Quinoa Genetics

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Abstract

Quinoa (*Chenopodium quinoa* Willd.) is a pseudocereal in the genus *Chenopodium* and is commonly known as "goosefoot." *C. quinoa* has a monophyletic origin from Andean crop/weed system and was first domesticated in the Altiplano region south of Lake Titicaca. Quinoa is predominantly an inbreeding species and an allotetraploid having a chromosome number of $2n = 4x = 36$; however, mixoploidy has been reported in *C. quinoa* with chromosome numbers of $2n = 18$, $2n = 27$, $2n = 36$, and $2n = 45$. Quinoa genome has been identified and confirmed to be divided into two subgenomes by several authors. Characters controlled by major genes in quinoa have been reported to exhibit simple disomic-monogenic inheritance. Few successes have been recorded for attempts to manually hybridize *C. quinoa* with either of its related wild or cultivated tetraploids, and this has hindered the creation of segregating generations large enough for genetic analysis. Genetic improvement of quinoa has so far received little attention unlike other major cereal crops which have been fully involved in modern plant breeding techniques and genetic research. A number of molecular markers (AFLP, SSR, and SNP) have been developed for quinoa and are being used today to enhance quinoa improvement programs.

Keywords

Quinoa · Inheritance · Genetic improvement · Cytogenetics · Genetic diversity

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4.1 Introduction

Quinoa (*Chenopodium quinoa* Wild.), commonly known as "goosefoot" (Giusti 1970), is a pseudocereal and one of the 250 species included in the genus *Chenopodium* (Amaranthaceae). Although most species of the genus are colonizing annuals, other habits such as herbaceous, suffrutescent, and arborescent perennials also exist (Wilson 1990; Fuentes et al. 2012). *C. quinoa*, *C. berlandieri* subsp. nuttalliae, and *C. album* are of economic importance as they are used as a leafy vegetable, grain, and forage (Risi and Galwey 1989a), while other *Chenopodium* species such as *C. ambrosioides*, *C. botrys*, and *C. murale* have been identified with various medicinal uses (Kirtikar and Basu 2001).

Quinoa has been cultivated for more than 5000 years in the Andes and was probably domesticated by ancient civilizations at different times and in different geographic zones (Bhargava and Ohri 2016). Many wild characters such as seed shattering, seed dormancy, and thick seed coats that were disadvantageous to the farmers were lost, while useful characters such as larger and starchier seeds, fewer and larger inflorescences, uniform maturity, and environmental adaptations were preserved during domestication (Bhargava and Ohri 2016).

Quinoa is a highly nutritious crop with remarkable agronomic adaptations to different adverse climatic conditions such as drought, high salinity, and frost (Ruiz et al. 2014, 2016), which makes it suitable for cultivation in countries that are susceptible to the effects of climate change. Due to its high level of adaptability, quinoa can survive in diverse environments such as lowlands, deserts, and areas over 4000 m above sea level (Jacobsen and Mujica 2003; Jacobsen et al. 2003, 2009; Maughan et al. 2009; Hariadi et al. 2010). Quinoa has the potential to become a sustainable food supply globally under rapidly changing climatic pattern shifts while at the same time ameliorating pressure on arable land (Ruiz et al. 2016) and is therefore considered as a climate change-resilient crop. Because of its resilience and nutritional benefits, quinoa, together with amaranth, has been described as "one of the grains of the 21st century" (Konishi 2002) that will play a key role in the provision of sustainable food in adverse environmental conditions resulting from climate change scenarios. It has exceptional capacity to grow in water-deficient soil due to its inherent low water requirement and the ability to resume its photosynthetic rate and maintain its leaf area after a period of drought (Galwey et al. 1989; Jensen et al. 2000; Jacobsen et al. 2003). Saponins are the main antinutritional compounds of quinoa, and they confer bitterness when present in the integuments of mature achenes. The developmental stage of the crop affects saponin content; it is low during branching and high during flowering (Bhargava et al. 2006a). Seed components have been reported to exhibit diversity with regard to the environment as considerable increase of saponins and other seed components has been reported in an arid location (irrigated) as opposed to a cold temperate climate (rain-fed) site (Miranda et al. 2012, 2013); this suggests that environment plays a major role in the expression of genes responsible for seed components. Development of varieties with little or no saponin is one of the vital breeding objectives (Spehar and Rocha 2010), and MAS combined with recently available linkage mapping can be valuable for

advanced genetic analysis of important agronomic traits (Mastebroek et al. 2000; Maughan et al. 2004, 2012).

Increasing but insufficient knowledge of quinoa genetics and its complex allotetraploid nature, together with its small flowers and self-pollination nature, makes emasculation, hybridization, and breeding difficult. The primary breeding objective is to develop a variety with a dwarf, non-branching, and uniformly early maturing plant type to aid mechanical harvesting (Jacobsen et al. 1996) and high grain yield with high protein and low saponin content (Bhargava et al. 2006a). However, for any breeding program to work, the genetics of the traits of interest should be well understood.

4.2 Genome Size

Studies on genome size of *C. quinoa* using Feulgen micro-densitometry found 4C DNA amounts ranging from 6.34 to 6.47 pg in 21 accessions, which showed a nonsignificant 1.02-fold (Bhargava et al. 2007a). Likewise, 4C DNA amounts of 5.79 and 5.90 pg were recorded in two accessions of related tetraploid species *C. berlandieri* subsp. nuttalliae, and their average is 8.31% less than the mean of 4C DNA values of the studied 21 accessions of *C. quinoa* (Bhargava et al. 2007a). Similar results have been obtained using flow cytometry in *C. quinoa* cv. Barandales, which showed 2C values of 2.96 pg. Also a range of 2.96–3.04 pg was obtained for six accessions of *C. berlandieri* subsp. nuttalliae (Palomino et al. 2008). The findings of Palomino et al. (2008) correspond to that of Kolano et al. (2012), who showed 2C values ranging from 2.9 to 3.0 pg in 20 *C. quinoa* accessions; however, significantly lower 2C values of 2.01 pg using flow cytometry (Stevens et al. 2006) and 2.66 pg (Bennett and Smith 1991) using micro-densitometry have been reported.

Kolano et al. (2011) demonstrated the occurrence of two subgenomes in quinoa by FISH using two repetitive sequences, 12-P and 18-24J. The specificity of 18-24J to one of the two subgenomes was revealed by strong signals on 18 chromosomes in the form of bands of differing intensities on chromosome arms, while only minor signals on the remaining 18 chromosomes occur in terminal and centromeric positions.

Two genomes involved in the ancestry of *C. quinoa* have also been recognized by Storchova et al. (2015) through phylogenetic analysis of two flowering locus T-like genes CrFTL1 and CrFTL2. One parent was assigned to subgenome "A" and was shown to be related to North American *C. standleyanum*, *C. incanum*, or any other related diploid, while the other parent belonging to the Eurasian species *C. suecicum*, *C. ficifolium*, or some related diploid species was assigned to subgenome "B."

