QTL mapping for agromorphological traits in Quinoa (*Chenopodium quinoa* Willd.)

Major thesis report

Diana Pastrana Cervantes
(910226642130)
Plant Sciences - Breeding and Genetic Resources

Supervisor:
Dr. EN van Loo

Date:
30-January-2017

WAGENINGEN UR
For quality of life

QTL mapping for agromorphological traits in Quinoa (*Chenopodium quinoa* Willd.)

Course

Name:	MSc Thesis Plant Breeding
Code:	PBR-80436
Credits:	36 credits
Submission date:	January 23th, 2017

Author

Name:	Diana del Rosario Pastrana Cervantes
Registration number:	910226642130
Study program:	MSc Plant Sciences - Breeding and Genetic Resources
E-mail:	diana.pastranacervantes@wur.nl

Supervisor

Name:	dr. EN (Robert) van Loo
E-mail:	robert.vanloo@wur.nl

Institute data

Name:	Laboratory of Plant Breeding - Wageningen UR
Address:	6708 PB, Wageningen

Acknowledge

I wish to express my foremost gratitude to Dr. Robert van Loo who guided me during this major thesis project. I am very grateful because the support and enthusiasm of my supervisor kept me motivated throughout. I also want to thank my examiner, Dr. Luisa Trindade, and the Bio-based Economy group for the support and feedback. I also owe an immense debt of gratitude to Afrida Ali, Bihani Thapa, Giuliana Nakasato and Luis Rosado for their support on the academic field but especially for being my family in the Netherlands. I want to thank all the people who have supported me, cheered me and accompanied me through the realization of this dream. Last but not least, I would like to thank my family for their unconditional love and support.

Index

1. INTRODUCTION

1.1. Chenopodium quinoa

Chenopodium quinoa Willd. (2n=4x=36) belongs to the family *Amaranthaceae*. It is a dicotyledonous species with a dispersal unit botanically known as achene, a single seed surrounded by a dry and indehiscent pericarp (Burrieza et al., 2014). Quinoa is considered a pseudocereal because the grains of this species can be used in the same manner as true cereals. Archaeological research revealed that quinoa has been cultivated by pre-Colombian cultures in the Andes for approximately 8,000 years (Dillehay et al., 2007). Since the Spanish conquest, the cultivation of quinoa declined with displacement by the introduction of crops like wheat and barley (Martínez et al., 2009; Maughan et al., 2007). Earlier, quinoa cultivation was relegated to subsistence farming in some areas of South America (Bhargava et al., 2006).

In the last two decades, the interest for this crop has greatly increased worldwide due to its excellent nutritional profile and its potential as an alternative to feed the growing world population in a sustainable manner (Zurita-Silva et al., 2014; Jacobsen et al., 2013). Since the selection process of quinoa cultivars took place under several adverse conditions of the Andes, the germoplasm with abiotic stress tolerance to aridity, salinity, highland and frost represent good choice for marginal environments. The latitude range of quinoa fluctuates from sea level up to 2,000 m a.s.l. (González et al., 2011). There are ecotypes growing well in limited rainfall or under extreme aridity (Martínez et al., 2009), and in salt-affected soils (Ruiz-Carrasco at al., 2011).

In 2015, worldwide quinoa production accounted for 228,870 tons (mostly cultivated in Peru, Bolivia and Ecuador) from which 32% is imported (IAI, 2016). The demand for quinoa has particularly grown in North America and Europe, the value of exportations increased from $135.53 million in 2012 to $321.56 million in 2015 (Bellemare et al., 2016). The strong dependence on quinoa from the Andean region have led to concerns about the impact in the food security of rural households. Successfully experiences in the adaptation of quinoa have been reported in Europe, North America, Africa and India. In 1978 Quinoa germoplasm from Chile was introduced to Europe (Bazile & Baudron, 2015), relevant characteristics of these accessions are early maturity, short and unbranched stem, and compact inflorescence (Limburg & Mastebroek, 1996). The Centre for Plant Breeding and Reproduction Research (CPRO-DLO) in Wageningen, the Netherlands have been working since 1986 in the adaptation of quinoa to the climatic conditions of North Western Europe (Mastebroek & Limburg, 1996).

The improved genotypes for North Western Europe must be less sensitive to the principal unfavourable environmental factors: strong wind and prolonged wet weather. The windy conditions may result in lodging, stem breakage and seed loss while humidity favour infection by *Botrytis* and pre-harvest sprouting. Another important breeding objective in quinoa has been the reduction of the saponin content, these major anti-nutritional compounds (Zúrita-Silva at al., 2014) are predominantly found in the seed pericarp which is often removed to prevent an unpleasant bitter flavor (Gómez-Caravaca et al., 2012). Saponin-free or sweet quinoa varieties

are currently available being 'Atlas' the first one launched outside of the Andean region (Jacobsen, 2015).

"*Quinoa is under-researched, under-supported and considered a neglected crop*" (Rojas et al. 2015). The majority of the studies for this species have been focused in the phylogenetic relationships and characterization of its diversity. Until quite recently the molecular tools to speed up the improvement of this crop were developed. Consequently, for most of the important commercial characters in quinoa the genetic basis is not well understood yet. Advance trait analysis in quinoa research is crucial. At present, quinoa is only at the start of its productivity development. For further improvement, it is central to take into consideration the preferences of the consumers. Despite of the nutritional value and the saponin content, the most important commercial quality characters of quinoa seeds are size and color. Until 2000, the consumers and the industry preferred white or cream-colored quinoa seeds (Gomez-Pando, 2015) but this situation changed with the discover of high carotenoid content in accessions with dark seed coat color (Bhargava et al., 2007). The assumed health benefits of carotenoids are considered the main motivation for the introduction of colored quinoa in the market.

There is a marked increase in the available information about quinoa genetics, its allotetraploid nature, self-pollination and small flowers as it yet remains insufficient. A fairly level of complexity has been reported in the quinoa breeding system, emasculation and hybridization (Zurita-Silva et al., 2014). The identification of the markers that predict certain trait is expected to accelerate the process of breeding elite cultivars using marker-assisted selection (MAS) (Maughan et al., 2015). In the case of quantitative traits, the phenotype is the result of small contributions from many individual genes (Acquaah, 2009). These groups of genes known as quantitative trait loci (QTL) are mapped by finding which molecular markers are significantly linked with an observed trait. With the availability of the next-generation sequencing technologies and the development of tools for SNP genotyping, the use of SNP markers for QTL mapping studies have increased (Mammadov et al., 2012; Zurita-Silva et al., 2014).

1.2. Genetics and molecular tools

The cultivated quinoa is an allotetraploid (2n=4x=36), the most closely related species are *C. berlandieri* and *C. hircinum*. Although quinoa is a self-pollinating species, cross pollination or outbreeding may occur varying in a range (10–17 %) in response to flowering and incidence of pollen vectors (Mastebroek et al., 2002; Spehar & Santos 2005). For most qualitative traits, inheritance occurs in a disomic fashion but tetrasomic inheritance has also been detected (Simmonds, 1971; Risi and Galwey 1984; Ward, 2000).

Maughan et al. published the first genetic linkage map of quinoa in 2004. It was based predominantly on AFLP (amplified fragment length polymorphism) markers covering approximately 60% of the genome. However, the potential of these markers was limited by the complications that emerged when transferring this technology in the developing world, where most quinoa is cultivated. Another genetic map was delivered four years later. It was based on the available molecular resources developed in quinoa and the characterization of more than 400 SSR (simple sequence repeat) markers reported by Mason et al. (2005) and Jarvis et al. (2008). In comparison to other molecular markers, once developed the SSR are relatively inexpensive,

highly reproducible and informative (Jarvis et al., 2008). Single nucleotide polymorphisms (SNPs) are the most abundant forms of genetic variation among individuals of the same species. Compared to other marker systems, the high-throughput SNPs can deliver the highest map resolution. The first SNP-based quinoa linkage map was constructed with 511 SNP markers reported by Maughan et al. (2012).

1.3. Agromorphological traits

1.3.1. *Color features*

The coloration of vegetative tissues is due to the presence and interaction of pigments. There are four major classes of plant pigments: chlorophyll, carotenoids, flavonoids and betalains. The visible colors result from the emission of a specific wavelength of light by pigments that have absorbed other specific to their molecules (Davies, 2009). The most common plant pigment are chlorophylls, they have photosynthetic function consisting of light energy capture (Chen, 2015). Chlorophyll is responsible of the green color in all plants and some algae, it reflects these wavelengths by absorbing primarily at the blue and red ends of the visible spectrum (Karban, 2015).

In the *Amaranthaceae* family, it is well known that betalains are responsible for the pigmentation in leaf and seed (Cai et al., 2001; Repo-Carrasco-Valencia et al., 2010). Betalains are water-soluble class of vacuolar pigments that contain nitrogen, two main groups have been recognized: red–violet betacyanins and the yellow betaxanthins (Moreno et al., 2008). These pigments are found in most plants from the Caryophyllales families where anthocyanin is absent (Strack et al., 2003; Repo-Carrasco-Valencia et al., 2010) for instance, in beetroots (*Beta vulgaris*), prickly pears (*Opuntia spp.*) and purple-fleshed pitayas (*Hylocereus polyrhizus*). In a similar way as with anthocyanin, when present in flowers or fruits, betalains help to attract vectors for the pollination process and seed dispersal (Delgado-Vargas et al., 2000). Tang et al. (2015a) confirmed the presence of betacyanins, mainly betanin and isobetanin, in red and black quinoa grains. Before this study, Pasko et al. (2009) wrongly characterized betalains present in quinoa as anthocyanin due to the similar UV/Vis absorption spectrum of these mutually exclusive pigments. Red-violet betacyanins absortion espectra includes values at 536–538 nm, which is larger than in anthocyanin (520 nm).

Carotenoids represent another important source of pigmentation in both quinoa leaf and seed (Bhargava et al., 2007; Dini et al., 2010). This group of lipid-soluble phytochemicals accumulated in chloroplasts of all green plants confers the yellow-to-red colors of fruits, vegetables, flowers and seeds. Besides the same type of contribution from anthocyanin and betalains in plant reproduction, carotenoids also play an important role in photosynthesis (Delgado-Vargas et al., 2000). Tang et al., (2015b) reported the presence of carotenoids in white, red and black quinoa seeds with a concentration of 11.87, 14.97 and 17.61 μg/g, respectively. These results suggest that the darker the seed coat, the higher the total carotenoid content.

Although anthocyanin is not synthetized by *C. quinoa*, other classes of flavonoids have been reported for this species. Flavonoids are water-soluble phenolic compounds stored in vacuoles

(Tanaka et al., 2008). The best known functions of flavonoids are their role in plant pigmentation with colors ranging from red or purple to yellow as well as copigmentation by complexation with anthocyanins (Winkel-Shirley, 2002). However, there exist some classes of noncolored flavonoids such as flavones, flavonols, and isoflavonoids (Waksmundzka-Hajnos & Sherma, 2010). According to Delgado-Vargas et al. (2000), flavonoids are UV-B photoprotectors and the noncolored types offer better protection against severe illumination. The flavonoid content of Chenopodium species ranges from 36.2 to 144.3 mg/100 g. The most abundant flavonoids found in quinoa seeds belong to the flavonol class, these are quercetin and kaempferol and for some varieties myricetin and isorhamnetin.

During the vegetative stage quinoa plants may display green, purple, red and mixtures of these colors, the shade of the leaves may intensify or fade during the subsequent developmental stages (Gómez & Eguiluz, 2011). According to the inheritance study of Granadillas (1968) for plant color, red is dominant over the purple strain and both types of colored plants are dominant over the green with the allelic forms R R for red, r^p r^p for purple and r r for green.

The emergence of floral buds indicates the transition from vegetative to reproductive phase. The inflorescence of this species is a panicle which emerge on the upper part of the plant, it is full of bunches (racemose) and non-branched (Wrigley et al., 2015). New colors are expressed after the panicle have emerged and during the start of flowering (Rojas et al., 2015). The color of the pericarp is commonly used to define the color of quinoa seed but when this coat is translucent or when it has been removed, the color of the episperm become apparent (Jacobsen and Stølen, 1993). According to Cayoja (1996) commercial seeds are characterized by three colors: white, red and black.

At least 66 different seed colors have been reported for this specie in the national quinoa collection of Bolivia, the largest ex situ seed bank (Cayoja, 1996). Seed colors result from complementary interacting genes, the allelomorphic genes A and C has been suggested, A has 5 alleles (A, a, a^r, a^c, $a^{cc)}$ and C has 3 (C, c, c^c). The associated genotypes to most common colors are: black (A- C-), brown ($a^c a^c$ $c^c c^c$, a^c- c^c-), light brown (a^{cc} a^{cc} cc), Yellow (A- cc, aa C-, a^c- cc, aa c^c-), red (a^r a^r) and white (aa cc) (Jacobsen and Stølen, 1993).

Figure 1. Quinoa seed and color diversity. Source: Gómez-Pando & Eguiluz (2011).

Natural segregation is mainly associated with changes in plant and grain color. At physiological maturity spontaneous color variations might be observed, for instance from white to dark seeds or from red to brown seeds. Bonifacio (1995) suggests that the instability of this trait can be attributed to paramutation, genetic transposition or both simultaneously. Currently it is known that these changes are related to a phenomenon of natural selection present as an adaptation mechanism to stress (Bonifacio at al., 2015).

1.3.2. *Saponin content*

The seed-coat of quinoa is rich in triterpenoind saponins, they are amphipathic plant glycosides that confer bitter taste and protect against predators (Gomez-Pando, 2015). Saponins have also been found in quinoa leaves (Mastebroek et al., 2010). As the quinoa consumers generally perceive bitterness as an undesired trait, the removal of the pericarp previous to consumption became indispensable. In response to the demands for seeds that are easier to clean and process, since 1990 sweet varieties were developed (Bonifacio et al., 2015). Koziol (1990) determined that a genotype is considered sweet when it contains 0.11% or less saponins (fresh weight basis) and bitter when the concentration is higher.

For saponin content it was found that bitter seeds AA are completely dominant over the sweet ones aa (Granadillas,1968). The low content of saponins is an attribute that results from the reduction of seed-coat thickness, a genetically recessive trait that requires artificial selection (Planella et al., 2015).

