Field Crops Research 166 (2014) 46–57

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Multi-environmental evaluation for grain yield and its physiological determinants of quinoa genotypes across Northwest Argentina

R.N. Curti [a,1,*], A.J. de la Vega [b], A.J. Andrade [c], S.J. Bramardi [d,e], H.D. Bertero [a]

[a] Departamento de Producción Vegetal, CONICET/Facultad de Agronomía, Universidad de Buenos Aires, Avenida San Martín 4453, C1417DSE, C.A. Buenos Aires, Argentina
[b] DuPont Pioneer, 41300 San José de la Rinconada, Sevilla, Spain,
[c] CRSJ-INTA (Instituto Nacional de Tecnología Agropecuaria), EEA Abra Pampa, Ruta Prov. 11 km. 17 (4640). Jujuy, Argentina
[d] Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, Avenida 60 y 119-S/N°. La Plata, Argentina
[e] Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Ruta 151-C.C. 85 (8303) Cinco Saltos, Río Negro, Argentina

ARTICLE INFO

Article history:
Received 5 October 2013
Received in revised form 7 June 2014
Accepted 9 June 2014
Available online 26 June 2014

Keywords:
Chenopodium quinoa Willd
G × E interaction
Groups of environments
Downy mildew
Quinoa
Yield components

ABSTRACT

The quinoa growing region of Northwest Argentina (NWA) shows a strong environmental variability, both seasonal and spatial. In consequence, the site-year combinations in which yield trials are established can complicate quinoa genotypic selection through strong genotype-by-environment interactions (G × E). The magnitude and nature of the genotype (G) and G × E interaction effects for grain yield, its physiological determinants and components, and days-to-flower exhibited by quinoa at NWA were examined in a multi-environment trial involving a reference set of 12 genotypes tested in six environments. The tested genotypes were selected based on their known contrasting relative performance to environments and different geographical origin. They represent three out of the four genotypic groups identified in previous studies. The G × E interaction to G component of variance was 3:1, 30:1 and 1.3:1 for grain yield, harvest index and grain number, respectively. Conversely, the G effect was large for biomass, grain weight and days-to-flower. Two-mode pattern analysis of the double-centered matrix for grain yield revealed four genotypic groups with different response pattern across environments. This clustering which separates genotypes from highlands and valleys showed a close correspondence with the genotypic groups previously proposed based on phenotypic and genetic characterization. On the other hand, a strong and repeatable negative association was observed between highland and valley sites, in terms of their G × E interaction effects. Phenological variation among genotypes in combination with environmental differences in the incidence of mildew or frost risk gave rise to significant crossover yield responses to site changes and determined specific adaptation to different ecological conditions. All yield components and determinants were involved in the genotype-specific yield responses. The genotypic variability observed for time to flowering determined the form of the G × E interactions observed for total above-ground biomass in valley environments, while in the highland sites, harvest index made a significant contribution. On the other hand, grain number was the major component in grain yield determination, while grain weight showed a weak to strongly negative association with grain number across both types of environment. In this sense, the future breeding programs in NWA region should focus on these physiological attributes underlying grain yield variation among genotypes across groups of environments for faster genetic progress.

1. Introduction

The certainty of selection decisions in plant breeding programs testing networks would be improved if the relative magnitudes of the genotype (G) and genotype-by-environment interaction (G × E) effects are quantified and at least a partial understanding of the target population of environment (TPE) is developed. The multi-environment trials (METs) that breeders routinely conduct for genotype selection can be also used to this purpose. In METs, a set of

* Corresponding author. Tel.: +54 387 4255434; fax: +54 387 4255434.
E-mail addresses: rcurti@agro.uba.ar (R.N. Curti), abelardo.delavega@pioneer.com (A.J. de la Vega), ajandrade@correo.inta.gov.ar (A.J. Andrade), sbramardi@gmail.com (S.J. Bramardi), bertero@agro.uba.ar (H.D. Bertero).
[1] Present address: Laboratorio de Investigaciones Botánicas (LABIBO/CONICET), Facultad de Ciencias Naturales, Universidad Nacional de Salta, Avenida Bolivia 5150 (4400) Captital, Salta, Argentina.

http://dx.doi.org/10.1016/j.fcr.2014.06.011
0378-4290/

genotypes is evaluated across several environments (typically site-year combinations) that are expected to represent the environmental range across which the genotypes should partially (specific adaptation) or wholly (wide adaptation) perform well (van Eeuwijk et al., 2005).

The performance of genotypes in METs is analyzed by statistical methods developed to describe and interpret G × E data (van Eeuwijk et al., 2005). The variance components estimated from the combined analysis of variance in conjunction with patterns analysis (clustering and ordination) (Williams, 1976) have been used to predict the response to selection across the TPE, to understand the relationships between genotypes and environments and to determine the relative merit of subdividing the TPE into mega-environments in terms of the effect of this strategy on the magnitude of the correlated response to selection (de la Vega et al., 2001; Yan et al., 2000). This information is particularly useful to breeders because it can help determine the relative convenience of developing cultivars for all environments of interest versus developing specific cultivars for identified mega-environments (de la Vega and Chapman, 2010; Windhausen et al., 2012).

Better knowledge of the physiological bases of the differential responses of genotypes to specific environments should contribute to the overall efficiency with which breeding programs characterize and use the available germplasm accessions according to their specific adaptation patterns (de la Vega and Hall, 2002a,b). Commonly, investigations of the physiological bases of genotypic variation for grain yield have been based on correlations between components of the grain yield determination models. When interest is focussed on the G × E interactions for grain yield, a directed investigation of the association between yield and its physiological determinants (i.e., total accumulated biomass and harvest index) or numerical components (i.e., grain number and weight) is possible by focussing on the attributes which show high G × E interaction (Cooper et al., 1994).

Quinoa (*Chenopodium quinoa* Willd.) is an Andean grain crop of exceptionally high nutritive quality, broadly adapted to grow in the heterogeneous environments that characterise much of the Andean region (Wilson, 1990). Results of large-scale METs have revealed that large and regional G × E interactions can be a major impediment to genetic progress in breeding for this highly heterogeneous TPE (Bertero et al., 2004). Current quinoa breeding programs in the Andean countries are based on decentralized and farmer participatory methods, which exploit locally adapted cultivars (often landraces) (Danial et al., 2007). Whilst this approach appeared to be successful in terms of cultivar adoption by small-scale farmers (McElhinny et al., 2007), it also implies more breeding efforts due to fragmentation of testing resources (Atlin et al., 2000). In order to determine if this participatory approach is also the most convenient breeding strategy for other, i.e., non traditional, Andean quinoa agricultural systems, some understanding of the magnitude, repeatability and predictability of the G × E interactions is needed. This information is useful to determine the relative merit of exploiting only local adaptation versus selecting for both wide and specific adaptation across a broader range of environments (Basford and Cooper, 1998).

The Andean region of Northwest Argentina (NWA) shows a large variability in terms of rainfall, humidity and temperature; the longitude and direction of the slopes being the major factors affecting the amount and distribution of rainfall (Bianchi et al., 2005). Quinoa production systems in NWA are hand-labour intensive and operate with minimal management and external input (Curti et al., 2012). Thus, their capacity to ensure local food security depends largely on the agro-ecological adaptation of the cultivars in use. In this study, we applied linear mixed models and multivariate analysis to a MET where a reference set of 12 quinoa genotypes was tested across six NWA environments to: (i) examine the relative size of the G and G × E interaction components of variance for grain yield, above-ground biomass, harvest index, grain number and weight and time to flowering (first anthesis); (ii) group quinoa genotypes according to their relative responses to testing environments for grain yield, and testing environments according to the way they discriminate among genotypes; (iii) interpret changes in relative yield across environments in terms of the changes in the physiological determinants and numeric components of yield; and (iv) investigate the physiological basis of the observed G × E interaction effects for grain yield in terms of the genotype-specific responses for time to flowering, above-ground biomass, harvest index, grain number and weight across environmental groups previously defined on the basis of cluster analysis. The hypothesis of the present study are: (1) since small-scale farmers grow locally developed quinoa cultivars that typically posses a narrow range of adaptation, large G × E interactions complicate the analysis of genotypic performance across large agro-ecological zones; (2) since phenotypic and genetic diversities are mainly structured according to ecogeography (Costa Tártara et al., 2012; Curti et al., 2012), genotypes from the same origin respond in a similar way across different environments; and (3) similar climatic agro-ecological zones discriminate in a similar fashion among genotypes.