4.3 Cytogenetics

The basic chromosome number in the genus *Chenopodium* is $x = 8$ and $x = 9$ (Kawatani and Ohno 1950, 1956). The number $x = 9$ is found in section *Chenopodia*, which has been further subdivided into three subsections, viz., Leiosperma, Cellulata, and Undata (Risi and Galwey 1984). Cytological studies have established that *C. quinoa* is a tetraploid having a chromosome number of $2n = 4x = 36$ (Palomino et al. 1990; Wang et al. 1993; Bhargava et al. 2006b); however, mixoploidy has been reported by Gandarillas (1979) in *C. quinoa* with chromosome numbers of $2n = 18$, $2n = 27$, $2n = 36$, and $2n = 45$. According to Nelson (1968), the basic chromosome number for the genus *Chenopodium* is $x = 9$, and this is in line with the high degree of self-fertility and low levels of inbreeding depression seen in the species.

The results of Ward (2000) are consistent with allotetraploidy. This suggests that functional alleles have been retained at some duplicate loci, and there is some association occurring between homologous chromosomes. Also, tetrasomic segregation ratios have been observed in a minority of families, which may be due to reciprocal fragment exchange between homologues (Ward 2000).

Bhargava et al. (2006b) divided the karyotypes of *C. quinoa* into two groups based on the ratio between the longest and the shortest chromosomes in the complement, which was <2.0 in 1a and >2.0 in 1b types of karyotypes. All taxa they studied were characterized by one satellite pair, the position of which varies according to its comparative size in the complement. The satellite pair was found to be morphologically similar in all the accessions, being median (m) or median-submedian (msm), and has the satellite on the short arm. The symmetry index (TF%) on the basis of arm ratios varies from 43.9% (most asymmetrical) to 47.4% (most symmetrical).

They further observed that the longest chromosome in different complements is either m or msm with arm ratios varying between 1.18 and 1.56, while 4th, 9th, and 18th pairs are the most conserved in being median (M or m) in all the accessions studied (Figs. 4.1a–e and 4.2a, b). The greatest variability was observed in 10th and 13th pairs with the arm ratio ranging between 1.0–1.86 and 1.0–1.78, respectively (Figs. 4.1a–e and 4.2a, b).

C. quinoa has a monophyletic origin from Andean crop/weed system (Wilson 1990); this was confirmed by Bhargava et al. (2006b) in the seven accessions of *C. quinoa* studied, which show only minor though consistent differences in their karyotypes. These minor differences in karyotypes due to chromosomal alterations (mainly pericentric inversions and translocations) are being maintained due to predominantly self-pollinating behavior (Risi and Galwey 1984), and this is consistent with some degree of variability in morphological characters (Risi and Galwey 1984; Wilson 1988a, b; Bhargava et al. 2007b), protein profiles (Bhargava et al. 2005), and RAPD profiles (Ruas et al. 1999). This implies that variation in morphological characters, karyotypic alterations, and protein and RAPD profiles is similar (Bhargava et al. 2006b).

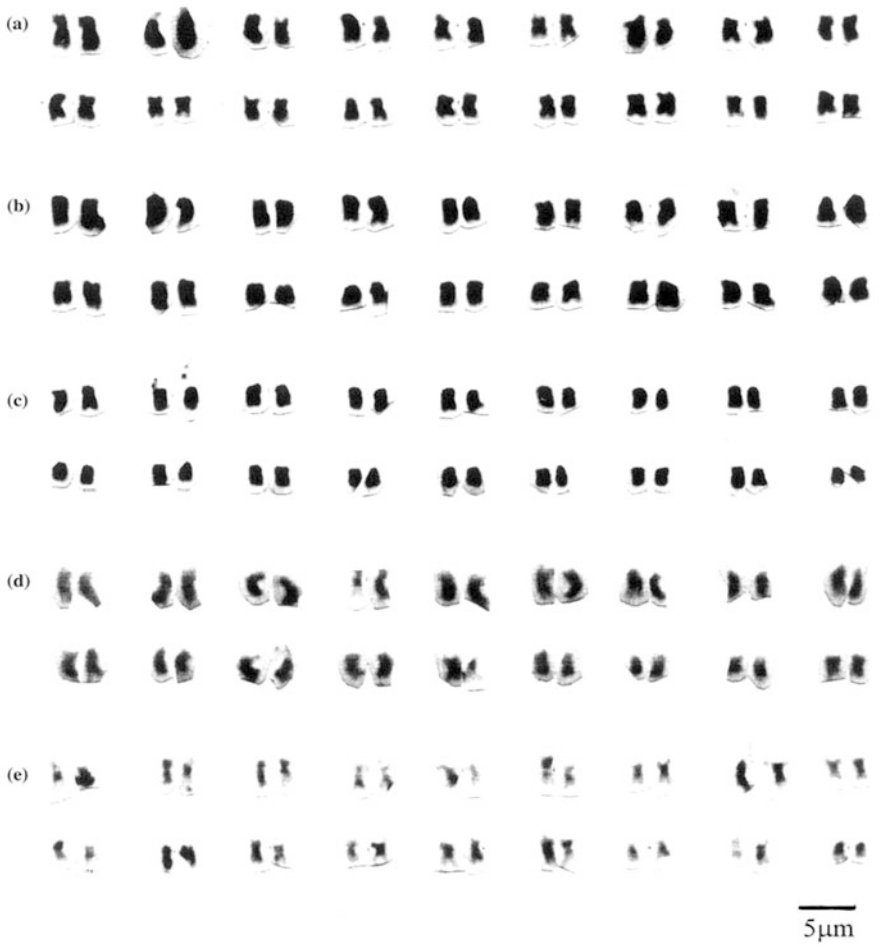

Fig. 4.1 Karyotypes of (**a**) *C. quinoa* PI 587173, (**b**) *C. quinoa* PI 584524, (**c**) *C. quinoa* PI 596498, (**d**) *C. quinoa* PI 510537, (**e**) *C. quinoa* CHEN 71/78 (Bhargava et al. 2006b)

In an earlier study by Catacora (1977), *C. quinoa* chromosomes could be arranged into nine groups of four homologues based on length and ratio between long and short arm. However, a more detailed analysis by Bhargava et al. (2006b) has resulted in clearly identifiable 18 pairs, thereby indicating allotetraploidy. This is also supported by duplication of Lap loci (Wilson 1976), disomic inheritance of some characters (Simmonds 1971), and allelic segregation ratios of F1 and F2, which indicated disomic-digenic and tetrasomic inheritance in some traits (Ward 2000).

