



Genotype and genotype-by-environment interaction effects for grain yield and grain size of quinoa (*Chenopodium quinoa* Willd.) as revealed by pattern analysis of international multi-environment trials

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Abstract

The size and nature of the genotype (G) and genotype \times environment (G \times E) interaction effects for grain yield, its physiological determinants, and grain size exhibited by the Andean grain crop quinoa at low latitudes were examined in a multi-environment trial involving a diverse set of 24 cultivars tested in 14 sites under irrigation across three continents. These environments included a wide latitudinal (from 21°30'N to 16°21'S), altitudinal (from 5 to 3841 m a.s.l.) and temperature (average daily temperatures during crop cycle varied from 9 to 22.1 °C) range; while average daily photoperiods exhibited a smaller variation, from 11.2 to 12.8 h. The G \times E interaction to G component of variance ratio was 4:1 and 1:1 for grain yield and grain size, respectively. Two-mode pattern analysis of the environment-standardised matrix of grain yield revealed four genotypic groups of different response pattern across environments. This clustering, which separates cultivars from mid-altitude valleys of the northern Andes, northern altiplano, southern altiplano and sea level, showed a close correspondence with adaptation groups previously proposed. The results of the genotype clustering can be used to choose genotypes of contrasting relative performance across environments for further studies aimed at assessing the opportunity to select for broad or specific adaptation. Classification of sites for grain yield grossly discriminated between cold highland sites, tropical valleys of moderate altitude, and warmer, low altitude sites. As expected from the size of the G \times E interaction component, no single genotype group showed consistently superior grain yield across all environment groups. The G and G \times E interaction effects observed for the duration of the crop cycle had a major influence on the average cultivar performance and on the form of G \times E interactions observed for total above-ground biomass and grain yield. Although different environment types showed contrasting effects on the physiological attributes underlying grain yield variation among cultivars, it was observed that good average performance and broad adaptation could come from the combination of medium-late maturity and high harvest index. Correlation analysis revealed no association between the average cultivar responses for grain yield and grain size. Three-mode pattern analysis have

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also shown no association between the $G \times E$ interaction effects for both traits. Both observations indicate that simultaneous progress for grain yield and grain size can be expected from selection.

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1. Introduction

The Andean grain crop quinoa (*Chenopodium quinoa* Willd.) has received increasing attention in the last decades because of its high nutritive value (Ruales and Nair, 1992) and its capacity to grow under conditions of extreme aridity and low temperatures, as those experienced in the highlands of the central Andes of Bolivia, Peru, Chile, and Argentina (Tapia et al., 1979). This species is cultivated over a range of almost 50° in latitude, from southern Colombia to southern Chile (Wilson, 1990) and over a large altitudinal range, from over 4000 m as in Bolivia to almost sea level in Chile. Recently, it has been evaluated as a new crop outside its original areas of cultivation (Risi and Galwey, 1989; Johnson and Ward, 1991; Jacobsen and Stolen, 1993).

Grain yield and grain size, a determinant of its commercial quality, are frequently used as selection criteria for quinoa breeding. The Andean quinoa agricultural system has been identified as an extremely complex population of environments in terms of the diversity of the environmental factors affecting crop yield and quality across the toposequence and latitudinal range (Grace, 1985; Aguilar and Jacobsen, 2003). Quinoa breeding is mainly conducted on a local basis and exploits local adaptation to narrowly defined target areas, i.e. the environmental variation generated by the topographical and latitudinal range creates a need for genotypes with different characteristics within relatively small areas (Aguilar and Jacobsen, 2003). As a consequence of this, the species exhibits a strong variability for cultivar-specific responses to environmental variation, i.e. large genotype \times environment ($G \times E$) interactions for grain yield and size are observed when a diverse set of cultivars is evaluated in multi-environment trials (i.e. Ballón et al., 1991; Risi and Galwey, 1991). $G \times E$ interaction results when there is a change in the relative performance of genotypes across environments and

has the potential to influence the nature and magnitude of the selection response achieved by a breeding program (Cooper and DeLacy, 1994). The highly variable quinoa genotype–environment system is suitable for maintaining a high degree of biodiversity through in situ conservation (Ceccarelli, 1996), but complicates the identification of superior genotypes for target environments, potentially limiting future genetic progress. Consideration of the impact of $G \times E$ interactions on selection is central to assess the relative merits of different breeding strategies aimed at developing improved varieties for traditional and new quinoa growing environments.

The germplasm developed by locally-focussed breeding programs can be used to exploit specific adaptation to widely occurring environment types, as characterised by particular types of stress, management systems, etc. However, the identification of useful sources of specific adaptation requires a more extensive and precise testing than that normally conducted by locally-based breeding programs (see discussion in Atlin et al. (2001)). There is also no strong evidence to suggest that it is not possible to recombine some of the components of specific adaptation shown by the quinoa germplasm base in a way that contributes to an improvement in broad adaptation. Some understanding of the nature and magnitude of the G and $G \times E$ interaction effects on grain yield and size in the quinoa target population of environments would lead to a more accurate formulation of appropriate breeding strategies for selecting for broad and/or specific adaptation to different target environments.

The focus of the present study is to investigate the implications of $G \times E$ interactions for genetic improvement of grain yield and grain size of quinoa in low-latitude environments. Grain size (maximum diameter) is a relevant determinant of commercial quality in this species. Observation and interpretation of patterns of genotype adaptation in multi-environment

trials provide the stimulus for the investigations into the magnitude, nature and underlying causes of $G \times E$ interactions. The variance components estimated from the combined analysis of variance can be used to judge the relative magnitude of G and $G \times E$ interaction variances and predict the response to selection for broad adaptation. When $G \times E$ interactions account for a large proportion of variation among genotypes, this suggests complex $G \times E$ interactions that warrant further investigation (Cooper and DeLacy, 1994). Many methods have been proposed for extraction and interpretation of patterns of $G \times E$ interaction (DeLacy et al., 1996). Pattern analysis (Williams, 1976), the complementary use of classification and ordination, attempts to: (i) identify genotypes that have similar patterns of response across a range of environments; (ii) environments that are similar in the manner in which they discriminate among genotypes (DeLacy et al., 1996; Chapman et al., 1997). The characterisation of variation for genotypic adaptation from these analyses provides a sound basis for selection decisions (Cooper and DeLacy, 1994).

Better knowledge of the physiological basis for the differential responses of genotypes to specific environments should contribute to the formulation of ideotype-based selection criteria that improve the overall efficiency of a selection strategy (Wright et al., 1996). A useful physiological framework to investigate environmental and genotypic effects on crop performance defines crop yield as the product of total biomass produced and the fraction of that biomass partitioned to harvestable yield, i.e. harvest index (Charles-Edwards, 1982). Combining these physiological attributes with economic traits, such as yield and quality, to assess relative genotype response across environments leads to a three-way dataset of genotype \times environment \times attributes. A three-mode principal component analysis (PCA) (Tucker, 1966; Kroonenberg, 1983), an extension of standard PCA to handle three-way datasets, has been used for handling genotypes, environments and attributes simultaneously (Kroonenberg and Basford, 1989; Crossa et al., 1995; de la Vega et al., 2002). Thus, allowing an examination of the relationships between genotypes and attributes associated with specific patterns of environmental variability.

In this study we applied combined analysis of variance and two- and three-mode pattern analysis to

three subsets of trial data selected from the European and American Test of Quinoa Cultivars (Mujica et al., 2001), an international multi-environment trial in which a set of genetically diverse cultivars was tested in several countries. The objectives are: (1) to examine the relative size of components of variance for G and $G \times E$ interaction for grain yield, time to physiological maturity, above-ground biomass, harvest index, and grain size; (2) to group quinoa cultivars according to their relative responses to testing environments for grain yield, to group environments according to the way they discriminate among cultivars, and to contribute to a definition of a reference set of genotypes (Fox and Rosielle, 1982) which could be used to investigate differences among environments; (3) to investigate the biological basis of the observed G and $G \times E$ interaction effects for grain yield in terms of the genotype-specific responses for phenology, biomass and harvest index; (4) to examine the prospects for improving grain yield and grain size simultaneously in the selection process.