1.3.3. *Seed and yield*

The crop cycle of quinoa is related to photoperiod sensitivity, the duration rates from 120 to 240 days (González et al., 2015) while some varieties reach physiological maturity 90 days after sowing (Apaza et al., 2015). The diversity in seed size has been classified into four categories according to its diameter. The 'extra-large' seeds present a diameter greater than 2.20 mm, the 'large' category ranges from 1.75 – 2.20 mm, for "medium" 1.35 – 1.75 mm and less than 1.35 mm is considered "small" (IBNORCA, 2007). The seed weight ranges from 2 to 6 mg (Jacobsen and Stølen, 1993). The maximum yield per plant recorded is 250 g varying in response of the genotype, stem diameter, plant height, panicle length and diameter, and grain diameter (Rojas et al., 2015).

2. AIM OF RESEARCH

The main purpose of this study was to construct a map of quantitative trait loci (QTL) for seed color features and agronomical traits in segregating F3 families of quinoa sweet genotypes using whole genome sequence data.

Phenotypic data was recorded for seeds of the F3 families and along the complete crop cycle in a field trial. The data is analyzed in a Principal Component Analysis in order to detect relationships between the phenotypic traits.

Although color is often referred as a qualitative trait in most quinoa studies, quantiative measurements are feasible. In fact, modern tools such as VideometerLab (multispectral imaging device) captures reflection properties from which measurements of color attributes of a large number of seeds can be obtained. The software covers geometrical features of the seeds as well. The potential of VideometerLab to provide measurements for the small quinoa seeds was investigated.

3. MATERIALS AND METHODS

3.1. Plant materials and field experiment

The F1 from the cross between cv. Carina Red (bitter, dark seed) and Atlas (non-bitter EU variety) were used to obtain an F2 mapping population resulting in 1000 genotypes segregating for color and size of seeds, bitterness among other traits. From this population, 94 non-bitter genotypes were selected. Whole genome sequence data of these 94 genotypes (at 1X coverage per genotype) and of the parents (at 30X coverage) were obtained from 6 Illumina Hiseq2500PE runs. Evaluation of the F2 mapping population was based on the F3 progeny.

For the field trial an augmented design was chosen. This experimental design is commonly used in the initial stages of a breeding program in order to evaluate the performance of accessions when the number of genotypes is large and seed is scarce. This is done by using a single experimental unit per genotype additionally, standard check genotypes are systematically placed. When the experiment is designed with rows of columns, it is possible to assess the environmental variation in the field in two directions for any number of genotypes and replicates (Federer and Crossa, 2012). For this study, the 94 sweet genotypes were arranged in an augmented row–column design together with six check varieties. These varieties are Jessie and Pasto with 2 replications and, 3 for Carina Red, Atlas, Dutchess and CQ21050442. The total number of plots was 110 from which 16 correspond to the standard varieties.

The size of the net plot was 40 x 50 cm and it contained a total of 22 plants from a given genotype. Border rows composed of 20 plants from the variety Pasto were established around each plot at a distance of 10 cm. Additionally, two empty rows were left at each side making a

gross plot size of 90 x 100 cm. Seeds were planted on March 7, 2016. Two seeds of each genotype were sown in a cell of the seed tray. After germination additional seedlings were removed and one plant was kept per cell. Seedlings were grown under controlled conditions and transplanted into the field on April 18 to 19.

3.2. Phenotyping

3.2.1. *Seed data*

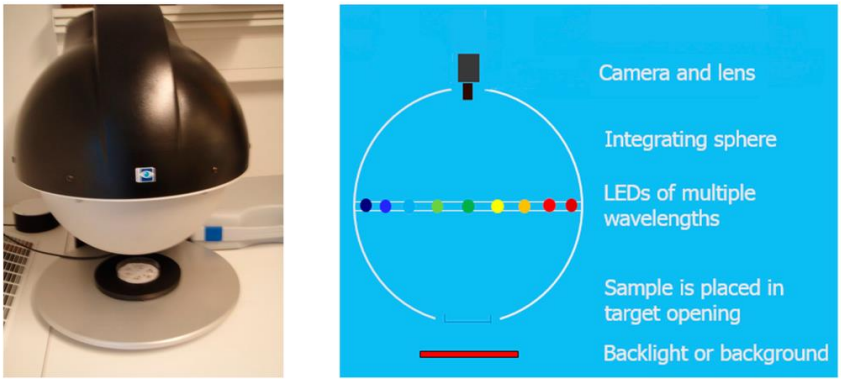
3.2.1.1. Seed weight of sowing seed

The thousand seed weight (TSW) of each genotype of the mapping population and the parents was estimated. Samples consisted of three sets of 100 seeds randomly selected. The number of seeds was determined by an automatic seed counter and the weights were measured with an analytical balance. This variable was calculated as $TSW = (weight\ in\ g / number\ of\ seeds) \times 1000$.

3.2.1.2. VideometeLab

VideometerLab (Figure 2) is a system for multispectral imaging that cover reflectance values from 375 to 970 nm (Table 1) with a resolution of 2056 x 2056 pixels, each pixel represents a spectrum. Before image acquisition, the device calibration was performed with assortment of seeds representative of the color diversity in the mapping population. For each genotype of the mapping population and the parents, 80 seeds were randomly selected and placed in a dark plate. The images were labeled into areas of dark background and foreground (the seeds), the resulting images are known as binary-labelled objects (BLOBs) where each BLOB represent a seed. A total of 28 variables were extracted and calculated in the blob toolbox. The size-related variables were area, length and width. The variables associated with color are CIE L*a*b*, intensity, hue, saturation and 19 spectral bands.

Figure 2. VideometerLab: A) device picture and B) setup (Source: Olesen et al., 2015).



(A) **(B)**

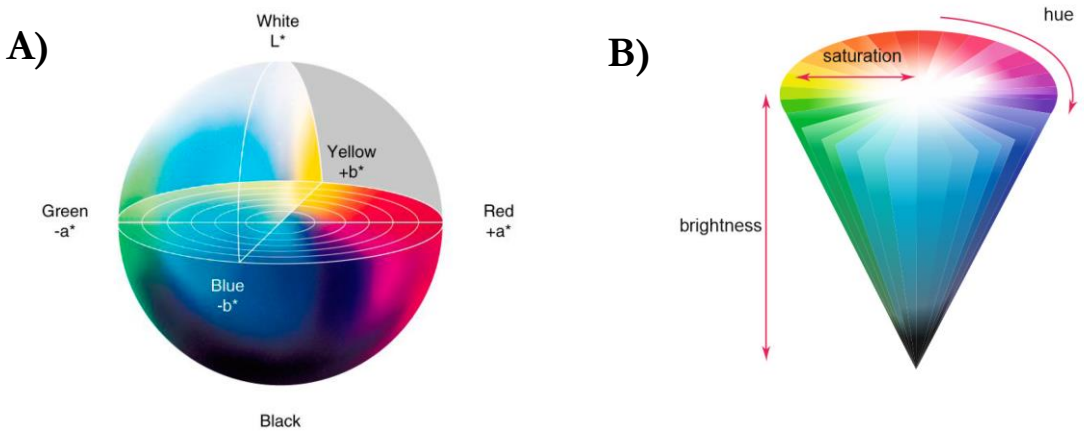
Table 1. VideometerLab spectral bands and description.

Band	Wavelength (nm)	Spectrum
1	375	UV
2	405	
3	435	
4	450	
5	470	
6	505	
7	525	Visible light
8	570	
9	590	
10	630	
11	645	
12	660	
13	700	
14	780	
15	850	
16	870	NIR
17	890	
18	940	
19	970	

Highly correlated color bands were identified in a correlation matrix constructed in Genstat (18th edition). Groups of bands within the visible light spectrum and the infrared region were constructed. The correlation coefficients and p-values are shown in Annex 1. The UV spectrum is represented by 375 nm the unique color band in this region. The visible light spectrum included the categories 405 - 470 nm (blue), 505 - 590 nm (green) and 630 - 700 nm (red). In the infrared region the first category was 780 nm followed by 850-890 nm and 940-970 nm. The wavelengths values for categories including more than one band were estimated as the average of the consecutively correlated bands.

CIELAB is a color system that works based on complementary pairs of color dimensions. The color space is recorded in coordinates of L* (psychometric light-ness channel), a* (red-green channel) and b* (yellow-blue channel) including colors beyond the visible spectrum (Figure 3A). Intensity refers to how bright or dull a color looks; bright colors are considered of high intensity while dull colors tend to grey. Hue is a color appearance parameter associated with the principal wavelength in an assortment of colors, just as an observer perceives it. For example, when an object is said to be red, blue, green or a combination, the hue is being specified. Saturation is the colorfulness perceived, it represents the intensity or purity of a hue (Figure 3B).

Figure 3. Variables related to color. A) CIELAB color space (Agudo et al., 2012). B) The hue, saturation, brightness cone (Dekel, 2016).



3.2.2. *Field data*

The leaf color of the plants before flowering was documented on May 6. The number of plants showing red leaves per plot (or otherwise green) were recorded and the percentage was estimated as $LCBF = (number\ of\ plants\ with\ red\ leaves\ /\ total\ number\ of\ plants\ in\ the\ plot) \times 100$.

The number of plants presenting floral bud was recorded per plot during the days 10, 12, 16 and 19 of may, in the last date the majority of the plots already had 90% of plants showing this trait. The number of days after sowing necessary to achieve the 90% of plants with floral bud presence per plot was estimated with a simple linear equation.

Flowering time was assessed in each genotype. The criteria to evaluate when the buds have started flowering was the exhibition of anthers in the opened flowers. Data was recorded in five dates, this was by the end of May the days 24, 27 and 31 plus 3 and 7 of June. The number of days required to achieve the 90% of plants with flowers was calculated from a simple linear regression equation.

Harvest took place the 17 of August. The hardness of the grains when pressed against the thumb's fingernails was used as a criterion to determine the harvest date. Mature grains will hardly break when pressure is applied while the unripe seeds will crack and show a starchy white liquid. The number of broken plants in the field was recorded to further correct mean values. The plots and their respective border were harvested separately and transported to UNIFARM facilities.

The plot plants were divided into head and stems. Since the seeds of this study belong to a plant breeding program, special care was taken to maintain their viability for further use. Heads were dried first at 35 °C during 3 days and the stems at 105 °C overnight. Whole plants from border rows were dried in the same way as the stems. An abrasive method was used to clean the seeds.

The dry panicles were crushed and sieved to separate the seeds from the rest of the heads. Another step for seed cleaning was the removal of remaining powder with an air blowing machine. The residuals of the triturated heads were collected and dried at 105 °C overnight. All dry weights were documented.

With available data of stems dry weight measured at 35 and 105 °C, the percentage of dry matter was calculated with the formula: $DM\% = (DW_{105\,°C}\ in\ g\ /\ DW_{35\,°C}\ in\ g) \times 100$. These results were used to estimate the DW of seeds at 105 °C with the formula: $DW_{105\,°C} = DW_{35\,°C}\ in\ g \times DM\%$. The dry weights at 105 °C for stem and the heads (without dust and seeds) were added as plant biomass. These results together with seed DW were extrapolated from the area of each plot (0.2 m^2) to hectares with the formula $DW_{kg\ per\ ha} = (10 \times DW_{105\,°C}\ in\ g)\ /0.2\ m^2$.

3.3. Statistical analyses

Analysis of variance were calculated in Genstat for the mapping population using average scores of the 94 lines. Mean genotype values correspond to three sets of seeds for TSW and 80 seeds for the traits measured with VideometerLab. In the case of the field experiment, the analysis comprised scores from the 110 plots (including the F3 and the check varieties). Table 2 provides a summary of the analysis for the F3; the descriptive statistics for the parents were included as reference.

The varieties were also analyzed in ANOVA in order to obtain an estimation of the environmental variance. For TSW and VideometerLab data from Atlas and Red Carina were included, number of replication per genotype was equal as in the F3. Field experiment includes data of 16 plots corresponding to only to check varieties.

The output of the ANOVAs was used to estimate the broad sense of heritability. The formula for heritability was $H^2 = genetic\ variance\ (\sigma^2 G)/phenotypic\ variance\ (\sigma^2 P)$. Due to the lack of replicates, the genetic variance for field traits was stimated as $\sigma^2 Genotypic(F3) = \sigma^2\ phenotypic\ (F3) - \sigma^2 Environmental\ (Varieties)$. The data for the estimation of H^2 is shown in annex 2 and the results are included in annex 2.

The mean values of the mapping population show more similarities when compared to those of Carina Red. Significant differences were found in the mapping population for the seed related traits (P = <.001) (TSW and VideometerLab). The ranges of the values in the F3 for the traits flowering time, grain and residual biomass are more extreme than the values observed in the parents. The transgressive segregation is more noticeable for the traits grain and residual biomass dry weights. However, except for the trait red leave color, no significant differences were detected in the mapping population for the field traits bud appearance (P = 0.43), flowering time (P = 0.11), grain dry weight (P = 0.33), and residual biomass dry weight (P = 0.13).