2. Material and methods

2.1. Genotypes and testing environments

A reference set (Fox and Rosielle, 1982) of 12 quinoa genotypes (Table 1) was evaluated in six environments as determined by combinations of three sites (Abra Pampa, Calete and Colanzulí) and two seasons (2008/2009–2009/2010) (Table 2). The experimental sites were located in farmer's field (e.g., Colanzulí and Calete) and an experimental research station belonging to the Instituto Nacional de Tecnología Agropecuaria (EEA-INTA, Abra Pampa), including some of the major agro-ecological zones in which quinoa is grown in Northwest Argentina (Curti et al., 2012). The Abra Pampa site (Department of Cochinoca, province of Jujuy), located at high altitude (3400 masl) represents a typical highland environment; Calete (Department of Humahuaca, province of Jujuy) located at lower altitude (2939 masl) represents a typical dry valley environment; while, Colanzulí (Department of Iruya, province of Salta) located at high altitude (3600 masl) represents a transition zone between dry and humid valleys environments (Curti et al., 2012). In this MET, other major agro-ecological zones where quinoa is grown as the dry valleys located to the south (Valles Calchaquíes) and the humid valleys located to the east (Santa Victoria Oeste) of Salta province respectively, were not represented (Curti et al., 2012).

The genotypes composing the reference set were selected from the Faculty of Agronomy of the University of Buenos Aires Germplasm Collection based on their contrasting environments of origin and relative performance (Bertero, personal communication). According to a previous classification, four genotypic groups (highlands, transition zone, dry valleys and humid valleys) were defined within the germplasm collection (Curti et al., 2012). In this evaluation, genotypes from three out of the four genotypic groups were represented, including three from highlands (CHEN 420, 426 and 431), seven from dry valleys (CHEN 58, 60, 182, 231, 252, 414 and 435) and two from Humid valleys (CHEN 212 and 456) (Table 1). These genotypes represent a wide range of genetic diversity according to microsatellite markers (Costa Tártara et al., 2012).

Since only three genotypes (CHEN 60, 182 and 435) were tested across the six environments, the trial dataset was unbalanced across years and locations. The genotype CHEN 456 was only

Table 1
Adaptation group and agronomic characters of 12 genotypes of quinoa evaluated during two seasons (2008/2009–2009/2010) across three localities in Northwest Argentina. Values of agronomic traits are means ± 1 standard error of six trials for grain yield, above-ground biomass, harvest index, grain number and weight, and five trials for time to flowering.

Genotype	Adaptation group[a]	Origin (locality, department, province)	Grain yield ($g\,m^{-2}$)	Above-ground biomass ($g\,m^{-2}$)	Harvest index	Grain number ($\#m^{-2}$)	100 grain weight (g)	Time to flowering (days)
CHEN 58	Dry valley	Coctaca, Humahuaca (Jujuy)	155.4 ± 20.3	421.2 ± 44.8	0.36 ± 0.01	49,658 ± 7,675	0.32 ± 0.013	67 ± 1.8
CHEN 60	Dry valley	Abralaite de Colanzulí, Iruya (Salta)	220.2 ± 40.7	638.3 ± 95.5	0.32 ± 0.03	98,124 ± 18,916	0.23 ± 0.01	70 ± 2.7
CHEN 182	Dry valley	QQ 95-NSL 106,394, Humahuaca, (Jujuy)	109.7 ± 18.7	342.4 ± 49.5	0.31 ± 0.02	44,819 ± 8,975	0.26 ± 0.01	67 ± 3.5
CHEN 212	Humid valley	San Felipe, Santa Victoria Oeste (Salta)	214.7 ± 29.3	692.4 ± 68.9	0.31 ± 0.02	101,253 ± 15,117	0.22 ± 0.01	106 ± 1.3
CHEN 231	Dry valley	Ocumaso, Humahuaca (Jujuy)	140.5 ± 21.4	375.1 ± 51	0.37 ± 0.02	55,347 ± 8,974	0.27 ± 0.01	74 ± 4.3
CHEN 252	Dry valley	Maimará, Tilcara (Jujuy)	161.1 ± 35.8	501.4 ± 90.9	0.28 ± 0.03	57,780 ± 12,204	0.26 ± 0.01	86 ± 3.8
CHEN 414	Dry valley	La Poma, La Poma (Salta)	115 ± 22.8	427.2 ± 93.7	0.30 ± 0.03	41,508 ± 8,591	0.28 ± 0.01	87 ± 6.1
CHEN 420	Highland	Antofallita, Los Andes (Salta)	69 ± 5.8	263.6 ± 17.3	0.26 ± 0.01	19,422 ± 1,501	0.35 ± 0.01	48 ± 1.4
CHEN 426	Highland	Santa Rosa de los Pastos Grandes, Los Andes (Salta)	71.3 ± 5.3	373.2 ± 67.2	0.23 ± 0.02	24,737 ± 2,028	0.30 ± 0.01	41 ± 2.2
CHEN 431	Highland	Susques, Susques (Jujuy)	73.4 ± 6.5	244.3 ± 21.8	0.31 ± 0.02	22,357 ± 1,987	0.33 ± 0.01	46 ± 1.3
CHEN 435	Dry valley	Cangrejillos, Yavi (Jujuy)	96.1 ± 11.6	358.9 ± 33.2	0.28 ± 0.03	32,676 ± 3,904	0.30 ± 0.01	72 ± 3.8
CHEN 456	Humid valley	Trigo Huaico, Santa Victoria Oeste (Salta)	194.4 ± 46	1271 ± 135	0.16 ± 0.03	105,940 ± 22,437	0.18 ± 0.004	86 ± 2.3

[a] Genotype group identified by hierarchical agglomerative clustering of morpho-phenological traits (Curti et al. 2012).

included in the second season (2009/2010). No grain yield was recorded in Colanzulí in the first season (2008/2009) for genotype CHEN 58. Grain yield was not recorded for highland genotypes in Colanzulí during the first season (2008/2009) because plots suffered a severe systemic infection by downy mildew (*Peronospora farinosa* f.sp. *chenopodii* Fr.) at visible flower buds stage (Bertero and Ruiz, 2008) causing complete defoliation and poor plant development. Since in the present evaluation we did not recorded the incidence of mildew at each environment other than visually, this fact precluded their further consideration in statistical analyses. For the two seasons in Abra Pampa, grain yield was not recorded for genotypes of the Andean valleys (CHEN 58, 212, 252 and 414) due to abiotic stress caused by frost at the end of the growing season that inhibited grain-filling.

2.2. Field experiments

In each environment, a randomized complete block design with three replicates was used. In Calete and Colanzulí, the sowing date across the two seasons was the conventional for the zone (October), while in Abra Pampa, December and November plantings were used for the first and second seasons, respectively. In Abra Pampa and Colanzulí genotypes were cultivated on sandy loam soil (Hidric Medifibrists and Torriorthents Thapto Argids, respectively, Soil Taxonomy, U.S. Department of Agriculture), while in Calete on a sandy soil (Typic Haplargids, *ibid*). Plot size was 5 rows, 5 m long, with an inter-row spacing of 0.5 m. Sowing density was 14 seeds m^{-1}, equivalent to 280.000 seeds ha^{-1}.The experiment was kept free of weeds and pests and fertilised at a rate of 43 kg N ha^{-1}, 35 days after crop emergence. In Colanzulí and during the two growing seasons, experiments were carried out under local farming practices (i.e, organic fertilization before sowing and without the use of insecticides or fungicides to control pests and diseases during the growing season). For all environments the experiments received deep irrigation before sowing and then every 10 or 15 days following local practices (furrow irrigation) to avoid water deficit during the crop cycle. Because of the experimental design, all genotypes were exposed to the same irrigation regime.

Grain yield and its determinants, i.e., above-ground biomass and harvest index, and its numerical components, i.e., grain

Table 2
Testing sites where the reference set of genotypes was evaluated. Values of agronomic traits are means ± 1 standard error of 11 genotypes for the season 2008/2009 and 12 for 2009/2010, respectively. Different letters within a column indicate significant difference ($P < 0.05$) between environments according to Fisher's test of LSD.

Location	Trial code (location, year)	Mean daily temperature; (°C)[a]	Mean Photoperiod (h)[d]	Total precipitations (mm)	Relative humidity (%)	Grain yield ($g\,m^{-2}$)	Above-ground biomass ($g\,m^{-2}$)	Harvest index	Grain number ($\#m^{-2}$)	100 grain weight (g)	Time to flowering (days)	Genetic variance[e]
Abra Pampa	AP 08	10.3	12.4	385	40–50[c]	65.4 ± 3.7b	254.4 ± 15.7bc	0.26 ± 0.01ab	24,915 ± 1,788bc	0.27 ± 0.01b	54 ± 2.6b	0.2
	AP 09	12.2	12.6	247	40–50[c]	70.7 ± 5.2b	265.3 ± 9.6bc	0.26 ± 0.01b	22,985 ± 1,170c	0.30 ± 0.01ab	54 ± 0.5b	452
Colanzulí	CLZ 08	9.7[b]	12.7	329[b]	77[b]	100.8 ± 15.7b	299.6 ± 52.6c	0.35 ± 0.03a	41,839 ± 7,319bc	0.25 ± 0.01ab	97 ± 1.8a	4,705
	CLZ 09	12.3[b]	12.8	244[b]	68[b]	149.6 ± 17.5ab	561.0 ± 57.3a	0.28 ± 0.02ab	57,659 ± 8,013abc	0.29 ± 0.01a	–	6,098
Calete	KLT 08	13.0	12.7	178	50–60[c]	170.3 ± 23.5a	554.1 ± 61.2a	0.30 ± 0.02ab	67,235 ± 1,102a	0.29 ± 0.01ab	68 ± 3.5b	12,579
	KLT 09	14.2	12.8	145	50–60[c]	150.0 ± 13.0ab	513.1 ± 54.6ab	0.31 ± 0.01ab	62,582 ± 7,263ab	0.27 ± 0.01ab	66 ± 3.2b	3,281

[a] Average daily values of mean temperature for time to physiological maturity (visually determined from examination of seeds on the medium third of the inflorescence, according to Bertero and Ruiz, 2008), were obtained from a temperature sensor (TC1047, Microchip Technologies, Chandler AZ) monitored by an automated control unit (Cavadevices, Buenos Aires, Argentina) located inside the experimental plots.