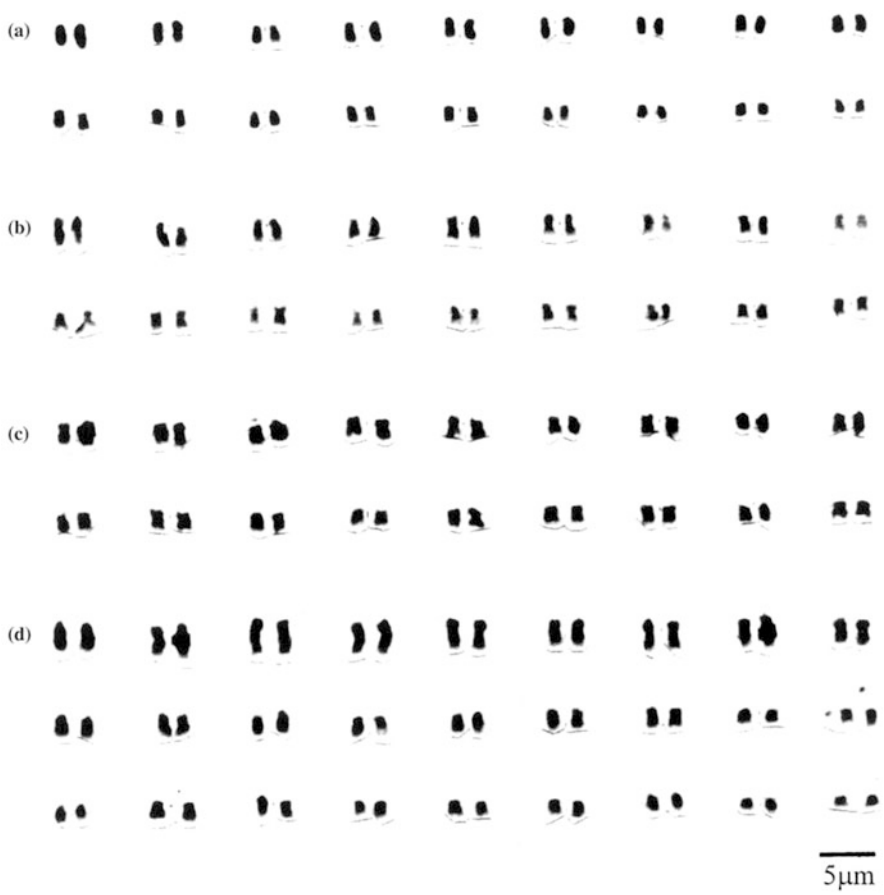

Fig. 4.2 Karyotypes of (**a**) *C. quinoa* CHEN 58/77, (**b**) *C. quinoa* CHEN 33/84, (**c**) *C. berlandieri* subsp. nuttalliae PI 568156, (**d**) *C. bushianum* 22,376 (Bhargava et al. 2006b)

4.4 Pattern of Trait Inheritance in Quinoa

An understanding of how alleles will segregate at loci controlling agronomically important traits is essential to quinoa breeders. Estimation of the heritability coefficient in the narrow sense (hr^2) is a very useful factor for breeders because one can predict the possibility of success with selection, as it reflects the proportion of phenotypic variation that can be inherited; that is to say that heritability coefficient measures the reliability of the phenotypic value as an pointer of genotypic value (Vasconcelos et al. 2012).

Characters controlled by major genes have been reported to exhibit simple disomic-monogenic inheritance (Simmonds 1971; Gandarillas 1979). This type of segregation has led to suggestions that quinoa possesses genes which suppress

pairing between homologous chromosomes, which to an extent places species as functionally diploid (Risi and Galwey 1984; Fleming and Galway 1995). The small size of the chromosome of quinoa makes study of the meiotic chromosome pairing difficult (Ward 2000). Meiotic chromosome configurations in both allo- and autotetraploid are often erratic, and several authors (Soltis and Reiseberg 1986; Krebs and Hancock 1989; Beaver and Iezzoni 1993) pointed out that allelic segregation analysis gives a more precise way of determining polyploidy type and whether inheritance is disomic or tetrasomic.

Homologous chromosome pairing from the same progenitor species in an allotetraploid would normally result in independent assortment at the duplicated loci and disomic inheritance. In autotetraploid, random association of the four homologous chromosomes and independent assortment at any one locus will result in tetrasomic inheritance (Ward 2000). However, segregation ratios which do not fit a simple disomic pattern have been observed in quinoa populations containing a fertility restoration gene (Ward 1998).

Ward (2000) carried out a research to use allelic segregation analysis of these traits: restoration of male fertility in CMS quinoa plants due to the presence of the *Frv* allele, with male fertile being dominant to male sterile (Ward 1998), red inflorescence and stem color due to the presence of the *R* allele with red being dominant to green (Gandarillas 1979), and pigmented axils due to the presence of the *Ax* allele, with pigmented being dominant to non-pigmented (Simmonds 1971) to determine the type of inheritance occurring in quinoa. The allelic segregation analysis was performed in a cross using male sterile plants as female parents produced F1 and F2 generations segregating for different single-gene morphological traits. The analysis revealed a range of F1 and F2 ratios indicative of both disomic-digenic and tetrasomic inheritance in two traits observed (Ward 2000). Also, distorted F2 ratios pointed to erratic multivalent formation at meiosis (Ward 2000). Certainly, tetrasomic segregation of "erratic multivalents" as observed by Ward (2000) would lead to distorted segregation ratios and may also contribute to the low levels of segregation distortion seen in the dataset studied by Maughan et al. (2004).

The level of bitterness of seeds (which is directly associated with saponin content of the seed) is quantitatively inherited (Risi 1986; Kenwright 1989). This has been confirmed by an earlier study by Gandarillas (1948), who observed a 3:1 segregation ratio for bitter versus sweet genotypes, suggesting that bitterness associated by saponin content is controlled by a single dominant gene.

Ward (2000) carried out an investigation in three cycles of pedigree selection with ten quinoa accessions and established that the action of a single dominant gene is an important part of the genetic variation regulating this trait. Due to the allotetraploid nature of the species, fixed heterozygosity at the locus controlling saponin content may also occur. Although identification of precise molecular markers of the dominant genetic locus could significantly accelerate breeding programs (Mastebroek et al. 2000) for selection of sweet genotypes, those efforts may be hindered if saponin content in leaves of bitter and sweet genotypes and their F2 progeny plants did not vary during the vegetative phase of plant development, signifying that the

sweet genotypes cannot be selected before anthesis, hence hampering the speed of a breeding program for this particular trait (Mastebroek et al. 2000).