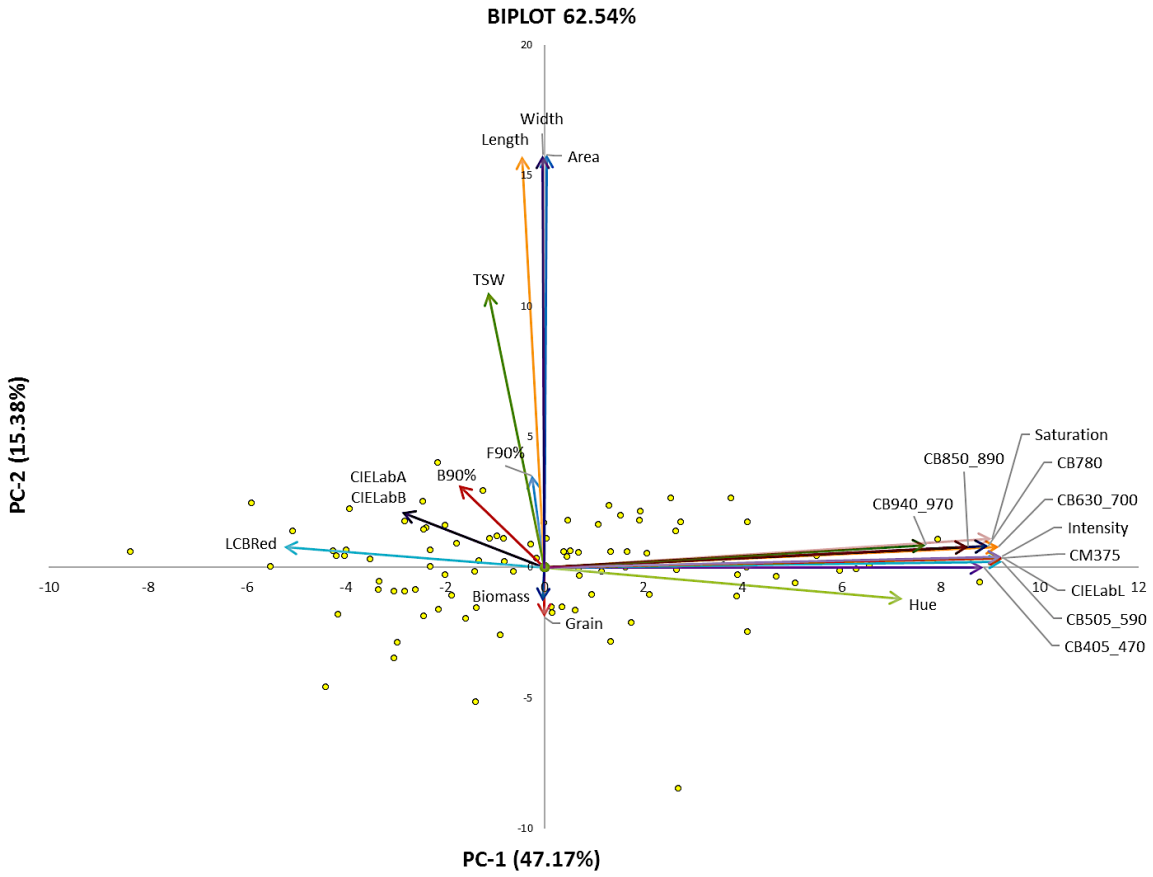
Table 2. Statistical analysis of traits of the mapping population. Standard deviation for the Mapping population correspond to the average of 94 lines. SD in each parent correspond to means of three sets of seeds (TSW), 80 seeds (VideometerLab) and three plots (Field traits).

Trait	Unit	H^2	Mapping population						Atlas				CR			
			Mean	Min	Max	SD	P-value	LSD	Mean	Min	Max	SD	Mean	Min	Max	SD
1000 seed weight	g	97	1.8	0.7	2.5	0.28	<.001	0.121	2.7	2.7	2.7	0.0	2.2	2.1	2.2	0.0
Area	mm^2	98	2.7	1.8	3.3	0.25	<.001	0.102	3.5	2.1	4.4	0.5	2.6	1.7	3.3	0.4
Length	mm	97	2.0	1.6	2.2	0.09	<.001	0.039	2.3	1.8	2.7	0.2	1.9	1.5	2.2	0.2
Width	mm	97	1.9	1.5	2.0	0.09	<.001	0.038	2.1	1.6	2.4	0.2	1.8	1.3	2.0	0.2
CIELABL	L*	98	44.3	29.3	58.2	5.34	<.001	1.817	67.4	54.0	73.3	4.0	32.5	25.6	41.3	3.4
CIELABA	a*	94	8.7	5.7	16.2	1.59	<.001	1.055	3.2	-0.3	9.1	2.1	9.0	6.2	12.3	1.1
CIELABB	b*	99	22.5	11.7	30.5	3.45	<.001	1.113	24.2	16.5	35.1	4.4	15.6	8.8	23.2	3.1
Intensity	C*	98	14.2	6.9	23.7	3.12	<.001	1.074	33.8	19.5	42.3	5.0	8.0	5.6	11.8	1.3
Hue	º	97	141.1	132.2	148.5	2.87	<.001	1.428	152.3	144.5	159.5	3.1	135.2	125.8	140.5	2.4
Saturation	C*	99	11.6	3.7	18.9	2.84	<.001	0.883	20.2	14.4	24.9	2.1	5.7	3.0	11.0	1.7
Color band 1	nm	98	11.9	6.5	19.1	2.35	<.001	0.847	27.8	15.2	35.8	4.6	7.5	5.8	10.0	1.0
Color band 2	nm	97	7.8	5.0	12.1	1.37	<.001	0.601	20.1	8.0	28.9	4.8	5.3	4.2	6.6	0.5
Color band 3	nm	98	14.8	6.9	25.9	3.59	<.001	1.225	36.8	21.3	45.4	5.3	8.0	5.5	12.2	1.4
Color band 4	nm	99	23.9	10.6	37.1	4.96	<.001	1.605	47.3	35.2	53.3	3.9	13.7	9.0	21.4	2.6
Color band 5	nm	99	34.9	17.6	46.1	5.51	<.001	1.803	54.1	46.8	59.6	2.8	23.8	17.0	32.9	3.7
Color band 6	nm	99	41.9	24.3	51.6	5.00	<.001	1.676	55.6	46.8	61.2	2.6	32.7	23.5	42.7	3.9
Color band 7	nm	99	46.4	31.0	54.2	4.09	<.001	1.439	55.2	45.8	61.0	2.6	40.1	29.1	48.8	3.7
Red leave color	%	100	65	-	100	34	<.001	4	-	-	-	-	98	95	100	3
Floral bud appearance	DAS	14	67	65	73	2	0.42	6	68	67	71	2	68	66	69	2
Flowering time	DAS	51	88	77	95	3	0.11	8	84	77	89	7	87	85	91	3
Grain yield	Kg/ha	24	3531	1126	6985	1,342	0.33	2,154	3,250	1,167	4,385	1,806	2805.3	1,894	4,181	1,212
Biomass yield	Kg/ha	48	6,359	2,041	12,039	2294	0.13	3,088	5,819	2,497	7,850	2,900	5366	4,395	7,186	1,578

3.4. PCA

In order to investigate the relationships of the variables, a principal component analysis (PCA) was performed. With this approach it is possible to reduce the dimensionality of a data set containing several interrelated variables. This is achieved by transforming the data into a new set of uncorrelated variables: the principal components (PCs). The few first PCs retain most of the variation present in the original data. The analysis was performed on Z-score data. All the traits measured on the mapping population were included and the option of two vectors was selected. The scores were copied in an excel file to improve the graph, multiplier for vector loadings was set at 30.

Figure 2. PCA biplot of all measured traits in the mapping population.

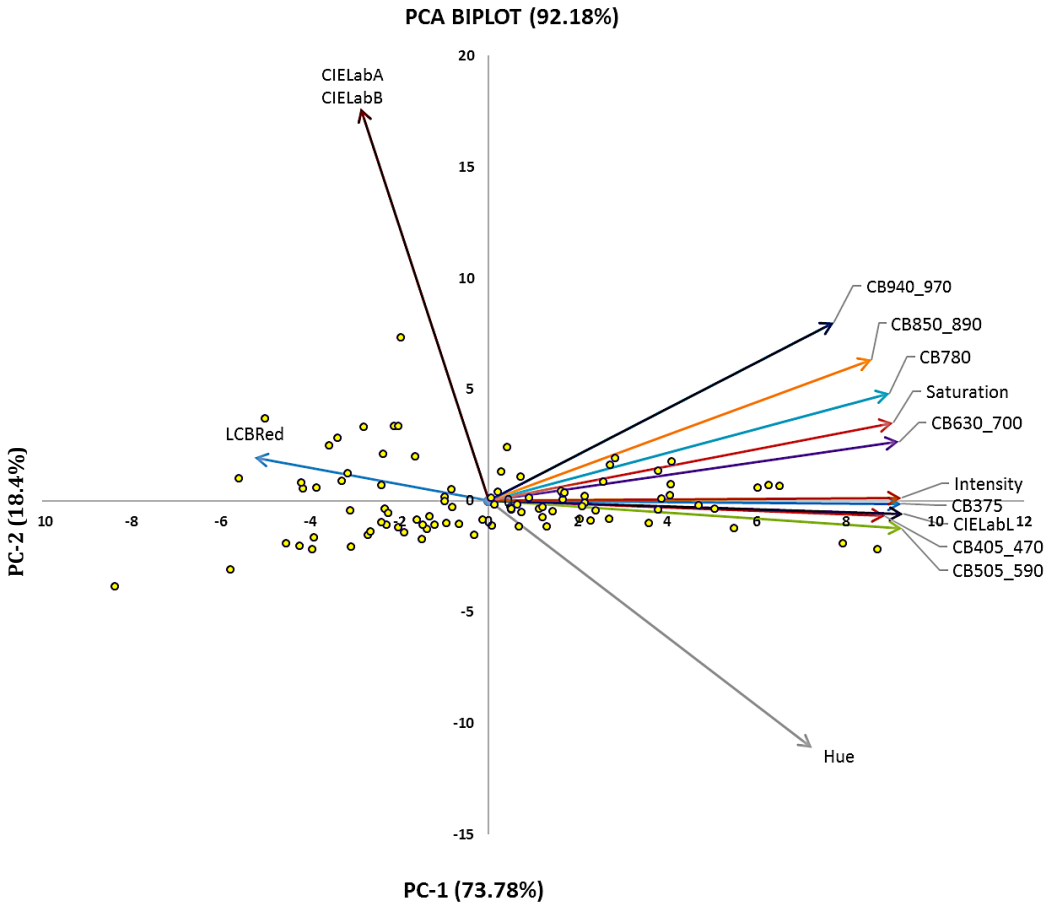


The PCA biplot summarizes 62.54% of the variation corresponding to 47.17% and 15.38% successively for PC-1 and PC-2 (Figure 2). Variation of the mapping population is greater along the PC-1 axis in which seed color traits are shown, the cluster of vectors corresponding to these variables suggest a positive correlation. In the opposite direction of the same axis, the trait red-colored leaves shows a negative relationship with the color attributes except for CIELabB and CIELabA. The last two variables were fitted in the same position suggesting a perfect positive

correlation. In PC-2 a close relationship between seed-size traits (AR, WI, LN), flowering time and TSW is shown. The effects of grain and residual biomass dry weight are in the opposite direction indicating a negative correlation furthermore, variables close to 0 indicate that the effects are not consistent with the major part of the variation in the data. Phenotypes comprising green leaves and clear seeds are positioned at the left of PC-1 while individuals with colored leaves and seeds are at the right side. It also seems that the last category mentioned have larger segregation for seed size and yield. In the lower part of the plot a phenotype with extreme values for both grain and biomass was detected.

After analyzing the results, a second PCA was carried out including only the color-related variables. The selected variables are better predictors of the observed variation in color traits, the biplot accounted for 92.18% of the variation, PC-1 contributes with 78.78% and PC-2 with 18.40% (Figure 3). The order of the vectors is similar to the one in the previous analysis. Beside what has already been described, groups of variables are observed in PC1, those representing the NIR and red color appear near to saturation. Another group is composed of the variables of the UV spectrum, green, blue, CIELabL and intensity. Hue represents the predominant wavelength perceived for example as the result or the mixture of several wavelengths, in the biplot this vector has a closer distance with the left side of the light spectrum than the opposed NIR end.

Figure 3. PCA biplot of all measured traits in the mapping population.



3.5. QTL analysis

QTL analysis was performed using MapQTL 6. The linkage map used in the analysis was constructed by van Erp (2016). Restricted MQM were performed for each trait, the mapping step size was set at 1 cM. The forward regression method was selected; the model includes cofactors with a LOD value of at least 2.5. According to the permutation test LOD score peaks greater than 5.0 indicated the existence of QTLs with a probability level of 99%. The average scores of the 22 traits were used in the QTL analysis. A 1-LOD confidence interval was estimated for the position of the flanking markers. The QTL mapping of the traits was performed using MapChart 2.2. Cofactors are show in annex 2 and QTLs above the threshold in annex 3.

4. RESULTS

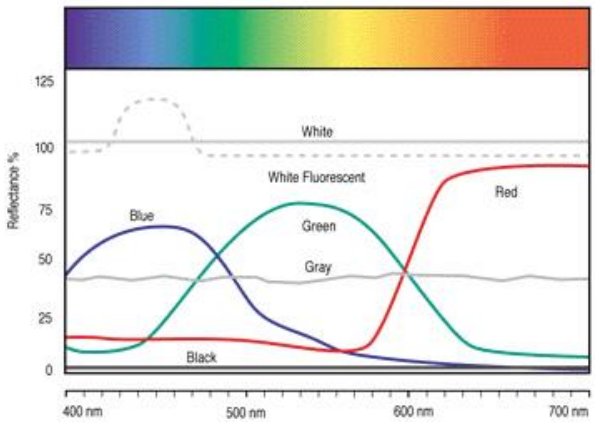
4.1. Color traits

A quinoa plants can express more than one seed color or different shades in the panicle, therefore more variation is expected when individual seeds are compared than when the average reflectance of the whole set is taken into account.

4.1.1. *Spectral bands*

The measurement at different color bands do not necessarily reflex the complexity of the seed colors as these are perceived, but rather represent the different elements that contribute to the observed color. In the UV and visible spectrum, Atlas is expected to have higher values because the white (or cream) color have higher reflectance in comparison to the red seeds of the other parent. The differences between seed colors of the parents decreased along the NIR spectrum (figure 4).

Figure 4. Reflectance curves



a. Color band 1

CB1 measures reflectance of the seeds in the UV spectrum (375 nm). Seven QTLs were found for this trait in LG-3B, 11B, 12A, 13A, 16B, 17B, N1B. These QTLs explain 76% of the variation, individual R^2 ranges from 5-21% and LOD values of 5-17. In the segregating F3 population, individuals did not have seeds as white as the seeds of parent A, suggesting that a homozygous condition is necessary to express white color which has been previously described as a recessive trait. Additive effects were detected but 60% of the QTLs for this trait had dominant effect. The average contribution of A allele to C1 is 15.30 and 14.8 for RC, this matched with the observed phenotypes. Combining all the best alleles found this trait a maximum average reflectance of 27.7 could be reached (this is equal to the mean of parent A). The broad sense of heritability per seeds was 98%.

b. Color band 2

CB2 (blue 405-470 nm), had eleven QTLs (LG-2A, 3B, 5B, 6-B, 11B, 12A, 13A, 15A, 16B, 17B and N1B) which accounted for 80% of the variation. The variation explained by each QTLs fluctuates from 3-19% and LOD values are within a range of 5-20. Dominance effects were observed in 45% of the QTLs; two of these (LG-3B and 15B) were overdominant. The allele from parent A increases the reflectance in this color band 9.31 nm and RC allele have an average contribution of 8.9. By taking into account the effects of the best QTLs, the estimated highest reflectance is about 17.5, which falls between the ranges of parent A (8.0-28.9 nm). The broad sense of heritability was 97%.

c. Color band 3

C3 (green 505-590 nm) had seven QTLs (LG-3B, 5B, 7A, 13A, 16B, 17B and N1B) which together explain 57% of the variation. The explained variance of each QTL is between 5 and 19% with LOD values ranging from 5 to 15. All the QTLs for this color band show additive effect, in average allele A contributes with 15.7nm while CR adds 13.93nm. The combined effects of the best QTLs for this trait was 16.6 nm, this is higher than the effect observed from parent A suggesting the possibility of transgressive segregation, this was not observed in the mapping population. The estimated H^2 for this trait was 98%.

d. Color band 4

For C4 (red 630-700 nm) eight QTLs were identified (LG-3B, 4A, 5B, 11B, 13A, 15B, 16B and 17B) which explain 62% of the variation. The R^2 of each QTL varies from 4-19% and LOD scores within a range of 5-16. The allele from parent A had positive dominant effect in LG-4A and 15B. Half of the QTLs have additive effect and the other half had dominant effect, overdominance was observed in QTLs from LG-11B 12B and 4B. For this color band the average effects of the parents was similar (24.2 nm for A and 23.38 nm for RC). The combined effect of the best QTLs for CB4 would produce phonotypes with approximately 34.4 nm.

