#### RESEARCH ARTICLE



# Trade-off between seed yield components and seed composition traits in sea level quinoa in response to sowing dates

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#### Abstract

**Background and objectives:** The relative influences of genetic and environmental factors on seed composition traits as well as the interrelations among these attributes and seed yield are largely unknown in quinoa. These aspects are approached here through experiments conducted at a low elevation temperate environment with four quinoa genotypes sown at three dates and the hypothesis that variation in seed composition traits can be explained by the relative embryo size was tested.

**Findings:** There was an important range of variation for almost all seed composition traits, and the genotype-by-sowing date ( $G \times S$ ) interaction effect was significant for yield and its components plus protein and oil concentrations. Variation in fat and protein concentration was associated with embryo and seed size but not with relative embryo size (trait indifferent to environmental and genetic factors). A winter sowing date induced positive associations between fat and carbohydrate concentrations, seed, and embryo weight, but negative associations among almost all of these traits and seed yield and protein content. On the other hand, a mid-spring sowing date induced positive associations between seed yield and protein content.

**Conclusions:** Winter sowing dates are suited for obtaining heavier seeds associated with higher fat and carbohydrates concentrations under the explored conditions; whereas under mid-spring sowings higher seed yield, associated with high protein content but at the expense of smaller seeds are achieved.

**Significance and novelty:** Variability in the main seed composition traits in sea level quinoa cultivars was explained mostly by  $G \times S$  interaction. The choice of genotypes and sowing dates that modify the trade-offs between the main yield and seed composition traits might contribute to obtain a specific quality and higher yields. Variation in protein and fat concentrations was no associated with the relative embryo size.

#### **KEYWORDS**

embryo weight, genotype-by-environment interaction, proximate composition, seed quality

# **1** | **INTRODUCTION**

In most annual crops grain, yield and quality vary considerably due to genotype (G), environment (E), and their interaction  $(G \times E)$  effects. Studies of the covariation among crop physiological traits and grain compositional attributes provide useful information to implement management strategies aimed at obtaining a specific quality and high vield (Aguirrezábal, Martre, Perevra-Irujo, Echarte, & Izquierdo, 2015). The above information is not available for new grain crops which have recently risen in value due to their nutritional composition and capacity to grow in marginal environments (Haros & Schoenlechner, 2017). The study of genetic and environmentally determined associations among yield and grain compositional attributes will have profound implications to define breeding targets and crop management strategies as new environments are expected to affect productivity and quality (Aguirrezábal et al., 2015).

Quinoa (Chenopodium quinoa Willd.) is an ancient Andean crop that gained worldwide attention as a highly nutritious grain (Bazile, Bertero, & Nieto, 2015). Its main nutritional attractives are the high quality of its proteins, fatty acids, and minerals compared to other cereal and crops and also closer species such as amaranth and buckwheat (Haros & Schoenlechner, 2017; Vilcacundo & Hernández-Ledesma, 2017; Wijngaard & Arendt, 2006). According to Prego, Maldonado, and Otegui (1998), localization of stored reserves shows a marked compartmentation within the mature quinoa seed. Most carbohydrate reserves are found in the perisperm, while most protein and lipid reserves are located in the embryo tissue. This feature raises two main questions to be addressed to set the basis for improving the nutritional quality of this crop: (a) What is the size and nature of the associations among seed components and how are they determined by genetic and/or environmental factors and (b) whether seed composition (e.g., protein and fat content) is determined by the relative size of the tissue in which they are located as this last could be modified by genotypic and environmental factors.

Several studies reported variation in seed composition traits among quinoa cultivars or accessions from the Andean region and sea level sites in Central and Southern Chile (Aluwi, Murphy, & Ganjyal, 2017; Bhargava, Shukla, & Ohri, 2007; De Santis, D'Ambrosio, Rinaldi, & Rascio, 2016; Gonzalez, Konishi, Bruno, Valoy, & Prado, 2012; Miranda et al., 2013; Vidueiros et al., 2015). However, only few of these studies analyzed the relative influences of genotypic and environmental effects or the association between variation in seed quality and that in seed yield or weight in a range of genotypes and environments. Bhargava et al. (2007) recorded high genotypic effects in most seed yield components and seed composition traits; however, they did not find a significant genetic association among protein content, seed yield, and weight. On the other hand, Miranda et al. (2013) found that different environmental conditions induced different relations among seed yield and seed composition traits. Recently, De Santis et al. (2016) found that genotypic effects were the major source of variation explaining seed yield components, whereas  $G \times E$  interaction effects were significant for seed composition traits.