2. Materials and methods

2.1. International trial dataset

A set of 24 cultivars of quinoa was tested in 14 sites across three continents during the growing season 1998/1999 (Tables 1 and 2). Of the original 25 sites (Mujica et al., 2001), only those where at least yield data for all cultivars were available were selected. Thus, environments outside the tropics, where most Andean cultivars failed to produce yield, were excluded from the analyses. Quinoa cultivars can be classified into five major adaptation groups (Tapia et al., 1979):

- *valley type*: from the Andean valleys in Peru, Bolivia, Colombia and Ecuador, where quinoa is grown between 2000 and 4000 m;
- *altiplano type*: from high altitudes (ca. 4000 m) of the highlands (altiplano) around lake Titicaca in Peru and Bolivia;
- *salares type*: from the salt flats in the southern Bolivian altiplano, resembling the altiplano type but differing in having greater tolerance to saline stress;

Table 1

Agronomic characters of 24 cultivars of quinoa evaluated in 14 international trial environments during 1998/1999

Code	Cultivar	Origin	Adaptation group	Time to physiological maturity (days)	Grain yield (g m ⁻²)	Grain size (mm)	Above-ground biomass (g m ⁻²)	Harvest index
1	CICA-127	Peru	Valley	146.1	186.3	2.0	998.8	0.25
2	CICA-17	Peru	Valley	143.8	216.8	2.1	931.8	0.31
3	Huariponcho	Peru	Altiplano	135.1	204.9	1.8	721.4	0.33
4	Kancolla	Peru	Altiplano	133.6	192.9	1.8	727.2	0.31
5	Nariño	Colombia	Valley	156.5	198.0	1.9	1209.9	0.20
6	Salcedo	Peru	Altiplano	129.5	190.6	2.0	831.0	0.27
7	Ratuqui	Bolivia	Altiplano	126.1	161.4	2.1	568.8	0.29
8	Kamiri	Bolivia	Altiplano	133.1	165.8	2.1	827.5	0.24
9	Real	Bolivia	Salar	124.4	135.4	2.2	553.7	0.34
10	Jujuy	Argentina	Altiplano	127.9	155.9	2.0	619.0	0.28
11	Baer-II	Chile	Sea level	123.5	130.6	1.8	574.9	0.25
12	RU-2-PQCIP	UK	Sea level	105.8	113.3	1.8	467.2	0.32
13	RU-5-PQCIP	UK	Sea level	110.3	136.3	1.8	601.9	0.31
14	NL-6-PQCIP	Holland	Sea level	113.1	112.6	1.8	467.1	0.33
15	E-DK-4-PQCIP	Denmark	Sea level	109.7	111.1	1.9	513.0	0.28
16	G-205-95-PQCIP	Denmark	Sea level	107.4	115.8	1.9	498.2	0.30
17	Sayaña	Bolivia	Altiplano	126.9	174.4	2.1	669.4	0.26
18	Ingapirca	Ecuador	Valley	140.8	183.5	1.8	835.7	0.27
19	03-21-079BB	Peru	Altiplano	134.6	257.4	1.8	878.2	0.33
20	03-21-072RM	Peru	Altiplano	135.4	206.8	1.8	1124.7	0.27
21	ECU-420	Ecuador	Valley	156.4	185.6	1.8	1026.4	0.24
22	02-Embrapa	Brazil	Sea level	120.2	122.5	1.9	492.1	0.30
23	Canchones	Chile	Altiplano	117.9	119.7	2.1	466.1	0.33
24	Illpa	Peru	Altiplano	130.3	167.2	2.1	806.2	0.27

Values of agronomic traits are means of 14 (grain yield), 10 (time to physiological maturity), 8 (grain size), or 9 (above-ground biomass and harvest index) trials.

- *sea-level type*: grown at low altitudes in central and southern Chile;
- *subtropical type*: a late flowering material from the Yungas (low altitude humid valleys) in Bolivia.

Cultivars from four of these adaptation groups were included in the trial (Table 1). Cultivar selection was based on diversity of origin and wide distribution. They originated from different breeding programs, and a short description of their pedigree follows. Cultivars CICA-17 and CICA-127 were selected from the local variety Amarilla de Maranganí at Centro de Investigaciones en Cultivos Andinos (CICA), Cuzco, Peru. Nariño, though originally from the region of Pasto, Southern Colombia, was also selected for adaptation to the conditions of Cuzco. The other two valley-type cultivars, Ecu-420 and Ingapirca, were selected at Instituto Nacional de Investigaciones Agropecuarias (INIAP), Quito, Ecuador for cultivation at mid-altitude

valleys. Cultivars Huariponcho, Kancolla, Salcedo, 03-21-079BB, 03-21-072RM and Illpa were selected at Instituto Nacional de Investigaciones Agrarias (INIA), Puno, Peru from local cultivars (Peruvian coast of lake Titicaca) or crosses between them. Cultivar Jujuy, although derived from a local landrace collected at Purmamarca (province of Jujuy, Argentina) was selected in Puno, Peru. Cultivars Ratuqui, Kamiri and Sayaña were selected for the Central Bolivian Altiplano at Estación Experimental Patacamaya, Instituto Boliviano de Tecnología Agropecuaria (IBTA). Real is a cultivar selected from landraces collected at Salar de Uyuni, southern Bolivia. Canchones was selected at Universidad Arturo Prat, Iquique, Chile, from materials originating in the Chilean Altiplano. Baer-II was selected at Temuco (Semillas Baer, Temuco, Chile). Cultivars RU-2, RU-5, NL-6, E-DK-4 and G-205-95 were donated by the Danish International Development Agency (DANIDA). These lines

Table 2
International trial environments where the set of 24 genotypes of quinoa was evaluated

Code	Location	Country	Latitude	Altitude a.s.l. (m)	Mean daily temperature (°C)	Mean photoperiod (h)	Sowing month	Time to physiological maturity (days)	Grain yield (g m ⁻²)	Grain size (mm)	Above-ground biomass (g m ⁻²)	Harvest index
1	Salcedo	Peru	15°50'S	3822	10.2	12.7	October	160.5	172.2	2.0	841.4	0.31
2	Huancayo	Peru	12°00'S	3212	–	–	October	–	116.5	1.9	357.8	0.29
4	Alto Catacha	Peru	15°24'S	3841	14.7	12.7	October	163.0	165.0	–	–	–
5	Sutuca	Peru	15°24'S	3841	14.5	12.6	October	168.5	169.9	–	–	–
6	Cuzco	Peru	14°10'S	3485	12.2	12.8	October	136.1	334.3	2.1	1207.8	0.29
7	Arequipa	Peru	16°21'S	1441	16.0	12.8	October	131.2	153.0	1.8	–	–
8	Cajamarca	Peru	7°9'S	2667	–	–	–	–	71.6	–	–	–
9	Ayacucho	Peru	13°15'S	2760	–	–	November	–	69.3	–	–	–
10	Brasilia	Brazil	15°35'S	1007	22.1	12.0	July	115.9	239.1	1.8	915.3	0.26
13	Choquenaira	Bolivia	16°03'S	3816	–	–	–	–	229.1	–	674.6	0.33
14	Belén	Bolivia	16°03'S	3816	9.0	12.4	October	159.2	91.1	–	245.5	0.37
19	Gia Loc	Vietnam	21°30'N	5	21.9	11.2	October	90.9	121.9	1.7	781.3	0.16
23L	Nairobi L	Kenya	1°15'S	1819	18.9	12.4	March	77.1	209.7	2.1	698.7	0.31
23S	Nairobi S	Kenya	1°15'S	1819	18.2	11.7	October	84.5	158.3	2.0	806.5	0.25

Location code numbers are the same as those in the original report (Mujica et al., 2001). Nairobi L and Nairobi S are crops grown during the long (L) and short (S) rainy season in that environment (Maurice, 2001). Crop duration is expressed as days from sowing to maturity. Temperature and photoperiod data are means for that period. Agronomic traits are means for the 24 cultivars.

were selected from materials of a breeding program started at Cambridge University, UK, and can be considered as predominantly sea-level type (N. Galwey, University of Cambridge, personal communication). Finally, 02-Embrapa was selected at Empresa Brasileira de Pesquisa Agropecuaria (Embrapa), Brasilia, Brazil for adaptation to the Brazilian Cerrados, from late flowering lines that were obtained by diallelic crosses between valley-, altiplano- and sea-level type cultivars at Cambridge University (C. Spehar, Embrapa, personal communication). The sites included in the analysis were mostly located within university experimental fields or government agricultural research stations, and covered a wide range of environmental conditions, from almost sea level (Gia Loc, Vietnam) to over 3800 m (Salcedo, Peru), and from the Equator (Nairobi) to 21° of latitude (Gia Loc). One experiment (Alto Catacha) was grown under a raised field agriculture system (Waru Waru), a pre-Columbian technique similar to the Mexican chinampas, a method that creates a slightly warmer microclimate thereby protecting crops from the killing frost of the harsh altiplano nights (Sanchez de Losada et al., 1998). Average daily temperatures during crop cycle ranged from 9 to 22.1 °C, and photoperiods from 11.2 to 12.8 h (Table 2).