Individuals with such phenotype would exceed the ranges of parent A (-0.29-9.14nm) and parent RC (6.20-12.31mn). The broad sense of heritability for H^2 accounted for 99%.

e. Color band 5

C5 (NIR 780 nm) had five QTLs (LG-4A, 5B, 12A, 16B, and 17B); the total explained variance is about 50%. Effect of individual QTLs is between 5-20% with LOD values of 5-15. The QTLs were in the range of additive and dominant effects. Two QTL had dominance effect and the one in LG-4B presented overdominance. The QTL in 5B was the only QTL in this study that show additive effects without dominance deviation. The average allelic effect of the parents was very similar (35.86 nm for A and 33.65 nm for parent RC). Combining the effect of the best QTLs for this trait an effect of 37.26 units is expected and a phenotype of 59.8 nm, which would be above the ranges obtained for both parents. H^2 for this trait was about 99%.

f. Color band 6

CB6 (NIR 850-890 nm) eight QTLs were found in LG-3B, 4A, 5B, 7A, 12A, 15A, 16B and 17B. These QTLs together explain 70% of the variance, each QTL 5-12% and LOD values from 5-9. Half of the QTls had dominance effect, from these LG in 4A shows overdominance. The average allelic effect of parent A was 40.88nm and for parent RC this was 39.66nm. The combined effect of the best QTLs accounted for 42.4 nm which would result in a phenotypic value of 56.6 nm (above the maximum values obtained by parent A). Broad sense of heritability for this trait was 99%.

g. Color band 7

(NIR 940-970 nm) had eight QTLs (LG-3B, 4A, 5B, 7A, 12A, 15A, 16B and 17B) which in total explain 76% of the variation. The R2 per QTL ranges from 6-14% and LOD values from 5-11. QTL with strongest effect correspond to LG-15A. Half of the QTLs had dominance effect. Allelic effect of the parents were alike, A scored 45.51nm and RC 44.80nm. H^2 for this trait was 99%.

4.1.2. *CIELAB*

In CIELabL Atlas had higher scores as result of his bright color. The range of colors of the mapping population overlaps with RC but the maximum value obtained by F3 exceeds the RC. This indicates the presence of more bright colors in the mapping population, for instance pink and yellow. For CIELabL three QTLs were found, the total explained variance is 36%. The QTLs were located at LG-17B, 3B and 15B that respectively accounted for 16.2%, 14.5% and 5.5% of the variation. The LOD scores were between 5 and 12. Allele from parent A had additive

effect for QTLs in LG-17B and 3B. For QTL in LG-15B overdominance was detected. Average allelic effect of parent A is 49.38. H^2 for this trait was 98%.

CIELabA provides information about the chroma hence, the white-seeded parent shows values within a range of -0 and 9. This variable might be good for measuring colored-seed. The results of the phenotypes show that in the F3 there are seeds more redish than the observed among RC. This trait had five QTLs (LG-1B, 3B, 11B, 15A and 1NB), the most significant QTL was found in LG-1B. The total explained variance is about 60%, each QTL ranging from 10% to 16% and LOD values of 6-9. The QTL with strongest effect was found in LG-1B. Effect of QTLs include additive and dominance. Dominance was detected in N1B and 15A, the last shows overdominance. H^2 for this trait was 94%.

For CIELabB, Atlas show more positive values due its approximation to cream (yellow) color. The value of the F3 is not as high as in the case of parent A but there were some phenotypes beyond the ranges of RC. Eight QTLs were found (LG-2A, 3B, 8A, 11B, 15B, 17B, 18B and 1NB), together these QTLs explain 79% of the variation. Individual R^2 scores are within a range of 7-12 with LOD values of 5-8. The QTL with strongest effect correspond to LG-2A. 50% of the QTLs show overdominace. The broad sense of heritability was 99%.

4.1.3. *Color appearance parameters*

Intensity is higher for parent A, in the mapping population some phenotypes had more intense color than RC but not better than the scores for parent A. The trait intensity of seed color had ten QTLs (LG-3B, 5B, 6B, 11B, 12A, 13A, 15B, 16B, 17B and N1B) which together explain 84% of the variation. The R^2 of each QTL varies from 4-21% and LOD values within a range of 5-17. The most significant QTL was found in LG-17B. Five QTLs presented dominance, from these three show overdominance (LG-15B, 16B and 6B). Broad sense of heritability accounted for 98%.

For the character hue of the seed color five QTLs (LG-1NB, 10B, 12A, 15B, 17B), the total explained variance was 46% and the QTL with biggest effect is located in LG- 1NB. Each QTL explains 7-12% of the variation and the LOD scores were between 5 and 8. Hue had two QTLs with dominance effect (LG-15B and 17B), overdominance was observed in QTL from 17B. The estimation of H^2 for this trait resulted in 97%.

The trait saturation had two QTLs, one in linkage group 17B and another in 3B successively explaining 19.4% and 7% of the variation and LOD values of 12.5 and 5. Both QTLs had additive effect. The broad sense of heritability accounted for 99%.

4.1.4. *Leave color*

The character red color of the leaves (before flowering) had two QTLs. The QTL in LG-3B explained 22% of the variation and obtained a LOD value of 12. The second QTL was detected

in LG-5B, the effect of this QTL accounted for 10% of the variation with a LOD value of 7. The QTL in LG-5B show overdominance effect and the QTL in LG-3B has additive effect. The H^2 for this trait was 100%

4.2. Phenological traits

4.2.1. *Time of floral bud appearance*

This trait had six QTLs (LG-6B, 8A, 10A, 14A, 16B and 17B) which together explain 65% of the variation. The explained variance per QTL was between 7-14% with LOD values in a range of 5-9. The QTLs with higher R^2 were found in LG-17B and 6B (14% each). Except for the QTL in LG-16B, all QTLs had dominant effect. Overdominace was observed in QTL from LG-10A, 8A and 17B. Broad sense of heritability accounted for 14%.

4.2.2. *Flowering time*

For flowering time four QTLs were detected (LG-10A, 15B, 16B and 17B), the total explained variance was approximately 50 %. The R^2 of each QTL varies from 9.1 to 14.4% and the LOD scores were between 5 and 8. The most significant QTLs belong to 10A and 16B. A part from QTL in LG-10A which had additive effect, all QTLs show overdominance. Broad sense of heritability accounted for 51%.

4.3. Yield related traits

4.3.1. *TSW of sowing seed*

For TSW, five QTLs were identified in LG-3B, 4B, 11B, 12A and 17B explaining in total about 80% of the variance (individual QTLs 10-19% each and LOD-values of 6-10); the QTL on LG17B had the highest strongest effect. Dominance effects were found for all QTLs, four of these QTLs have overdominance. H^2 for this trait was 97%.

4.3.2. *Size-related traits of sowing seed*

Seed area had five QTLs located in LG-1B, 3B, 10A, 10B and 14A that together explain 46.5% of the variation. The R^2 per QTL is between 7.4% and 11.13% and LOD values from 5.4 to 7.6. The QTL with highest R^2 effect was found in LG-1B. All the QTLs have dominant effect, overdominance corresponds to QTLs in LG-14A, 10A, 03B. Heritability for this trait was 98%.

The trait length of seed had six QTLs (LG-1B, 3B, 5B, 7A, 11B and 14A) which together explain 70% of the variation. Individual R^2 of QTLs is between 8 and 17, LOD values ranging from 5.6 to 10.6. The QTL with the strongest effect was found in LG-1B. QTLs in LG-3B and 14A shows overdominance. Heritability for this trait was 97%.

The trait width had four QTLs positioned in LG-1B, 10A, 10B and 11B together explain 46% of the variation. The R^2 of these QTLs is between 9.8%-13.4% and LOD values of 5.5-7. The most significant QTL was found in LG10A. All the detected QTLs had dominant effect and overdominance was detected in QTL from LG-1B and 10B. H^2 for this trait was 97%.

