter varieties to protect their crops against bird damage to some degree. The selection criteria and preference of genotype depend on the location, the type of grower, the grain use and the market demand (McElhinny et al. 2007). Nevertheless, high levels of saponin are considered a major impediment to the diversification of the crop (Bhargava et al. 2006) because they can affect the absorption and digestibility of nutrients (Maughan et al. 2004). Consequently, the development of varieties with low or no saponin is one of the important breeding objectives for quinoa (Spehar and Rocha 2010), in which MAS combined with recently available linkage mapping can be effective for advanced genetic analysis of agronomic traits (Mastebroek et al. 2000; Maughan et al. 2004, 2012). It has been suggested that bitterness is controlled by a single dominant gene, a suggestion supported by the 3:1 segregation ratio observed for bitter versus sweet genotypes (Gandarillas 1948), and by the fact that the level of bitterness is quantitatively inherited (Risi 1986; Kenwright 1989). In three cycles of pedigree selection with 10 quinoa accessions, Ward (2000) demonstrated that the action of a single dominant gene is an important component of the genetic variation regulating this trait. Moreover, fixed heterozygosity at the locus controlling saponin content may also occur due to the allotetraploid nature of the species. While identification of precise molecular markers of the dominant genetic locus (Mastebroek et al. 2000) could significantly accelerate breeding programs, those efforts may be hampered in the light of a study in which saponin content in leaves of bitter and sweet genotypes and their F2 progeny plants did not differ during the vegetative phase of plant development, suggesting that the sweet genotypes cannot be selected before anthesis, thus restricting the pace of a breeding program for this particular trait (Mastebroek et al. 2000). Relative saponin contents of traditional quinoa cultivars in the Andes are described in Table 1.

Harvest index and yield

Average harvest index values for quinoa are low (i.e. 0.30, Bertero et al. 2004), similar to those of wheat and rice before the Green Revolution. However, based on the history of breeding these two crops, for instance, an increase in quinoa yield might be achieved by affecting gibberellic acid (GA) metabolism and thus manipulating plant height (Sakamoto and Matsuoka 2004; Gómez et al. 2011). The hypothesis underlying this strategy is that yield in quinoa is limited by a low sink capacity, and that a reduction in competition between stem and panicle for photoassimilates will result in higher seed number and yield as a

consequence of increased reproductive partitioning (Reynolds 2009; Gómez et al. 2011). To assess the potential impact of genetic manipulation of GA content in this species, the effect of the GA synthesis inhibitor paclobutrazol on quinoa yield, biomass, partitioning, seed number and weight was evaluated. As a consequence of paclobutrazol application, plant height decreased and yields increased by ca. 50 %, seed numbers augmented and the harvest index increased from 0.282 to 0.398, without affecting biomass accumulation and seed weight (Gómez et al. 2011). Thus, higher yields can be accomplished by increasing reproductive partitioning, which could imply many advantages for quinoa's development, and this crop is a very good candidate in the search for high-quality plant protein sources considering the current and the near-future food demands in the world.

Grain yield and grain size, determinants of crop commercial quality, are frequently used as selection criteria for quinoa breeding, and they are some of the most important traits that need to be addressed in the future (Bertero et al. 2004). Quinoa exhibits a strong variability of cultivar-specific responses to environmental variation; i.e. large genotype × environment interactions for grain yield and size are observed when a diverse set of cultivars is evaluated in multi-environment experiments, ranging between 0.4 and 6.0 ton/ha, depending upon the specific genotype (Table 1). Comprehensive multi-environment trials involving multiple cultivars were tested in 14 sites under irrigation across three continents to assess the size and nature of the genotype (G) and genotype × environment (G × E) interaction effects (Bertero et al. 2004). In this study, no single genotype group displayed consistently superior grain yield across all the environments, and the G and the G × E interaction effects observed for the duration of the crop cycle had the major influence on the cultivar performance and on the form of G × E interactions observed for the total above-ground biomass and grain yield.

