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Research paper

Trade-off between grain weight and grain number in wheat depends on GxE interaction: A case study of an elite CIMMYT panel (CIMCOG)

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ABSTRACT

Identifying the functionally linked mechanisms of grain yield (GY) and its components —i.e. grain number (GN) and grain weight (GW) is necessary for boosting GY potential of wheat. The objectives of the current study were to: (i) analyze the trade-off between GW and GN in 27 elite wheat genotypes grown in two contrasting locations with different yield potential, (ii) assess its causes, and (iii) gain a better understanding of the physiology behind the trade-off between GW and GN. A set of 27 elite wheat genotypes was evaluated during three years in Ciudad Obregón, Mexico (CO), and two years in Valdivia, Chile (Val). GY was higher in Val than CO (783 g m^{-2} and 665 g m^{-2}, respectively) and positively associated with above-ground biomass (BM) in both locations. In CO, 15,850 grains m^{-2} were recorded and 15,197 grains m^{-2} in Val, while thousand-grain weight (TGW) was higher ($P < 0.001$) in Val than in CO by 23% (52.2 and 42.5 g, respectively). Also, individual grain weight (IGW) of most categories was higher in Val than in CO. Remarkably, the relationships between GY and GN showed contrasting responses between locations despite the similar GN. A very low GY/GN relationship was found in CO, while a positive and linear relationship was plotted in Val. The virtual lack of association found in CO (11%) was due to a clear trade-off between TGW and GN, while the positive association in Val was the result of a very low trade-off between the two main yield components. Interestingly, the IGW of grains set in the G2 and G4 positions showed negative association with GN in CO across years as well as during each year, while in Val no association was found across years, though a very low association was found in each year. The source-sink treatments applied ten days after anthesis by halving the spikes showed that, G2 and G4 responded to the increased source by 7.7% and 16%, respectively in CO, while in Val the responses were 15% and 5.1% in Val_{y13} and 6.5% and 9.6% in Val_{y14}, respectively. In conclusion, the lack of association between GY and GN found in CO was due to the trade-off between the two main yield components (GW and GN), which was mainly explained by higher average temperature and lower photothermal quotient during grain filling recorded in this location than in Val. These results highlight the need to employ different strategies aimed at increasing yield potential depending on the environment. The increase of grain number could be proposed for environments with favorable growing conditions as in Val. On the contrary, increasing GW would be the objective in environments with little chance of taking advantage of increased GN such as CO.

1. Introduction

During the "Green Revolution" a quantum leap in wheat yield was achieved through improved biomass partitioning as a result of introgressing the *Rht1* and *Rht2* alleles. This, in turn, improved grain yield, harvest index and grain number due to the higher amount of assimilate partitioned to the spike during pre-flowering (Miralles et al., 1998; Slafer and Andrade, 1993). However, genetic gains in yield potential are currently well under 1% per year (Crespo-Herrera et al., 2017), and global wheat production would have to increase ~2.4% per year to feed the increasing human population (Ray et al., 2013), underlining the need to accelerate genetic gains. Studies published recently have reported that grain yield (GY) of wheat and other crops are asymptotically related to grain number (GN) suggesting that GY tends to level off at a very high GN (Bomford, 2009; Bustos et al., 2013; García et al., 2013), which could be ascribed to the trade-off between grain weight (GW) and GN. This trade-off could be due to: (i) source limitation during grain filling (Sinclair and Jamieson, 2006), (ii) the setting of smaller grains in distal position of the spikes, with lower weight potential (Acreche and Slafer, 2006; Fischer, 2008), or (iii) a

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combination of both. The former assumes source limitation during grain filling while the latter could be related either to source limitations at pre-grain filling or to intrinsic limitations in the grain weight potential of distal grain positions (Acreche and Slafer, 2006).

Taking into account the negative relationship generally reported between TGW and GN in wheat (Acreche and Slafer, 2006; Bustos et al., 2013; García et al., 2013; Miralles and Slafer, 1995; Sadras, 2007; Slafer and Miralles, 1993) and other grain crop species (Bulman et al., 1993; Gambín and Borrás, 2010; López Pereira et al., 1999), future increases of yield potential both in wheat as well as other crops could be achieved by improving individual grain weight (IGW) as a necessary breeding strategy to counteract the trade-off between the two main yield components (Calderini and Ortiz-Monasterio, 2003). Therefore, to quantify the degree of the trade-off between the two major yield components of wheat, and to understand the causes behind the negative association between TGW and GN, is a key for wheat breeding efficiency aimed at continuing increasing grain yield. Recent published evidences suggest that the trade-off between TGW and GN could be affected by the environment taking into account that the relationship between these yield components showed different values in the same wheat doubled haploid population across the explored environments (Bustos et al., 2013; García et al., 2013). Although the trade-off between TGW and GN has been reported since long ago (e.g. Villareal et al., 1992) little is known about the environmental effect on this association. This information can provide important knowledge for wheat breeding strategies aimed at different kinds of high yielding environments.

The objectives of the current study were to (i) gain a better understanding of the trade-off between GW and GN and its interaction with the environment in 27 elite wheat genotypes from the CIMMYT Core Germplasm (CIMCOG) population grown in two contrasting locations (both corresponding to mega-environment 1) and (ii) assess its physiological bases. The answer to these objectives would accelerate the breeding of wheat with higher grain yield potential.

