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Agronomic and physiological traits associated with breeding advances of wheat under high-productive Mediterranean conditions. The case of Chile

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ABSTRACT

Wheat yields in Chile have increased significantly during the last four decades as a consequence of plant improvement and better crop husbandry. Central Chile is characterised by high-yield Mediterranean conditions, where precipitation received by the crop in most years does not represent a major limitation to productivity. This study assesses the changes in agronomic and physiological traits of spring cultivars released in the country between 1920 and 2000. A total of 95 spring bread wheat accessions, representing 20 old and 75 modern cultivars (released before and after 1960, respectively) were tested in a humid Mediterranean-type climate, with irrigation. Modern genotypes exhibited higher grain yield, harvest index, number of grains per ear and sedimentation values and lower height, test weight, wet gluten content and hardness index. No differences were found for days to heading, and ear length, whereas kernel weight decreased with the Green Revolution. Principal component (PC) analysis using ten agronomic traits clearly separated modern from old cultivars. Grain yield, a trait not included in PC analysis, was highly correlated with the first PC ($r = 0.80$, $P < 0.0001$), where modern cultivars presented lower plant height, higher harvest index and better grain quality, as indicated by the higher sedimentation values and lower hardness index values. The year of release of cultivars was related negatively to plant height and positively to harvest index, number of grains per ear and sedimentation value. In a further study, changes in photosynthetic and transpirative traits were investigated in a subset of 14 genotypes covering the same 80-year range. Differences in grain yield across genotypes were related positively to stomatal conductance and transpiration rates of the flag leaves during grain filling and negatively to oxygen isotope composition and (to a lesser extent) carbon isotope composition in kernels. The results suggest that the higher grain yield of modern varieties is related to higher stomatal conductance and transpiration.

1. Introduction

Wheat is one of the three main crop staples worldwide and is the principal staple under Mediterranean conditions. The conservation and use of wheat genetic resources is essential to support future genetic progress, and is an insurance against unexpected threats to crop productivity such as diseases or abiotic stresses (Gepts, 2006). As researchers characterise and evaluate germplasm, they create information that is potentially useful to a broad range of research processes and that might help to speed breeding (Rubenstein et al., 2006). Genetic resources will be useful if rigorous agronomic, grain quality (DeLacy et al., 2000; Alvarez et al., 2007; Hailu et al., 2006) and physiological characterisation (Araus et al., 2002, 2008) is available alongside the molecular characterisation (Roussel et al., 2005; Landjeva et al., 2006; Pagnotta et al., 2009). In that regard, retrospective studies, where genotypes released in different years are grown together under similar agronomic conditions (Loss et al., 1989; Slafer and Andrade, 1989; Calderini et al., 1995), are a way to study not only the progress of yield in a specific region or country but are also a means of investigating the agronomic, physiological and quality traits associated with the evolution of breeding.

Grain yield of wheat has increased significantly worldwide from the early sixties (Miralles and Slafer, 2007), coinciding with the adoption of the Green Revolution. Chile has followed the same trend, with the average yield in the seventies (1970–1979) being 1.6 Mg ha^{-1} and further increasing to reach 4.6 Mg ha^{-1} in the last decade (2000–2009) (Engler and del Pozo, 2013). Breeding efforts

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during the past decades have had not only a great impact on productivity but also on the grain quality of wheat in different countries (Trethowan et al., 2007; Zhou et al., 2007), including Chile (Mellado, 2007).

The introduction of semi-dwarfing genes in the sixties allowed a reduction in plant size that increased harvest index, the number of grains per unit area and grain yield (Flintham et al., 1997; Donmez et al., 2001; Brancourt-Hulmel et al., 2003; Zapata et al., 2004; Shearman et al., 2005), and improved grain quality, particularly grain protein content, sedimentation value and wet gluten (Ortiz-Monasterio et al., 1997; Dencic et al., 2005; Trethowan et al., 2007; Matus et al., 2012). Nevertheless, reports indicating a global trend towards lower grain quality in highly yielding agronomical conditions and modern cultivars are also abundant (Oury et al., 2003; Triboi et al., 2006; Oury and Godin, 2007). In addition the nature of the physiological changes associated with breeding advance in grain yield during or after the Green Revolution remains elusive. Studies in wheat under the highly yielding conditions of North West Mexico (CIMMYT) have reported a progressive increase in photosynthetic rates and stomatal conductance (on area basis) together with higher carbon isotope discrimination (Δ^{13}C; or a lower carbon isotope composition δ^{13}C) and lower oxygen isotope composition (δ^{18}O) in the more modern wheats (Fischer et al., 1998; Barbour et al., 2000). In the same way for durum wheat under Mediterranean conditions, a higher Δ^{13}C (or lower δ^{13}C) in the modern varieties compared with landraces has been reported (Araus et al., 2007, 2013; Royo et al., 2008), whereas no clear differences were found for δ^{18}O (Araus et al., 2013). However, no information exits for high yielding, wet Mediterranean conditions.