Another strategy to improve grain yield is to take advantage of heterosis reported on quinoa (Wilson 1990), which is associated with hybrid seed production. Various sources of male sterility used in hybridizations for breeding quinoa are available. Initially, a single nuclear gene was reported by Gandarillas (1969) and a cytoplasmic source was reported by Simmons (1971). Galwey and Risi (1984) reported another cytoplasmic source in 1984. Wilson (1990) observed heterosis for yield ranging between 201 and 491 % for different crosses in experiments conducted in Colorado (USA). Subsequently, Ward (1991) obtained two potential sources of male sterility, one from the cultivar Amachuma and another from the cultivar Apelawa. The Amachuma type appears to be a simply inherited, nuclear gene for male sterility. The Apelawa type has cytoplasmatic male sterility and Ward (1991) transferred this trait into four additional genotypic backgrounds.

Germplasm collections and programs

There are 16,263 ex situ *Chenopodium* accessions collected in the world, mainly obtained and maintained in the Andean Region (mostly in Bolivia and Peru) (FAO 2010). The largest ex situ seed bank is the Bolivian National Collection located at the Fundación para la Promoción e Investigación de Productos Andinos (PROINPA) and is now under custody of the Instituto Nacional de Innovación Agropecuaria y Forestal (INIAF), which comprises 4,312 quinoa accessions preserved under ex situ conditions (FAO 2010). These accessions have been characterized (i.e., growth habit, shape of panicle, physiological maturity, grain diameter, nutritional and industrial value of the seeds), and molecular tools are being developed in conjunction with Brigham Young University (Jellen 2013, personal communication). Other important seed collections maintained in South America are the Universidad Nacional del Altiplano (UNAP, Peru), the National Institute of Agricultural Research (INIA, Peru), the Research Center for Andean Studies (CICA, Peru) and, more recently, the National Seed Bank of Chile (managed by INIA-Intihuasi, Vicuña). In addition, other complete ex situ germplasm collections are maintained at the Royal Botanical Gardens Kew (UK), the USDA-ARS (USA), the National Bureau of Plant Genetic Resources (India) and IPK-Gatersleben (Germany) (Fuentes et al. 2009b). Only the USDA-ARS and the Royal Botanical Gardens Kew have wild Chenopodiaceous species available, and the USDA-ARS has currently 357 accessions of *Chenopodium* and allied genera (Brenner 2013, personal communication).

Overall, research on the genetics and breeding of quinoa has been limited, and indeed it is necessary to boost more research for quinoa genetic improvement (Jacobsen et al. 2003; Danial et al. 2007; Rojas et al. 2009). Quinoa research breeding programs were not

initiated until the 1960s in Andean countries (McElhinny et al. 2007). Subsequently, quinoa breeding programs were started in the 1980s in the USA and Europe with the objectives of adapting quinoa, with respect to uniformity and early maturity, to new climatic and agronomic conditions. In Europe breeding work was initiated in the UK, followed by Denmark, both countries working on a broad range of genotypes obtained from previous British collections. Uniform lines were developed and given identification codes, but no varieties were registered. Quinoa breeding in the Netherlands began in 1986 based on accessions from seed banks, botanical gardens and universities. After evaluation, uniform lines adapted to the climate of Western Europe were selected (Mastebroek et al. 2002). A stability analysis of the selection time for some quantitative traits of quinoa concluded that height, inflorescence size and stage of development of quinoa could be satisfactorily selected in the early stages of a breeding program, and potential parental lines were identified in one population (i.e., from 14 lines grown during five seasons) for their use in the development of new varieties suitable for northern European conditions (Jacobsen et al. 1996). At present, there are four Dutch and two Danish varieties of quinoa registered (Jacobsen and Bendevis 2013). Another major quinoa breeding program, the Project for Durable Resistance in the Andean Zone (PREDUZA), was started in the late 1990s, funded by Wageningen University, and focusses on improving quinoa's abiotic and biotic stress tolerance.

The McKnight Foundation has been supporting breeding efforts conducted by PROINPA in Bolivia. National breeding programs in Ecuador, Peru and Bolivia have been characterized by irregular and inconsistent funding (McElhinny et al. 2007). In Asia, The National Botanical Research Institute (India) initiated a breeding program with the main objective of adapting quinoa to local conditions (Bhargava et al. 2006). In Chile, private efforts have generated cultivars and advanced lines using coastal/lowland genotypes. Additionally, different lines of quinoa from Salares have been analyzed for their morphological and qualitative traits in desert coastal and highlands conditions so as to determine their genetic diversity and therefore usefulness for breeding programs (Fuentes et al. 2009b; Fuentes and Bhargava 2011). In Brazil, pioneering quinoa varieties free of saponin (sweet genotypes) and adapted to the growing conditions of the savannah (i.e., acid soils) have been bred (Spehar and Rocha 2010). This was the initial goal for improving the crop and a turning point in the agricultural diversification of the savannah.