In an attempt to reveal the genetic components of saponin biosynthesis, Reynolds (2009) reported the annotation of a large-scale EST collection from maturing seed tissues expressing saponins. Moreover, 39,366 unigenes, comprising of 16,728 contigs and 22,638 singletons, were assembled using Sanger and 454 GS-FLX pyrosequencing technologies. The identification of a set of candidate genes transcriptionally related with saponin biosynthesis included genes having homology to cytochrome P450s, cytochrome P450 monooxygenases, and glycosyltransferases was done using microarray analysis.

Plant color in quinoa, as reported by Fleming and Galway (1995), is governed by a single gene with three major alleles: red (R), dominant to purple (rP), which is dominant to green (r). Plant color-inflorescence phenotypes (R vs r) were determined for the parents and F1 and F2 populations.

4.5 Hybridization

Different attempts have been made to hybridize *C. quinoa* with either related wild or cultivated tetraploids by several researchers. In a study by Pal and Ohri (unpublished), *C. quinoa* was found to be inter-crossable with a diploid cytotype of *C. album* occurring in North Indian Plains. The resulting triploid shows 18II and 18I, which implies that one of the genomes of *C. quinoa* is homologous with that of 2x *C. album*. This close genetic relationship between *C. quinoa* and 2x *C. album* has been confirmed on the basis of RAPD and DAMD studies by Rana et al. (2010).

Nelson (1968) created artificial hybrids between *C. quinoa* and *C. quinoa* var. melanospermum and also confirmed the presence of natural hybrids. In another study, Heiser and Nelson (1974) produced F1 hybrids between *C. quinoa* and *C. nuttalliae* or "huauzontle," but these lacked pollen grains as male sterile parent was involved. The F1 hybrids, however, produced seed when backcrossed with the parents showing the close relatedness of the two species. Surprisingly, the F1 had black fruit, while both parents had a light-colored fruit, which was interpreted as a consequence of genetic complementation, thereby showing that light-colored fruit arose independently in Mexico and S. America.

C. quinoa cultivated in N. America has been shown to naturally hybridize freely with related wild species *C. berlandieri*; 30% of the progeny of *C. berlandieri* was found to be F1 crop/weed hybrids; this was confirmed by the presence of polymorphic quinoa isozyme alleles and morphologically intermediate leaves (Wilson and Manhart 1993).

Crosses between *C. berlandieri* subsp. nuttalliae and *C. quinoa/C. hircinum* (Andean complex) resulted in extremely low pollen stainability of 3–4% with no seed set after selfing, although the pollen stainability increases after backcrossing of the hybrid with *C. berlandieri* subsp. nuttalliae (Wilson and Heiser 1979). However, *C. berlandieri* subsp. zschackei of North American complex produces fertile hybrids in crosses with *C. quinoa/C. hircinum*, therefore showing closest affinity to the

Andean complex, and this can be a possible link between North and South American tetraploids (Wilson and Heiser 1979). A study by Bhargava et al. (2006b) seems to support this view point because of the close overall karyotypic similarity between *C. quinoa* and *C. berlandieri* subsp. nuttalliae. High sterility in F1 hybrids between these cultigens has been attributed to the accumulation of chromosomal differentiation following their origin and evolution in extensively separated geographical areas (Wilson 1980).

The karyotype of *C. bushianum* has marked differences in comparison with *C. quinoa* and *C. berlandieri* subsp. nuttalliae, with reference to number and morphology of satellite pairs and a very high ratio between longest and shortest chromosomes in the complement. This is reflected in its crossability relationships showing very low fertility and complete sterility of F1 hybrids (Bhargava et al. 2006b). The 2x types are cross compatible. However, 4x cytotype, which grows in Northern India, has an unusually asymmetrical karyotype as compared with those of diploid and hexaploid cytotypes (Bhargava et al. 2006b). This is reflected in complete crossing compatibility of 4x cytotype with 2x and 6x cytotypes of *C. Berlandieri* sp. nuttalliae and *C. quinoa*, respectively (Wilson 1980).

Owing to the small flower size and clustering of huge numbers of flowers on an inflorescence, there is difficulty of manual hybridization in quinoa, which has hindered the creation of segregating generations large enough for genetic analysis. Also, the existence of tetraploid segregations at some loci in quinoa makes breeding and genetic studies in the crop complex (Ward 2000). The occurrence of both disomic and tetrasomic segregations at the same locus is uncommon but could be explained by mutual exchange of fragments between homologous 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 make genetic analyses and mapping of the quinoa genome very difficult (Ward 2000).

Despite these difficulties, mass selection and hybridization have been practiced in quinoa (Risi and Galwey 1984). A practical approach of effective selection can be the utilization of morphological markers to distinguish the hybrid from the parents (Bhargava and Ohri 2016).

4.6 Genetic Diversity of Morphological Traits of Quinoa

Genetic analysis studies are designed to determine the degree of heterogeneity among potential genotypes for selection to guarantee that only the best genotypes are selected in a breeding program (Silva et al. 2009); this is the same for quinoa which exhibits a high degree of heterogeneity, both within and among different geographic locations. The variability among cultivars reflects the heterogeneity of the genetic material, improves food security which is currently threatened by fluctuations in climatic conditions, and presents the possibility of identifying promising material for use in a plant breeding program (Ruiz et al. 2014).

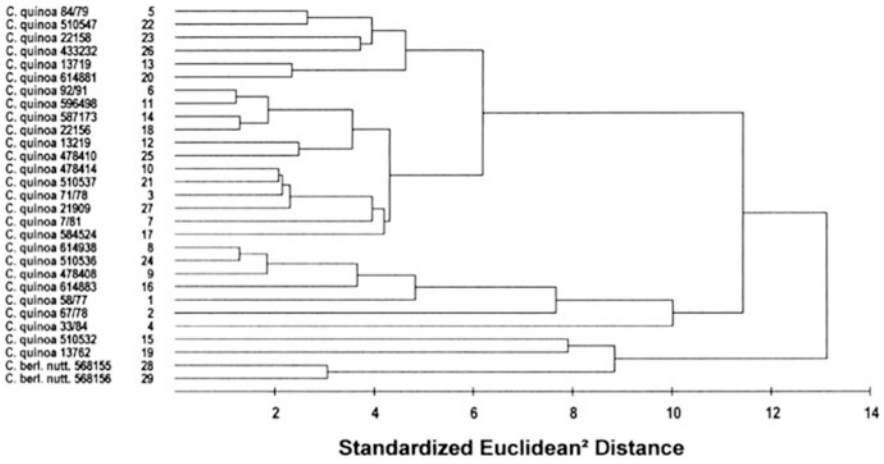

Fig. 4.3 Dendrogram of 29 germplasm lines derived from average linkage method (Bhargava et al. 2007b)

Quinoa exhibits ample genetic diversity for both qualitative and quantitative traits, which enables attaining a wide range of adaptability to various agroecological conditions (Rodriguez and Isla 2009). Gonzalez et al. (2012) showed that variability in the cultivation area of quinoa caused variation in yield and seed quality. High coefficients of heritability estimates are associated with a greater genetic variability, better selective accuracy (Cargnelutti Filho et al. 2009), and greater potential for success in selecting lineages with higher productivity of grain (Vasconcelos et al. 2016). Quinoa diversity, at a continental scale, has been associated with five main ecotypes, viz., Highlands (Peru and Bolivia), Inter-Andean valleys (Colombia, Ecuador, and Peru), Salares (Bolivia, Chile, and Argentina), Yungas (Bolivia), and Coastal/Lowlands (Chile), each of which is connected to subcenters of diversity that originated around Lake Titicaca (Risi and Galwey 1984).