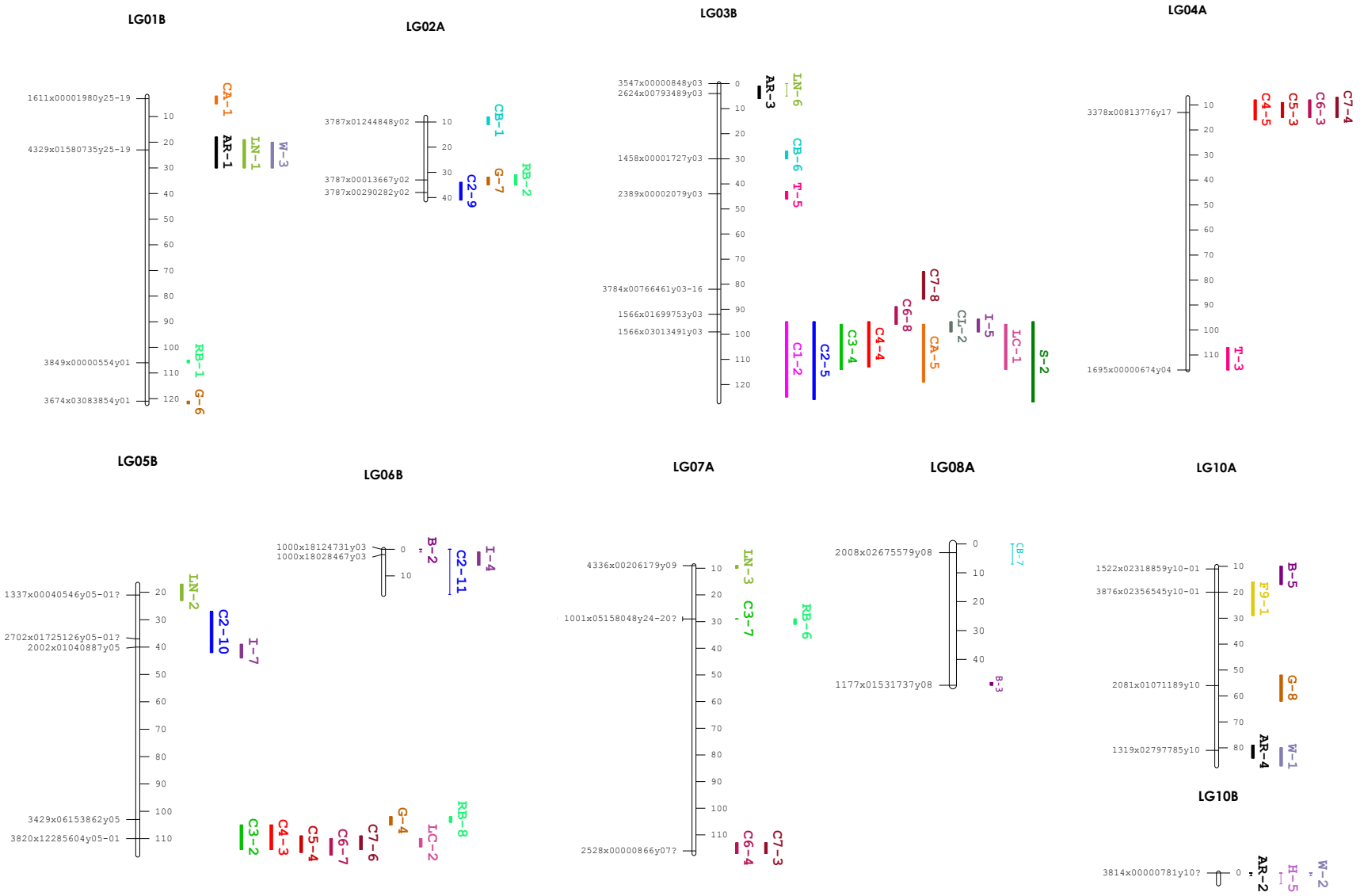
4.3.3. *Grain yield*

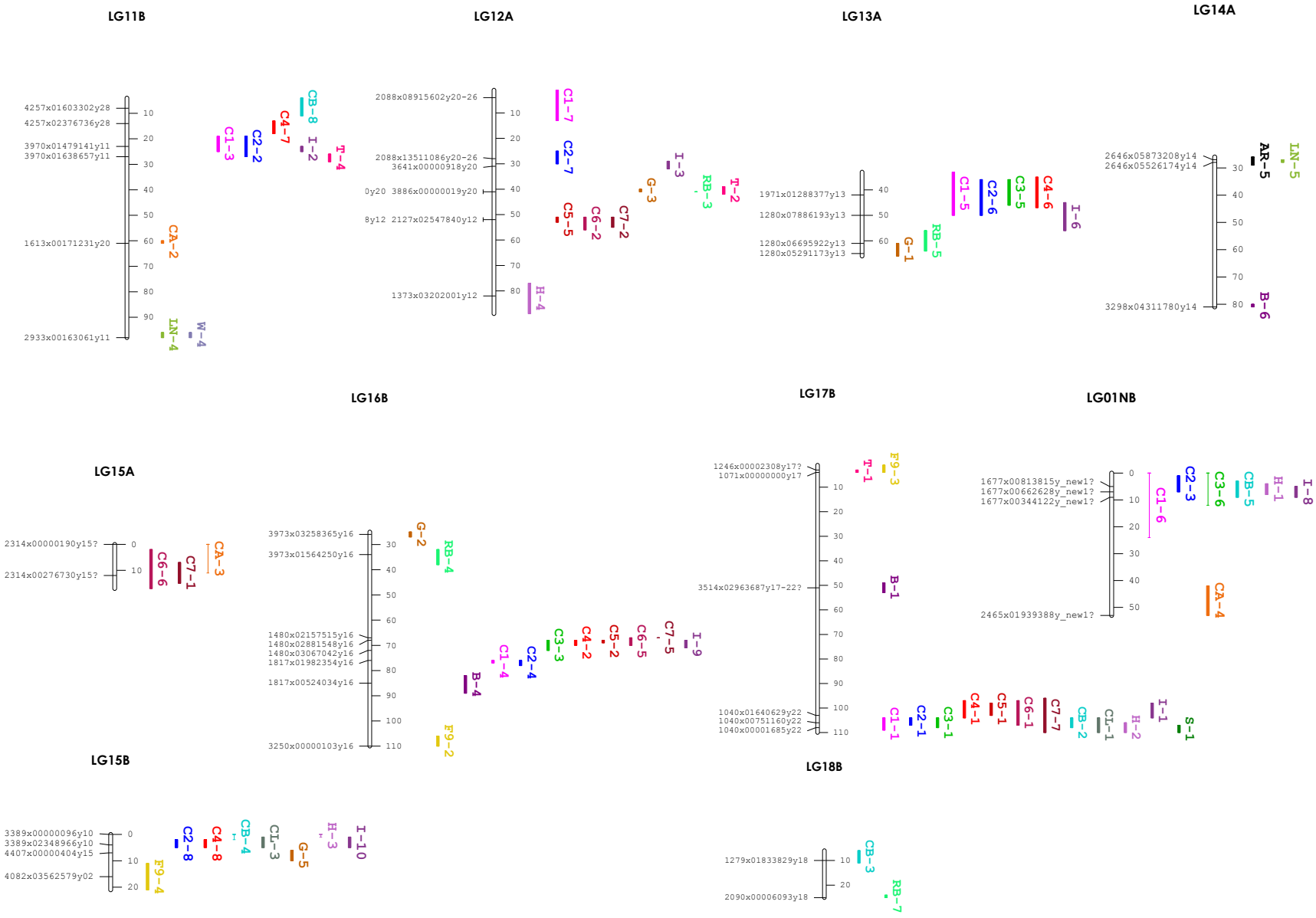
For grain dry weight eight QTLs were identified (LG-1B, 2A, 5B, 10A, 12A, 13A, 15B and 16B). The explained variation per QTL ranges from 6.1% and 15.5% with a total of 87%. LOD values were in a range of 5-11. The QTLs with the most significant values correspond to 13A, 16B these had additive effects. For the rest of the QTLs dominance was detected, overdominance was present in QTLs from LG-12A, 5B, 15B and 1B. H^2 for this trait was 24%.

4.3.4. *Residual biomass*

The trait residual biomass dry weight had eight QTLs (LG-1B, 2A, 5B, 7A, 12A, 13A, 16B and 18B) accounting for 88% of the variation. Individual explained variance is between 7-15 and LOD values from 5-10. The QTLs explaining more variation belong to LG-1B (15.1%), 2A (15.1%) and 12A (11.9%), these QTLs presented overdominance. The dominance effect was also detected in LG-7A and 5B, the rest of the QTLs had additive effects. The broad sense of heritability for this trait was 48%.

Fig. 5. Quinoa QTL map based on an F3 population derived from Atlas and Red Carina. Bars indicate 1-LOD confidence` interval, QTL loci are shown at the right.




LG11B
4257x01603302y28
4257x02376736y28
3970x01479141y11
3970x01638657y11
1613x00171231y20
2933x00163061y11
CA-2
LN-4
W-4
C1-3
C2-2
C4-7
CB-8
I-2
T-4
LG12A
2088x08915602y20-26
2088x13511086y20-26
3641x00000918y20
0y20 3886x00000019y20
8y12 2127x02547840y12
1373x03202001y12
H-4
C1-7
C2-7
C5-5
C6-2
C7-2
G-3
I-3
RB-3
T-2
LG13A
1971x01288377y13
1280x07886193y13
1280x06695922y13
1280x05291173y13
G-1
RB-5
C1-5
C2-6
C3-5
C4-6
I-6
LG14A
2646x05873208y14
2646x05526174y14
3298x04311780y14
B-6
AR-5
LN-5
LG16B
3973x03258365y16
3973x01564250y16
1480x02157515y16
1480x02881548y16
1480x03067042y16
1817x01982354y16
1817x00524034y16
3250x00000103y16
G-2
RB-4
B-4
F9-2
C1-4
C2-4
C3-3
C4-2
C5-2
C6-5
C7-5
I-9
LG17B
1246x00002308y17?
1071x00000000y17
3514x02963687y17-22?
1040x01640629y22
1040x00751160y22
1040x00001685y22
T-1
F9-3
B-1
C1-1
C2-1
C3-1
C4-1
C5-1
C6-1
C7-7
CB-2
CL-1
H-2
I-1
S-1
LG01NB
1677x00813815y_new1?
1677x00662628y_new1?
1677x00344122y_new1?
2465x01939388y_new1?
C1-6
C2-3
C3-6
CB-5
H-1
I-8
CA-4
LG15A
2314x00000190y15?
2314x00276730y15?
C6-6
C7-1
CA-3
LG15B
3389x00000096y10
3389x02348966y10
4407x00000404y15
4082x03562579y02
F9-4
C2-8
C4-8
CB-4
CL-3
G-5
H-3
I-10
LG18B
1279x01833829y18
2090x00006093y18
CB-3
RB-7

5. DISCUSSION

To our knowledge, this is the first QTL map including several traits of agronomic importance in quinoa. QTLs above the LOD threshold were find for all traits. In total 135 putative QTL were identified on 20 linkage groups, 56% of these had dominance effect and 35% of them presented overdominance. The linkage groups in which more QTLs were detected are 3B (15), 17B (15) and 16B (12). There were several cases in which co-location of QTLs was observed. For example, in linkage group 17B were QTLs interval of 12 different color traits were mapped at approximately 95 -110 cM. The number of QTLs per trait ranges between 2 and 11 suggesting multifactorial inheritance. The traits red leaves and color saturation in the seeds had two QTLs which might correspond to oligogenic characters. Other traits that could be included in this category were CIELabL*, Flowering time and width of the seeds. The rest of the traits seems to be polygenic; this was expected for the yield-related traits but not for the color attributes of the seeds. The traits with more QTLs were intensity of seed color and color band 2 with respectively 10 and 11 QTLs.

According to Jacobsen and Stølen (1993) quinoa seed color is determined by two allomorphic complementary interacting genes. Quinoa seed color is expected to follow Mendilian inheritance however, visual assessment of phenotype is not only tedious but difficult because a panicle might exhibit several seed colors. VideometerLab provided fast and accurate measurements of the seeds. The LSDs obtained for the seed traits measured with VideomenterLab indicate that differences between seeds are very small (for instance, in the size-related traits). However, for color traits it remains important to select a smaller set of variables depending on what is desired to compare. The spectral bands are very informative of the reflectance properties and the decomposition of the perceived color increases the complexity of the analysis. The spectral bands could be used when there is interest for measuring reflectance within certain range of the spectrum, for example UV properties. CIELAB color space model is better for phenotyping seeds, for example CIELabA can be used to determine the redness, for yellow CIELabB could be used and CIELabL for white seeds. Nevertheless, estimation of the expected phenotypes might be difficult since the position in the color space depend on the coordinates (L* a* b*).

In the field, experiment spatial variation from soil was observed as a gradient across the trial. The precision of the phenontypic measurements is a relevant factor because higher errors will decrease the estimated heritability and lower the detection power for QTLs (Xinmin et al., 2006). For the phenological traits no significant differences were found, this might be because the phenotypic scores does not accurately reflex the complexity of this biological process.

The result presented in this this study can be used to accelerate the development of elite cultivars once the markers that predict a given trait are confirmed. Further steps in the developing of markers requires the validation of QTLs and allele mining, this is to confirm that the linkage of QTLs and traits are not the result of statistical anomalies or errors.

6. Conclusions

A QTL linkage map for 22 agromorphological traits of quinoa. It remains important to validate the putative QTLs with other mapping populations and in homogeneous environments. Further research is necessary in other to understand the complex expression of seed colors in quinoa. This study also provides a framework for metric color characterization of quinoa seeds. The results of this study shows that it is possible to breed non-bitter varieties with dark or red colors beyond what has been described for Red Carina. Furthermore, some lines of the mapping population show transgressive segregation several traits, including grain yield, that might be exploited in quinoa breeding programs.

7. REFERENCES

Acquaah, G. (2009). Principles of plant genetics and breeding. John Wiley & Sons.386-402 pp.

Agudo, J. E., Pardo, P. J., Sánchez, H., Pérez, Á. L., & Suero, M. I. (2014). A low-cost real color picker based on arduino. Sensors, 14(7), 11943-11956.

Apaza, V., Cáceres, G., Estrada, R. and Pinedo, R. (2015). Catalogue of commercial varieties of quinoa in Peru: a future planted thousands of years ago. FAO, Regional Office for Latin America and the Caribbean, Lima. 9.

Bazile, D. and Baudron, F. (2015). The dynamics of the global expansion of quinoa growing in view of its high biodiversity. State of the Art Report on Quinoa around the World in 2013, 42-55.

Bellemare, M., Gitter, S., Kasterine, A., Obregon, E. & Zotz, A. (2016) Trade in Quinoa: Impact on the Welfare of Peruvian Communities. International Trade Centre. Geneva, Switzerland. 1-4.

Bhargava, A., Shukla, S., & Ohri, D. (2007). Genetic variability and interrelationship among various morphological and quality traits in quinoa (Chenopodium quinoa Willd.). Field Crops Research, 101(1), 104–116.

Bonifacio, A. (1995). Interspecific and intergeneric hybridization in Chenopod Species (master's thesis). Brigham Young University, Provo, Utah, USA. 150 p.

Bonifacio, A., Gomez-Pando, L., and Rojas, W. (2015). "Quinoa breeding and modern variety development," in State of the Art Report on Quinoa Around the World in 2013, eds D. Bazile, H. D. Bertero, and C. Nieto (Rome: FAO/CIRAD), 172–191.

Burrieza, H. P., López-Fernández, M. P. & Maldonado, S. (2014). Analogous reserve distribution and tissue characteristics in quinoa and grass seeds suggest convergent evolution. Frontiers in plant science, 5, 546. http://dx.doi.org/10.3389/fpls.2014.00546.

Cai, Y., Sun, M., & Corke, H. (2001). Identification and distribution of simple and acylated betacyanins in the Amaranthaceae. Journal of Agricultural and Food Chemistry, 49(4), 1971–1978.

Cayoja, M.R. (1996). Caracterización de variables continuas y discretas del grano de quinua (Chenopodium quinoa Willd.) del banco de germoplasma de la Estación Experimental Patacamaya (bachelor's thesis). Universidad Técnica Oruro, Bolivia. 129 p.

Chen, C. (2015). Overview of plant pigments. In Chen, C (Ed.), Pigments in fruits and vegetables: genomics and dietetics. Springer. 1-8. doi: 10.1007/978-1-4939-2356-4_1.

D. Strack, T. Vogt, W. Schliemann. Recent advances in betalain research. Phytochemistry, 62 (2003), pp. 247–269

Davies, K. (Ed.). (2009). Annual plant reviews: plant pigments and their manipulation (Vol. 14). John Wiley & Sons. 1-18.

Dekel, G. (2016). Hue, saturation and brightness. Retrieved from: http://www.poeticmind.co.uk/research/hue-saturation-brightness-hsb/.

Delgado-Vargas, F., Jiménez, A. R., & Paredes-López, O. (2000). Natural pigments: carotenoids, anthocyanins, and betalains—characteristics, biosynthesis, processing, and stability. Critical reviews in food science and nutrition, 40(3), 173-289.

Dillehay, T. D., Rossen, J., Andres, T. C., & Williams, D. E. (2007). Preceramic adoption of peanut, squash, and cotton in northern Peru. Science, 316(5833), 1890-1893. doi: 10.1126/science.1141395.

Federer, W. T., & Crossa, J. (2012). I.4 Screening Experimental Designs for Quantitative Trait Loci, Association Mapping, Genotype-by Environment Interaction, and Other Investigations. Frontiers in Physiology, 3, 156. http://doi.org/10.3389/fphys.2012.00156

Gómez-Caravaca, A. M., Iafelice, G., Lavini, A., Pulvento, C., Caboni, M. F., & Marconi, E. (2012). Phenolic compounds and saponins in quinoa samples (Chenopodium quinoa Willd.) grown under different saline and nonsaline irrigation regimens. Journal of agricultural and food chemistry, 60(18), 4620-4627.

Gómez-Pando, L. & Eguiluz, A. (2011). Catálogo del banco de germoplasma de quinua. Universidad Nacional Agraria La Molina, Lima. 13 -20. Retrieved from: http://sinia.minam.gob.pe/documentos/catalogo-banco-germoplasma-quinua.

Gomez-Pando, L. (2015). Quinoa Breeding. In Murphy, K. & Matanguihan, J. (Eds.), Quinoa: Improvement and Sustainable Production. Hoboken, NJ, USA. 87-108. doi: 10.1002/9781118628041.ch6

González, J. A., Bruno, M., Valoy, M., & Prado, F. E. (2011). Genotypic variation of gas exchange parameters and leaf stable carbon and nitrogen isotopes in ten quinoa cultivars grown under drought. Journal of Agronomy and Crop Science, 197(2), 81-93. doi:10.1111/j.1439-037X.2010.00446.x.

González, J. A., Eisa, S. S., Hussin, A. E. S., & Prado, F. E. (2015). Quinoa: an Incan crop to face global changes in agriculture. Quinoa: improvement and sustainable production, 7-11. doi: 10.1002/9781118628041.ch1.

IBNORCA. (2007). Granos Andinos. Quinua en grano: clasificación y requisitos. NB 312004. Norma Boliviana. Instituto Boliviano de Normalización y Calidad.

IAI. (2016). Quinoa Markets 2016, Trends and Opportunities. Informa Agribusiness Intelligence. Retrieved from: file:///C:/Users/User/Downloads/Agribusiness%20intelligence.%20Quinoa%20Markets%20Trends%20and%20Opportunities.pdf

Jacobsen, S. E. (2015). Adaptation and scope for quinoa in northern latitudes of Europe. In Bazile, D.; Bertero, D.; Nieto, C. (Eds.), State of the art report on quinoa. FAO, Regional Office for Latin America and the Caribbean

Jacobsen, S. E. & Stølen, O. (1993). Quinoa-morphology, phenology and prospects for its production as a new crop in Europe. European Journal of Agronomy, 2(1), 19-29.