[b] Average daily values obtained from nearest meteorological station located at 600 m from experimental plot. Database from Sistema Nacional de Información Hídrica (web site: http://www.hidricosargentina.gov.ar).

[c] Decadal ranges provided by La Quiaca meteorological station (22°06′S 65°34′W, 3412 masl, department of Yavi, province of Jujuy) from National Meteorological Service (web site: http://www.mineria.gov.ar/estudios/irn/jujuy).

[d] Photoperiod data are average from sunset to sunrise (Goodspeed, 1975) to the period from crop emergence to physiological maturity.

[e] Genetic variance calculated on the basis of grain yield according to the following model: $y_{ik} = \mu + g_i + b_k + \varepsilon_{ik}$; genotypes and block defined as random terms.

number and weight and time to flowering (first anthesis) were obtained for each plot at all experiments. Time to flowering (days) was determined as the time at which 50% of the plants in the plot reached anthesis (at least one flower opened) (Bertero and Ruiz, 2008). For each experiment grain yield and above-ground biomass were determined as follows: one week after physiological maturity (visually determined by seeds examination on the medium third of the inflorescence, Bertero and Ruiz, 2008), the distance between the first and last plant of 10 plants from the three central rows, discarding border plants, was measured with a ruler. The number of plants per meter was calculated as the ratio of the 10 harvested plants at harvesting and the distance harvested, while crop density (plants m^{-2}) was the product of the number of harvested plants by a factor of two. Grain yield ($g\,m^{-2}$), above-ground biomass ($g\,m^{-2}$) and grain number ($\#m^{-2}$) were determined as the product of grain and/or plant dry weight by plant density respectively. All yield data are presented at 0% moisture after samples were dried in an air-forced drying oven at 70 °C to constant weight. Harvest index was estimated as the ratio of grain yield to total above-ground biomass at harvest. Seed number per m^{-2} was estimated considering the final harvest data as the ratio of grain yield ($g\,m^{-2}$) to average individual seed weight (g per seed). Individual seed weight (mg seed $^{-1}$) was estimated using three replicates of 100 seeds in each replicate plot (Gómez et al., 2011).

2.3. Statistical analyses

2.3.1. Variance components analysis

The G and G × E interaction components of variance and their standard errors for grain yield, above-ground biomass, harvest index, grain number and weight and time to flowering were estimated by Residual Maximum Likelihood (REML) (Patterson and Thompson, 1974). The phenotypic observation y_{ijk} on genotype i in block k of environment j was modelled as:

$$y_{ijk} = \mu + g_i + e_j + (ge)_{ij} + \left(\frac{b}{e}\right)_{kj} + \varepsilon_{ijk} \quad (1)$$

where μ is the grand mean; g_i the random effect of genotype i and is $\sim NID(0, \sigma^2_g)$, $i = 1, \ldots, g$; e_j the fixed effect of the environment j; $(ge)_{ij}$ the random effect of the interaction between the genotype i and environment j and is $\sim NID(0, \sigma^2_{ge})$; $(b/e)_{kj}$ the random effect of the block k nested within the environment j and is $\sim NID(0, \sigma^2_b)$, $k = 1, \ldots, b$; ε_{ijk} is the residual effect for genotype i in the block k of environment j and is $\sim NID(0, \sigma^2_\varepsilon)$.

In the linear mixed model used, the trial environments were considered fixed because for most of the traits analysed, less than 10 degrees of freedom were available for this term. This does no allow proper checking of the distributional assumptions for terms defined as random (Yang et al., 2009). Chi-square test was used to test the significance for fixed environment effects, as implemented in lme4 R package (Bates et al., 2009). The genotypes were assumed to be a random sample of the current genetic variability, and therefore G and G × E interaction terms were defined as random effects. The Best Linear Unbiased Predictors (BLUPs) (Robinson, 1991) for the random terms (i.e. predictors that were adjusted for the unbalanced nature of the data) were computed from REML analysis. As environments were defined as fixed effects in model (1), their estimates computed from REML are the Best Linear Unbiased Estimates (BLUEs) (Piepho et al., 2008). REML using the sparse Average Information algorithm was used to estimate the variance components and standard errors of random terms, as implemented in GenStat 12th Edition (2008). To evaluate the significance of variance components for all attributes we used the Likelihood Ratio Test as implemented in lme4 R package (Bates et al., 2009).

2.3.2. Two-mode pattern analysis of grain yield

Pattern analysis (complementary use of clustering and ordination; Williams, 1976) was applied to the environment-standardized (Fox and Rosielle, 1982) array of G × E interaction BLUPs for grain yield. For the classification, a hierarchical agglomerative clustering method with incremental sum of squares (Ward, 1963) as the fusion criterion was utilised. The squared Euclidean distance was used as dissimilarity measure for Ward's method. A dendrogram was constructed on the basis of fusion level to investigate similarities in terms of genotype-specific responses to environments) and environments (in terms of the way they influence the relative performance of the genotypes). The performance's specific response plots of different genotype groups across different environmental groups were used to describe the adaptation profile of the genotype groups (DeLacy et al., 1996). Given that grain yield is the economic trait of interest; we used the groups derived from cluster analysis of this trait to interpret response for the other traits. The principal components of the Euclidean distance matrix of grain yield were estimated using singular value decomposition and a GE (AMMI2) biplot of the first two principal components was constructed from this analysis (Gabriel, 1971). Patterns analyses were carried out using the InfoStat package (Di Rienzo et al., 2011).

2.3.3. Physiological bases of G × E interaction effects for grain yield

To investigate the physiological basis of the observed G × E interaction effects for grain yield in terms of the genotype-specific responses, the BLUPs for time to flowering, above-ground biomass, harvest index, grain number and weight within environmental groups previously defined on the basis of cluster analysis (see Section 2.3.2) were used to assist in the interpretation of G × E interaction effects for grain yield. Partial correlation coefficients and t Student test were performed on the scatter diagrams of association between each pair of traits using the InfoStat package (Di Rienzo et al., 2011).

3. Results

3.1. Variance components analysis

A strong across-genotype and across-environments variation was found for grain yield, as well as for other phenotypic attributes (Tables 1 and 2). Combined analysis of variance for this multi-environmental trial evaluation revealed significant G and G × E interaction effects for all attributes (Table 3). The G × E interaction term accounted for a higher proportion of variation than the G effects for grain yield, harvest index and grain number, while for above-ground biomass, grain weight and time to flowering, the G variance component was higher than the G × E interaction effects (Table 3). The environmental effects were statistically significant

Table 3
Estimated variance components (±standard error) for above-ground biomass ($g\,m^{-2}$), grain yield ($g\,m^{-2}$), harvest index, grain number ($\#m^{-2}$) and weight (g) and time to flowering (days) measured in 12 genotypes of quinoa across six environments in Northwest Argentina. The significance for each component of variance was calculated using the Likelihood Ratio Test.

Variable	Source of variance		Ratio G × E/G
	$\sigma^2_{gxe} \pm$ s.e	$\sigma^2_g \pm$ s.e	$\sigma^2_{gxe}/\sigma^2_g$
Biomass	$17205 \pm 6544^{**}$	$54473 \pm 26106^{***}$	0.3
Grain yield	$3944 \pm 1148^{***}$	$1336 \pm 1087^{*}$	3.0
Harvest index	$0.006 \pm 0.002^{***}$	$0.0002 \pm 0.0008^{*}$	30.0
Grain number	$7.4e^8 \pm 2.2e^{8***}$	$5.7e^8 \pm 3.4e^{8***}$	1.3
Grain weight	$0.001 \pm 0.0002^{***}$	$0.002 \pm 0.0009^{***}$	0.5
Time to flowering	$62.1 \pm 17.7^{***}$	$241.1 \pm 112.4^{***}$	0.25

$P < 0.001^{***}$; 0.01^{**}; 0.05^{*}.