Regardless of narrowing of genetic base during domestication, large genetic diversity still exists for plant color, seed color, and types of branching and panicles in addition to grain productivity, abiotic stress tolerance, and disease resistance (Bhargava and Ohri 2016). This diversity, which is also revealed at the molecular level, is being used by the quinoa breeders all over world to develop improved plant (Bhargava and Ohri 2016).

Bhargava et al. (2007b) studied the genetic variation of 19 traits among 29 germplasm lines of quinoa; the analysis of variance indicated the presence of high degree of morphological and qualitative variations among the lines studied, which showed that a vast amount of genetic variability existed in the quinoa germplasm lines. Cluster analysis (Fig. 4.1) grouped together lines that had greater genetic similarity but did not include lines from the same origin, indicating heterogeneity of the lines within a given geographical region (Fig. 4.3).

The germplasm lines were grouped into six clusters based on average linkage method. Cluster I grouped lines that are early maturing and high yielding but had low carotenoid content together. Cluster II comprised lines with higher leaf quality components but low seed quality. Cluster III lines had highest seed yield and high values for protein and carotenoids. The lines in cluster IV are early maturing and had high seed protein, while cluster V had high seed yield, dry weight/plant, stem diameter, and maximum number of inflorescences. Lines in cluster VI had low values for traits related to seed morphology and quality but not for carotenoid content. Also, the study clustered two lines of *C. berlandieri* subsp. nuttalliae separately from the quinoa line that is phylogenetically correct (Bhargava et al. 2007b).

Such genetic diversity of population within the same geographical region might be due to factors like heterogeneity, genetic architecture of population, history of selection, and/or developmental traits (Singh 1991), and the same has been reported by other researchers in different crop species (Ghafoor et al. 2001; Alemayehu and Becker 2002; Singh et al. 2004).

4.7 Genetic Improvement of Quinoa Using Mutation Induction

Genetic improvement of wild or cultivated plants requires variability, selection, and conservation of the characteristics of the types that are cultivated. Genetic improvement has, until recently, received limited attention unlike other major cereal crops which have benefited greatly from the modern plant breeding techniques and genetic research (Jarvis et al. 2008). However, emphasis has been mainly on its introduction to newer agroecological zones (Bhargava et al. 2007a), although initial reports on quinoa trials from Europe and Africa are encouraging (Mujica et al. 2001). There are several ways of improving crop performance, one of which is genetic improvement via mutation induction.

There are a lot of reports of improved morphological as well as physiological characteristics in cereals, grain legumes, fiber crops, oil seeds, vegetables, and ornamentals after mutation induction, and more than 2500 mutant varieties of more than 170 different species have been released and are available in the IAEA database (IAEA 2012). Of the various mutagens available, gamma ray is the preferred agent, and plant type and yield are the traits most commonly reported (Ahloowalia et al. 2004; Chopra 2005; Fu et al. 2008). Although the quality of many crops has been improved through mutation induction, few reports are available for quinoa.

Gomez-Pando and la Barra (2013) irradiated dry seeds (cv. Pasankalla) with gamma ray doses of 150 Gy, 250 Gy, and 350 Gy. They reported a delayed germination process in the M1 generation with increasing radiation dose. Also seedling height, root length, and leaf development were most reduced at 250 Gy, and at 350 Gy, no plants survived. In M2, the maximum spectrum of chlorophyll mutations corresponded to 150 Gy, while the maximum frequency was at 250 Gy. They also observed chlorophyll mutations with chlorina mutation being

predominant, followed by xantha. Changes were recorded for branch number, pedicel length, plant height, lifecycle duration, stem and foliage color, and leaf morphology at the two doses, with improvements in plant type.

Farmers are still using land races of quinoa with very long maturity period and very tall plants (Tapia 2000); the identified mutants with reduced life cycle could be beneficial, considering that some of the actual cultivars have long cycle reaching over 7 months in the field with the flowering and grain maturity time under adverse weather conditions (drought and frost), which significantly reduce the performance (Gomez-Pando and la Barra 2013). The same trend has also been reported for African yam bean (Ihuoma and Adesoye 2017) and *Jatropha curcas* (Dhakshanamoorthy et al. 2011), and suggestions are made on the use of such early maturing mutants to overcome some adverse field conditions that may arise during the flowering period such as pest attack. Gomez-Pando and la Barra (2013) also proposed that the identified mutants with reduced plant height will be very useful because they will decrease the high tendency of lodging and could improve the yield in similar way to that achieved in wheat (Rutger 1984; Sasaki et al. 2002; Zhou et al. 2007).

4.8 Molecular Marker Analyses

Molecular markers offer unique and valuable tools for evaluating and characterizing plant genetic diversity in a manner that is unaltered by the environment (Gupta and Varshney 2000). Genetic markers are very vital for germplasm conservation and core collection development (Diwan et al. 1995; Tanksley and McCouch 1997); it is also used in enhanced breeding applications such as marker-assisted selection (Staub et al. 1996).

The foremost molecular studies were focused on establishing genetic variability undomesticated quinoa and wild species (*C. hircinum* and wild quinoa ajara) using allozyme markers (Wilson 1988a, b). The results highlighted two distinctive groups on the basis of molecular information: 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, Fairbanks et al. (1990) used protein-based approaches to characterize quinoa seed storage proteins as a valuable tool for cultivar identification and breeding programs for improved protein quantity and quality.