In each experiment, a randomised complete block design with four replicates was used. Plots size was 4 rows × 4 m, with an inter-row spacing of 0.5 m. Seeds were sown at a 10 kg ha⁻¹ rate, and thinned after sowing to reach a final density of 280 000 plants ha⁻¹. Crops received supplementary irrigation; nutrient deficiencies were prevented with fertilisation when necessary; and weeds and insect pests were controlled. The experimental protocol for the trial was the same for all sites. Thus, genotype × management interactions are not expected to be observed in this genotype–environment system. Grain yield (14 sites) and its determinants, i.e. above-ground biomass and harvest index (9 sites), at physiological maturity (defined as the date when seeds from the main panicle become resistant when pressed) were determined by hand harvesting of an area of 3 m² (two central rows, discarding 0.5 m at each border). Yield and yield determinants data (g m⁻²) are expressed on a dry weight basis. Harvest index was calculated for each sample as the ratio of grain dry matter to above-ground dry matter. Seed size (mm) was determined at eight

sites as the average of the maximum width of a random sample of 20 seeds in each replicate plot. When available, temperature data were collected from the nearest meteorological station, located within each experimental station.

2.2. Analysis of variance and two-mode pattern analysis of grain yield

The G and G × E interaction components of variance and their standard errors for grain yield, grain size, time from sowing to physiological maturity, above-ground biomass and harvest index were estimated from the genotype–environment means by residual maximum likelihood (REML) (Patterson and Thompson, 1975) using GENSTAT (2002). In the linear mixed model used, the cultivars evaluated in the international multi-environment trial were assumed to be a random sample of the current genetic variability, and therefore G and G × E interaction terms in the model were defined as random effects, $\sim\text{NID}(0, \sigma_g^2)$ and $\sim\text{NID}(0, \sigma_{ge}^2)$, respectively. Trial locations were considered fixed effects because, for most of traits analysed, less than 10 degrees of freedom were available for this term. This does not allow proper checking of the distributional assumptions for terms defined as random (van Eeuwijk, 1995). The best linear unbiased predictors (BLUPs) (Robinson, 1991) for the genotypic effects were computed from this analysis and used further as estimates of the average-genotype responses for the traits analysed.

Pattern analysis (Williams, 1976) was applied to the environment-standardised two-way (cultivar × environment) array of means for grain yield. The matrix was centred by removal of trial grand mean and normalised by division of the remainder by the within-environment standard deviation (Fox and Rosielle, 1982; Cooper and DeLacy, 1994). For classification, a hierarchical agglomerative clustering method (Williams, 1976) with incremental sum of squares (Ward, 1963) as the fusion criterion was utilised. The squared Euclidean distance was used as the dissimilarity measure for Ward's method. A dendrogram was constructed on the basis of fusion level to investigate similarities in pattern of performance among cultivars (in terms of their relative responses to environments) and environments (in terms of the way they influence the relative performance of the cultivars).

Given that grain yield is the most important economic trait, we used the grouping derived from cluster analysis of this attribute to interpret the results of the three-mode analyses, which also include other traits. The principal components of the squared Euclidean distance matrix of grain yield were estimated using a singular value decomposition procedure and a biplot of the first two principal components was constructed from this analysis (Gabriel, 1971).

2.3. Three-mode principal component analysis

Two subsets of trials were used to construct $24 \times 7 \times 4$ and $24 \times 8 \times 2$ three-mode, three-way (Carroll and Arabie, 1983) $G \times E \times A$ arrays of means for grain yield, time to physiological maturity, above-ground biomass and harvest index, and grain yield and grain size, respectively. These subsets were constructed using data from those sites for which this information was available. The three-mode three-way methodology is needed as each data point represents a measurement on a certain attribute of a particular genotype in a given environment and these data are not condensed or modified by re-expressing them as proximity measures (Cooper et al., 2001). Three-mode principal component analyses (PCA) (Kroonenberg, 1983) were conducted on the $G \times E \times A$ environment-standardised residual arrays using the program TUCKALS3¹ (Kroonenberg, 1994).

This procedure derives components, i.e. linear combinations of the levels of the modes, for each of the three modes. It can be assumed that these components together contain the only relevant systematic variation of the three-way array dataset. In this model each mode is allowed to have a different number of components. The number of components for each mode needs to be simultaneously determined for all modes. Therefore, several solutions have to be inspected to come to an adequate description of a dataset (Kroonenberg, 1983, chapter 2).

Prior to three-mode PCA, the three-way arrays of means ($G \times E \times A$) were centred within attributes by subtracting both the across-genotypes environment means and the across-environments genotype means, and adding the overall mean (residual from additivity,

Gabriel, 1978), as in the additive main effects and multiplicative interaction (AMMI) model for two-way tables (Gauch, 1988). This type of centring, in which both genotypic and environmental effects are removed from the data, and the $G \times E$ and $G \times E \times A$ interaction terms remain, allows the derivation of environmental components that explain different sources of $G \times E$ interaction (de la Vega et al., 2002). Next, the residual arrays were normalised within environments (Fox and Rosielle, 1982; Cooper and DeLacy, 1994).

It is very instructive to investigate the component loadings of the genotypes jointly with the component loadings of the attributes, by projecting them together in one space, as it then becomes possible to display the interaction between genotypes and attributes. The plot of the common space is called a joint biplot, a variant of Gabriel's (1971) biplot (Kroonenberg, 1983; Basford et al., 1996).

3. Results

3.1. Genotype and genotype \times environment interaction effects for grain yield

Strong across-cultivar and across-environment variations were found for grain yield, its physiological determinants, and grain size (Tables 1 and 2). For grain yield, the $G \times E$ interaction component of variance was four times larger than the genotypic component (Table 3). Both yield determinants, i.e. biomass and harvest index, also showed a large $G \times E$ interaction to G component of variance ratio. For time from sowing to physiological maturity the G variance component was 1.7 times larger than the $G \times E$ interaction variance component, while both components of variance for grain size were of similar magnitude (Table 3).

Cluster analysis of the environment-standardised matrix of grain yield showed that the 24 cultivars evaluated could be separated into four groups of different response patterns across environments (Fig. 1A). This truncation retained about 70% of the genotype sums of squares. Group 4 (G4), the last to join on the dendrogram, consisted of six entries corresponding to the sea-level type, which is composed of early-flowering genotypes grown at low altitudes in southern Chile or selected from materials of that origin. At the next join, Group 1 (G1) consisted

¹ This program can be obtained from Dr. Pieter Kroonenberg: <http://www.fsw.leidenuniv.nl/~kroonenb>.

Table 3

Estimates of components of variance (\pm S.E.) for the analysis of variance of grain yield (g m^{-2}), grain size (mm), time from sowing to physiological maturity (days), total biomass (g m^{-2}), and harvest index measured on 24 cultivars of quinoa evaluated in an international multi-environment trial

Trait	Locations	Source of variance	
		Genotype	Genotype \times environment
Grain yield	14	1216 \pm 462	4870 \pm 398
Grain size	8	0.0140 \pm 0.0047	0.0157 \pm 0.0018
Time to physiological maturity	10	186.8 \pm 58.3	110.7 \pm 10.9
Total biomass	9	38986 \pm 14445	88920 \pm 9271
Harvest index	9	0.00003 \pm 0.0004	0.0113 \pm 0.0012

of four cultivars classified as valley type. These are tall and late-flowering materials. At the last join, Group 2 (G2) and Group 3 (G3) were mostly composed of cultivars previously classified as altiplano type, from the Peruvian and Bolivian–Chilean Altiplano, respectively, with the exception of Ingapirca and 02-Embrapa. Altiplano-type genotypes are grown at high altitudes (ca. 4000 m) in Peru, Bolivia and Chile and are earlier-flowering than the valley-type cultivars.