While yield and seed size are two of the main selection criteria in quinoa breeding programs, seed composition traits have not been considered yet. Results of large and regional scale multienvironmental trials show that the vast size of  $G \times E$  interactions for guinoa seed yield can be a significant obstacle to the identification of superior genotypes across the target population of environments (Bertero, de la Vega, Correa, Jacobsen, & Mujica, 2004; Curti, de la Vega, Andrade, Bramardi, & Bertero, 2014). On the other hand, the higher contribution of G to  $G \times E$  interaction effects for seed weight opens a window for faster genetic progress for this trait (Curti et al., 2014). The lack of association found between yield and seed size indicates that progress for both yield components can be expected from simultaneous selection (Bertero et al., 2004). At present, however, there are few studies aimed at evaluating how much seed composition traits variation is related to that in seed yield and its components (i.e., seed number and weight) as well as the genetically and environmentally determined correlations among these attributes. Thus, to improve the efficiency of quinoa breeding, a study that evaluates the relations between breeding objectives and responses to the environment or management regimes for a combined analysis of yield components and composition traits is needed.

This study analyzes responses to a range of sowing dates of four Sea Level (Chilean) quinoa genotypes grown in a temperate environment in the humid pampas of Argentina that could provide information for management and breeding to improve seed composition traits. Our objectives were to: (a) evaluate the variability in seed yield components and seed composition traits among genotypes and sowing dates, (b) determine the nature and size of genotype (G), sowing date (S) and their interaction  $(G \times S)$  effects, and (c) explore the genotypically and environmentally determined correlations among seed yield and seed composition traits. It was hypothesized that: (a) There are substantial  $G \times S$  interaction effects on seed composition variation and (b) variation in protein and fat concentrations is correlated with that in relative embryo size (embryo to total seed weight<sup>-1</sup>), as this organ is the main reservoir of these components.

## 2 | MATERIALS AND METHODS

# 2.1 | Experimental design and growing conditions

Quinoa genotypes adapted to temperate environments were cultivated in a sowing date experiment conducted at the Faculty of Agronomy of the University of Buenos Aires (34°35'S, 58°29'W, 20 m above sea level). The soil is a silty clay loam (vertic argiudoll, USDA Taxonomy). Rainfall (mm), mean air temperature (°C), and total radiation values (MJ  $m^{-2} day^{-1}$ ) were obtained from a weather station (Li-COR 1200; Lincoln, NE, USA) located 50 m from the experimental field. Four genotypes: NL-6 (selected in Holland), CO-407 (USA), Salto de Agua (Chile), and 2-Want (USA) were sown at three sowing dates in a splitplot experiment arranged in a randomized complete block design with three replicates, with sowing date levels as main plots and genotypes as subplots. The first three genotypes were selected from germplasm originating from lowaltitude environments in Chile (the so-called Sea Level quinoas, Bertero et al., 2004) while 2-Want is the result of a cross between a Bolivian and a Chilean accession (E. Ballon, personal communication). Sowing dates were defined as July 2 (winter), October 10 (early spring), and November 15 (mid-spring). Plots were hand-planted and thinned to 20 plants/m<sup>2</sup> in rows 0.50 m apart. Plots were five rows wide by 3 m long with an area of 7.5  $m^2$ . Plants received supplementary irrigation and fertilization at sowing (20 kg P and 18 N kg/ha) and one urea application (totalling 100 kg N/ha) 30 days after emergence to minimize nutrient restrictions. Weeds were removed by hand and fungicides and insecticides applied upon diseases and pest detection in the field.

## 2.2 | Seed yield components

Seed yield and seed number were determined from the sample conducted at crop physiological maturity of ten contiguous plants in central rows after discarding border plants. Results are expressed as g/m<sup>2</sup> obtained by multiplying sample data by a factor of two. Samples were dried to constant weight in an air-forced drying oven at 70°C. Seed number was calculated as the ratio of individual seed weight (g/seed) to seed yield. Individual seed weight (g/ seed) was calculated using three replicates of 100 seeds in each replicate plot. Embryo weight was measured to estimate its relative size and contribution to variation in seed composition. To do that for each genotype, sowing date, and block, 15 seeds were separated. To isolate the embryo from other seed components (seed coats and perisperm), seeds were boiled in water for 20 min in glass beakers. At this stage, the perisperm tissue exhibited a gelatinous consistency. Then, the embryos were manually separated from the remaining seed material with tweezers, then dried in an air-forced drying oven at  $70^{\circ}$ C for 24 hr and weighed.