Fairbanks et al. (1993) were the first to use random amplified polymorphic DNA (RAPD) markers in quinoa, and they observed that 26 primers produced polymorphic markers among 16 randomly selected accessions. The RAPD markers were also used by Ruas et al. (1999) to identify genetic variation among 19 accessions of 6 species of the genus *Chenopodium*. The results showed that wild and cultivated populations of *C. quinoa* shared a low level of molecular variation, without delineation between sympatric domesticated and weedy populations. RAPD has also been used by Del Castillo et al. (2007) to study the hierarchical structure among gecotype

Table 4.1 Similarity matrix based on simple matching coefficients of potential quinoa parents for genetic linkage mapping

	Chucapaca	NL6	0654	Ku-2
Chucapaca	1.000			
NL6	0.245	1.000		
0654	0.576	0.327	1.000	
Ku-2	0.229	0.866	0.304	1.000

1 jump threshold = 5 (Kosambi mapping function) for all linkage groups (Maughan et al. 2004)

populations of Highlands and Inter-Andean valleys in Bolivia. The result revealed a marked geographical effect on the populations' structure and pointed out climatic and orographic barriers present in the studied zone contributed to the observed variations rather than to a distance effect. Hence, the population structure was associated with the three major biogeographic zones present in Bolivia, viz., Northern and Central Highlands, Inter-Andean valley, and southern Salar. The intra-population genetic diversity was higher than expected, basically due to autogamous reproduction, in addition to the limited seed exchange among isolated regions studied (Del Castillo et al. 2007).

Maughan et al. (2004) screened 60 RAPD primers in 4 mapping populations of quinoa; 6 (10%) created reproducible polymorphic markers and were included in linkage analysis for quinoa. One polymorphic band was scored from each of the six polymorphic RAPD primers, with an average of 3.8 prominent bands per RAPD reaction. One RAPD marker (O-F10), however, was scored in a co-dominant fashion, while the remaining five RAPD markers were scored as dominant markers. None of the RAPD markers deviated significantly ($P > 0.05$) from their expected segregation ratios.

The first step toward the development of genetic markers for quinoa was the development of a genetic linkage map by Maughan et al. (2004). The map was based primarily on amplified fragment length polymorphism (AFLP) and covered an estimated 60% of the genome. Eighty-eight (88) AFLP primer combinations were screened for polymorphism among four potential mapping parents ("Ku-2," "NL-6," "0654," and "Chucapaca"), representing two different ecotypes for quinoa: "Ku-2" and "NL-6" from the coastal region and "0654" and "Chucapaca" from the Altiplano region. A total of 597 polymorphic bands across the 4 potential parents were identified. The average number of bands identified for individual primer pairs ranged from 19 to 52, with an average of 6.8 polymorphic bands per primer combination. Moreover, 68 out of the 88 AFLP primer combinations screened for polymorphism between the mapping parents were polymorphic and highly reproducible based on duplicated samples. The similarity coefficients of the four potential parents for the linkage mapping (Table 4.1) ranged from 0.23 to 0.87 and the least genetic similarity between the Bolivian accession "Chucapaca" and the Chilean accession "Ku-2," while the highest similarity was between the two Chilean coastal accessions "NL-6" and "Ku-2." These findings supported the previous morphological and isozyme studies (Wilson 1988a, b; Risi and Galwey 1989a), which separated quinoa

germplasm into two distinct fundamental elements: Chilean coastal types and Andean Altiplano types.

The difficulties associated with AFLP marker technologies and the related transfer of this technology to developing world countries where quinoa is being cultivated have limited the use of AFLP markers to enhance quinoa improvement programs (Jarvis et al. 2008). This led to identification and characterization of more feasible SSR markers of quinoa which once developed can be used across different laboratories to determine genetic diversity in quinoa.

Maughan et al. (2004) screened 39 putative simple sequence repeat (SSR) loci previously identified from an SSR-enriched genomic library for polymorphism in 4 potential mapping population parents; they identified 21 SSR markers as polymorphic, while 13 produced simple monogenic banding patterns and were easily scored in a co-dominant fashion. A good number of the other SSR markers yielded amplification products with complex banding patterns that made scoring the marker in a co-dominant fashion difficult; however, a single, unambiguous, and clearly segregating band was scored in a dominant fashion. These complex banding patterns could be a result of the occurrence of duplicate chromosome regions (Rae et al. 2000), which may be the remains of quinoa's probable allotetraploid origin.

Mason et al. (2005) took the next step in quinoa marker development and characterized 208 SSR markers which were validated and characterized in 31 cultivated quinoa accessions, representing the main growing areas of South America. These SSR markers have been utilized to assess the genetic diversity among quinoa accessions within the USDA collection (Christensen et al. 2007).

Unfortunately, less than 10% of the 208 SSR markers identified by Mason et al. (2005) have been mapped genetically, and only 67 of these were considered highly polymorphic ($H > 0.7$), stressing the need for additional SSR marker development and genetic mapping. To this effect, Jarvis et al. (2008) developed a new set of polymorphic SSR markers to increase the number of SSR markers already available in quinoa and constructed a new genetic linkage map of quinoa based primarily on the SSR markers developed. From their result, out of the 402 SSRs tested, 54% (216) were polymorphic when tested on the screening panel of 7 quinoa accessions. An additional 4.7% (19) were polymorphic when the *C. berlandieri* accession was included in the analysis (interspecies polymorphism). The remaining 41.05% (165) primers were monomorphic or amplified poorly. In only 9 (2.2%) cases did a primer successfully amplify in quinoa but not in *C. berlandieri*, signifying that these two *Chenopodium* species share a high degree of DNA sequence homology.

All the 216 markers identified by Jarvis et al. (2008) were considered polymorphic (according to the recommendations of Ott (1992)), and 53 (25%) are considered highly polymorphic ($H \geq 0.70$), and H values ranged from 0.12 to 0.90, with an average value of 0.57.

Fuentes et al. (2009) genetically characterized Andean and Chilean germplasm to quantify the genetic diversity within 28 Altiplano and 31 coastal Chilean accessions of quinoa using microsatellite markers. Results of both cluster (UPGMA) and principal component analyses generated separated the accessions into two discrete groups, as was also revealed by isozyme analysis and morphological traits (Wilson

1988a, b), AFLP analysis (Pratt 2003), and microsatellites (Christensen et al. 2007). The first group contained quinoa accessions from the north (Andean highlands), and the second group consisted of accessions from the south (lowland or coastal). The result obtained in the diversity analyses emphasized the relationships both within and among northern and southern Chilean quinoa accessions and provides a new set of simple-to-use and highly informative genetic markers.

Fuentes et al. (2012) characterized 20 microsatellite genetic markers in a multi-origin set of 34 quinoa accessions to understand the impact of farmers' seed exchanges and local production practices on the genetic structure and diversity of quinoa on a national scale in Chile. The heritability for all quinoa accessions studied ranged between 0.12 (QGA17) and 0.87 (QAAT76) with a mean value of 0.65, which indicated the presence of wide genetic diversity in the quinoa samples and confirmed the highly informative quality of the markers used. The UPGMA analysis using the Jaccard coefficient identified two major groups which were further subdivided into five populations (Fig. 4.4). The genetic information obtained permitted the detection of variation among and within the populations identified, which corresponds to natural geographical-edaphic-climatic constraints to the expansion of biodiversity. This grouping also links with the social-linguistic context of ancient people inhabiting the Andes region, where agronomic and cultural traditions that have thrived until the current time are very different.