The classification of environments for grain yield gave rise to four groups, with a truncation retaining about 75% of the environment sums of squares (Fig. 1B). This clustering grossly discriminated between cold highland sites (E1), tropical valleys of moderate altitude (E2, E3), and warmer, low altitude sites (E4). E1 included most of the altiplano sites, with altitudes above 3400 m, with the exception of Ayacucho. Reported average temperatures during crop cycle for environments in this group ranged from 9.0 to 14.7 °C and had the longest crop durations (Table 2). E2 and E3 include two inter-Andean valley sites (Huancayo and Cajamarca) and the Kenya sites. Arequipa (E3) is considered a coastal environment (Soldevilla et al., 2001). The shortest crop durations reported are associated with E2, i.e. the two Nairobi trials. The last group (E4) included the two warmest locations, Brasilia and Gia Loc, situated at low altitudes, but also included a Peruvian altiplano site, Sutuca.

As expected from the domination of the dataset by G \times E interactions, no single genotype group was identified to show consistently superior grain yield across all environment groups. G1 (valley cultivars) showed its best performance in the valley sites (E2), above-mean yield in E1 (altiplano sites) and below-mean yields in E3 and E4. G2 (Peruvian altiplano

cultivars) performed best at E1 and E4, but exhibited a poorer performance in E2 and E3. G3 (Bolivian altiplano cultivars) had a below-mean performance in most environments, with the exception of E4; G4 (sea level cultivars) showed the highest relative yields at E3 (Arequipa and Cajamarca).

The results of the ordination analysis of grain yield are presented in the biplot of the first and second principal components (Fig. 2), which together accounted for 64% of the G and G \times E interaction variation of the system. The environment vectors covered a wide range of Euclidean space, which is consistent with the strong G \times E interaction effect revealed by REML analysis (Table 3). The angle between the vectors of the environments on the biplot ranged from small positive values (i.e. Belén cf. Choquenaira) to values close to 180° (i.e. Arequipa cf. Salcedo). This range in angles indicated that the correlations between the environment-standardised grain yields for the genotypes in individual environments ranged from strongly positive to strongly negative values.

Environments that were grouped together by the cluster analysis (Fig. 1B) were co-located on the biplot (Fig. 2). The first principal component (41% of the variation) appears to be associated with the strong contrast between E1 and E3 in the way they influence the relative performance of the cultivars evaluated. The maximum angle among the vectors of the sites of E1 is smaller than 90°, corresponding to Ayacucho and Alto Catacha in Fig. 2. This suggests that these environments are relatively similar in the manner they discriminate among genotypes. G2 and G1 cultivars are positively associated with E1 sites and tend to be on the left-hand side of the diagram. G4 cultivars

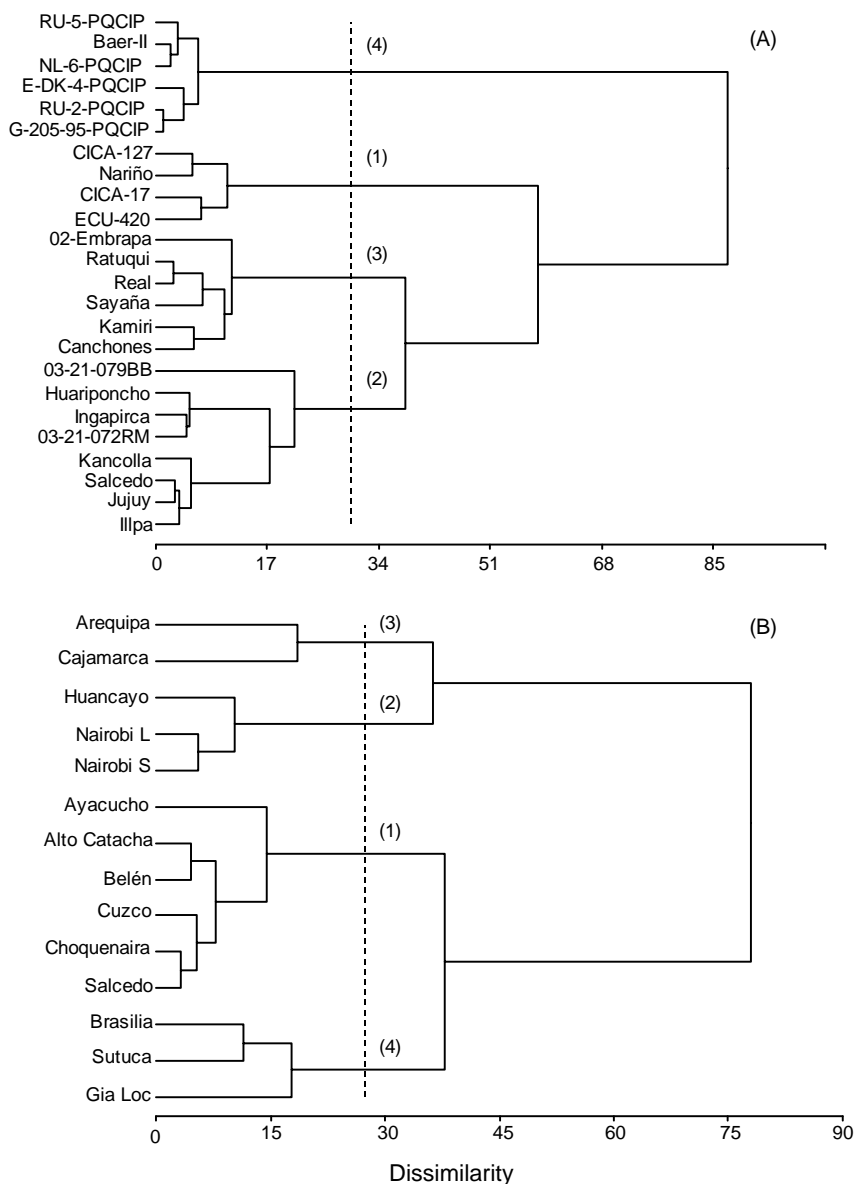


Fig. 1. Hierarchy for the classification of 24 cultivars of quinoa according to their relative responses for grain yield across 14 international testing sites (A) and for the classification of 14 environments, according to the way they differentiated among patterns of grain yield of 24 cultivars of quinoa (B).

improved their relative performance for grain yield in Arequipa (E3) and tend to be on the right side of the biplot. Cajamarca (E3) did not fit well in the system formed by the first and second principal components, according to the length of its vector. The second principal component contrasts E2 (Nairobi S, Nairobi

L, and Huancayo) and E4 (Sutuca, Gia Loc, and Brasilia), showing a strong negative association in terms of the manner they discriminate among genotypes. G1 cultivars showed a positive association with E2 sites, while G3 entries improved their relative performance for grain yield in the E4 sites.

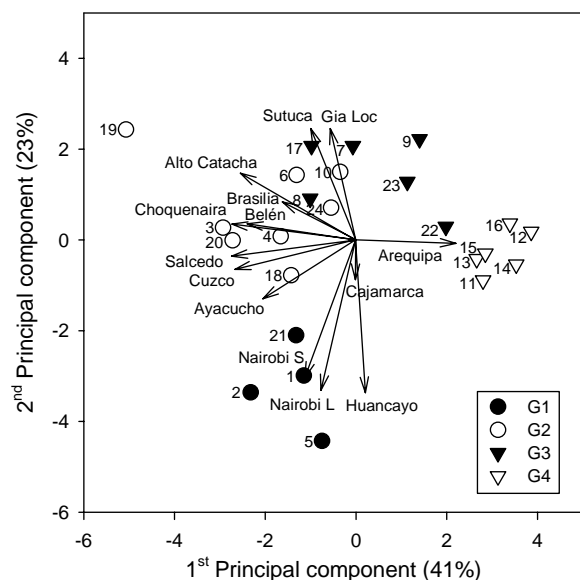


Fig. 2. Biplot of the first and the second principal components for grain yield of 24 cultivars of quinoa grown in 14 testing sites. Genotypes are represented by points and environments are represented by vectors. For any particular environment, genotypes can be compared by projecting a perpendicular from the genotype symbols to the environment vector, i.e. genotypes that are further along in the positive direction of the environment vector are higher yielding and vice versa. The cosine of the angle between any two environment vectors approximates their genetic correlation. Acute angles indicate positive association, i.e. the environments compared influence the genotypic relative performance in a similar manner; 90° angles indicate no association; and angles greater than 90° indicate negative association (Kroonenberg, 1997; Chapman et al., 1997). Same entry markers indicate genotype groups with members of a similar response pattern at the four-group level for grain yield (see Table 1 for genotype codes).