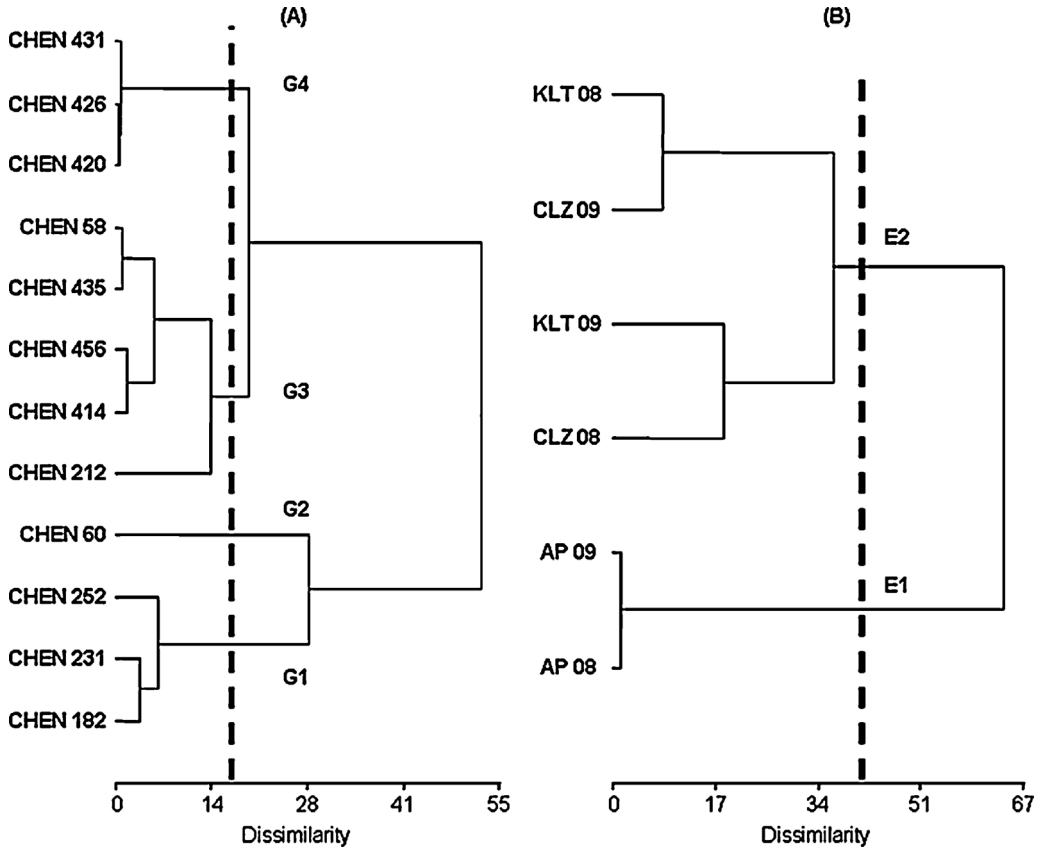

Fig. 1. Hierarchy for the classification of 12 genotypes of quinoa according to their relative responses for grain yield across six environments (A) and for the classification of six environments, according to the way they differentiated among patterns of grain yield of 12 genotypes of quinoa (B).

for all phenotypic attributes ($P = 0.01$), except for harvest index and grain weight.

3.2. Two mode pattern analysis for grain yield

Cluster analysis of environment-standardized array of G × E BLUPs for grain yield showed that genotypes could be grouped into four groups of different response patterns across environments (Fig. 1A), with a truncation retaining about 66% of the G × E interaction sum of squares. Group 1 consisted of three genotypes (CHEN 182, 231 and 252) previously assigned to dry valleys (Table 1) that showed, across-environments and compared with other genotypic groups, low grain yield, above-ground biomass and grain number and weight, but high harvest index and 73 days to flowering (Table 4). Group 2 consisted of one genotype (CHEN 60) previously assigned to dry valleys on the basis of morpho-phenological traits (Table 1) that showed the highest grain yield, above-ground biomass, grain number and harvest index, but low grain weight, while it was shorter for time to flowering compared to G1 and longer than G4 (Table 4).

At the next join, Group 3 consisted of five genotypes (CHEN 58, 212, 414, 435 and 456) from dry and humid valleys (Table 1), that showed the largest time to flowering, high grain yield, above-ground biomass and grain number, but low harvest index and grain weight (Table 4). Within this group, genotypes from dry and humid valleys were not differentiated according to relative performance across environments. The last group to join (G4), consisted of three genotypes (CHEN 420, 426 and 431) previously assigned to the highlands (Table 1), that showed the lowest phenotypic values for all traits except for grain weight (Table 4).

The classification of environments for grain yield gave rise to two groups, with a truncation level retaining about 63% of the G × E interaction sums of squares. This clustering roughly discriminated between highland (E1) and valley (E2) Environments (Fig. 1B). Within E2, dry and humid valley environments were not differentiated according to season or locality in the way they discriminate among genotypes (see genetic variance at each environment in Table 2). The environments did not show difference according to mean daily temperature, but Calete (dry valleys) tend to be hotter than Abra Pampa (highlands) and Colanzulí (humid valleys) respectively (Table 2). Environments showed differences in cumulative precipitation during the crop cycle, with more rain in the highlands and humid valleys compared to dry valleys. Besides that, the humid valleys were the wettest testing environments (Table 2).

Table 4
Agronomic traits of the four genotype groups resulting from a hierarchical agglomerative clustering method for BLUPs of grain yield.

Group	Grain yield ($g\,m^{-2}$)	Above ground biomass ($g\,m^{-2}$)	Harvest index	Grain number ($\#m^{-2}$)	Grain weight (g)	Time to flowering (days)
G1	126.2	389.1	0.31	49,478	0.26	73
G2	195.3	599.5	0.31	87,599	0.23	70
G3	126.6	552.6	0.29	53,711	0.26	82
G4	73.2	271.6	0.28	24,593	0.32	50

Results of the ordination analyses for grain yield are displayed in the biplot of the 1st and 2nd principal components, which together accounted for 80% of G × E interaction variability of the system (Fig. 2). The environments that grouped together in cluster analyses were co-located on the biplot (Fig. 1B and Fig. 2). The environmental vectors covered a wide range of Euclidean space, which is consistent with the strong G × E interaction effect revealed by REML analysis (Table 3). The angle between the environmental vectors on the biplot ranged from small positive values to values close to 180°, which suggest that the associations between environments in terms of their influence on the cultivar-specific responses for grain yield ranged from strongly positive to strongly negative. The angle between highland environments is smaller than 90°, which suggests that both environments are relatively similar in the way they discriminate among genotypes. A similar pattern was observed for the vectors of dry and humid valleys, but with lack of association, i.e., 90° angles, between environmental vectors corresponding to the same location in different years (Fig. 2). The average angle between highland and valley environments is larger than 90°, which indicates a negative association between both environmental groups in terms of their G × E interaction effects for grain yield.

The 1st principal component (PC1) explained 56.2% of the G × E interaction variation and seems to account for the highly contrasting effects of highland and valley environments on cultivar-specific responses, emphasizing the difference in relative performance between genotypic groups G3-G4 and G1-G2. Genotypic groups G3 and G4 are positively associated with highland environments, i.e., they present a positive component of G × E interaction in these environmental groups, and tend to sit on the right-hand side of the diagram, while G1 and G2 cultivars had negative loadings on the PC1 and were placed on the left side of the biplot (Fig. 2). The 2nd principal component (PC2) explained 23.3% of G × E interaction variation and seems to account for the contrasting environmental effects of the site-year combinations in the valley Environments, emphasizing the differences in performance between genotypic groups G3 and G1. Genotypic group G2 tend to be at the top left-hand quadrant of the biplot, which indicates that it had a positive G × E interaction component over all valley Environments. Cultivar CHEN 212 (G3) showed a positive G × E interaction component in three (KLT 08, CLZ 08 and KLT 09) out of the four valleys Environments. Genotypic group G1 showed improved relative performance in some site-year combinations (KLT 08 and CLZ 09), while G3 in some others (CLZ 08 and KLT 09) (Fig. 2). The strongly contrasting effects among site by year combinations observed in valley Environments could be attributed to the high pressure of downy mildew (*P. farinosa* f.sp. *chenopodii*), temperature and rainfall during pre and post-flowering stages. In CLZ 08 the high impact of downy mildew during the crop cycle affected mostly the performance of highland genotypes (G4), while in KLT 09 a lower downy mildew pressure affected the performance of most genotypes through defoliation, faster development and shorter plant height (Table 2). On the other hand, in KLT 08 and CLZ 09 there was a lower mildew pressure and favourable climatic conditions for the crop. High mean temperatures and low precipitation during pre and post-flowering stages determined higher grain number and weight (Table 2). The 3rd principal component (PC3) explained 14% of G × E interaction variation and did not differentiate between genotypic or environment groups according to origin.