4.9 Abiotic Stress Tolerance and Associated Genetic Mechanisms

Quinoa has been found to tolerate several abiotic stresses such as differing soil pH, soil salinity, frost, and drought; this could be due extreme climatic conditions where quinoa evolved. Tolerance to these abiotic stresses is determined by complex mechanisms and polygenically inherited traits.

4.9.1 Soil pH and Frost

Quinoa can tolerate both highly acidic and basic soils with pH ranging between 4.8 and 9.5 due to its mycorrhizal associations, which also facilitates the acquisition of scarce nutrients (Urcelay et al. 2010). Since frosts are common in the Andes, the effects of temperature on germination, phenology, and growth have been the focus of several studies (Jacobsen et al. 2005, 2007). Several genotypes and cultivars from the Andean highlands of Bolivia that show varying degrees of responses to low temperatures have been identified (Bertero et al. 2004; Fuentes 2008). Quinoa can also tolerate freezing preceding the formation of flower buds (Bhargava et al. 2006a). It grows properly at temperatures of −5 °C and endures temperatures as low as −16 °C during the vegetative stage (Bois et al. 2006). During flowering, it tolerates −8 °C up to a period of 2 h (Jacobsen et al. 2007). However, details of the physiological and the genetic mechanisms responsible for the observed frost

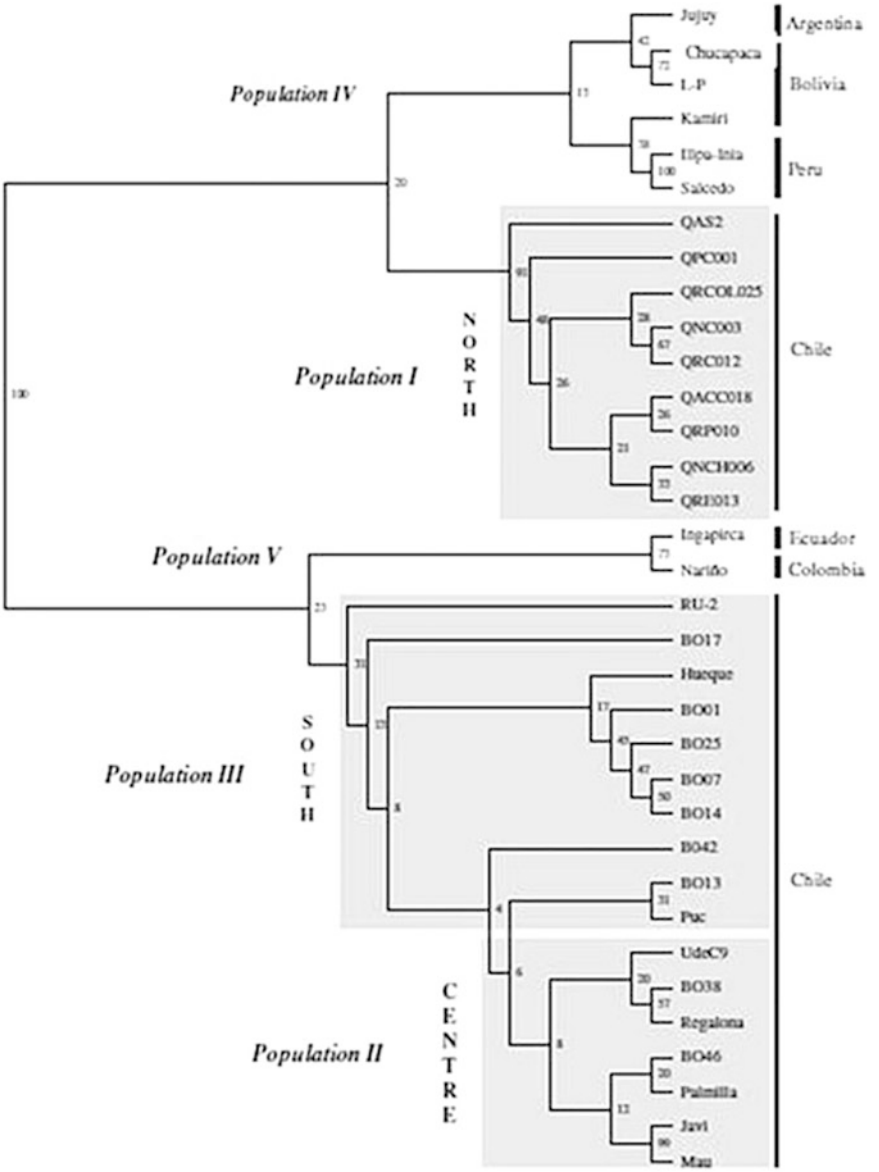

Fig. 4.4 UPGMA cladogram based on Jaccard's similarity coefficient of 34 quinoa accessions performed after 500 replicates for bootstrap test (percentage number between each node) (Fuentes et al. 2012)

resistance remain unknown (Jacobsen et al. 2007), but proline content and levels of soluble sugars such as sucrose might serve as markers of frost tolerance in quinoa breeding lines (Jacobsen et al. 2007).

4.9.2 Salinity

About 40% of quinoa genera are facultative halophytes; this advantageously places quinoa over glycophytes as it is known that it can thrive in saline conditions because of its capacity to avoid the harsh impacts of high salt accumulation, which will cause hyperosmotic stress in roots and other structures, thereby decreasing the plant's ability to absorb water efficiently (Adolf et al. 2012). Also, it has the ability to survive at salinity levels higher than that of seawater, and this makes it more suitable than some other halophytes under similar abiotic stress (Adolf et al. 2012). However, salinity increases the accumulation of sapogenins (Solíz-Guerrero et al. 2002; Pulvento et al. 2012); this implies that quinoa cultivated in areas with high soil salinity may tend to produce seeds that are bitter, a trait that is undesirable to many farmers.

A lot of the ~6000 global quinoa germplasm accessions have been subjected to salt treatments both in situ and field experiments, and they exhibited varying levels of tolerance both at germination and progressive developmental phases (Ruiz et al. 2014; Valencia-Chamorro 2003; Christiansen et al. 1999; Karyotis et al. 2003; Wilson et al. 2002). The significant characteristic of salinity tolerance has been thoroughly studied, particularly the physiological and the molecular mechanisms involved, the mechanisms specifically associated with salt ion accumulation in specialized tissues, and the adjustment of leaf water potential (Adolf et al. 2013). Quinoa species accumulate salt ions in its tissues by adjusting the water potential in its leaves; this allows the plant to sustain cell turgor and limit plant transpiration under saline conditions (Hariadi et al. 2010; Shabala et al. 2012). Other studies by Koyro and Eisa (2008) and Burrieza et al. (2012) suggest that dehydrin accumulation, subcellular localization, and phosphorylation state of mature seed embryos are related to high salt stress.