3.2. Physiological bases of genotype and genotype \times environment interaction effects for grain yield

For the analysis of the physiological determinants of G and G \times E interaction effects for grain yield, we used 7 of the 14 testing sites included in the two-mode pattern analysis, where data of maturity, biomass and harvest index were available. This dataset includes E1 (Salcedo, Cuzco and Belén), E2 (Nairobi L and Nairobi S), and E4 (Gia Loc and Brasília) environments. E3 is not represented in this genotype–environment system. Scatter diagrams were used to examine the relationships between the BLUPs for the genotypic

effects for grain yield and its physiological determinants (Fig. 3). The physiological basis of the G \times E interaction effects observed for grain yield were investigated using three-mode (genotype \times environment \times attribute) PCA. The BLUPs for time to physiological maturity, biomass, and harvest index within environmental groups were used to assist the interpretation of the G \times E interactions for grain yield.

The strong linear association between the average performance BLUPs for time to physiological maturity and total above-ground biomass (Fig. 3D) explains the similarity exhibited by the associations between both traits and grain yield Fig. 3A and B). There was a weak negative association between the BLUPs for maturity and harvest index (Fig. 3E), mainly determined by the low average harvest index values exhibited by the G1 cultivars. These are later than the G2 entries and produced on average a higher amount of biomass (Fig. 3D). However, their poorer average performance for harvest index explains the difference between the linear association between time to physiological maturity and total biomass (Fig. 3D) and the curvilinear association between time to physiological maturity and grain yield (Fig. 3A).

A $2 \times 2 \times 2$ (genotype \times environment \times attribute) solution for the three-mode PCA was considered adequate for fitting the data ($r^2 = 0.83$, Table 4), on the basis of informal judgements of the increases in r^2 as compared to the increases in dimensions and difficulty of interpretation. In this model, the two components for the genotype mode accounted for 78 and 5% of the variation, the components for the environment mode accounted for 80 and 3%, and the components for the attributes accounted for 76 and 6% of the variation (Table 4). The $1 \times 1 \times 1$ solution accounted for a large proportion of the variation of the system, but at least a $2 \times 2 \times 2$ model was necessary to construct the joint biplot of genotypes and attributes for the first environment component (Fig. 4). This joint biplot provides a good representation of the results of the analysis and displays those aspects of the relationships between genotypes and yield-related attributes determined by the contrast between E1 (negative scores) and E2 + E4 (positive scores, Table 4), after the removal of genotypic and environmental effects.

In this joint biplot the positive direction of the attribute vectors (indicated by arrowheads in the figure) indicates improved relative performance in Gia Loc,

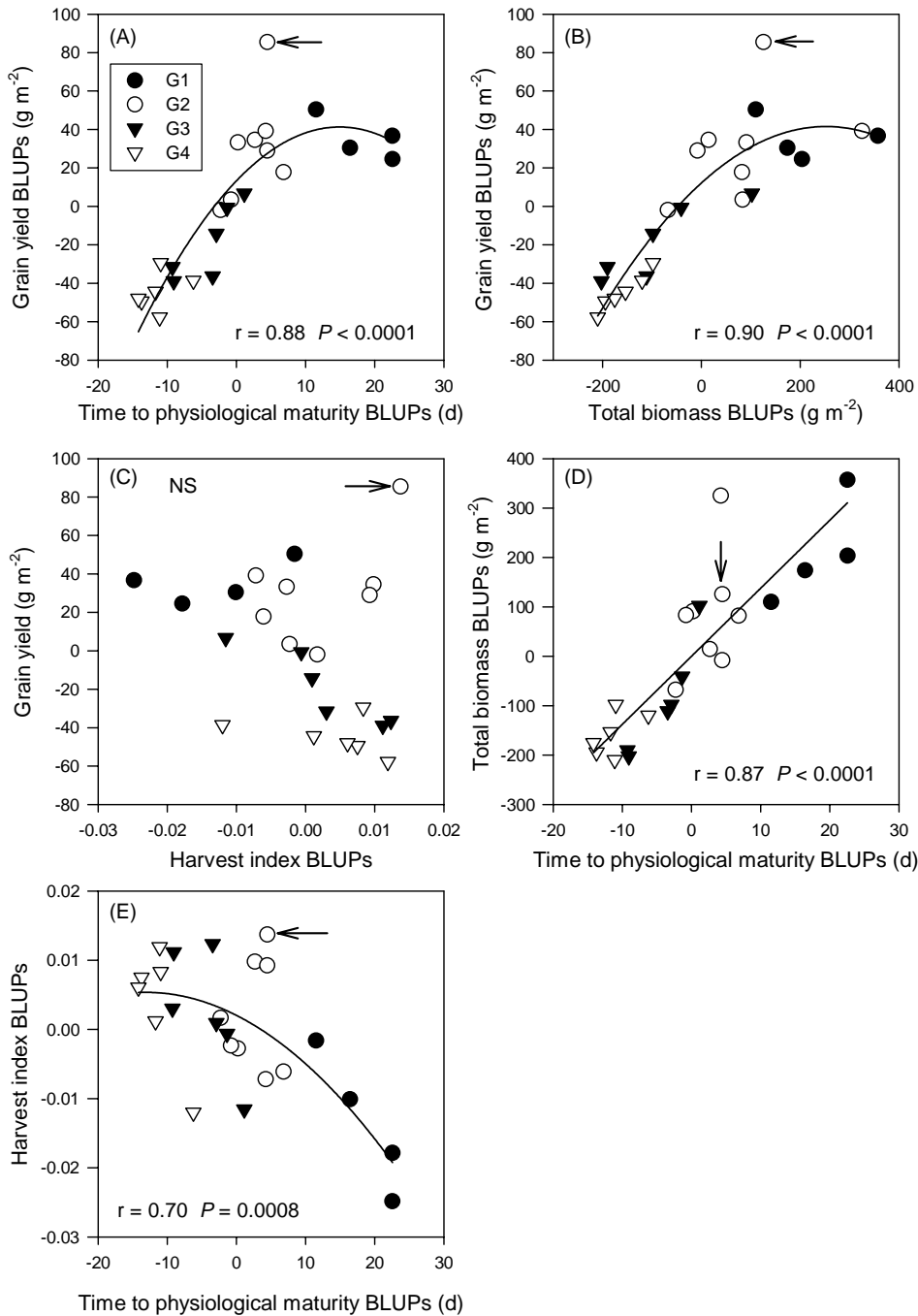


Fig. 3. Scatter diagrams of association between the best linear unbiased predictors (BLUPs) for grain yield, time to physiological maturity, above-ground biomass, and harvest index for 24 cultivars of quinoa evaluated in a subset of seven testing sites. Same entry markers indicate genotype groups with members of a similar response pattern at the four-level subset for grain yield. Arrows indicate cultivar 03-21-079BB.

Table 4

Mode component scores (with adequacy of fit) for four attributes (grain yield, total biomass, harvest index and time to physiological maturity) of 24 cultivars of quinoa grown over seven international trial environments ($2 \times 2 \times 2$ component model for genotypes \times environments \times attributes, respectively)