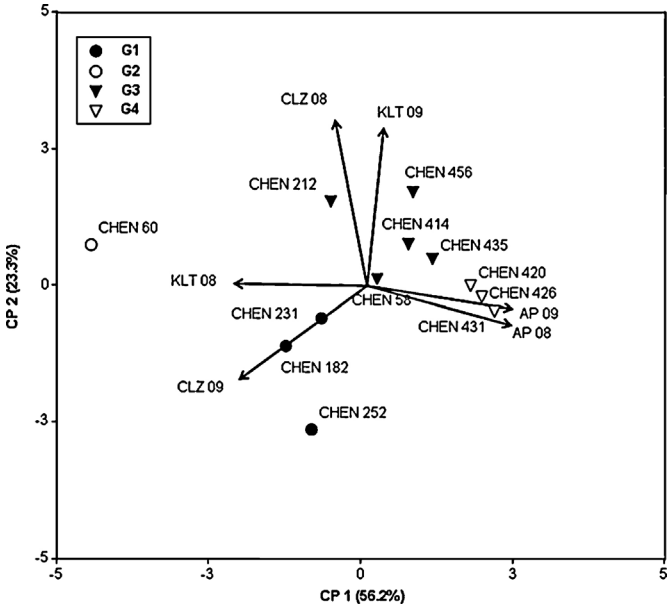

Fig. 2. Biplot of the 1st and 2nd principal components for grain yield of 12 genotypes grown in six environments. Genotypes are represented by symbols and environments by vectors. Same entry markers indicate genotype groups with members of a similar response pattern at the four-group level for grain yield.

3.3. Performance plots for grain yield, its physiological determinants and numerical components

The response plots of the five traits measured for the four genotype groups across two environmental groups indicated different patterns of genotype-specific performance across environments (Fig. 3A–E). G1 showed a relatively higher yield in the valleys and a poor relative performance in highland environments (Fig. 3A). G2 showed lower grain yield with respect to G1, G3 and G4 in highland Environments and was relatively superior to all genotypes groups in the valleys (E2), indicating a contrasting adaptation pattern to that of G4; both genotype groups showing specific adaptation. G3 showed a similar pattern of adaptation of G1, but slightly higher yield across environments. The adaptation profiles of G3 and G1 expressed nearly no interaction with the environmental groups in terms of grain yield and therefore may be considered to exhibit stable yields, i.e., broad adaptation, across all environmental groups. G4 showed high yield in highland environments and poor performance in valleys indicating a contrasting pattern of adaptation with respect to G2 (Fig. 3A).

The response plots for above-ground biomass and harvest index showed that G4 expressed a high values for both traits in highland environment and relatively poor performance in the valleys, while G2 showed the opposite pattern (Fig. 3B and C). This tendency indicates that both traits underlie the contrasting relative performance for grain yield of G2 and G4 across environments. On the other hand, G3, which showed stable yield, expressed stability for both traits, while G1 showed stable values for biomass, but contrasting responses for harvest index across environmental groups (Fig. 3B and C).

The response plots for grain number resemble that of grain yield and biomass, showing contrasting relative performances for G2 and G4 across environmental groups and stability for G1 and G3 (Fig. 3D). In contrast, G1 and G3 expressed high and poor relative performances for grain weight in highland and valley environments, respectively, while G4 showed a contrasting response (Fig. 3E). G2 expressed stability for this trait across all environmental groups.

3.4. Physiological bases of G × E interaction effects for grain yield

The association between BLUPs for the average performances for the five traits analyzed differed strongly between both pair of

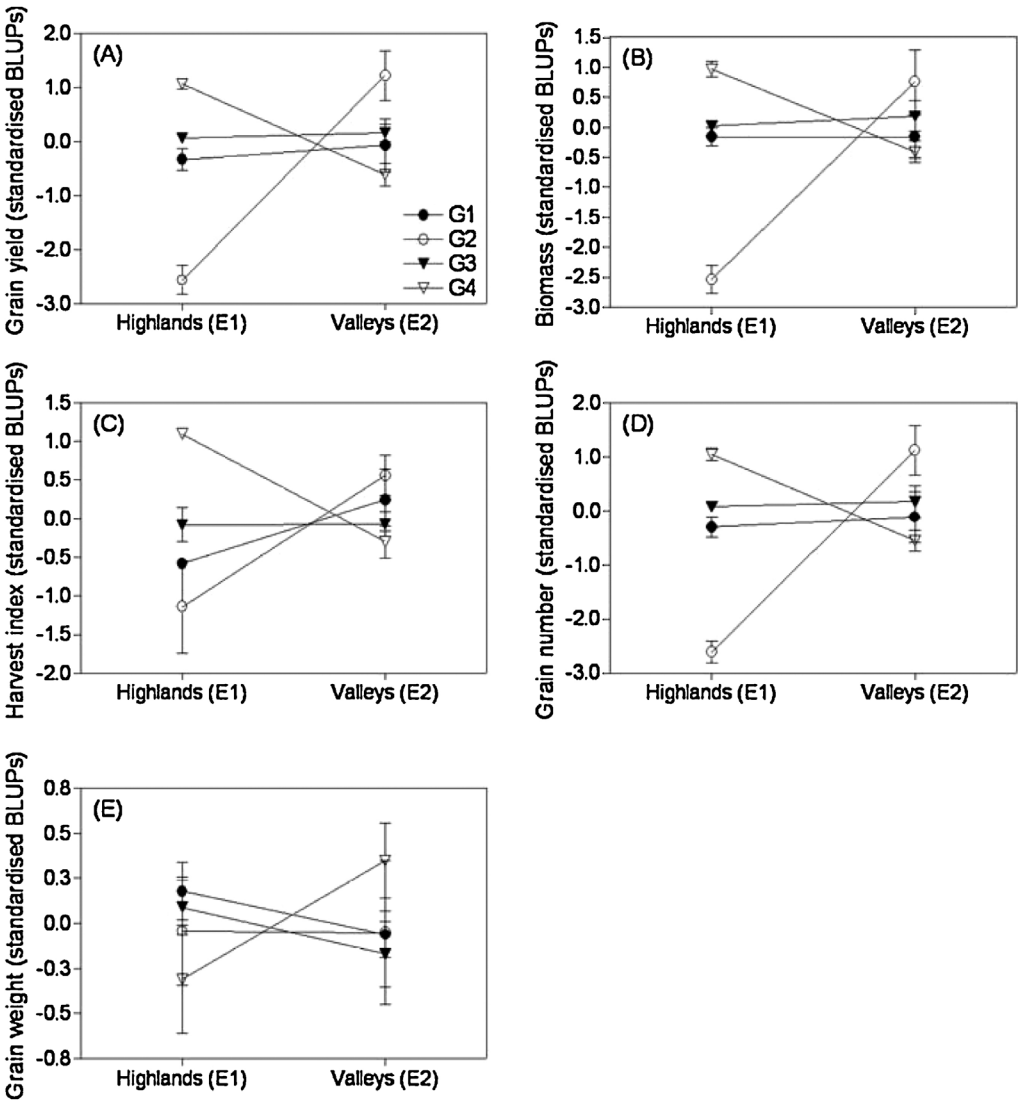

Fig. 3. Plot responses of the grain yield (A), above-ground biomass (B), harvest index (C), grain number (D) and grain weight (E) for the four groups of quinoa genotypes identified by cluster analysis plotted against two environments groups. Vertical bars indicate standard errors.

environments (Fig. 4). For highland environments (E1) there was a positive association between yield and above-ground biomass (Fig. 4A) and harvest index (Fig. 4B), but no association was detected between yield and time to flowering (Fig. 4C) and between above-ground biomass or harvest index and time to flowering (Fig. 4D and E). For valley Environments (E2) there was a positive association between yield, time to flowering (Fig. 4F) and above-ground biomass (Fig. 4G) and a slightly significant one between biomass and time to flowering (Fig. 4I).

For the numerical components, the association between average BLUPs performances analyzed show that grain number is the main component that determines yield in both highland and valley environments (Fig. 5A and F). There was a negative association between grain yield and grain weight in both environments, and it was highly significant in valley sites (Fig. 5B and G). A similar trend was observed for the association between grain number and weight across both environments (Fig. 5C and H). Otherwise, there was a positive association between grain number and time to flowering in both environments, although in valley sites that was slightly significant (Fig. 5D and I); while a strong negative association was detected between grain weight and the time to flowering across both environments (Fig. 5E and J).