### 2.3 | Proximate composition

The proximate composition of raw quinoa seeds was assessed according to the Association of Official Analytical Chemists (AOAC) methods (AOAC, 2000), moisture by AOAC N° 925.09, ash by AOAC N° 923.03, protein by AOAC N° 984.13, and fats by AOAC N° 930.09. The factor used to transform % nitrogen into % protein was 6.25 (Stikic et al., 2012). Total dietary fiber concentration was determined in oven-dried and defatted samples using AOAC N° 985.29 adopted by a Megazyme<sup>®</sup> commercial kit. All concentration values are expressed on a % of dry weight basis (g 100 of seeds). The carbohydrates percentage was determined according to the formulae:

- % Carbohydrates
- = 100 (% moisture + % ashes + % proteins + % fats
- +% total dietary fiber)

# 2.4 | Statistical analysis

Results were expressed as means plus standard errors, and coefficients of variation were calculated to evaluate the relative variability of attributes among genotypes and sowing dates. Analysis of variance was used to estimate the main and interaction effects for all attributes. Mean performance plots were used to study the nature of  $G \times S$  interactions. t tests and Pearson's correlations were used to quantify the significance and magnitude of the associations between protein and fat concentration and the absolute or relative embryo size (embryo  $\times$  total seed weight<sup>-1</sup>). To explore the genetically and environmentally determined correlations among seed yield components and seed composition traits, biplots were constructed. This was performed by plotting the symmetrically scaled principal component 1 (PC 1) against the principal component 2 (PC 2) scores obtained via principal component analysis (PCA) of a genotype  $\times$  attribute or environment  $\times$  attribute matrices, respectively, containing standardized attribute data. The rules for biplot interpretation are as follow: The cosine of the angle between two trait vectors approximates the environmental or genetic correlation between the traits. An acute angle indicates positive correlations, and an obtuse angle indicates a negative association, a right angle indicates no association between both traits (Yan & Rajcan, 2002). All statistical analyses were performed using the Infostat package (Di Rienzo et al., 2017).

# **3** | **RESULTS AND DISCUSSION**

# 3.1 | Genotype, sowing date, and genotype × sowing date interaction effects on seed yield components and seed composition traits

Rainfall, mean temperature, and solar radiation for the entire experiment were 354 mm, 18.6°C, and 18.1 MJ m<sup>-1</sup>  $day^{-1}$ , respectively. Table 1 shows the weather conditions during seed-filling period for each sowing date. The maximum and minimum temperatures values ranged from 24 and 13.7°C (winter sowing date) to 28.9 and 19.3°C (midspring sowing date), respectively, whereas solar radiation ranged from 21.1 to 23.3 MJ m<sup>-1</sup> day<sup>-1</sup>. The seed yield and its components for each genotype and sowing date are shown in Supporting Information Table S1. Means of seed yield, number and weight and their ranges of variation fitted within the range of values found in previous studies involving Sea Level quinoa cultivars and conducted in sea level environments (Bertero & Ruiz, 2008; Miranda et al., 2013). They were higher than values from experiments conducted in a tropical environment (Bhargava et al., 2007) and lower than results from experiments conducted in the Mediterranean Sea basin (De Santis et al., 2016). Nevertheless, these contrasts are secondary to the fact that, while significant  $G \times E$  interactions for these traits were observed in sea level environments (Table 2), they were lower or nonsignificant in the subtropical and Mediterranean environments (Bhargava et al., 2007; De Santis et al., 2016), thus complicating the selection of the best conditions to achieve higher yield and/or seed weight.

The proximate composition values are listed in Supporting Information Table S2. Comparison of proximate composition values and ranges gave contrasting results depending on the variable under analysis and also of whether comparisons were made with experiments involving Sea Level or Andean varieties. The mean protein content was lower than results usually reported (Aluwi et al., 2017; Bhargava et al., 2007; De Santis et al., 2016; Gonzalez et al., 2012; Miranda et al., 2013; Vidueiros et al., 2015); however, the range of variation was relatively high (Supporting Information Table S2), and associated with significant G × S interaction effects (Table 2). Some

 TABLE 1
 Weather conditions during the seed-filling period for each sowing date

Sowing date	Mean temperature (°C)	Rainfall (mm)	Solar radiation (MJ/m <sup>2</sup> )
Winter	18.4	43	21.1
Early spring	25.0	168	24.5
Mid-spring	25.0	177	23.3

previous studies did not discriminate between genotype and  $G \times E$  interaction effects (Gonzalez et al., 2012) or did not detect a significant  $G \times E$  interaction effect for protein content (Gonzalez et al., 2012; Miranda et al., 2013; Walters et al., 2016). An evaluation of a set of quinoa cultivars from different origins conducted recently in a Mediterranean site found significant  $G \times E$  interactions for protein content; however, the interaction component was smaller than the G component of variance (De Santis et al., 2016). According to our results, the  $G \times S$  interaction effect was of higher magnitude than G effects explaining variation in protein content under the conditions explored in the experiments reported here (Table 1).