Code	Name	Group ^a (two-mode)	Component scores		Proportion of SS explained
			1	2	
Genotype (G)					
1	CICA-127	1	1.27	-0.32	0.90
2	CICA-17	1	0.91	-0.29	0.85
3	Huariponcho	2	0.25	-0.11	0.35
4	Kancolla	2	0.33	-0.22	0.46
5	Nariño	1	1.93	-0.03	0.91
6	Salcedo	2	0.27	0.22	0.44
7	Ratuqui	3	-0.32	-0.11	0.55
8	Kamiri	3	-0.11	0.29	0.38
9	Real	3	-0.46	-0.30	0.59
10	Jujuy	2	-0.14	0.07	0.23
11	Baer-II	4	-0.56	-0.13	0.70
12	RU-2-PQCIP	4	-1.17	-0.08	0.97
13	RU-5-PQCIP	4	-0.91	-0.10	0.86
14	NL-6-PQCIP	4	-0.95	-0.07	0.82
15	E-DK-4-PQCIP	4	-0.98	-0.03	0.82
16	G-205-95-PQCIP	4	-1.03	0.10	0.92
17	Sayaña	3	-0.17	0.13	0.21
18	Ingapirca	2	0.66	0.13	0.83
19	03-21-079BB	2	0.41	0.26	0.32
20	03-21-072RM	2	0.82	0.64	0.84
21	ECU-420	1	1.80	-0.21	0.96
22	02-Embrapa	3	-1.11	0.00	0.88
23	Canchones	3	-0.83	-0.05	0.85
24	Illpa	2	0.08	0.22	0.27
Proportion of SS explained			0.78	0.05	0.83
Environment (E)					
1	Salcedo	1	-0.13	-0.21	0.45
6	Cuzco	1	-0.17	0.00	0.22
10	Brasilia	4	0.31	0.26	0.43
14	Belén	1	0.00	0.17	0.19
19	Gia Loc	4	2.34	-0.06	0.94
23L	Nairobi L	2	0.14	0.15	0.17
23S	Nairobi S	2	0.01	0.05	0.01
Proportion of SS explained			0.80	0.03	0.83
Attribute (A)					
1	Grain yield		0.58	0.12	0.59
2	Total biomass		0.80	0.37	0.87
3	Harvest index		-0.23	-0.14	0.20
4	Time to physiological maturity		1.43	-0.28	0.98
Proportion of SS explained			0.76	0.06	0.83

^a Genotype and environment groups identified by hierarchical agglomerative clustering of grain yield.

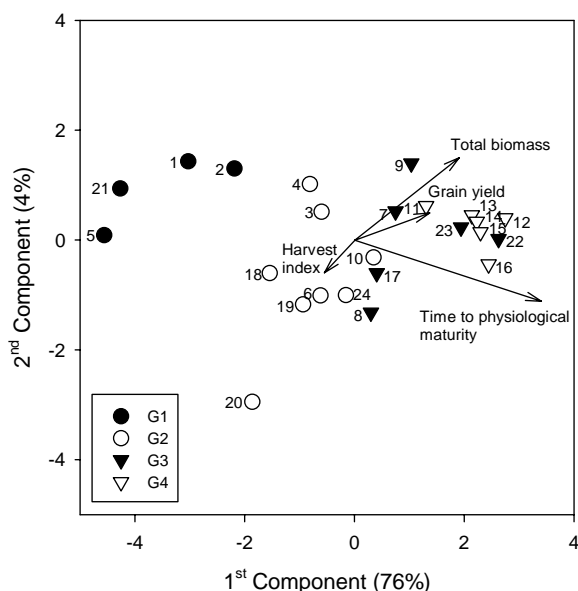


Fig. 4. Joint biplot of the first and second components of 24 quinoa cultivars and four attributes (grain yield, time to physiological maturity, above-ground biomass, and harvest index) associated with the first environment component. Genotypes are represented by points (see Table 1 for genotype codes) and attributes by vectors (positive direction shown by arrowhead) from the origin. For any particular attribute, genotypes can be compared by projecting a perpendicular from the genotype points to the attribute vector, i.e. entries that are further along in the positive direction of an attribute vector show higher values for this attribute and vice versa. Acute angles between any two attribute vectors indicate positive association; 90° angles indicate no association; and angles greater than 90° indicate negative association (Kroonenberg, 1997). Same entry markers indicate genotype groups with members of a similar response pattern at the four-group level for grain yield.

Nairobi and Brasilia, and the negative direction indicates improved relative performance in Salcedo and Cuzco. This is because the loadings on the first environment component are high and positive for the first three sites and high and negative for the second ones (Table 4). The harvest index vector is short, which indicates that most of the variation exhibited by this yield determinant was not fitted by the model (see percentage of explained variation in Table 4). The first component of the joint biplot accounted for 76% of the variation of the system (Fig. 4) and reflects the contrasting behaviour of G1 and G2 versus G3 and G4 in terms of their relative responses to the testing sites for grain yield, total biomass and time to physiological maturity. All these attributes showed positive scores

for the first component (Fig. 4), which suggest that the $G \times E$ interactions observed for the length of the ontogenic cycle and total biomass had a major positive influence on the form of the $G \times E$ interactions observed for grain yield. G2 cultivars were located around the origin in the joint biplot (Fig. 4) and were, on average, not very well fitted by the three-mode model (Table 4). The lower magnitude of the relative responses shown by the G2 cultivars, together with their high average performance for grain yield (Fig 3A), could be associated with broad adaptation to a wide range of environmental conditions and could be exploited in breeding strategies aimed at expanding the growing area of this species. The second component of the joint biplot accounted for a very low proportion of the total variation and highlighted the particular response patterns of cultivar 03-21-072RM, which showed a relative reduction for total biomass in Gia Loc, Nairobi and Brasilia, associated to a relative increase in time to physiological maturity (Fig. 4).

According to the magnitudes and signs of the environmental loadings on the first environment component, the most contrasting sites in terms of the relative responses exhibited by the cultivars were Salcedo and Cuzco (E1) versus Brasilia and Gia Loc (E4) (Table 4). The association between the average performance BLUPs for the four traits analysed strongly differed between both pairs of environments (Fig. 5). For Salcedo and Cuzco, there was a positive association between grain yield and time to physiological maturity (Fig. 5A) and total biomass (Fig. 5B), and a negative association between grain yield and harvest index (Fig. 5C). Total biomass showed a strong positive association with time to physiological maturity (Fig. 5D), while harvest index, which showed a negligible genotypic variation within this pair of environments, exhibited a negative association with the length of the crop cycle (Fig. 5E). For Gia Loc and Brasilia, there was a very weak positive association between grain yield and time to physiological maturity (Fig. 5F) and total biomass (Fig. 5G). Time to physiological maturity exhibited a negligible genotypic variation within this pair of environments and showed no association with total biomass (Fig. 5I) and harvest index (Fig. 5J). Conversely to the pattern observed in Salcedo and Cuzco, harvest index showed a strong positive association with grain yield in Brasilia and Gia Loc (Fig. 5H).