4. Discussion

The relative contributions of G and G × E interaction effects to total variation for grain yield, its physiological determinants and numerical components found in this study are similar to those found in quinoa crop adaptation studies in temperate and tropical environments (Risi and Galwey, 1991; Bertero et al., 2004). This scenario of environmental heterogeneity complicates the effective identification of superior genotypes in METs and indicates that it would be very difficult to achieve an indirect response to selection over all of the TPE for quinoa in NWA from selection in a few environments, ignoring the observed G × E interactions. The large and eco-regional nature of the observed G × E interactions require testing strategies structured to accommodate their effects by either avoiding or exploiting them. Conversely, the large relative contribution of the G effect for above-ground biomass, time to flowering and grain weight suggest that G × E interaction would not be a major impediment for achieving high responses to selection for these traits, even across the identified groups of environments for yield. However, these results should be taken cautiously because of the large unbalance of genotype representation across environments, and important differences regarding

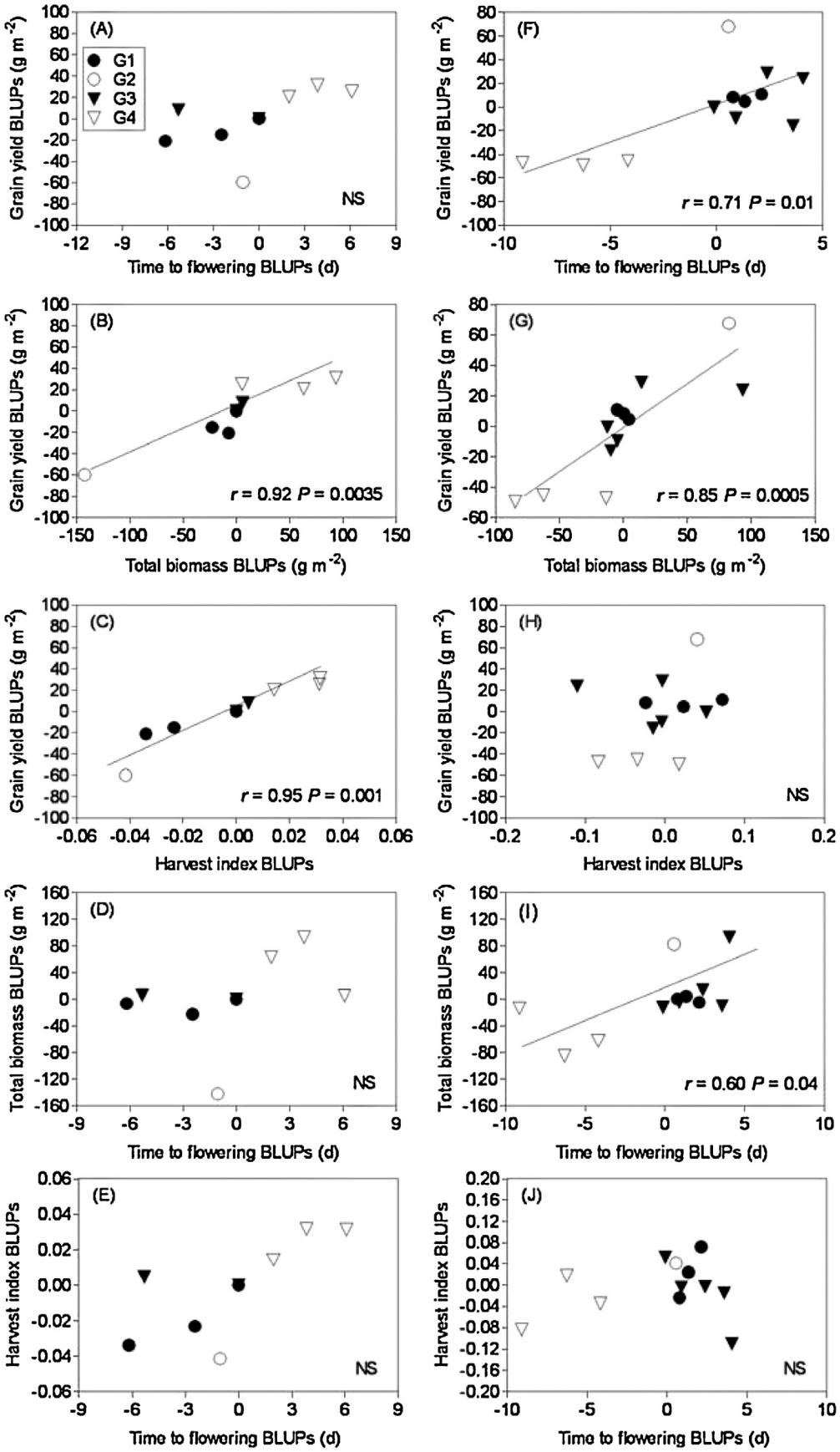

Fig. 4. Scatter diagrams of association between the best linear unbiased predictors (BLUPs) for grain yield, time to flowering, total biomass, and harvest index for 12 genotypes of quinoa for highland environment group (E1) (A–E), and for valley environment group (E2) (F–J). Partial correlation coefficient and *t* test were used to determine the magnitude and significance for each pair of associations.

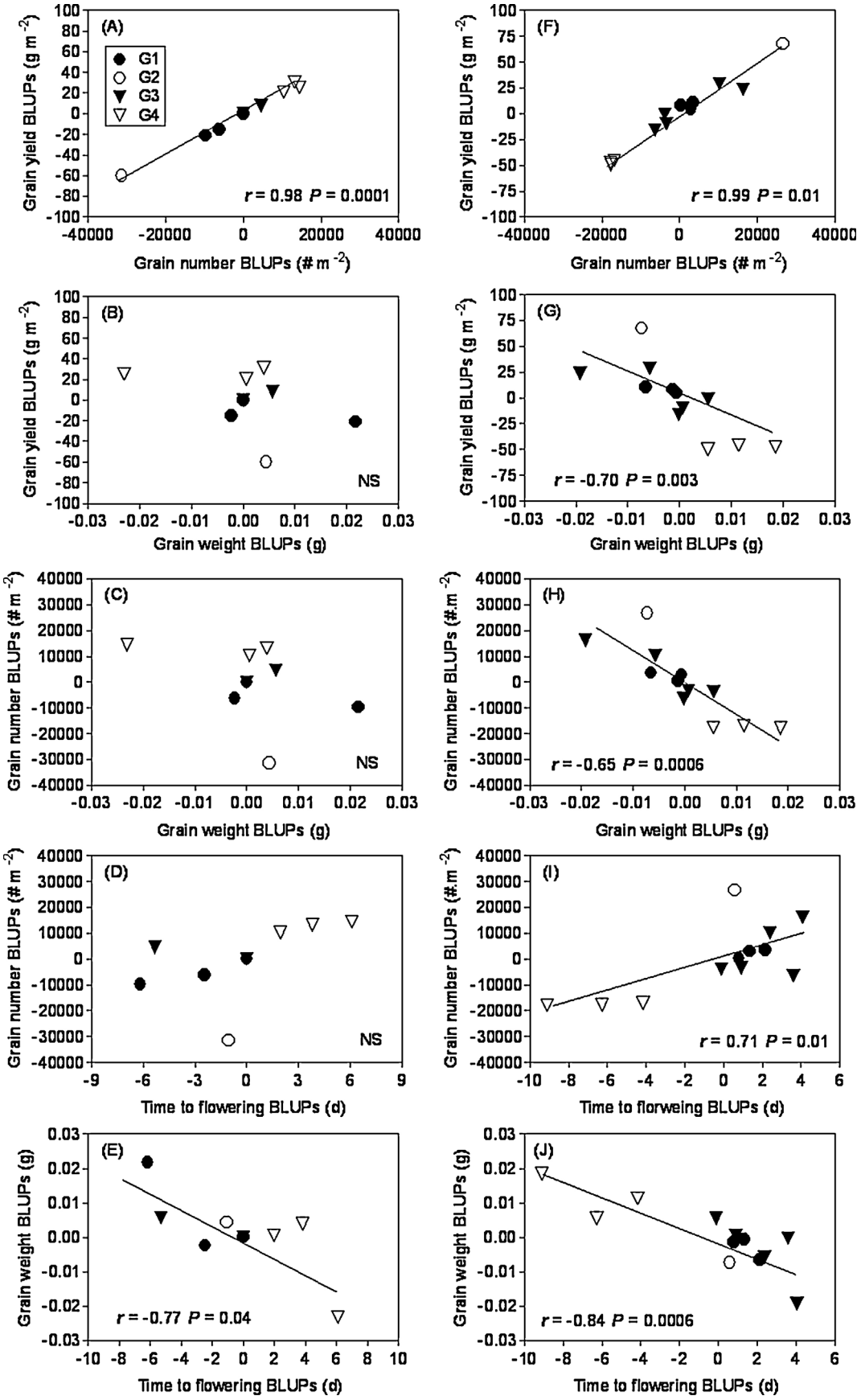

Fig. 5. Scatter diagrams of association between the best linear unbiased predictors (BLUPs) for grain yield, grain number and weight and time to flowering for 12 genotypes of quinoa for highland environment group (E1) (A–E), and for valley environment group (E2) (F–J). Partial correlation coefficient and *t* test were used to determine the magnitude and significance for each pair of associations.

management practices among environments that/which could introduce biases in the analysis of variance components.