Molecular genetic resources

The first molecular studies in quinoa were focused on allozyme markers to establish genetic variability in domesticated quinoa and wild species (*C. hircinum* and wild quinoa ajara) (Wilson 1988a, b). The results of these works highlighted for the first time, on the basis of molecular information, two distinctive groups: a coastal type from southwestern Chile and an Andean type from northwestern Argentina to southern Colombia, suggesting the co-evolutionary relationship between domesticated and free-living populations of the southern highlands (Wilson 1988b). Similarly, protein-based approaches have been carried out to characterize quinoa seed storage proteins as an effective tool for cultivar identification and breeding programs for improved protein quantity and quality (Fairbanks et al. 1990). Taken together, the findings reported in these studies were congruent with the taxonomic position of quinoa (subsect. *Favosa* of the sect. *Chenopodium*), crossability relationships and other biochemical characteristics previously reported on these species (Bhargava et al. 2005).

Fairbanks et al. (1993) reported the first DNA-based markers in quinoa on the basis of the random amplified polymorphic DNA (RAPD) method. These DNA markers have given the ability to detect genetic variation among quinoa and other Chenopodiaceae species (Ruas et al. 1999; Del Castillo et al. 2007), as well as to identify true hybrids from intergeneric crosses, to be used in generating genetic linkage maps (Maughan et al. 2004; Jarvis et al. 2008) (Table 2). Subsequently, simple sequence repeat (SSR) markers have been used widely in quinoa because of their co-dominant nature and their capacity to detect high levels of polymorphism (Mason et al. 2005). Interestingly, the differences in polymorphism between two- and three-nucleotide motifs (CA, GA, AAT, ATG and CAA) confirmed the common observation that the development of highly polymorphic microsatellite markers in quinoa should be focused on tri-nucleotide motifs with a repeat of >20 bp (Fuentes et al. 2012).

Table 2 Molecular studies reported in quinoa based on protein, DNA, RNA and cytogenetic approaches