Jacobsen, S. E., Sørensen, M., Pedersen, S. M., & Weiner, J. (2013). Feeding the world: genetically modified crops versus agricultural biodiversity. Agronomy for sustainable development, 33(4), 651-662.

Karban, R. (2015). Plant sensing and communication. University of Chicago Press, London. 45-59. doi: 10.7208/chicago/9780226264844.001.0001.

Koziol, M. J. (1990), Afrosimetric estimation of threshold saponin concentration for bitterness in quinoa (Chenopodium quinoa Wild.). J Sci Food Agric 54:211±219.

Limburg, H. & Mastebroek, H.D. (1996). Breeding high yielding lines of Chenopodium quinoa Willd. with saponin free seed. Proc COST 814 Workshop on Small Grain Cereals and Pseudo-cereals, Copenhagen, February, pp 103-114 (1996).

Mammadov, J., Aggarwal, R., Buyyarapu, R. & Kumpatla, S. (2012). SNP Markers and Their Impact on Plant Breeding. International Journal of Plant Genomics, Article ID 728398, 11 pages, 2012. doi:10.1155/2012/728398

Martínez, E. A., Veas, E., Jorquera, C., San Martín, R., & Jara, P. (2009). Re-Introduction of Quínoa into Arid Chile: Cultivation of two lowland races under extremely low irrigation. Journal of Agronomy and Crop Science, 195(1), 1-10. doi: 10.1111/j.1439-037X.2008.00332.x.

Mastebroek, H. D., Limburg, H., Gilles, T., & Marvin, H. J. P. (2000). Occurrence of sapogenins in leaves and seeds of quinoa (Chenopodium quinoa Willd).Journal of the Science of Food and Agriculture, 80(1), 152-156.

Mastebroek, H., van Loo R., Dolstra, O. (2002). Combining ability for seed yield traits of Chenopodium quinoa breeding lines. Euphytica 125:427–432

Mastebroek, H.D. & Limburg, H. (1996) Breeding harvest security in Chenopodium quinoa. In: Stølen O, Bruhn K, Pithan K, Hill J, editors. Proceedings of the COST 814 Workshop on Small Grain Cereals and Pseudo-cereals, Copenhagen, February 79-86

Maughan, P. J., Bonifacio, A., Coleman, C. E., Jellen, E. N., Stevens, M. R. & Fairbanks, D. J. (2007). Quinoa (Chenopodium quinoa). In Genome mapping and molecular breeding in plants: pulses, sugar and tuber crops. Springer Berlin Heidelberg. (pp. 147-158).

Maughan, P., Jellen, E., & Raney, J. (2015). Quinoa molecular and Genomic Tools. In Bazile, D.; Bertero, D.; Nieto, C. (Eds.), State of the art report on quinoa. FAO, Regional Office for Latin America and the Caribbean, 24.

Maughan, P.J., Kolano, B.A., Maluszynska, J., Coles, N.D., Bonifacio, A., Rojas, J., Coleman, C.E., Stevens, M.R., Fairbanks, D.J., Parkinson, S.E. & Jellen, E.N. (2006). Molecular and cytological characteriza on of ribosomal RNA genes in Chenopodium quinoa and Chenopodium berlandieri. Genome, 49(7): 825-839.

Medina, W., Skurtys, O., & Aguilera, J. M. (2010). Study on image analysis application for identification Quinoa seeds (Chenopodium quinoa Willd) geographical provenance. LWT-Food Science and Technology, 2(43), 238-246.

Moreno, D. A., García-Viguera, C., Gil, J. I., & Gil-Izquierdo, A. (2008). Betalains in the era of global agri-food science, technology and nutritional health. Phytochemistry Reviews, 7(2), 261-280.

Olesen, M. H., Nikneshan, P., Shrestha, S., Tadayyon, A., Deleuran, L. C., Boelt, B., & Gislum, R. (2015). Viability prediction of Ricinus cummunis L. seeds using multispectral imaging. Sensors, 15(2), 4592-4604.

Pasko, P., Barton, H., Zagrodzki, P., Gorinstein, S., Fołta, M., & Zachwieja, Z. (2009). Anthocyanins, total polyphenols and antioxidant activity in amaranth and quinoa seeds and sprouts during their growth. Food Chemistry, 115(3), 994–998.

Planella, M. T., López, M. L., Bruno, M. C., Amancai, S., & Condes, L. (2015). Domestication and prehistoric Distribution In Bazile, D.; Bertero, D.; Nieto, C. (Eds.), State of the art report on quinoa. FAO, Regional Office for Latin America and the Caribbean.

Repo-Carrasco-Valencia, R., Hellström, J. K., Pihlava, J.-M., & Mattila, P. H. (2010). Flavonoids and other phenolic compounds in Andean indigenous grains: Quinoa (Chenopodium quinoa), kañiwa (Chenopodium pallidicaule) and kiwicha (Amaranthus caudatus). Food Chemistry, 120(1), 128–133.

Risi, J. & Galwey, N. W. (1984). The Chenopodium grains of the Andes: Inca crops for modern agriculture. Advances in applied biology, 10, 145–216.

Rojas, W., Pinto, M., Alanoca, C., Gómez-Pando, L. G., León-Lobos, P., Alercia, A., Diulgheroff, S., Padulosi, S. & Bazile, D. (2015). Quinoa genetic resources and ex situ conservation. In Bazile, D.; Bertero, D.; Nieto, C. (Eds.), State of the art report on quinoa. FAO, Regional Office for Latin America and the Caribbean. 56-82.

Ruiz-Carrasco, K., Antognoni, F., Coulibaly, A. K., Lizardi, S., Covarrubias, A., Martínez, E. A., Molina-Montenegro, M.A., Biondi, S. & Zurita-Silva, A. (2011). Variation in salinity tolerance of four lowland genotypes of quinoa (Chenopodium quinoa Willd.) as assessed by growth, physiological traits, and sodium transporter gene expression. Plant Physiology and Biochemistry, 49(11), 1333-1341. doi: 10.1016/j.plaphy.2011.08.005.

Simmonds, N. (1971). The breeding system of Chenopodium quinoa. Male sterility. Heredity, 27, 73–82.

Spehar, C. & Santos R. (2005) Agronomic performance of Quinoa selected in the Brazilian Savannah. Pesq Agrop Brasil 40(6):609–612.

Tanaka, Y., Sasaki, N., & Ohmiya, A. (2008). Biosynthesis of plant pigments: anthocyanins, betalains and carotenoids. The Plant Journal, 54(4), 733-749.

Tang, Y., Li, X., Chen, P. X., Zhang, B., Hernandez, M., Zhang, H., Massimo, F., Liu, R., & Tsao, R. (2015b). Characterisation of fatty acid, carotenoid, tocopherol/tocotrienol compositions and antioxidant activities in seeds of three Chenopodium quinoa Willd. genotypes. Food chemistry, 174, 502-508.

Tang, Y., Li, X., Zhang, B., Chen, P. X., Liu, R., & Tsao, R. (2015a). Characterisation of phenolics, betanins and antioxidant activities in seeds of three Chenopodium quinoa Willd. genotypes. Food Chemistry, 166, 380-388.

Van Erp, W. (2016) Marker Development for Bitter-Tasting-Saponin Gene in Quinoa (Chenopodium quinoa). Msc thesis. Wageningen University, the Netherlands.

Waksmundzka-Hajnos, M., & Sherma, J. (2010). High Performance Liquid Chromatography in Phytochemical Analysis. 380 p

Ward, S. M. (2000). Allotetraploid segregation for single-gene morphological characters in quinoa (Chenopodium quinoa Willd.). Euphytica, 116, 11–16. http://dx.doi.org/10.1023/a:1004070517808.

Winkel-Shirley, B. (2002). Biosynthesis of flavonoids and effects of stress. Current opinion in plant biology, 5(3), 218-223.

Wrigley, C. W., Corke, H., Seetharaman, K., & Faubion, J. (Eds.). (2015). Encyclopedia of food grains (2nd edition). Academic Press. 345.

Zurita-Silva, A., Fuentes, F., Zamora, P., Jacobsen, S. E., & Schwember, A. R. (2014). Breeding quinoa (Chenopodium quinoa Willd.): potential and perspectives. Molecular Breeding, 34(1), 13-30.

Annex 1. Correlation coefficients for the 19 spectral color bands and p-values of the two-sided test of correlations different from zero ($\alpha = 0.05$).

CB1	1	-																
CB2	2	0.959	-															
CB3	3	0.977	0.993	-														
CB4	4	0.983	0.984	0.998	-													
CB5	5	0.984	0.976	0.994	0.999	-												
CB6	6	0.993	0.951	0.975	0.985	0.990	-											
CB7	7	0.995	0.943	0.966	0.975	0.979	0.997											
CB8	8	0.991	0.925	0.947	0.956	0.960	0.986	0.996	-									
CB9	9	0.994	0.928	0.950	0.958	0.962	0.985	0.994	0.999	-								
CB10	10	0.991	0.926	0.949	0.956	0.958	0.975	0.982	0.985	0.993	-							
CB11	11	0.989	0.924	0.947	0.954	0.956	0.972	0.979	0.982	0.990	1.000	-						
CB12	12	0.981	0.914	0.937	0.944	0.946	0.960	0.966	0.970	0.981	0.997	0.998	-					
CB13	13	0.970	0.900	0.923	0.929	0.931	0.946	0.952	0.958	0.971	0.992	0.993	0.998					
CB14	14	0.947	0.873	0.894	0.899	0.900	0.916	0.924	0.934	0.949	0.974	0.977	0.986	0.994	-			
CB15	15	0.910	0.837	0.854	0.857	0.857	0.873	0.882	0.896	0.913	0.943	0.947	0.960	0.974	0.993	-		
CB16	16	0.889	0.818	0.832	0.834	0.834	0.849	0.859	0.874	0.892	0.925	0.929	0.943	0.960	0.985	0.998	-	
CB17	17	0.865	0.796	0.809	0.809	0.808	0.822	0.833	0.849	0.868	0.903	0.908	0.923	0.943	0.973	0.994	0.998	-
CB18	18	0.810	0.747	0.755	0.752	0.750	0.762	0.773	0.792	0.812	0.851	0.856	0.875	0.900	0.941	0.974	0.985	0.993
CB19	19	0.754	0.698	0.701	0.696	0.693	0.702	0.713	0.734	0.755	0.797	0.803	0.824	0.853	0.902	0.946	0.962	0.976
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17

CB1	1	-																
CB2	2	<0.001	-															
CB3	3	<0.001	<0.001	-														
CB4	4	<0.001	<0.001	<0.001	-													
CB5	5	<0.001	<0.001	<0.001	<0.001	-												
CB6	6	<0.001	<0.001	<0.001	<0.001	<0.001												
CB7	7	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-										
CB8	8	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-									
CB9	9	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-								
CB10	10	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-							
CB11	11	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-						
CB12	12	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-					
CB13	13	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-				
CB14	14	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-			
CB15	15	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-		
CB16	16	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001		
CB17	17	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	
CB18	18	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-
CB19	19	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17

Annex 2. Data for H^2 estimation and results

Trait	Varieties	Mapping population				H^2
	MSresidual	MSresidual	MSPhenotype	S^2_genotype	S^2_Total	%
TSW	0.001	0.006	0.219	0.073	0.074	99
AR	0.200	0.109	4.948	0.059	0.260	23
LN	0.029	0.016	0.612	0.007	0.036	20
WI	0.024	0.015	0.593	0.007	0.031	23
CLBL	13.910	34.350	2279.700	28.322	42.232	67
CLBA	2.740	11.590	202.540	2.498	5.238	48
CLBB	14.470	12.900	954.600	11.752	26.222	45
INT	13.150	12.010	780.670	9.594	22.744	42
HUE	7.745	21.240	658.630	8.136	15.881	51
SAT	3.661	8.122	643.375	7.996	11.657	69
CB1	10.990	7.461	441.996	5.388	16.378	33
CB2	11.760	3.759	149.749	1.725	13.485	13
CB3	14.810	15.610	1032.570	12.722	27.532	46
CB4	11.240	26.820	1969.150	24.474	35.714	69
CB5	10.770	33.820	2424.670	30.174	40.944	74
CB6	11.110	29.230	2000.480	24.867	35.977	69
CB7	10.370	21.560	2000.480	24.876	35.246	71
LCR	1.260	1.512	1599.558	1598.298	1599.558	100
B90	3.227	3.529	4.098	0.871	4.098	21
F90	7.785	7.131	14.425	6.640	14.425	46
GDW	1401424	1401424	1840444	439020	1840444	24
RBM	2880964	2880964	5501861	2620897	5501861	48