4.1. Contrasts between highland and valley environments

The hierarchical grouping of genotypes according to their relative responses for grain yield found in this study is consistent with the previously proposed genotypic groupings on the basis of a morpho-phenological classification (Curti et al., 2012) and on pattern analysis of a wide range of cultivars evaluated across tropical environments (Bertero et al., 2004). However, a difference between this classification and that obtained on the basis of morpho-phenological traits was observed. Within G3, the cultivars from dry and humid valleys were not differentiated. One possible explanation for this result could be that in this multi-environmental evaluation, environments from dry and humid valleys located to the south (Valles Calchaquies) and east (Santa Victoria Oeste) of Salta province, were not included. Alternatively, the strong eco-regional nature of the observed G × E interactions across valley environments could explain the low discrimination power of these sites. More testing sites are needed across these environments to evaluate if genotypes of dry and humid valleys show differences in their relative performance along sites which includes their origins.

Although a larger environmental sampling is needed to accurately predict the amount of variation explained by the genotype × year and genotype × location × year interactions, the environment grouping resulting from classification analysis suggests that this is large within three main eco-regions (highland, dry and humid valleys). But there were extreme differences in the discrimination effects of the highland (E1) and valley (E2) environments in terms of their G × E interaction effects for grain yield, suggesting at least the existence of two groups of environments. The largely orthogonal association between E1 and E2 environments indicates that yield gains under highland environments would have been unlikely to occur if selection is done in valley environments and vice versa. On the other hand, within the E2 the genotype × year and genotype × location × year were large, which suggest that among this eco-region the G × E interaction is highly unpredictable. More sites and years of testing are needed across this eco-region to reach an objective decision about further subdivision into groups of environments. Conversely, with no subdivision of the TPE only broad adaptation could be exploited using genotypes from G3 which showed stability across environments of highland and valleys and G2 across valleys environments.

Testing sites in NWA did not show extreme differences in terms of photoperiod and mean temperature, but were strongly different with respect to rainfall and relative humidity during the growing season. Relative humidity differences among the Andean environments are an important factor for the development of downy mildew (*P. farinosa* f.sp. *chenopodii*) (Danial et al., 2007). It is known that cool and humid conditions are conductive to *P. farinosa* attacks and that late maturing genotypes in general are more resistant to downy mildew than earlier maturing genotypes (Danielsen and Munk, 2004). Thus, the strong crossover G × E interaction observed for G4 cultivars could be due to their precocity; which contributes to their adaptation to the highland environments (low mean temperature and rainfall), and their extreme susceptibility to downy mildew, which leads to low relative grain yields in valley environments. This susceptibility would be consequence of a low selection pressure for downy mildew resistance in the arid environment (highlands) where these cultivars were bred. At the other extreme, the differences between highland and valley environments with respect to the length of the growing season and frost risk (shorter length and higher frost risk in highland than in valley environments) (Pouteau et al., 2011), combined with genotypic variation in time to flowering could explain why cultivars belonging to G1, G2 and G3 with longer time to flowering suffered the largest yield losses in highland environments. This result shows that the identification of defined causes of G × E interactions between highland and valley environments could be used in defining selection strategies. For example, the identification of genetic variation in disease susceptibility and environmental variation in the incidence of diseases, including genetic variation in flowering time and that in the length of the growing season are two of the major defined causes of G × E interaction in major crops and those that are taken into account to define the selection strategies. Typical cases of such situations are observed in maize breeding for low input conditions (Bänziger and Cooper, 2001) for wheat in Australia (Basford and Cooper, 1998) and for barley in Syria (Ceccarelli et al., 1998). In summary, the observed similarity of these results with other crops suggests that these causes should be considered in defining selection strategies aimed to exploit specific components of adaptation in crop species growing in complex TPE.

4.2. Grain yield determinants and numerical components

The response pattern of the four genotype groups across environments for grain yield showed a re-ranking of the groups along this environmental range (Fig. 3A). This type of G × E interaction, known as crossover or due to the lack of genetic correlation between environments, severely complicates the recommendation or selection of genotypes (Cooper et al., 1996). The presence of crossover G × E interactions could have been determined by specific adaptation patterns that are the consequence of the breeding strategy followed by the quinoa breeding program across Andean environments. Typically these programs conducted breeding activities on a local basis and exploit local adaptation to narrowly defined target areas (Aguilar and Jacobsen, 2003; Danial et al., 2007; McElhinny et al., 2007).

The response plot for above-ground biomass and harvest index showed that both attributes were important for yield determination across the two groups of environments (Fig. 3). However, a major difference between highland and valley environments was that in the first both biomass and harvest index made a significant contribution to the genotypic effect for grain yield (Fig. 4A and B), while for the second only biomass production made a significant contribution (Fig. 4F) through its influence on time to flowering (Fig. 4I). Similar results (in terms of the contrasts between environments in yield generation strategy) were observed by Bertero et al. (2004) based on a broader evaluation of genotypes in tropical environments. This approach was useful for identifying how genetic effects influence the G × E interaction for yield. The difference in genetic effects for attributes across the groups of environments indicates that such characters could be used as indirect selection attributes to improve performance in each environmental group, but hardly can be combined into a single cultivar to increase performance throughout the population of environments (Bertero et al., 2004).

The relationships among yield numerical components showed that genotypic effects were more pronounced for grain number than grain weight, which indicate that genetic variation in grain yield was mainly explained by this component (Fig. 5). This means that selection for grain yield should indirectly increase grain number throughout the population of environments. The similarity observed among response plot for above-ground biomass and grain number (Fig. 3B and D) and between grain number and time to flowering in valley environments (Fig. 5I), suggest that genotypic effects for time to flowering partially explain the difference in grain number and yield observed within this environment and indicate that this attributes could be used as indirect selection attributes to improve performance for grain yield

in this environmental group. Previous study with quinoa commercial lines have showed that crop growth rate around flowering and genotypic variation for time to flowering are the most important factors determining grain number and total biomass produced, respectively (Bertero and Ruiz, 2008; Ruiz and Bertero, 2008).

Correlation analysis between BLUPs of the genotypic effects revealed a negative association between grain number and weight across both groups of environments, although this association was stronger and significant in valley than highland environments (Fig. 5C and H). This means that selection based on grain yield only, especially in valley environments, could lead to an indirect selection for smaller grains, possibly associated to a source limitation linked to more grains. These results are consistent with observations in other crops species, in which the negative relationships between both yield components have been attributed to compensation processes through limitations to grain weight caused by the low resources availability per grain in the presence of higher grains number (Sadras, 2007; Gambín and Borrás, 2010). If determination of a large number of grains is linked to a source limitation, the drop in resources availability per grain when potential grain weight is determined would lead to lower seed weight. These effects could be observed whether there is temporal overlapping between stages of determination of grain number and weight (as observed in quinoa) or not, as in the case of wheat where the number of grains is largely determined before flowering (Savin and Slafer, 1991).

The response plot for grain weight and the BLUPs relationship among grain number and weight within each group of environment suggest that in highland environments genotypes from valleys (G1, G2 and G3) achieved higher grain weight, while genotypes from the highlands (G4) did it in valley environments (Fig. 3E and Fig. 5C and H). Moreover genotypes from highlands showed longer time to flowering in highland than in valley environments, respectively (Fig. 5E and J). These results suggest that grain weight maximization was associated with genotypes that flower earlier in each environment. In this case, grain weight was determinated by post-flowering conditions, thus genotypes which showed longer time to flowering in each environment were exposed to unfavourable conditions (low radiation and mean temperature) that could have affected the grain filling (Capristo et al., 2007).

Overall these results reveal clearly contrasting patterns of genotype relative performance for grain yield and its physiological determinants in a relatively narrow geographical range of environments. In this aspect, these results differ from those obtained in crop species more evolved than quinoa in terms of history and investment in plant breeding, In crops such as wheat, sunflower or corn (Basford and Cooper, 1998; de la Vega et al., 2001; Windhausen et al., 2012), many sources of germplasm have been globally spread, which contributed to the creation of widely-adapted genotypes that require more comprehensive environmental sampling to reveal repeatable patterns of G × E interaction. Quinoa, as experimental model for the study of the physiological basis of G × E interaction, presents the particular advantage that all or almost all genotypes present a narrow pattern of specific adaptation to local conditions, due to the small, local and isolated breeding efforts applied to this species, expressing very contrasting relative responses in a relatively narrow range of environments.

5. Conclusions

This study reveals that G × E interaction in quinoa in the NWA region was significant and repeatable across the eco-regions. Pattern analysis indicates that these interactions are mainly explainable as subsets of genotypes and environments and suggest that subdivision and selection for specific adaptation is a potential strategy to increase the selection response. However, the relative performance of genotypes from G2 and G3 across the groups of environments identified suggests that selection for broad adaptation is possible and both strategies should be compared. Improved adaptation to complex TPE characterized by large variations in environmental conditions and biotic challenges, should contemplate the importance of time to flowering and the degree of resistance/susceptibility to diseases since both predictable sources of variation are primarily responsible for the differences of individual genotypes in those environments. On the other hand, the narrow pattern of specific adaptation to the local conditions of quinoa genotypes provide an optimal experimental model to study the physiological bases of G × E interaction in a narrow range of environments with highly contrasting environments conditions.