The response pattern for protein content of the four genotypes across sowing dates shows a re-ranking (crossover) of genotypes performance when modifying the sowing date (Figure 1a). This crossover interaction severely complicates the choice of genotypes (Basford & Cooper, 1997), which for this sea level site should contemplate their specific adaptation patterns. If crossover interactions are emphasized, choice of genotypes to increase protein content must contemplate their specific patterns of performance. Thus, Salto de Agua should be chosen for early-spring sowing date while CO-407, NL-6, or 2-Want for the late sowing date (Figure 1a). On the other hand, NL-6 ensures stability of protein content across sowing dates (Figure 1a). However, these statements should be taken cautiously because of our study lacks of replicability among years. Thus, additional experiments are needed to confirm this pattern.

The mean fat content agrees with results reported in the literature. The variability found in this study was higher than that reported by Aluwi et al. (2017) and Vidueiros et al. (2015), and fitted within the range of values reported by

**TABLE 2** Analysis of variance for four sea level quinoa

 genotypes across three sowing dates in a sea level environment

	Source of variation			
Traits	Genotype	Sowing date	Genotype × Sowing date	
Moisture	5.4**	0.3 <sup>ns</sup>	0.3 <sup>ns</sup>	
Protein	2.3 <sup>ns</sup>	5.7*	2.5*	
Fat	4.2**	3.0**	0.4**	
Ash	1.7**	6.5**	0.1 <sup>ns</sup>	
Total dietary fiber	19.0**	24.6*	1.6 <sup>ns</sup>	
Carbohydrates	21.6**	81.1**	3.1 <sup>ns</sup>	
Seed yield	79,484.2**	89,216.1**	16,714.9*	
Seed number	1.82e <sup>10</sup> **	3.61e <sup>10</sup> **	6.78e <sup>10</sup> **	
Seed weight	$2.9e^{-6}$ **	$1.0e^{-5}**$	3.2e <sup>7</sup> **	
Embryo weight	0.005**	0.01**	0.002**	

Notes. ns: no significant.

 $p < 0.01^{**}; 0.05^{*}.$ 



**FIGURE 1** Responses plots of the protein (a) and fat content (b) for CO-407 (●), Salto de Agua (○), NL-6 (■) and 2-Want (□) at each of the three sowing dates (winter, early spring and mid spring). Vertical bars indicate standard errors

Miranda et al. (2013). The resemblance between our results and those of Miranda et al. (2013) is due to the large range of variation among genotypes and environments found in both studies for this trait (Supporting Information Table S1). Generally, the pattern of response among genotypes for this trait is the opposite to that found for proteins (Figure 1b). As genotype 2-Want exhibits the best performance for fat content in all sowing dates, choice of this genotype at the mid-spring sowing date will maximize both nutrient contents (Figure 1b).

The mean carbohydrates content was higher than values reported for Chilean genotypes (Aluwi et al., 2017; Miranda et al., 2013) and generally coborrate previous reports from Andean cultivars (Aluwi et al., 2017). In contrast to Miranda et al. (2013), who observed that only environmental effects determined carbohydrate content variation, here, it depended on genotype and sowing date effects (Table 2). The mean ash and total dietary fiber contents corroborate previous reports and their variation was explained by both the genotype and the sowing date effects.

# **3.2** | Are protein and fat concentrations associated with embryo relative weight?

We hypothesized that, as both proteins and fats are located in the embryo, genotypic or sowing date effects affecting

variation in embryo weight would influence these nutrients contents if they also modify its relative proportion, for example, by affecting more the weight of the tissue where carbohydrates are accumulated (perisperm) than that of the embryo. A significant association was found between protein or fat concentrations and embryo weight (Figure 2) and these relations were maintained when considering the seed weight. However, the association with the relative embryo weight was not significant (results not shown). Given the strong correlation found between embryo and seed weight (r = 0.94; p < 0.001) over the range of sowing dates explored in our study, the seed weight rather than embryo weight as a trait determining seed components in quinoa can be used as an indirect criteria to improve quality composition in this crop. Both salinity and water stress affect seed size and protein and fat concentrations in quinoa (Fischer et al., 2017; Koyro & Eisa, 2008). Our results suggest that these factors affected protein and fat accumulations and seed size in a way which is not related to the distribution of nutrients among different tissues within the seed and point out the specific environmental and genetic effects on each of these components. The positive association found between embryo/seed size and lipid content is consistent with results found previously in quinoa (Graf et al., 2016; Miranda et al., 2013), the negative association with protein content contrast with results found in those studies. On the other hand, the correlations found in this study are consistent with results found in sunflower for seed oil concentration (where changes were also explained by those in seed weight and not by the embryo relative proportion) (Aguirrezábal et al., 2015). They were also consistent with results or for protein concentration in wheat (Triboi & Triboi-Blondel, 2002). As sowing date conditions did not affect differentially embryo and seed weight, our initial hypothesis was rejected.