References	Approach	Description
Wilson (1988a, b)	Isozyme	Characterization of 99 populations of quinoa and relatives (SA-LC-HL-IAV)[a] using 21 isozyme loci-based analysis: glutamate oxaloacetate transaminase (GOT), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malic dehydrogenase (MDH), phosphoglucoisomerase (PGI) and phosphoglucomutas (PGM) systems
Fairbanks et al. (1990)	Protein	Characterization of quinoa seed proteins, revealing in a wide genetic base the presence of three polymorphic polypeptides from the globulin fraction of approximately 34.3, 35.6 and 36.2 kDa
Fairbanks et al. (1993)	RAPD	Characterization of 30 RAPD markers revealed 26 polymorphic markers among 16 randomly selected quinoa accessions, indicating a relatively common presence of multiple polymorphic markers
Ruas et al. (1999)	RAPD	A total of 33 10-mer primers generated 399 molecular markers with an average of 12 polymorphisms per RAPD primer, which discriminated the germplasm collection into five different clusters: (1) cultivated varieties of *C. nuttalliae*, (2) cultivars and wild varieties of *C. quinoa*, (3) *C. berlandieri* and *C. album*, (4) *C. pallidicaule* and (5) *C. ambrosioides*
Kolano (2004)	Molecular cytogenetic characterization	Characterization of sequences homologous to retrotransposons (15-5D, 21-5D and 22-19A) and to transposase genes (20-20I) using fluorescent in situ hybridization (FISH) technique
Maughan et al. (2004)	Genetic map	First quinoa genetic map constructed using AFLP, SSR and RAPD markers. Map yielded 35 genetic linkage groups spanning 1,020 cM (4.0 cM per marker) in a map population composed of 80 F2 individuals from KU-2 (L/C) × 0654 (HL) genotypes
Mason et al. (2005)	SSR	Generation of 208 SSR markers assessed in 31 quinoa accessions from Ecuador, Colombia Peru, Bolivia, Chile and Argentina (SA-L/C-HL-IAV). 0.2–0.9 range of heterozygosity
Bhargava et al. (2005)	Protein	Characterization of seed protein profiles of 40 cultivated and wild taxa of *Chenopodium* (SA-L/C-HL-IAV). Accessions of *C. quinoa* were clustered together showing genetic similarity with closely related *C. bushianum* and *C. berlandieri* subsp. *nuttalliae*
Coles et al. (2005)	SNP/EST	Generation of 51 SNP markers and 424 EST sequences obtained from both an immature seed and floral EST libraries. SNP markers comprised 38 single-base changes and 13 insertions–deletions (Indels), with an average of one SNP per 462 base pairs (bp) and one Indel per 1,812 bp
Maughan et al. (2006)	Molecular cytogenetic characterization	Characterization of organization and genomic distribution of 45S (NOR, nucleolus organizer region) and 5S ribosomal RNA (rRNA) genes using fluorescent in situ hybridization (FISH) technique
Stevens et al. (2006)	Bacterial artificial chromosome (BAC) library	Two libraries (*Bam*HI and *Eco*RI) yielded 26,880 and 48,000 clones respectively, from "Real" quinoa type, with an average insert size of approximately 123 kb.
Christensen et al. (2007)	SSR	Characterization of 151 quinoa accessions from Ecuador, Peru, Bolivia, Chile and Argentina (SA-L/C-HL-IAV) using 36 SSR markers (420 alleles). 0.45–0.94 range of heterozygosity
Del Castillo et al. (2007)	RAPD	Characterization of 87 Bolivian quinoa accessions (HL) using 10 RAPD markers (38 alleles). 0.10–0.22 range of averaged genetic diversity
Jarvis et al. (2008)	SSR	Generation of 216 SSR markers (888 alleles) assessed in 23 quinoa accessions from Ecuador, Colombia Peru, Bolivia, Chile and Argentina (SA-L/C-HL-IAV). 0.12–0.90 range of heterozygosity
	Genetic map	Second quinoa genetic map constructed using SSR, AFLP, 11S seed storage protein loci, a nuclear organizing region (NOR) and a betalain color locus. Map yielded 38 genetic linkage groups spanning 913 cM in a map population composed of a RIL population consisting of 82 F5 individuals from KU-2 (L/C) × 0654 (HL) genotypes

Table 2 continued

References	Approach	Description
Kolano et al. (2008)	Molecular cytogenetic characterization	Characterization of repetitive sequence (pTaq10) isolated from the *Taq*I digest of genomic DNA of quinoa using fluorescent in situ hybridization (FISH) technique
Fuentes et al. (2009a, b)	SSR	Characterization of 59 Chilean quinoa accessions (SA-L/C) using 20 SSR markers (150 alleles). 0.07–0.90 range of heterozygosity
Maughan et al. (2009)	Gene characterization	Characterization of *Salt Overly Sensitive 1* (*SOS1*) gene (Na^+/H^+ antiporter), yielding two homeologous SOS1 loci: cqSOS1A and cqSOS1B
Reynolds (2009)	EST	Annotation of a large-scale EST collection from maturing quinoa seed tissues expressing saponins to elucidate the genetic components of its biosynthesis using microarray assay. 39,366 unigenes were characterized, consisting of 16,728 contigs and 22,638 singletons
Anabalón-Rodríguez and Thomet-Isla (2009)	AFLP	Characterization of 18 Chilean quinoa accessions (L/C-SA) using three AFLP markers (130 alleles). 0.54–0.97 range of genetic similarity
Rana et al. (2010)	RAPD/DAMD	Characterization of 55 accessions belonging to 14 species of Chenopods using 12 RAPD and four mini-satellite or variable number of tandem repeat (VNTR) markers (350 polymorphic markers)
Kolano et al. (2011)	Molecular cytogenetic characterization	Characterization of a repetitive DNA sequence (18–24 J) and 12–13P sequence using fluorescent in situ hybridization (FISH) technique
Ruiz-Carrasco et al. (2011)	Gene characterization and expression	Characterization of *NHX1* gene (vacuolar Na^+/H^+ antiporter), analysing by quantitative RT-PCR sodium transporter genes *CqSOS1* and *CqNHX*, and their expression in root and shoot tissues of genotypes (L/C-HL) in response to salinity
Costa-Tártara et al. (2012)	SSR	Characterization of 35 Argentinian quinoa accessions (SA) using 22 SSR markers (354 alleles). 0.58–0.93 range of heterozygosity
Fuentes et al. (2012)	SSR	Characterization of 34 quinoa accessions from Ecuador, Colombia, Peru, Bolivia, Chile and Argentina (SA-L/C-HL-IAV) using 20 SSR markers (118 alleles). 0.12–0.87 range of heterozygosity
Maughan et al. (2012)	SNP	Generation of 427 SNP markers (854 alleles) assessed in 113 quinoa accessions from Ecuador, Peru, Bolivia, Chile and Argentina (SA-L/C-HL-IAV). 0.02–0.50 range of MAF (minor allele frequency). 46 % of markers were highly polymorphic and 90 % polymorphic. Transitions (A/G or C/T) were more frequent, being 1.6 times higher than transversions (A/T, C/A, G/C and G/T)
	Genetic map	Third quinoa genetic map constructed using 427 SNP markers. Map yielded 29 genetic linkage groups spanning 1,404 cM (3.1 cM per marker) in a map population composed of 128 individuals from two advanced F2:8 RIL populations sharing a common paternal parent (0654, HL)