Annex 3. Cofactors used in QTL analysis

Trait	LG	Position	Locus	LOD
AR	1B	23.451	4329x01580735y25-19?	7.69
AR	10B	0	3814x00000781y10?	6.91
AR	3B	4.139	2624x00793489y03	6.85
AR	10A	81.13	1319x02797785y10	5.84
AR	14A	27.424	2646x05873208y14	5.4
AR	11B	87.288	2751x06172613y11	4.84
AR	17B	73.495	3670x02102392y22	4.26
AR	15B	0	3389x00000096y10	3.91
AR	5B	21.152	1337x00040546y05-01?	3.79
AR	2A	75.535	4446x03992405y02	3.24
AR	7A	9.306	4336x00206179y09	2.77
B90	17B	50.867	3514x02963687y17-22?	8.88
B90	6B	0	1000x18124731y03	8.75
B90	8A	48.923	1177x01531737y08	7.03
B90	16B	85.2	1817x00524034y16	6.14
B90	10A	11.475	1522x02318859y10-01	5.49
B90	14A	80.933	3298x04311780y14	5.03
B90	1B	120.307	1694x00000088y01	4.22
B90	7A	10.625	1748x00000114y03-09	3.86
B90	15A	50.375	1257x03385525y15	3.47
B90	11B	86.82	2187x03279969y11	2.75
B90	2A	119.45	2896x00512907y02	2.73
CB1	17B	107.778	1040x00001685y22	17.3
CB1	3B	99.488	1566x03013491y03	14.19
CB1	11B	23.425	3970x01479141y11	11.52
CB1	16B	76.2	1817x01982354y16	8.15
CB1	13A	42.401	1971x01288377y13	7.01
CB1	N1B	5.491	1677x00813815y_new1?	6.88
CB1	12A	4.048	2088x08915602y20-26	5.86
CB1	2A	26.356	2715x00414490y02	4.81
CB1	15B	4.27	3389x02348966y10	3.68
CB1	6B	16.7	1000x11511170y03	3.63
CB1	5B	33.323	2822x05020357y05-01	3.04
CB2	17B	105.893	1040x00751160y22	20.1
CB2	11B	23.425	3970x01479141y11	16.44
CB2	N1B	5.491	1677x00813815y_new1?	12.9
CB2	16B	76.2	1817x01982354y16	8.58
CB2	3B	99.488	1566x03013491y03	7.59
CB2	13A	42.401	1971x01288377y13	7.48
CB2	12A	28.244	2088x13511086y20-26	7.14
CB2	15B	4.27	3389x02348966y10	6.8
CB2	2A	38.069	3787x00290282y02	6.65
CB2	5B	36.645	2702x01725126y05-01?	6.44
CB2	6B	2	1000x18028467y03	5.59
CB2	10A	23.038	3876x02088218y10-01	3.58
CB2	7A	42.017	1001x07508457y24-20?	3.11
CB3	17B	105.893	1040x00751160y22	15.54
CB3	5B	110.058	3820x12285604y05-01	7.62
CB3	16B	71.7	1480x03067042y16	7.48
CB3	3B	99.488	1566x03013491y03	6.49
CB3	13A	42.401	1971x01288377y13	6.19
CB3	N1B	6.643	1677x00662628y_new1?	5.72
CB3	7A	28.884	4480x06879032y20	5.1
CB3	11B	16.697	4257x02761910y28	4.26
CB3	14A	55.477	1229x00000124y14	3.91
CB3	15B	4.27	3389x02348966y10	3.61
CB3	12A	52.437	2127x02547840y12	3.34
CB3	4A	12.732	3378x00813776y17?	3.06
CB4	17B	102.512	1040x01640629y22	16.09
CB4	16B	67.9	1480x02881548y16	9.22
CB4	5B	110.058	3820x12285604y05-01	7.15
CB4	3B	99.488	1566x03013491y03	6.57

CB4	4A	12.732	3378x00813776y17?	6.38
CB4	13A	42.401	1971x01288377y13	5.86
CB4	11B	13.915	4257x02376736y28	5.13
CB4	15B	4.27	3389x02348966y10	5.1
CB4	N1B	5.491	1677x00813815y_new1?	4.71
CB4	12A	52.437	2127x02547840y12	4.62
CB4	7A	28.884	4480x06879032y20	4.3
CB4	14A	55.477	1229x00000124y14	2.97
CB5	17B	102.512	1040x01640629y22	15.36
CB5	16B	67.9	1480x02881548y16	10.24
CB5	4A	12.732	3378x00813776y17?	7.58
CB5	5B	110.058	3820x12285604y05-01	5.85
CB5	12A	52.437	2127x02547840y12	5.18
CB5	11B	13.915	4257x02376736y28	4.85
CB5	N1B	5.491	1677x00813815y_new1?	4.73
CB5	3B	99.488	1566x03013491y03	4.58
CB5	7A	28.884	4480x06879032y20	4.56
CB5	15B	4.27	3389x02348966y10	4.53
CB5	13A	42.401	1971x01288377y13	3.91
CB5	2A	137.257	3799x02552444y02	3.2
CB6	17B	102.512	1040x01640629y22	9.53
CB6	12A	52.437	2127x02547840y12	9.04
CB6	4A	12.732	3378x00813776y17?	7.95
CB6	7A	116.223	2528x00000866y07?	7.28
CB6	16B	67.9	1480x02881548y16	6.84
CB6	15A	11.828	2314x00276730y15?	6.59
CB6	5B	110.058	3820x12285604y05-01	6.26
CB6	3B	91.849	1566x01699753y03	5.21
CB6	15B	4.27	3389x02348966y10	3.48
CB6	2A	137.257	3799x02552444y02	3.29
CB7	15A	11.828	2314x00276730y15?	11.51
CB7	12A	51.831	2127x02752418y12	9.77
CB7	7A	116.223	2528x00000866y07?	9.32
CB7	4A	12.732	3378x00813776y17?	8.79
CB7	16B	66.9	1480x02157515y16	6.57
CB7	5B	110.058	3820x12285604y05-01	6.45
CB7	17B	102.512	1040x01640629y22	5.74
CB7	3B	81.526	3784x00766461y03-16	5.69
CB7	2A	137.257	3799x02552444y02	4.59
CB7	15B	4.27	3389x02348966y10	3.67
CLBA	1B	2.64	1611x00001980y25-19	9.35
CLBA	11B	60.805	1613x00171231y20	6.86
CLBA	15A	0	2314x00000190y15?	6.83
CLBA	N1B	52.677	2465x01939388y_new1?	6.45
CLBA	3B	99.488	1566x03013491y03	6.39
CLBA	2A	14.883	3787x00754203y02	4.81
CLBA	7A	75.725	2716x00000075y07	4.7
CLBA	10B	7.826	2370x04142848y10?	4.19
CLBA	10A	31.421	3876x00000251y10-01	3.26
CLBA	17B	63.035	3514x00896819y17-22?	2.8
CLBB	2A	9.892	3787x01244848y02	8.32
CLBB	17B	107.778	1040x00001685y22	7.76
CLBB	18B	9.784	1279x01833829y18	7.5
CLBB	15B	0	3389x00000096y10	7.49
CLBB	N1B	6.643	1677x00662628y_new1?	6.38
CLBB	3B	29.702	1458x00001727y03	5.78
CLBB	8A	3.01	2008x02675579y08	5.6
CLBB	11B	7.649	4257x01603302y28	5.56
CLBB	13A	82.386	1280x04649786y13	3.72
CLBB	10A	81.13	1319x02797785y10	2.78
CLBB	7A	20.436	2008x06145570y09	2.72
CLBL	17B	105.893	1040x00751160y22	12.21
CLBL	3B	99.488	1566x03013491y03	11.25
CLBL	15B	4.27	3389x02348966y10	5.01
CLBL	N1B	9.468	2596x00000649y_new1?	4.37
CLBL	16B	76.2	1817x01982354y16	4.36
CLBL	7A	42.017	1001x07508457y24-20?	3.86
CLBL	5B	116.391	3429x04212727y05-29	3.66

CLBL	13A	26.69	1971x02525578y13	2.98
CLBL	11B	19.373	3970x00389595y11-16	2.93
CLBL	12A	8.626	2088x09859989y20-26	2.78
CLBL	4A	116.108	1695x00000674y04	2.52
F90	10A	19.698	3876x02356545y10-01	7.7
F90	16B	110.2	3250x00000103y16	7.46
F90	17B	3.484	1246x00002308y17?	6.37
F90	15B	16.18	4082x03562579y02	5.16
F90	1B	158.707	4250x00998082y01	4.96
F90	11B	58.165	2909x00731364y03	4.57
F90	3B	38.256	1166x00000197y03	4.34
F90	7A	92.235	2716x05003960y07	3.82
F90	2A	69.78	2889x02737315y02	3.46
F90	14A	69.821	1105x04160753y14	3.1
GDW	13A	65.4	1280x05291173y13	11.42
GDW	16B	25.9	3973x03258365y16	10.13
GDW	12A	40.797	3925x00000020y20	9.91
GDW	5B	102.57	3429x06153862y05	8.58
GDW	15B	7.102	4407x00000404y15	8.19
GDW	1B	121.358	3674x03083854y01	7.76
GDW	2A	32.724	3787x00013667y02	7.47
GDW	10A	56.111	2081x01071189y10	5.27
GDW	7A	28.84	1001x05433299y24-20?	4.78
GDW	4A	70.151	1584x00002712y04	4.14
GDW	18B	24.954	2090x00006093y18	3.54
GDW	17B	7.343	3859x02456260y17?	2.88
GDW	11B	16.697	4257x02761910y28	2.85
HUE	N1B	6.643	1677x00662628y_new1?	7.89
HUE	17B	107.778	1040x00001685y22	6.53
HUE	15B	0	3389x00000096y10	5.97
HUE	12A	81.539	1373x03202001y12	5.27
HUE	10B	0	3814x00000781y10?	5.06
HUE	8A	3.01	2008x02675579y08	4.97
HUE	13A	42.401	1971x01288377y13	4.71
HUE	18B	6.057	3165x00381645y18	4.36
HUE	3B	99.488	1566x03013491y03	4.27
HUE	7A	24.153	4480x08645627y20	3.7
HUE	11B	18.852	4261x00000223y11-16?	3.7
HUE	16B	29.9	3973x02785002y16	3
INT	17B	102.512	1040x01640629y22	17.41
INT	11B	23.425	3970x01479141y11	14.03
INT	12A	30.776	3641x00000918y20	8.46
INT	6B	2	1000x18028467y03	7.17
INT	3B	99.488	1566x03013491y03	6.85
INT	13A	50.329	1280x07886193y13	6.3
INT	5B	40.374	2002x01040887y05	6.18
INT	N1B	8.909	1677x00344122y_new1?	6.12
INT	16B	67.9	1480x02881548y16	5.83
INT	15B	4.27	3389x02348966y10	5.04
INT	8A	3.01	2008x02675579y08	4.91
INT	2A	137.257	3799x02552444y02	3.22
LCR	3B	99.488	1566x03013491y03	12.7
LCR	5B	110.058	3820x12285604y05-01	7.06
LCR	17B	6.813	3859x01678873y17?	3.58
LCR	1B	141.985	1352x00001128y01	3.56
LCR	10A	49.644	2081x03647444y10	3.43
LCR	15A	0	2314x00000190y15?	3.42
LCR	2A	9.892	3787x01244848y02	3.35
LCR	4A	68.072	2365x00000261y04?	3.26
LCR	12A	25.67	2088x12394310y20-26	3.15
LCR	7A	42.017	1001x07508457y24-20?	2.84
LCR	8A	3.01	2008x02675579y08	2.26
LN	1B	23.451	4329x01580735y25-19?	10.65
LN	5B	21.152	1337x00040546y05-01?	10.24
LN	7A	9.306	4336x00206179y09	7.2
LN	11B	98.222	2933x00163061y11	6.38
LN	14A	27.939	2646x05526174y14	6.16
LN	3B	0	1390x00004335y03	5.6

LN	10A	81.13	1319x02797785y10	4.27
LN	10B	0	3814x00000781y10?	3.83
LN	17B	33.14	3298x07083874y14-17?	3.06
LN	16B	7.8	1358x00000993y16	2.67
LN	2A	69.78	2889x02737315y02	2.52
SAT	17B	110.006	2587x00638488y22	12.05
SAT	3B	99.488	1566x03013491y03	5.45
SAT	5B	110.058	3820x12285604y05-01	4.91
SAT	2A	9.892	3787x01244848y02	4
SAT	16B	71.7	1480x03067042y16	3.83
SAT	12A	8.626	2088x09859989y20-26	3.77
SAT	4A	12.732	3378x00813776y17?	3.32
SAT	7A	42.017	1001x07508457y24-20?	3.28
SAT	N1B	10.022	1677x00000563y_new1?	2.99
TSW	17B	3.936	1071x00000000y17	10
TSW	12A	41.433	3886x00000019y20	9.91
TSW	4A	116.108	1695x00000674y04	9.78
TSW	11B	27.125	3970x01638657y11	7.28
TSW	3B	44.488	2389x00002079y03	6.19
TSW	7A	72.338	1895x02115964y07	4.88
TSW	5B	21.152	1337x00040546y05-01?	4.66
TSW	15A	11.828	2314x00276730y15?	4.46
TSW	15B	27.66	2888x00661124y20	3.3
TSW	10A	111.687	1850x00000087y01?	3.21
TSW	1B	111.293	3674x00000564y01	3.15
WI	10A	81.13	1319x02797785y10	7.18
WI	10B	0	3814x00000781y10?	6.42
WI	1B	23.451	4329x01580735y25-19?	6.14
WI	11B	98.222	2933x00163061y11	5.5
WI	3B	4.139	2624x00793489y03	4.61
WI	14A	27.939	2646x05526174y14	4.08
WI	5B	21.152	1337x00040546y05-01?	3.89
WI	7A	2.034	3654x01807732y09	3.51
WI	2A	75.535	4446x03992405y02	3.26

Annex 3. Selected QTLs (A= Additive effect and D= Dominance deviation)