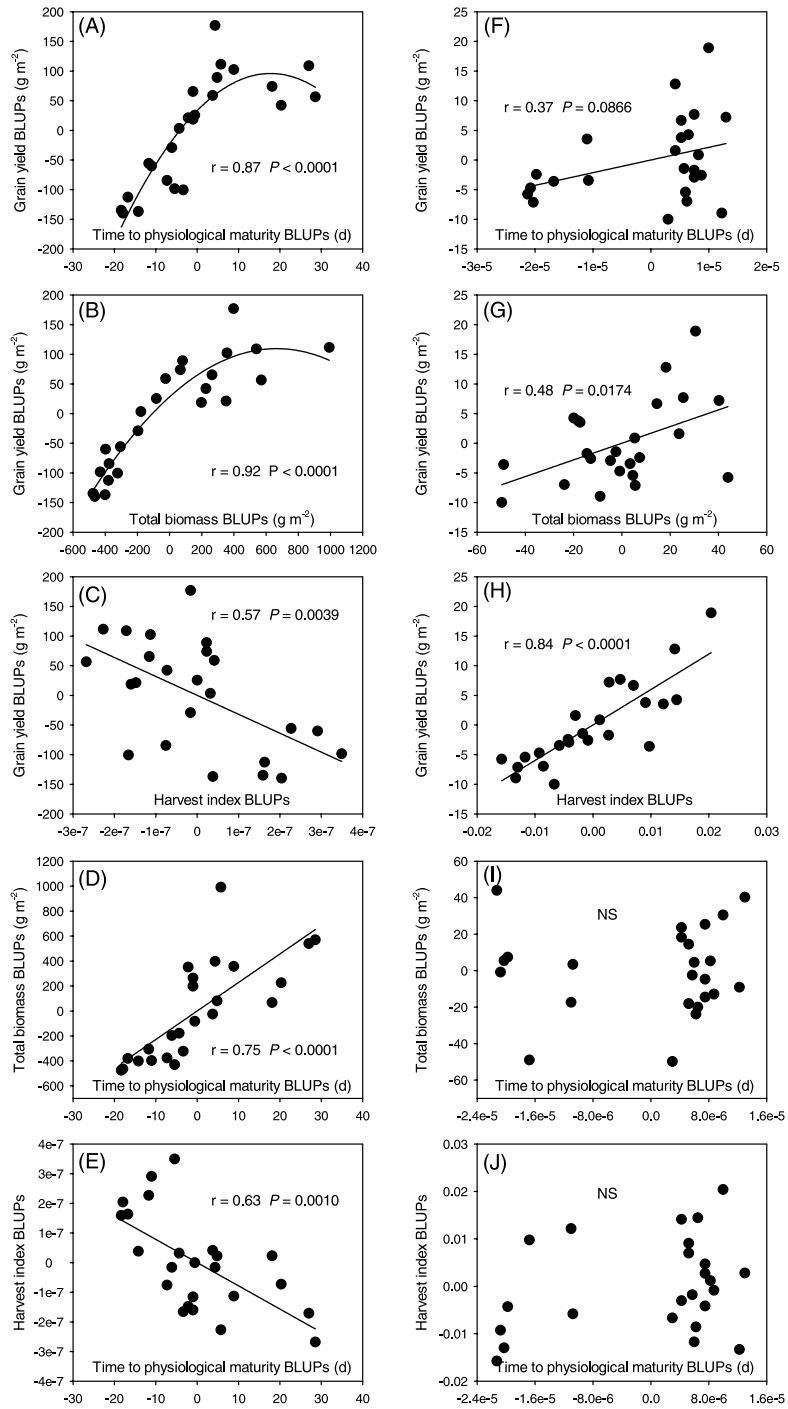


Fig. 5. Scatter diagrams of association between the best linear unbiased predictors (BLUPs) for grain yield, time to physiological maturity, above-ground biomass, and harvest index for 24 cultivars of quinoa for Salcedo and Cuzco, i.e. environment group 1 (A–E), and for Brasilia and Gia Loc, i.e. environment group 4 (F–J).

Fig. 5 emphasises a major difference between E1 and E4 environments, in terms of the physiological determinants of the genotypic effects observed for grain yield. For E1 sites, the genotypic variation for

time to physiological maturity made a significant contribution to the genotypic variation for grain yield, through its influence on the total biomass produced. These environments showed low to medium average

Table 5

Mode component scores (with adequacy of fit) for two attributes (grain yield and grain size) of 24 cultivars of quinoa grown over eight international trial environments ($2 \times 2 \times 2$ component model for genotypes \times environments \times attributes, respectively)

Code	Name	Group ^a (two-mode)	Component scores		Proportion of SS explained
			1	2	
Genotype (G)					
1	CICA-127	1	-0.93	0.15	0.66
2	CICA-17	1	-1.41	0.17	0.82
3	Huariponcho	2	-0.29	-0.09	0.18
4	Kancolla	2	-0.59	-0.10	0.60
5	Nariño	1	-1.21	0.20	0.69
6	Salcedo	2	-0.42	0.39	0.36
7	Ratuqui	3	0.59	0.52	0.74
8	Kamiri	3	0.32	0.59	0.65
9	Real	3	1.20	0.45	0.91
10	Jujuy	2	0.20	0.09	0.17
11	Baer-II	4	0.18	-0.46	0.48
12	RU-2-PQCIP	4	0.62	-0.63	0.69
13	RU-5-PQCIP	4	0.22	-0.49	0.52
14	NL-6-PQCIP	4	0.59	-0.37	0.66
15	E-DK-4-PQCIP	4	0.86	-0.32	0.67
16	G-205-95-PQCIP	4	0.48	-0.19	0.52
17	Sayaña	3	0.64	0.49	0.59
18	Ingapirca	2	-0.33	-0.24	0.27
19	03-21-079BB	2	-0.77	-0.01	0.44
20	03-21-072RM	2	-0.58	-0.28	0.69
21	ECU-420	1	-0.94	-0.25	0.81
22	02-Embrapa	3	0.58	-0.72	0.74
23	Canchones	3	0.86	0.42	0.80
24	Illpa	2	0.11	0.66	0.77
Proportion of SS explained			0.50	0.16	0.66
Environment (E)					
1	Salcedo	1	-0.38	0.15	0.44
2	Huancayo	2	0.17	-0.76	0.59
6	Cuzco	1	-0.35	0.22	0.50
7	Arequipa	3	0.85	-0.09	0.52
10	Brasilia	4	0.04	0.09	0.02
19	Gia Loc	4	1.88	0.17	0.94
23L	Nairobi L	2	-0.06	0.02	0.01
23S	Nairobi S	2	0.16	0.12	0.12
Proportion of SS explained			0.57	0.09	0.66
Attribute (A)					
1	Grain yield		1.01	0.06	0.72
2	Grain size		0.12	-0.53	0.51
Proportion of SS explained			0.52	0.14	0.66

^a Genotype and environment groups identified by hierarchical agglomerative clustering of grain yield.

temperatures, which allowed the expression of a high genotypic variability for developmental rate (time from sowing to maturity) and, consequently, for time to physiological maturity. In hotter environments such as Gia Loc and Brasilia, developmental rate exhibited a very small range of genotypic variation and the G3 and G4 cultivars showed a relative increase in total biomass. In such environments, harvest index was the main determinant of grain yield.

3.3. Grain yield and grain size relationship

For the analysis of the relationships between grain yield and grain size, we used 8 of the 14 testing sites included in the two-mode pattern analysis, where data for both traits were available. This dataset include E1 (Salcedo and Cuzco), E2 (Huancayo, Nairobi L and Nairobi S), E3 (Arequipa), and E4 (Gia Loc and Brasilia) environments. The relationship between the BLUPs for the genotypic effects for grain yield and grain size was examined and the $G \times E$ interaction effects observed for both traits were handled simultaneously using three-mode (genotype \times environment \times attribute) PCA.

There was no significant association between the average performance BLUPs for grain yield and grain size (data not shown). A $2 \times 2 \times 2$ (genotype \times environment \times attribute) solution for the three-mode PCA was considered adequate for fitting the data ($r^2 = 0.66$, Table 5). The first genotype component distinguishes between the G1 and G2 cultivars, with negative scores, and those of G3 and G4, with positive scores. The second genotype component contrasted G1 and G3 versus G2 and G4 (Table 5). These patterns of contrasting relative performance among genotype groups in terms of their responses for grain yield and grain size are clearly expressed in the joint biplot of genotypes and attributes for the first environment component (Fig. 6). This joint biplot provides an appropriate representation of the main features of the results of the analysis and displays those aspects of the relationships between genotypes and attributes that are influenced by the contrast between E1 (negative scores) and E3 and E4 (positive scores, Table 5), after the genotypic and environmental effects have been removed.

In this joint biplot the positive direction of the attribute vectors (indicated by arrowheads in Fig. 6)

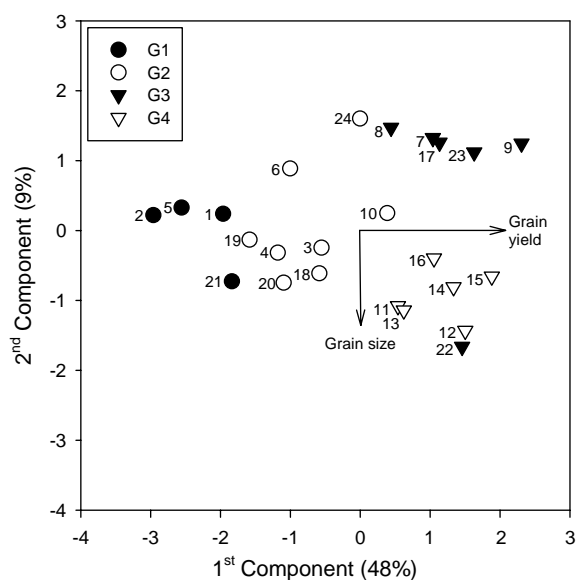


Fig. 6. Joint biplot of the first and second components of 24 quinoa cultivars and two attributes (grain yield and grain size) associated with the first environment component. Genotypes are represented by points (see Table 1 for genotype codes) and attributes by vectors (positive direction shown by arrowhead) from the origin. See caption of Fig. 4 for interpretation rules. Same entry markers indicate genotype groups with members of a similar response pattern at the four-group level for grain yield.

indicates improved relative performance in Arequipa and Gia Loc, and the negative direction indicates improved relative performance in Salcedo and Cuzco. This is because the loadings on the first environment component are high and positive for the first two sites and high and negative for the second ones (Table 5). In general terms, cultivars of G3 and G4 showed a relative increase in grain yield in Arequipa and Gia Loc, since their perpendicular projections on this attribute vector intercept it in positive direction (Fig. 6). The opposite was observed for G1 and G2 cultivars. The first component of this joint biplot (48% of the variation) accounted for the contrasting genotype-specific responses for grain yield, since the vector of this attribute is parallel to the axis of this component. The second component (9% of the variation) accounted for the $G \times E$ interaction observed for grain size and differentiates between G2 and G4, with improved performance for this trait in Arequipa and Gia Loc, and G1 and G3, which showed a contrasting response. The differences in percentage of explained

variation between the first and second components of the joint biplot is consistent with the differences in the $G \times E$ interaction to G variance component ratios showed by grain yield and grain size (Table 3). The attribute vectors of grain yield and grain size almost form a right angle (Fig. 6), suggesting that the genotype-specific responses for grain yield have almost no effect on the $G \times E$ interactions observed for grain size.