**FIGURE 2** Scatter plot of protein ( $\bigcirc$ ) and fat contents ( $\bigcirc$ ) against the embryo weight. The *r* and *p* values for each correlation and lineal trends arising from the regression are shown

# **3.3** | Implications of interrelationships among seed yield components and seed composition traits

The way seed composition traits and yield components variables relations are affected by genetic and environmental factors is critical for decision making. We approached these questions using as a reference both seed yield and weight as determinants of productivity the first one and quinoa commercial quality the second. The genetically and environmentally determined correlations among yield and seed composition traits are shown in Figure 3. The PCA results show that the first two components concentrate 95% and 100% of the total variation for either genetic or environmentally determined correlations, respectively. The vectors (traits) occupied a wide range of the Euclidean space, which implies strong genotype or sowing date x trait interactions. The angle between trait vectors on the biplots ranged from small to close to 180°, which suggest that the genetically or environmentally determined correlations



**FIGURE 3** Genetically and environmentally determined correlations between seed compositional attributes, seed yield and its components (arrows) for: (a) sea level quinoa genotypes (●) and (b) sowing dates (■). Numbers between brackets indicate the percentage of total variation explained by each component

between traits ranged from the strongly positive to the strongly negative ones.

The genetically determined relations shown by the genotype-by-traits biplot in Figure 3a indicated that higher yields and seed number were more associated with fat content than with seed protein and ash contents, whereas both traits were less associated with seed weight, fiber and carbohydrate contents. Seed weight, on the other hand, was more associated with fiber and ash contents. As for genotypes, they were represented by a contrast between CO-407 and the other genotypes along PC1, and between 2-Want and NL-6 along PC2 (Figure 3a). CO-407 has the biggest seeds with intermediate yield and higher fiber and ash contents, while the other three genotypes have lower seed weight but higher carbohydrate and fat contents. The contrast between 2-Want and NL-6 shows that the first has higher yield, seed number, and fat content, but lower protein, while NL-6 has lower yield, but higher protein content and embryo weight. These relations show that there is a trade-off between the main yield and seed composition traits (seed number and weight, oil and protein contents) among the genotypes analyzed here.

Sowing dates induced contrasting associations among seed yield components and seed composition traits, having several implications for management strategies aimed at optimizing the level and stability of seed yield and quality. The winter sowing date induced positive associations between fat and carbohydrate concentrations, seed and embryo weight, but negative associations among almost all of these traits and seed yield and protein content while the mid-spring sowing date induced positive associations between seed yield and protein content (Figure 3b). As for the particular conditions of the Argentinian humid Pampas, winter sowing dates would be suitable for obtaining heavier seeds associated with high concentration of fat and carbohydrates, at the expense of lower yield and seed protein content. On the other hand, a mid-spring sowing would be suitable for obtaining high seed yield, associated with high protein content but at the expense of smaller seed size. It should be noted that fat concentration was positively associated with seed yield, thus fat content would not be largely penalized. Consequently, maximizing seed yield through the mid-spring sowing date could favor an increase in protein concentration while maintaining fat concentration.

# 4 | CONCLUSIONS

Our results showed high variability in the main seed composition traits in sea level quinoa cultivars which were explained in most cases by  $G \times S$  interaction effects. Variation in both fat and protein concentrations seems not to be associated with the proportion of embryo tissue, but rather with its weight or in a simpler way with seed weight. The associations among traits showed that there is a trade-off between the main yield and seed composition traits (yield, seed weight, oil and protein contents) both among genotypes and sowing dates. Accordingly, the choice of genotype (e.g., among those studied here) and management practices (e.g., sowing date) that modify that trade-offs might contribute to obtain a specific quality and acceptable yield. Thus, winter sowing date would be suitable for obtaining heavier seeds associated with high concentration of fats and carbohydrates; whereas mid-spring sowing would be suitable for obtaining high seed yield, associated with high protein content but at the expense of smaller seed size.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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