Wheat is the primary crop in Chile in terms of planted area and geographical distribution. Central Chile is characterised by high-yield Mediterranean conditions, where precipitation received by the crop does not represent a major limitation to productivity during most years. This paper reports on the main changes in grain yield, agronomical yield components, grain quality and photosynthetic and transpirative gas-exchange traits in wheat varieties in Chile during the twentieth century for high-yielding Mediterranean conditions. Thus, instantaneous gas-exchange rates were measured in the flag leaf during grain filling, whereas δ^{13}C and δ^{18}O were measured in mature kernels as a time-integrated (i.e. during grain filling) indicator of photosynthetic and transpirative performance (Barbour et al., 2000; Cabrera-Bosquet et al., 2011). Nitrogen isotope composition was also analysed in mature kernels as a way to assess genotypic differences in nitrogen metabolism and the efficiency of nitrogen fertiliser usage (Serret et al., 2008; Yousfi et al., 2012). The final aim is to identify which agronomical and physiological traits have been involved in the genetic improvement of wheat cultivars in under high-yielding Mediterranean conditions.

2. Material and methods

2.1. Experimental site, plant material and growing conditions

The experiments were conducted in the experimental field of CRI-Quilamapu, located 25 km from Chillán, Chile (36°32′ S; 71°54′ W and 217 m.a.s.l.). The climate corresponds to a humid Mediterranean type. The average annual temperature in this region is 13.9 °C, the monthly minimum average is 3.0 °C (July) and the maximum 28.6° C (January), and the average annual precipitation is 1270 mm (del Pozo and del Canto, 1999). The soil was a sandy loam, humic haploxerand (Andisol). Soil chemical characteristics of the top 10 cm were: pH 6.0, 8.87 mg kg^{-1} of N-N0$_3$; 17.05 mg kg^{-1} of P (Olsen), 0.45% of N-total, 4.5% of C and 0.33, 5.75, 0.65 and 0.48 cmol kg^{-1} of available K, Ca, Mg and Na, respectively (Zagal et al., 2002).

Two different experiments were conducted. In the first experiment a total of 95 spring bread wheat accessions, including 20 old and 75 modern cultivars (released before and after 1960, respectively) were tested in field conditions. Seeds were obtained from the Germplasm Bank of CRI-Quilamapu of INIA. Cultivars had been released or introduced into Chile between 1920 and 2003 (Supplementary Table S1). Two rows of 2 m length, and 0.20 m between rows were sown for each cultivar with no replicates on 28 July 2003. The seed rate was the equivalent of 180 kg ha^{-1}. Before sowing, plots were fertilised with 260 kg ha^{-1} of ammonium phosphate (46% P_2O_5 and 18% N), 90 kg ha^{-1} of potassium chloride (60% K_2O), 200 kg ha^{-1} of sulpomag (22% K_2O, 18% MgO and 22% S), 10 kg ha^{-1} of boronatrocalcita (11% B) and 3 kg ha^{-1} of zinc sulphate (35% Zn). After sowing an extra 80 kg ha^{-1} of N was applied at tiller initiation (Zadoks 20). Weeds were controlled with MCPA at 750 g a.i. ha^{-1} + metsulfuron-methyl 8 g a.i. ha^{-1}. Plots were furrow irrigated according to the requirements of the crop. For each plot, the number of days from planting to heading was recorded when 50% of culms showed emerged ears. Plant height from the culm base to the top of the awns was measured at maturity. In addition, harvest index was assessed in 0.5 m row per plot and then spike length, number of kernels per spike and thousand kernel weight were evaluated in 20 ears. Finally, the rest of the plot was harvested to evaluate grain yield and test weight.

In the second experiment a subset of 14 cultivars released from 1920 and 2008, chosen from the initial set of 95 (roughly 1–2 cultivars per decade) plus one cultivar released in 2008, were evaluated during four consecutive seasons (2008–2011). The experimental design was a complete block with four replicates. Each plot consisted on ten rows of 2.5 m in length and 0.2 m apart. Sowing dates were between the 15th and 30th of August of each year. Before sowing, plots received the same fertilisation described above. After sowing, an extra 47 kg ha^{-1} of N was applied at tiller initiation (Zadoks 20), the first node (Zadoks 31) and booting (Zadoks 40). Weeds were controlled using the pre-emergence herbicide, Artist (0.5 kg ha^{-1}; 24.0:17.5% (w/w) a.i. of flufenacet/metribuzin), and the post emergence Hussar 20 WG (300 g ha^{-1}; 5.26% (w/w) a.i. of iodosulfuron-methyl-sodium). Plots were furrow irrigated according the requirements of the crop. All the plots were protected from fungal diseases using Juwel Top (0.8 L ha^{-1}; 125:125:150 g L^{-1} a.i. of kresoxim methyl + epoxiconazole + fenpropimorph). Plant height was measured at maturity. Additionally, the number of spikes per m^2 was determined and the harvest index evaluated in 1.0 m of each row, and the number of kernels per spike and thousand kernel weight were determined in 25 spikes taken at random from each plot and grain yield assessed by harvesting 2 m^2 (five rows, 2 m long).

2.2. Grain quality

Wet gluten content, sedimentation value and the grain hardness index were determined in grains of the two experiments. In addition, total nitrogen content of the kernels was evaluated for the last two seasons of the second experiment (see below). For sedimentation, a sample of 0.64 g of pure flour was mixed with 10.0 ml of bromophenol blue and 5.0 ml of a lactic acid and isopropyl alcohol solution (Zeleny, 1947). The sediment volume corresponds to the sedimentation value and is composed mainly by swollen gluten and occluded starch. For the gluten content, 10 g of pure flour was mixed with 5 ml of a 2% saline solution, homogenised and then placed in a gluten washer (Promylograph type TIK, Austria) for 5 min. The grain hardness index was determined as the grain resistance to abrasion in a pearler machine (Strong Scott N° 17810, USA), and therefore low values in hardness index (%) mean harder grains.