Genetic constituents related to salt tolerance exhibit additive effects, recessive or dominant relationships, and heterosis. Less than 25% of the salt-regulated genes that have been identified by Ma et al. (2006) are salt stress-specific. Adolf et al. (2012) in a review paper elucidated the mechanisms contributing to salt tolerance in quinoa to 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. Shabala and Mackay (2011) suggested that salinity tolerance may also be improved by pyramiding key genes regulating salinity tolerance, which is a very essential physiological trait, and quinoa might serve as a valuable donor of salt-tolerant genes to other crops. The large genetic variability for salinity tolerance in quinoa is a huge resource for the selection and breeding for higher tolerance; however, this poses challenges and opportunities for the future (Maughan et al. 2009; Gomez-Pando et al. 2010; Ruiz-Carrasco et al. 2011; Adolf et al. 2012).

While studying the molecular basis of salt tolerance in quinoa, Maughan et al. (2009) described the molecular characterization of Salt Overly Sensitive 1 (SOS1) gene. They reported a complete genomic sequence of two homologous SOS1 loci, cqSOS1A and cqSOS1B, which extended from 98,357 to 132,770 bp, respectively.

Relative gene expression of SOS1 in roots under saline conditions (450 m mol/L) was consistently three- to fourfold higher than in leaf tissue. A constitutive expression of SOS1 genes was observed in the roots, while an inducible expression occurred in leaves under stress; this is probably because the SOS1 expression was more strongly upregulated by salt stress in leaves as compared to the roots.

Similarly, Ruiz-Carrasco et al. (2011) reported gene expression analyses for two sodium transporter genes: CqSOS1 and CqNHX genes. Quantitative RT-PCR analyses of these genes revealed that their expression was differentially induced at the shoot and root level (as was reported by Maughan et al. (2009)) and between genotypes by 300 mM NaCl.

4.9.3 Drought

Quinoa has inherently low water requirements and is therefore highly drought-tolerant and responds to drought stress through drought escape, tolerance, and avoidance (Jacobsen et al. 1999; Jacobsen and Mujica 2003; Garcia et al. 2007). Other defensive mechanisms used by quinoa include tissue elasticity, low osmotic potential, decreased leaf area through dehiscence, and the presence of vesicular calcium oxalate and structurally with small and think-walled cells (Canahua 1977; Garcia 2003; Jacobsen et al. 2009; Abugoch et al. 2009). Drought reduces the accumulation of sapogenins by 45% in quinoa seeds, based on a study of severe water deficit conducted in Southern Europe (Gomez-Caravaca et al. 2012).

However, lack of understanding of the genetic behavior of such a complicated trait as well as biochemical constituents and anatomical attributes responsible for drought tolerance has led to the delay of plant breeders to incorporate drought stress tolerance into breeding programs (Al-Naggar et al. 2002a, b). Reports on heritability and genetic advance from selection for leaf anatomical traits of quinoa subjected to drought stress are scarce; this led to an investigation by Al-Naggar et al. (2017) on five genotypes of quinoa.

From their result, the effect of soil moisture content on leaf tissues had showed significant differences among the studied genotypes. The genotype CICA 17 (the most drought-tolerant) had the thickest leaf under well-watered condition (WW), moderate water stress condition (WS), severe water stress (SWS), and when all irrigation regimes were combined, while the thinnest leaf was shown by the genotype CO-407 and Ollague (drought-sensitive) under WS and when all irrigation regime conditions were combined. Heritability estimates in the broad sense for anatomical traits were very high in magnitude (>87.5%), except for the lower epidermis (41.18, 59.41, and 33.33) under WW, WS, and SWS, respectively, indicating that environment had minimal effect on the phenotype of most studied anatomical traits in the leaves of quinoa (Al-Naggar et al. 2017). The highest heritability estimate (100%) was shown by upper epidermis under severe water stress. The genetic advance (GA%) from selection was generally higher under moderate water stress (WS) for three anatomical traits (leaf thickness, lower epidermis, and palisade layer) and under well watering for two traits (upper epidermis and

spongy layer). GA ranged from 15.40% for the upper epidermis to 72.97% for palisade layer under SWS, from 52.66% for leaf thickness to 82.72% for palisade layer under water stress, and from 30.40% for leaf thickness to 87.12% for spongy layer under well watering (WW). Therefore, palisade and spongy layers under all environments were characterized by having high heritability accompanied by high values of expected genetic advance, especially under WS and SWS. Since efficiency of selection depends on the degree of heritable variability, higher heritability together with high expected genetic advance for the leaf anatomical traits studied should be quite valuable in future breeding programs for drought tolerance in quinoa (Al-Naggar et al. 2017).

Some authors (Blum 1988; Hefny 2007; Al-Naggar and Shehab-El-Deen 2012; Al-Naggar and Atta 2017; Al-Naggar et al. 2009, 2011, 2016a, b) opined that heritability and expected genetic advance is higher under stress than non-stress conditions and that selection should be practiced in the stressed environment to obtain higher genetic advance. However, another group of researchers found that heritability and GA from selection for grain yield is higher under non-stress than those under stress (Shabana et al. 1980; Atlin and Frey 1990; Banziger and Lafitte 1997; Worku 2005).

There is a need for further investigation on the type of gene action controlling the inheritance of drought tolerance traits to help plant breeders in tackling the physiologically and biochemically complex drought tolerance.

4.10 Conclusion

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 unstable (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, 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.

The wide range of environments in which quinoa can grow has a direct influence on its genetic diversity (Matanguihan et al. 2015). The adaptation of quinoa to vastly different climatic conditions over a long period of time may have contributed to its broad genetic diversity (Costa Tártara et al. 2012). Genetic variability has a spatial structure and distribution; this can be seen in quinoa as phenotypic and genetic diversity studies have shown that quinoa accessions are most often clustered according to their geographic origin (Risi and Galwey 1989a, b; Ortiz et al. 1998; Rojas et al. 2000; Del Castillo et al. 2007; Costa Tártara et al. 2012; Curti et al. 2012). Also, regardless of narrowing of genetic base during domestication, wide genetic diversity still exists for plant color, seed color, types of branching and panicles, as well as grain productivity, abiotic stress tolerance, and disease resistance

(Bhargava and Ohri 2016). This diversity, which is also reflected at the molecular level, is being used by the plant breeders all over world to develop improved plant (Bhargava and Ohri 2016).

The application of informative molecular markers has made it possible to reveal the genetic diversity of quinoa accessions. Seed exchanges and germplasm distribution have considerably affected the genetic diversity as well as genetic structure of quinoa (Costa Tártara et al. 2012). The results of genetic diversity studies of important agronomic traits in quinoa and associated genetics of such traits will greatly aid conservation efforts and, consequently, plant breeding programs.

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