2. Material and methods

2.1. Plant material

A set of 27 elite wheat genotypes [26 *Triticum aestivum* (22 elite lines, 4 historic lines) and 1 *T. turgidum* var. *durum*] from the CIMMYT Core Germplasm (CIMCOG) panel were provided by CIMMYT's breeding programs (Table A1). The 27 genotypes were selected because they represent historical genetic gains and similar phenology. Some lines are synthetic-derived wheat materials, and one is a recently released and extremely high yielding durum wheat (Table A1). Five field trials in two locations (three experiments in Cd. Obregón, Mexico, and two in Valdivia, Chile) were carried out to evaluate the CIMCOG panel.

2.2. Experimental design and treatments

2.2.1. Ciudad Obregón (CO), Mexico

The 27 CIMCOG wheat genotypes were evaluated at CIMMYT's experimental station (CENEB) (27°23′N, 109°55′W) in Sonora, Mexico, for three consecutive growing seasons (CO_{y11}, CO_{y12} and CO_{y13}), under fully irrigated conditions. The wheat genotypes were sown on beds arranged in a completely randomized design with 2 replicates the first year and 3 replicates the second and third years. Seed rates were 245 seeds m^{-2} in CO_{y11} and CO_{y12}, while 236 seeds m^{-2} were sown in CO_{y13}. These seed rates are within the optimum recommended range for this location.

The plots consisted of 4 beds (5 m long and 3.2 m wide) with 2 rows per bed the first year; the other two years, the genotypes were sown on 3 beds (8.5 m long and 2.4 m wide) with an additional shared bed on the side of each plot to avoid border effects. During CO_{y13}, a source-sink ratio treatment was applied to 20 plants in each plot 10 days after anthesis by halving the spikes along the rachis to compare them with a control without manipulation. Plots were sown at the optimal sowing date in this region, i.e. December 6, 8 and November 23 during CO_{y11}, CO_{y12} and CO_{y13}, respectively. The soil type at CENEB is a coarse sandy clay, mixed montmorillonitic typic caliciorthid, low in organic matter, and slightly alkaline (pH 7.7) in nature (Sayre et al., 1997). All plots were grown under optimal conditions: they were adequately fertilized and irrigated to avoid abiotic stress, plus weed, disease and pest control were implemented to avoid yield limitations. During the three growing seasons, the plots were fertilized by applying 50 kg N ha^{-1} (as urea) and 50 kg P ha^{-1} during soil preparation and another 150 kg N ha^{-1} with the first irrigation. Weather data were recorded in the three years and a summary of key variables during different phenological stages is presented in Tables A2 and A3.

2.2.2. Valdivia (Val), Chile

The 27 CIMCOG wheat genotypes were also assessed at the Estación Experimental Agropecuaria Austral (EEAA) (39° 47′ 18"S, 73° 14′ 5"O), of the Universidad Austral de Chile (UACh), Valdivia, Chile, during two growing seasons (Val_{y13} and Val_{y14}). The 27 elite wheat genotypes were sown on paired plots; 3 rows at 0.15 m apart and 1.2 m long, flanked by a row (0.15 m apart and 1.2 m long) of spring wheat cultivar Pantera INIA that served as border, as in previous studies (Bustos et al., 2013). The genotypes were arranged in a completely randomized design with 3 replicates. The source-sink ratio treatment was applied to 5 plants of each plot 10 days after anthesis by halving the spikes along the rachis to compare with a control without manipulation. Plots were sown within the sowing date period in the region, i.e. on September 10 and 14 in Val_{y13} and Val_{y14}, respectively, and at the recommended seed rate of 333 seeds m^{-2} in both growing seasons. The soil type at EEAA is a volcanic ash, classified as Typic Hapludand, 14% of organic matter content, and pH 5.8. Before sowing, 7 Mg $CaCO_3$ ha^{-1} was applied to the soil to avoid Al toxicity, which is common in the acidic soils of southern Chile. All plots were grown under adequate fertilized rates and irrigated to avoid water shortage. Weed, disease and pest control were implemented to avoid yield limitations. During the two growing seasons, the plots were fertilized with 125 kg N ha^{-1}, 300 kg P_2O_5 ha^{-1} and 150 kg K_2O ha^{-1} and additional fertilization of 125 kg N ha^{-1} was applied at tillering. Likewise, in Val, the climatic data were recorded during the two years and a summary of the key variables during different phenological stages is presented in Tables A2 and A3.

2.3. Crop measurements

The phenological stages of plants were recorded at both locations using the decimal code (Zadoks et al., 1974), following the average phenology in each plot (when 50% of the plants reached the developmental stage). The recorded stages were seedling emergence (Em), booting or Z45 (Bt), heading or Z55 (Hd), anthesis or Z65 (Ant), 20 days before anthesis (A-20), 10 days after anthesis (A + 10) and physiological maturity (PM). In CO, grain yield (GY) and yield components were determined on approximately 5.7 m^2 using standard protocols (Pask et al., 2012). To avoid edge effects caused by extra solar radiation reaching border plants, 50 cm of the plot edges were discarded before harvesting. Yield and harvest index (HI) were measured independently, but BM was calculated from GY/HI. In Val, at harvest, the plant number (PLN) and aboveground biomass (BM) were recorded in the middle row of a 1 m length of the plot; the biomass samples were divided into blade leaves, stems plus sheath, leaves and spikes. Fresh biomass was oven-dried at 60°C for 48 h for dry weight measurement. Spike number (SPK) was calculated and later the spikes were threshed