[a] Ecotype: *IAV* inter-Andean valley, *HL* highlands, *SA* salares, *C/L* coastal/lowland

This set of SSR markers also revealed the potential utility for further genetic analysis of related species of the genus such as *C. pallidicaule* (Canihua, South America), *C. berlandieri* subsp. *nuttaliae* (Huazontle, Central America) and *C. giganteum* (Khan chi, Asia).

Single nucleotide polymorphism (SNP) markers have also been developed in quinoa from specific tissues to construct expressed sequence tag (EST) libraries to report homology to many protein-encoding genes from other plants (Table 2) (Coles et al. 2005). A large-scale set of SNP markers has been described to develop functional SNP assays for quinoa (Maughan et al. 2012). In this study, the most frequent point mutation among all SNPs identified corresponded to transitions (A/G or C/T), being 1.6 times higher than transversions (A/T, C/A, G/C, G/T). In spite of the potential transferability of these markers to related species such as *C. hircinum*, *C. berlandieri* (subsp. *nuttaliae*, var. *macrocalycium*, var. *boscianum*, var. *zschackei*), *C. watsonii* and *C. ficifolium*, the inability

to separate related species into discrete groups suggests the limited use of this set of SNP markers for phylogenetic studies at genus level.

The first quinoa genetic linkage map of molecular markers was reported by Maughan et al. (2004) and, 4 years later, a second version of the genetic linkage map was published by Jarvis et al. (2008), and was based on different molecular resources developed in quinoa, including SSR, amplified fragment length polymorphism and RAPD markers, 11S seed storage protein loci, the NOR and the morphological betalain color locus (Table 2). Recently the first SNP-based linkage map was developed from the large-scale set of SNP markers reported by Maughan et al. (2012). In this context, this SNP-based map consisted of approximately twofold more marker loci and spanned a greater genetic distance than the previous reported maps, being closer to the 1,700 cM total length of the quinoa map predicted by Maughan et al. (2004). These latter results suggest that new molecular resources and much larger recombinant inbred line (RIL) populations are still required to cover the remaining undetected areas of the quinoa genome.

Another approach to boost the exploitation of the quinoa genome has been the development of bacterial artificial chromosome (BAC) libraries (Stevens et al. 2006). Results of this study allowed the determination of the di-haploid genome (1C) of quinoa to be 967 Mbp, or $2C = 2.01$ pg. To demonstrate the utility of this BAC library for gene identification, the study revealed the presence of two distinct genetic loci encoding 11S globulin seed storage proteins. The different pattern of the hybridized bands occurring in a single copy by Southern blotting was consistent with the differences between quinoa genotypes from highland and lowland, suggesting the utility of this locus for improving the protein content and quality (Stevens et al. 2006).