The second environment component reflects the contrast between Huancayo and the other testing sites. As this contrast accounted for a very low proportion of the total variation (9%) we did not analyse the relationship between genotypes and attributes associated with this environment component.

4. Discussion

The relative contributions of G and $G \times E$ interaction effects to the total variation for grain yield found in this study are similar to those found in other crop adaptation studies in rain-fed environments (i.e. wheat, Cooper et al., 1996; maize, Chapman et al., 1997; sorghum, Alagarswamy and Chandra, 1998; rice, Cooper et al., 1999a; sunflower, de la Vega et al., 2001) and indicate that it would be very difficult to achieve an indirect response to selection over all of the quinoa low-latitude target population of environments from selection in a few environments, ignoring the observed $G \times E$ interactions. The extremely high level of environmental variation encountered within the quinoa growing region, often expressed within relatively small areas across the topographical range, requires breeding and testing strategies structured to accommodate the effects of large $G \times E$ interactions.

The hierarchical grouping of the cultivars based on their relative responses for grain yield showed a strong degree of correspondence to the adaptation groups proposed by Tapia et al. (1979). This clustering was also consistent with that obtained using morphometric and electrophoretic data on a quinoa germplasm collection (Wilson, 1988), which distinguished three groups of accessions, namely central Chile, northern Andes and southern Andes, corresponding to G4, G1 and G2–G3 of this study, respectively. A distinction between northern- and southern-altiplano types, G2 and G3, respectively, was proposed by Rojas (2003),

on the basis of the results of multivariate analyses of morphological and agronomic traits measured on a set of accessions from the Bolivian quinoa germplasm collection.

Testing sites were clustered in cold highland (E1), tropical valleys of moderate altitude (E2, E3), and warmer, low altitude (E4) environment types. These environment groups showed strong differences in the manner they influenced the relative genotypic performance for grain yield, according to the angles between environmental vectors on the biplot of Fig. 2. Although no single genotype group was identified to show consistently superior grain yield across all environment groups, more years of testing are needed to reach an objective decision about subdividing the low-latitude quinoa target population of environments and selecting for specific adaptation to appropriately defined environment types. The large $G \times E$ interaction component and the strong correspondence between the classifications of cultivars based on their origin and relative responses for grain yield detected in this exploratory study can stimulate interest in further studies aimed at improving the effectiveness of the selection strategies implemented by the quinoa breeding programs. To determine the scope to select for specific adaptation, test environments can be indirectly characterised by the relative performance of a reference set of genotypes (Cooper and Fox, 1996). There is also a need for an environmental characterisation strategy that will assist in identification of the causes of repeatable $G \times E$ interactions for grain yield (Cooper et al., 1999b). The results of the cluster analysis described in this paper, together with 'agronomic wisdom' about quinoa cultivars, can be used to choose genotypes of contrasting relative performance across environments for further studies aimed at assessing the opportunity to select for broad or specific adaptation. A potential reference set of genotypes composed by broadly distributed cultivars representing the four genotype groups detected in this study could be as follows: cvs. CICA 17 and Nariño for G1; cvs. 03-21-079BB and 03-21-072RM for G2; cvs. Real and Sayaña for G3; cvs. RU-2 and NL-6 for G4.

Combined analysis of variance indicated that the average cultivar performance for time to physiological maturity had a major influence on the genotypic effects observed for grain yield. The genotypic groups that showed longer durations of the crop cycle, i.e. G1

and G2, produced higher amounts of biomass, which was in turn the main physiological determinant of grain yield in the genotype–environment system under study (Fig. 3A and B).

The highest yielding cultivar, 03-21-079BB (Table 1), indicated by arrows in Fig. 3, showed similar maturity and slightly higher above-ground biomass (Table 1, Fig. 3A, B and D), but much higher harvest index (Table 1, Fig. 3C and E) than the G2 across-cultivar means for these attributes. This suggests that the good average performance showed by this cultivar could come from a relatively high harvest index for its maturity type (Fig. 3E). The broad adaptation shown by cultivar 03-21-079BB (see genotype relative positions on the biplot of Fig. 2) could be explained by a relatively high biomass production in environment types such as that represented in Fig. 5B and a relatively high harvest index in environment types such as that of Fig. 5H.

Three-mode PCA have further served to establish the importance of time to physiological maturity and total above-ground biomass in determining the $G \times E$ interaction effects for grain yield. Different environment types showed contrasting effects on the physiological attributes underlying grain yield variation among cultivars. If the observed differences between sites of E1 and E4 in terms of the manner they influence the relative genotypic performance for grain yield were repeatable across years, specific adaptation to low-latitude environment types differing in temperature regime could be exploited in quinoa breeding. In the biplot of the environment-standardised grain yield, Gia Loc and Brasilia form almost a right angle with Salcedo and Cuzco (Fig. 2), indicating no association between their ability to discriminate among genotypes. Exploiting $G \times E$ interactions through simultaneous selection for both environment types, i.e. selecting for broad adaptation, should bring successive advances toward the top left corner of the biplot of Fig. 2. The relatively good performance of cultivar 03-21-079BB across both environment types, as well as its response patterns for biomass and harvest index, suggest that selecting for broad adaptation to E1 and E4 is a reliable breeding strategy. This would lead to avoid the subdivision of at least part of the quinoa target population of environments. However, an objective decision between selecting for broad or specific adaptation should come from the analysis of a multi-

environment trial replicated across years (Cooper and DeLacy, 1994) and from the characterisation of the frequency of occurrence of these types of temperature environment, over a long-time sequence. Although subdivision of a crop's growing region implies more work for plant breeders and seed producers, it also implies higher heritabilities and faster progress for plant breeders, potentially stronger competitiveness for seed producers, and higher yield for growers (Gauch and Zobel, 1997).

It should be noted that we were unable to include the temperate testing sites in this analysis. At these sites the tropical-adapted cultivars produced a high amount of vegetative biomass, but failed in producing grain. If a diverse set of genotypes could be appropriately grown in high- and low-latitude environments, it is expected that photoperiod will appear as a main determinant of the $G \times E$ interactions for grain yield, through its effects on the genotypic variation for harvest index. Photoperiod effects on developmental rate values were not significant for the dataset analysed in this work, perhaps because of the narrow latitudinal range explored (see Table 2). However, a strong inhibition of seed filling is observed in quinoa cultivars from tropical origin when cultivated in long days (in interaction with high temperatures) that limits their cultivation in higher latitudes (Bertero et al., 1999). Future work could assess whether harvest indices differences as those observed in E4 environments are associated to differential photoperiod (and temperature) sensitivities for seed filling.

Correlation analysis between the BLUPs of the genotypic effects and three-mode pattern analysis revealed no association between the average cultivar performance and environment-specific genotypic responses for grain yield and size. This means that grain size gains would have been unlikely to occur if selection had been done based on grain yield only and vice versa. The four genotype groups identified by cluster analysis occupied different quadrants on the joint biplot of Fig. 6, and each one shows a unique combination of responses for both traits. The lack of association between grain yield and grain size in terms of the manner they discriminate among the relative responses of the genotypic groups suggests that genetic progress for both traits can be achieved through simultaneous selection.

This paper highlights the relevance of $G \times E$ interaction effects on the determinations of crop yield and

some of its determinants in quinoa and suggests some strategies for its consideration or exploitation. The relative importance of $G \times E$ interaction effects was considerably higher than that estimated in the analysis of Risi and Galwey (1991) as expected for the much wider environmental and genotypic range explored in this work. A point to note is the close correspondence found between genotypic groups derived from this analysis and previous classifications of adaptation groups. Future efforts on improving the characterisation of environments, using a reference set of genotypes as that proposed in this work, would aid in distinguishing between predictable and unpredictable sources of $G \times E$ interactions and its causes.

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