Acknowledgements

The authors thank the handling editor and the anonymous reviewers for insightful comments that have improved this manuscript. We are grateful to Gustavo Giménez for statistical advice and Mónica Cuevas and Raúl Viveros for field technical assistance. This work was supported by FONCYT (Fondo Nacional de Ciencia y Técnica, BID 1728 OC-AR PICT 2005-23382) and CONICET (the Argentine Scientific Research Council).

References

Aguilar, P.C., Jacobsen, S.E., 2003. Cultivation of quinoa on the Peruvian Altiplano. Food Rev. Int. 19, 31–41.
Atlin, G.N., Baker, R.J., McRae, K.B., Lu, X., 2000. Selection response in subdivided target regions. Crop Sci. 40, 7–13.
Bänziger, M., Cooper, M., 2001. Breeding for low input conditions and consequences for participatory plant breeding examples from tropical maize and wheat. Euphytica 122, 503–519.
Basford, K.E., Cooper, M., 1998. Genotype × environment interactions and some considerations of their implications for wheat breeding in Australia. Crop Pasture Sci. 49, 153–174.
Bates D., Maechler M., Dai D., 2009. lme4: linear mixed effects models using S4 classes. R package version 0.999375-31. (http://cran.r-project.org/web/packages/lme4).
Bertero, H.D., de La Vega, A.J., Correa, G., Jacobsen, S.E., Mujica, A., 2004. 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. Field Crops Res. 89, 299–318.
Bertero, H.D., Ruiz, R.A., 2008. Determination of seed number in sea level quinoa (*Chenopodium quinoa* Willd.) cultivars. Eur. J. Agron. 28, 186–194.
Bianchi, A.R., Yánez, C.E., Acuña, L.R., 2005. Base de Datos Mensuales de Precipitaciones del Noroeste Argentino. Instituto Nacional de tecnologáa Agropecuaria. Proyecto Riesgo Agropecuario Convenio Específico, pp. 41.
Capristo, P.R., Rizzalli, R.H., Andrade, F.H., 2007. Ecophysiological yield components of maize hybrids with contrasting maturity. Agron. J. 99, 1111–1118.
Ceccarelli, S., Grando, S., Impiglia, A., 1998. Choice of selection strategy in breeding barley for stress environments. Euphytica 103, 307–318.
Cooper, M., Byth, D.E., Woodruff, D.R., 1994. An investigation of the grain yield adaptation of advanced CIMMYT wheat lines to water stress environments in Queensland. I. Crop physiological analysis. Crop Pasture Sci. 45, 965–984.
Cooper, M., DeLacy, I.H., Basford, K.E., 1996. Relationships among analytical methods used to analyse genotypic adaptation in multi-environment trials. In: Cooper, Hammer, M., GL (Eds.), Plant Adaptation and Crop Improvement. CAB International, Wallingford, UK, pp. 193–224.
Costa Tártara, S.M., Manifesto, M.M., Bramardi, S.J., Bertero, H.D., 2012. Genetic structure in cultivated quinoa (*Chenopodium quinoa* Willd.), a reflection of landscape structure in Northwest Argentina. Conserv. Genet. 13, 1027–1038.
Curti, R.N., Andrade, A.J., Bramardi, S., Velásquez, B., Bertero, H.D., 2012. Ecogeographic structure of phenotypic diversity in cultivated populations of quinoa from Northwest Argentina. Ann. Appl. Biol. 160, 114–125.
DeLacy, I.H., Basford, K.E., Cooper, M., Bull, J.K., McLaren, C.G., 1996. Analysis of multi-environment trials – an historical perspective. In: Cooper, M., Hammer, G. L. (Eds.), Plant Adaptation and Crop Improvement. CAB International, Wallingford, UK, pp. 39–124.
Danial, D., Parlevliet, J., Almekinders, C., Thiele, G., 2007. Farmers' participation and breeding for durable disease resistance in the Andean region. Euphytica 153, 385–396.
Danielsen, S., Munk, L., 2004. Evaluation of disease assessment methods in quinoa for their ability to predict yield loss caused by downy mildew. Crop Prot. 23, 219–228.
de la Vega, A.J., Chapman, S.C., Hall, A.J., 2001. Genotype by environment interaction and indirect selection for yield in sunflower: I. Two-mode pattern

analysis of oil and biomass yield across environments in Argentina. Field Crops Res. 72, 17–38.
de la Vega, A.J., Hall, A.J., 2002a. Effects of planting date, genotype, and their interactions on sunflower yield: I. Determinants of oil-corrected grain yield. Crop Sci. 42, 1191–1201.
de la Vega, A.J., Hall, A.J., 2002b. Effects of planting date, genotype, and their interactions on sunflower yield: II. Components of oil yield. Crop Sci. 42, 1202–1210.
de la Vega, A.J., Chapman, S.C., 2010. Mega-environment differences affecting genetic progress for yield and relative value of component traits. Crop Sci. 50, 574–583.
Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., Robledo, C.W., 2011. InfoStat Version 2011. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
Fox, P.N., Rosielle, A.A., 1982. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. Euphytica 31, 645–656.
Gabriel, K.R., 1971. The biplot graphic display of matrices with application to principal component analysis. Biometrika 58, 453–467.
Gambín, B.L., Borrás, L., 2010. Resource distribution and the trade-off between seed number and seed weight: a comparison across crop species. Ann. Appl. Biol. 156, 91–102.
GenStat, 2008. Genstat release 12, statistics software. VSNI. UK.
Gómez, M.B., Castro, P.A., Mignone, C., Bertero, H.D., 2011. Can yield potential be increased by manipulation of reproductive partitioning in quinoa (*Chenopodium quinoa*)? Evidence from gibberellic acid synthesis inhibition using Paclobutrazol Func. Plant Biol. 38, 420–430.
Goodspeed, M.J., 1975. Computer Routines for Solar Position, Day Length and Related Qualities. Tech. Mem. No. 75/11. CSIRO. Division of Land Use Research, Canberra, Australia, pp. 75/.
McElhinny, E., Peralta, E., Mazon, N., Danial, D.L., Thiele, G., Lindhout, P., 2007. Aspects of participatory plant breeding for quinoa in marginal areas of Ecuador. Euphytica 153, 373–384.
Patterson, H.D., Thompson, R., 1974. Maximum likelihood estimation of components of variance. Proceedings of the Eighth International Biochem. 197–209.
Piepho, H.P., Möhring, J., Melchinger, A.E., Büchse, A., 2008. BLUP for phenotypic selection in plant breeding and variety testing. Euphytica 161, 209–228.
Pouteau, R., Rambal, S., Ratte, J.P., Gogé, F., Joffre, R., Winkel, T., 2011. Downscaling MODIS-derived maps using GIS and boosted regression trees: the case of frost occurrence over the arid Andean highlands of Bolivia. Remote Sens. Environ. 115, 117–129.
Risi, J., Galwey, N.W., 1991. Genotype × environment interaction in the Andean grain crop quinoa (*Chenopodium quinoa*) in temperate environments. Plant Breed. 107, 141–147.
Robinson, G.K., 1991. That BLUP is a good thing: the estimation of random effects. Stat. Sci. 6, 15–32.
Ruiz, R.A., Bertero, H.D., 2008. Light interception and radiation use efficiency in temperate quinoa (*Chenopodium quinoa* Willd.) cultivars. Eur. J. Agron. 29, 144–152.
Sadras, V.O., 2007. Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Res. 100, 125–138.
Savin, R., Slafer, G.A., 1991. Shading effects on the yield of an Argentinian wheat cultivar. J. Agric. Sci. 116, 1–7.
van Eeuwijk, F.A., Malosetti, M., Yin, X., Struik, P.C., Stam, P., 2005. Statistical models for genotype by environment data: from conventional ANOVA models to eco-physiological QTL models. Crop Pasture Sci. 56, 883–894.
Ward, J.H., 1963. Hierarchical grouping to optimise an objective function. J. Am. Stat. Assoc. 58, 236–244.
Wilson, H.D., 1990. Quinua and relatives (*Chenopodium* sect. *Chenopodium* subsect. Celluloid). Econ. Bot. 44, 92–110.
Williams, W.T., 1976. Pattern Analysis in Agricultural Science. Csiro, Australia, pp. 340.
Windhausen, W.S., Wagner, S., Magorokosho, C., Makumbi, D., Vivek, B., Piepho, H.P., Melchinger, A.E., Atlin, G.N., 2012. Strategies to subdivide a target population of environments: results from the CIMMYT-led maize hybrids testing programs in Africa. Crop Sci. 52, 2143–2152.
Yang, R.C., Crossa, J., Cornelius, P.L., Burgueño, J., 2009. Biplot analysis of genotype × environment interaction: proceed with caution. Crop Sci. 49, 1564–1576.
Yan, W., Hunt, L.A., Sheng, Q., Szlavnics, Z., 2000. Cultivar evaluation and mega-environment investigation based on the GGE biplot. Crop Sci. 40, 597–605.