In recent years a significant change of pace in crop genomics has taken hold through the development of next-generation sequencing technologies, which have increased the ability to generate sequence data from any species, so that molecular markers can be generated at affordable cost in species where little or no information is available. In quinoa, the annotation of a large-scale EST collection from maturing seed tissues expressing saponins was reported in an attempt to elucidate the genetic components involved in their biosynthesis (Reynolds 2009). Additionally, the analysis of repeated sequences from unigene sequences identified a new set of 291 SSR markers (unpublished data). The assessment of transcriptional variation between sweet and bitter quinoa varieties at two different stages of development was developed using 102,834 oligonucleotide probes in a microarray assay. The microarray analysis allowed the identification of a set of candidate genes transcriptionally related to saponin biosynthesis, including genes with shared homology to cytochrome P450s, cytochrome P450 monooxygenases and glycosyltransferases, representing a potential new approach to quinoa grain improvement related to this economically important trait. Table 2 gives an extensive description of other molecular studies reported in quinoa.

Future trends and conclusions

Non-traditional crops with high nutritional value, outstanding capacities to cope with unfavorable soil and climatic conditions, and acceptable yields even without options for applying irrigation and fertilization are of special interest in the world today (Jacobsen et al. 2013). Sustainable agriculture and food security are of crucial importance in rainfed areas and where human and productive resources are limited, as in low-input Andean farming and in Africa. These crops represent an economic potential not only for local markets but also for exports, and could provide growers with better prices to improve their revenues. Quinoa, an Andean annual seed crop, fulfills all these attributes and has been selected by FAO as one of the crops destined to offer food security in the 21st century.

Although highly autogamous, quinoa can also display obligate outcrossing by self-incompatibility and male sterility (Nelson 1968; Gandarillas 1969), suggesting that quinoa has a fairly versatile breeding system. Increasing but insufficient knowledge of quinoa genetics and its allotetraploid nature, self-pollination and small flowers make emasculation, hybridization and breeding complex. Emasculation techniques (i.e., hand emasculation) remain cumbersome and expensive and limit the production of high-yield hybrids (Wilson 1990). Hand emasculation could be circumvented if stable male sterile lines existed for hybrid production, a subject little researched with the exception of Ward's work (Ward 1991, 1998; Ward and Johnson 1994).

Downy mildew is the main biotic factor causing serious yield losses (Danielsen and Munk 2004; Kumar et al. 2006). The nature of its resistance, as well as its interaction with pathogen populations of different geographical origin, has been little characterized. Breeding efforts are concentrated on increasing durable resistance against downy mildew and combining resistance with other desirable traits such as earliness, sweetness and drought tolerance. Additional sources of downy mildew resistance seem to be present in wild *Chenopodium* species that grow more or less in association with the cultivated crop. There are indications that wild species such as *C. hircinum*, *C. nuttalliae*, *C. petiolare*, *C. album* and *C. ambrosioides* harbor downy mildew resistance genes (Bonifacio 1995). These sources may be useful for incorporating resistance into commercial varieties; interspecific hybrids are viable but, unfortunately, may carry undesirable characteristics of the donor species that can decelerate a quinoa-breeding program.

Saponin content has also presented a problem for introducing quinoa worldwide. There is consensus that development of sweet cultivars with little or no saponin is one of the most important breeding objectives for the future (Bhargava et al. 2006; Spehar and Rocha 2010). However, breeding this trait into quinoa varieties is still a challenge to breeders due to their inability to measure pertinent saponin levels prior to anthesis and the difficulties in fixing desirable alleles due to allotetraploidy (Mastebroek et al. 2000).

Despite these limitations, there is still enormous potential for introducing quinoa to countries in need of protein because its seeds have high quantity and quality of proteins as food source. Quinoa cultivation constitutes an important opportunity to diversify low-input farming of growers in the Andes and elsewhere. Because of its well-documented tolerance to several abiotic stresses, such as drought, salinity, low soil fertility and frost, this ancient crop could make vulnerable cropping systems much less precarious (McElhinny et al. 2007; Kitz et al. 2009; Razzaghi et al. 2012). Pivotal to achieving this aim are breeding programs focused on increasing yield potential, pyramiding of abiotic tolerances, incorporation of downy mildew resistance and diminishing seed saponin levels to obtain sweet genotypes. Conventional as well as molecular tools should be utilized to unlock the rich biodiversity and potential of quinoa.

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