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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

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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 ($G \times E$). The magnitude and nature of the genotype (G) and $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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.

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* 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) Capital, Salta, Argentina.

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 ($G \times E$) 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

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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 $G \times E$ 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 possess a narrow range of adaptation, large $G \times E$ 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, Caleta and Colanzulí) and two seasons (2008/2009–2009/2010) (Table 2). The experimental sites were located in farmer's field (e.g., Colanzulí and Caleta) 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; Caleta (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

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