Trait	LG	Position	Locus	LOD	mu_A	mu_H	mu_B	R^2.	A	D
AR-1	1B	23.451	4329x01580735y25-19?	7.69	2.50	2.52	2.31	11.30	0.09	0.11
AR-2	10B	0	3814x00000781y10?	6.91	2.51	2.27	2.31	9.90	0.10	-0.14
AR-3	3B	4.139	2624x00793489y03	6.85	2.41	2.57	2.41	9.80	0.00	0.17
AR-4	10A	81.13	1319x02797785y10	5.84	2.33	2.59	2.49	8.10	-0.08	0.18
AR-5		27.424	2646x05873208y14	5.4	2.45	2.28	2.36	7.40	0.05	-0.13
B-1	17B	50.867	3514x02963687y17-22?	8.88	64.66	66.71	65.68	14.70	-0.51	1.55
B-2	6B	0	1000x18124731y03	8.75	65.77	66.61	64.56	14.40	0.61	1.44
B-3	8A	48.923	1177x01531737y08	7.03	64.79	66.62	65.54	11.10	-0.37	1.45
B-4	16B	85.2	1817x00524034y16	6.14	63.90	64.36	66.43	9.40	-1.27	-0.80
B-5	10A	11.475	1522x02318859y10-01	5.49	65.41	66.38	64.92	8.30	0.25	1.22
B-6	14A	80.933	3298x04311780y14	5.03	66.23	63.71	64.10	7.50	1.07	-1.46
C1-1	17B	107.778	1040x00001685y22	17.3	16.52	13.24	12.96	21.60	1.78	-1.50
C1-2	3B	99.488	1566x03013491y03	14.19	16.27	14.06	13.21	16.20	1.53	-0.68
C1-3	11B	23.425	3970x01479141y11	11.52	13.92	13.15	15.56	12.30	-0.82	-1.59
C1-4	16B	76.2	1817x01982354y16	8.15	15.50	13.88	13.97	7.90	0.77	-0.86
C1-5	13A	42.401	1971x01288377y13	7.01	13.78	14.24	15.69	6.60	-0.96	-0.50
C1-6	1NB	5.491	1677x00813815y_new1?	6.88	15.61	14.85	13.86	6.50	0.87	0.11
C1-7	12A	4.048	2088x08915602y20-26	5.86	15.47	14.15	14.00	5.40	0.73	-0.59
C2-1	17B	105.893	1040x00751160y22	20.1	10.11	8.24	8.11	18.80	1.00	-0.87
C2-10	5B	36.645	2702x01725126y05-01?	6.44	9.55	9.04	8.67	4.20	0.44	-0.06
C2-11	6B	2	1000x18028467y03	5.59	9.24	8.53	8.97	3.50	0.13	-0.58
C2-2	11B	23.425	3970x01479141y11	16.44	8.32	8.27	9.89	13.90	-0.78	-0.84
C2-3	1NB	5.491	1677x00813815y_new1?	12.9	9.78	9.44	8.44	9.90	0.67	0.33
C2-4	16B	76.2	1817x01982354y16	8.58	9.66	8.90	8.55	5.90	0.55	-0.20
C2-5	3B	99.488	1566x03013491y03	7.59	9.64	8.86	8.58	5.10	0.53	-0.25
C2-6	13A	42.401	1971x01288377y13	7.48	8.62	8.90	9.59	5.00	-0.48	-0.21
C2-7	12A	28.244	2088x13511086y20-26	7.14	9.54	8.70	8.68	4.70	0.43	-0.41
C2-8	15B	4.27	3389x02348966y10	6.8	9.36	9.63	8.85	4.40	0.26	0.52
C2-9	2A	38.069	3787x00290282y02	6.65	8.59	9.03	9.63	4.30	-0.52	-0.08
C3-1	17B	105.893	1040x00751160y22	15.54	17.51	13.14	12.19	19.40	2.66	-1.71
C3-2	5B	110.058	3820x12285604y05-01	7.62	13.26	14.93	16.44	7.70	-1.59	0.09
C3-3	16B	71.7	1480x03067042y16	7.48	17.33	15.06	12.37	7.50	2.48	0.22
C3-4	3B	99.488	1566x03013491y03	6.49	16.53	14.55	13.17	6.40	1.68	-0.29
C3-5	13A	42.401	1971x01288377y13	6.19	13.46	15.01	16.23	6.00	-1.39	0.16
C3-6	1NB	6.643	1677x00662628y_new1?	5.72	16.11	14.73	13.59	5.50	1.26	-0.12
C3-7	7A	28.884	4480x06879032y20	5.1	16.15	14.37	13.55	4.80	1.30	-0.48
C4-1	17B	102.512	1040x01640629y22	16.09	27.26	21.07	20.38	19.50	3.44	-2.76
C4-2	16B	67.9	1480x02881548y16	9.22	27.16	23.14	20.48	9.30	3.34	-0.68
C4-3	5B	110.058	3820x12285604y05-01	7.15	21.80	23.75	25.84	6.80	-2.02	-0.07
C4-4	3B	99.488	1566x03013491y03	6.57	26.02	23.03	21.62	6.20	2.20	-0.79
C4-5	4A	12.732	3378x00813776y17?	6.38	22.46	26.44	25.18	6.00	-1.36	2.62
C4-6	13A	42.401	1971x01288377y13	5.86	21.95	23.59	25.69	5.40	-1.87	-0.23
C4-7	11B	13.915	4257x02376736y28	5.13	23.20	21.51	24.45	4.60	-0.63	-2.31
C4-8	15B	4.27	3389x02348966y10	5.1	24.25	26.23	23.40	4.60	0.43	2.41
C5-1	17B	102.512	1040x01640629y22	15.36	38.79	31.97	30.73	20.20	4.03	-2.79
C5-2	16B	67.9	1480x02881548y16	10.24	38.35	33.00	31.16	11.70	3.60	-1.76
C5-3	4A	12.732	3378x00813776y17?	7.58	33.37	38.29	36.15	8.10	-1.39	3.53
C5-4	5B	110.058	3820x12285604y05-01	5.85	32.67	34.76	36.85	6.00	-2.09	0.00
C5-5	12A	52.437	2127x02547840y12	5.18	36.15	32.90	33.37	5.20	1.39	-1.86
C6-1	17B	102.512	1040x01640629y22	9.53	43.15	38.55	37.40	11.90	2.88	-1.73
C6-2	12A	52.437	2127x02547840y12	9.04	42.11	37.83	38.44	11.10	1.84	-2.44
C6-3	4A	12.732	3378x00813776y17?	7.95	38.44	43.35	42.11	9.50	-1.84	3.07
C6-4	7A	116.223	2528x00000866y07?	7.28	41.77	38.18	38.78	8.50	1.50	-2.10
C6-5	16B	67.9	1480x02881548y16	6.84	43.26	39.60	37.28	7.90	2.99	-0.67
C6-6	15A	11.828	2314x00276730y15?	6.59	37.67	39.97	42.88	7.60	-2.60	-0.30
C6-7	5B	110.058	3820x12285604y05-01	6.26	38.51	41.67	42.04	7.10	-1.76	1.40
C6-8	3B	91.849	1566x01699753y03	5.21	42.16	39.47	38.39	5.80	1.89	-0.80
C7-1	15A	11.828	2314x00276730y15?	11.51	42.16	44.79	48.15	14.90	-3.00	-0.37
C7-2	12A	51.831	2127x02752418y12	9.77	46.70	42.90	43.61	12.00	1.55	-2.25
C7-3	7A	116.223	2528x00000866y07?	9.32	46.57	43.03	43.74	11.40	1.41	-2.12
C7-4	4A	12.732	3378x00813776y17?	8.79	43.36	47.63	46.95	10.60	-1.79	2.48
C7-5	16B	66.9	1480x02157515y16	6.57	47.61	44.74	42.70	7.40	2.46	-0.41

C7-6	5B	110.058	3820x12285604y05-01	6.45	43.87	46.66	46.44	7.30	-1.28	1.50
C7-7	17B	102.512	1040x01640629y22	5.74	46.93	44.35	43.38	6.40	1.78	-0.80
C7-8	3B	81.526	3784x00766461y03-16	5.69	46.89	44.28	43.42	6.30	1.73	-0.87
CA-1	1B	2.64	1611x00001980y25-19	9.35	9.61	8.25	9.95	16.30	-0.17	-1.53
CA-2	11B	60.805	1613x00171231y20	6.86	10.63	9.54	8.93	11.20	0.85	-0.24
CA-3	15A	0	2314x00000190y15?	6.83	9.77	8.56	9.79	11.20	-0.01	-1.22
CA-4	1NB	52.677	2465x01939388y_new1?	6.45	9.03	9.19	10.53	10.40	-0.75	-0.59
CA-5	3B	99.488	1566x03013491y03	6.39	8.90	9.37	10.65	10.30	-0.88	-0.41
CB-1	2A	9.892	3787x01244848y02	8.32	21.92	23.42	20.19	12.50	0.86	2.37
CB-2	17B	107.778	1040x00001685y22	7.76	23.02	19.78	19.09	11.50	1.96	-1.28
CB-3	18B	9.784	1279x01833829y18	7.5	18.45	22.05	23.66	11.10	-2.60	1.00
CB-4	15B	0	3389x00000096y10	7.49	21.81	23.50	20.30	11.00	0.76	2.45
CB-5	1NB	6.643	1677x00662628y_new1?	6.38	22.59	20.50	19.52	9.10	1.53	-0.55
CB-6	3B	29.702	1458x00001727y03	5.78	21.93	22.89	20.18	8.20	0.88	1.84
CB-7	8A	3.01	2008x02675579y08	5.6	21.36	23.29	20.74	7.90	0.31	2.24
CB-8	11B	7.649	4257x01603302y28	5.56	19.52	21.97	22.59	7.80	-1.54	0.91
CL-1	17B	105.893	1040x00751160y22	12.21	50.49	44.24	43.17	16.20	3.66	-2.60
CL-2	3B	99.488	1566x03013491y03	11.25	50.17	45.45	43.49	14.60	3.34	-1.38
CL-3	15B	4.27	3389x02348966y10	5.01	47.47	49.36	46.20	5.50	0.64	2.53
F9-1	10A	19.698	3876x02356545y10-01	7.7	87.47	85.27	84.22	14.40	1.62	-0.58
F9-2	16B	110.2	3250x00000103y16	7.46	85.42	83.27	86.27	13.90	-0.43	-2.58
F9-3	17B	3.484	1246x00002308y17?	6.37	85.95	88.09	85.74	11.50	0.10	2.25
F9-4	15B	16.18	4082x03562579y02	5.16	86.62	87.37	85.07	9.10	0.78	1.53
G-1	13A	65.4	1280x05291173y13	11.42	3888.49	4690.63	5881.81	15.50	-996.66	-194.52
G-2	16B	25.9	3973x03258365y16	10.13	5696.82	4517.09	4073.48	13.30	811.67	-368.06
G-3	12A	40.797	3925x00000020y20	9.91	5249.90	5835.96	4520.40	12.90	364.75	950.81
G-4	5B	102.57	3429x06153862y05	8.58	5240.82	3789.68	4529.48	10.80	355.67	-1095.47
G-5	15B	7.102	4407x00000404y15	8.19	5175.90	3937.22	4594.40	10.20	290.75	-947.93
G-6	1B	121.358	3674x03083854y01	7.76	5248.97	5775.51	4521.33	9.60	363.82	890.36
G-7	2A	32.724	3787x00013667y02	7.47	4315.75	4357.89	5454.55	9.20	-569.40	-527.26
G-8	10A	56.111	2081x01071189y10	5.27	4402.18	5395.47	5368.12	6.10	-482.97	510.32
H-1	1NB	6.643	1677x00662628y_new1?	7.89	141.54	139.19	138.60	12.30	1.47	-0.88
H-2	17B	107.778	1040x00001685y22	6.53	141.52	138.72	138.61	9.80	1.46	-1.35
H-3	15B	0	3389x00000096y10	5.97	140.86	141.61	139.27	8.80	0.79	1.55
H-4	12A	81.539	1373x03202001y12	5.27	138.48	140.38	141.65	7.70	-1.59	0.31
H-5	10B	0	3814x00000781y10?	5.06	141.40	140.11	138.73	7.30	1.33	0.05
I-1	17B	102.512	1040x01640629y22	17.41	19.69	15.72	14.93	21.30	2.38	-1.59
I-10	15B	4.27	3389x02348966y10	5.04	17.81	18.66	16.81	4.40	0.50	1.35
I-2	11B	23.425	3970x01479141y11	14.03	15.51	15.27	19.11	15.60	-1.80	-2.04
I-3	12A	30.776	3641x00000918y20	8.46	18.81	16.44	15.82	8.10	1.49	-0.87
I-4	6B	2	1000x18028467y03	7.17	17.10	15.41	17.52	6.70	-0.21	-1.90
I-5	3B	99.488	1566x03013491y03	6.85	18.65	16.91	15.97	6.30	1.34	-0.40
I-6	13A	50.329	1280x07886193y13	6.3	16.35	15.93	18.27	5.70	-0.96	-1.38
I-7	5B	40.374	2002x01040887y05	6.18	18.47	17.47	16.15	5.60	1.16	0.16
I-8	1NB	8.909	1677x00344122y_new1?	6.12	18.29	17.83	16.33	5.50	0.98	0.52
I-9	16B	67.9	1480x02881548y16	5.83	17.91	15.70	16.71	5.20	0.60	-1.61
LC-1	3B	99.488	1566x03013491y03	12.7	44.50	77.58	98.48	22.10	-26.99	6.09
LC-2	5B	110.058	3820x12285604y05-01	7.06	82.36	52.78	60.62	10.60	10.87	-18.71
LN-1	1B	23.451	4329x01580735y25-19?	10.65	1.92	1.95	1.85	17.30	0.03	0.06
LN-2	5B	21.152	1337x00040546y05-01?	10.24	1.83	1.86	1.94	16.50	-0.06	-0.03
LN-3	7A	9.306	4336x00206179y09	7.2	1.93	1.91	1.84	10.70	0.05	0.03
LN-4	11B	98.222	2933x00163061y11	6.38	1.93	1.91	1.85	9.30	0.04	0.03
LN-5	14A	27.939	2646x05526174y14	6.16	1.90	1.84	1.87	8.90	0.02	-0.05
LN-6	3B	0	1390x00004335y03	5.6	1.88	1.94	1.90	8.00	-0.01	0.05
RB-1	1B	105.565	3849x00000554y01	10.23	9275.23	9839.58	7433.48	15.10	920.87	1485.22
RB-2	2A	32.724	3787x00013667y02	10.19	7430.68	6944.47	9278.03	15.10	-923.67	-1409.88
RB-3	12A	40.797	3925x00000020y20	8.41	8532.31	10182.00	8176.41	11.90	177.95	1827.61
RB-4	16B	34.4	3973x01564250y16	7.58	10125.80	8480.01	6582.96	10.50	1771.40	125.66
RB-5	13A	60.918	1280x06695922y13	7.21	7107.50	8499.02	9601.21	9.80	-1246.85	144.66
RB-6	7A	29.425	1001x05158048y24-20?	7.1	7387.32	7435.32	9321.39	9.70	-967.03	-919.04
RB-7	18B	24.954	2090x00006093y18	6.12	9680.62	7685.74	7028.10	8.10	1326.26	-668.61
RB-8	5B	102.57	3429x06153862y05	5.81	9108.50	7169.48	7600.22	7.70	754.14	-1184.87
S-1	17B	110.006	2587x00638488y22	12.05	14.24	11.45	10.07	19.40	2.08	-0.71
S-2	3B	99.488	1566x03013491y03	5.45	13.45	11.71	10.86	7.40	1.30	-0.45
T-1	17B	3.936	1071x00000000y17	10	1.54	1.85	1.84	19.20	-0.15	0.16
T-2	12A	41.433	3886x00000019y20	9.91	1.57	1.48	1.80	18.90	-0.11	-0.21
T-3	4A	116.108	1695x00000674y04	9.78	1.77	1.98	1.61	18.60	0.08	0.29
T-4	11B	27.125	3970x01638657y11	7.28	1.79	1.50	1.58	13.00	0.10	-0.19

T-5	3B	44.488	2389x00002079y03	6.19	1.58	1.51	1.80	10.70	-0.11	-0.18
W-1	10A	81.13	1319x02797785y10	7.18	1.75	1.85	1.81	13.40	-0.03	0.08
W-2	10B	0	3814x00000781y10?	6.42	1.82	1.73	1.74	11.70	0.04	-0.05
W-3	1B	23.451	4329x01580735y25-19?	6.14	1.80	1.83	1.75	11.20	0.02	0.05
W-4	11B	98.222	2933x00163061y11	5.5	1.81	1.81	1.74	9.80	0.04	0.03