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Sink-strength determines differences in performance between bread and durum wheat

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ABSTRACT

In a large comparison of experimental and published data across a wide range of environmental conditions, a cross-over interaction of durum *vs.* bread wheat yield was found to be the reverse of expectations, where the former would outyield the latter under low-yielding conditions and *vice-versa*. In this study, we aimed to establish the physiological basis of this species cross-over interaction, analysing whether it was established before or after anthesis and to determine if it was related to differences in sink-strength.

Our study indicates that the consistent species-by-environment interaction for yield is the consequence of a few traits related to sink-strength that are determined around anthesis. Thus, differences in the spike weight and N accumulated at anthesis, which produced important variations in the number of grains and presumably generated differences in sink-strength, seemed to be involved. This conclusion is supported by the strong relationship between grain yield and the biomass produced during grain filling, in addition to the fact that the variation in individual grain weight, as well as its rate or the duration of grain filling, was poorly related to yield and the post-anthesis biomass.

1. Introduction

Wheat species are among the most important staple crops in the world, being the source of *c.* 20% of the carbohydrates and proteins destined for human consumption (Braun et al., 2010). For this reason, increasing wheat production is of critical importance to cope with the continuously increasing demand of food and feed from a global population that is not only growing but in many regions also becoming wealthier and changing diets. Therefore, wheat is crucial to ensure food security (*e.g.* Reynolds et al., 2012).

A common approach to raise the yield of crops is through gains in yield potential, which have facilitated increases in yield, not only in high-yielding areas, but also in a wide range of environments (Richards, 1992; Calderini and Slafer, 1999; Trethowan et al., 2001; Slafer and Araus, 2007; Marti and Slafer, 2014). Crop performance is both a function of the genotype and the environment (Fischer and Maurer, 1978; Blum, 2005; Marti and Slafer, 2014), highlighting the need to understand the genotype by environment (G × E) interactions for traits governing yield. That information will ultimately help to design strategies to effectively increase productivity of field crops. Analysing the bases of the differences in performance among genotypes (either within a species or across related species) could help to identify traits responsible for the G × E interactions.

Recently, we found evidence that the traditional land allocation for the two most commonly grown species of wheat, bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* L. ssp. *durum* (Desf.) Husn.), goes against the common view about the differential responsiveness of both species, in terms of yield, to environmental conditions. Briefly, durum wheat is most commonly grown in relatively lower-yielding environments (like the Mediterranean basin) than bread wheat (*e.g.* Ceccarelli et al., 1987), which would imply that durum wheat would perform better under stress and bread wheat would possess higher yield potential (*e.g.* Percival, 1921; Bozzini, 1988; Trethowan et al., 2001; Elias and Manthey, 2005; Dias et al., 2011; Monneveux et al., 2012). In agreement with that, it was found that durum cultivars were well adapted to post-anthesis warm conditions (Zhang and Oweis, 1999; Reynolds et al., 2004) and maintained photosynthesis during periods of heat (Dias et al., 2011). Unexpectedly, a major conclusion from our recent study that combined experiments under a wide range of environmental conditions and a comprehensive meta-analysis, was that

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bread wheat yielded more under low-yielding conditions while durum wheat exhibited a higher yield potential (Marti and Slafer, 2014), and this was the reverse of our assumptions.

Little is known about the causes of the G × E interaction for yield between bread and durum wheat. The few studies that have compared the physiological traits of bread and durum wheat have suggested that the latter seems to have higher sensitivity to pre-anthesis growth (Reynolds et al., 2004), which affects the number of grains set (Zubaidi et al., 1999). However, differences in the number of grains may well be a consequence of the constitutively heavier kernels of durum wheat, which would be reflected in a constitutively different fruiting efficiency (Marti and Slafer, 2014). These differences in the capacity of setting a certain number of grains and the potential size of the grains may imply differences between both species in sink-strength after anthesis, and this strength may be relevant for determining differences in yield across environments (Serrago et al., 2013).

In this study, we aimed to determine whether differences in performance between durum and bread wheat across a range of environmental conditions were established before or after anthesis and in the latter case if this is related to the establishment of certain differences in sink-strength at around anthesis. The basic hypothesis is that the consistent species-by-environment interaction for yield is the consequence of a few characters determined around anthesis and related to sink-strength.

2. Materials and methods

Three field experiments were carried out in the Mediterranean location of Agramunt, in the province of Lleida (Catalonia, north-eastern Spain; lat. 41°47′17″N, long. 1°5′59″E, altitude 337 m). Overall the study included 20 different environmental conditions in which durum and bread wheat cultivars were compared side-by-side, given by the combination of different growing seasons (2004–05, exp. 1; 2005–06, exp. 2; 2006–07, exp. 3) and water × nitrogen treatments imposed in each of the experiments. In all cases the experiments were installed in actual farmer's fields within the optimal period for sowing cereals in the region and plant densities within the ranges normally recommended (200–250 plants m^{-2}). Weeds, pests and diseases were controlled with agrochemicals following the manufacturer's recommendations (doses and timings) for application.

Details of the experiments are available in a previous paper (Marti and Slafer, 2014) that tested and rejected the hypothesis (based on both the available literature and the pattern of geographical distribution of these species) that durum wheat would outyield bread wheat under low-yielding conditions and *vice-versa*.

To recap this briefly:

- The first experiment consisted of the factorial combination of six genotypes (three bread and three durum wheat cultivars), two levels of water availability and two N fertilization levels, arranged in a split-block split-plot design with three replicates. The main plots were a combination of genotypes and irrigation levels: they consisted of the genotypes sown in strips, randomized within blocks, with two water regimes paired across the strips (also randomized within blocks) in the entire replicate. The sub-plots (16 rows, 18 cm apart and 4 m long) consisted of different N levels, randomized within main plots. The three cultivars of each species were well adapted to the region based on comparative yield trials of previous years, published in reports of the GENVCE network (Group for the Evaluation of New Varieties of Field Crops; GENVCE, 2013). Two contrasting water regimes were applied: rainfed (accumulated rainfall during the crop cycle was 163 mm) and irrigated from early spring (roughly coinciding with jointing) onwards on a weekly basis (accumulated irrigation was 165 mm). The two contrasting levels of N availability were an unfertilized and a heavily fertilized condition (200 kg ha^{-1}).
- The other two experiments consisted of the factorial combination of two of the cultivars from exp. 1, the same two levels of N availability used, and four levels of irrigation, arranged in a split-split-plot design with three replicates, with the irrigation treatments assigned as the main plot, the genotypes as the sub-plot and the N treatments as the sub-sub-plot, in 17 rows, 18 cm apart and 5 m long. One cultivar from each species (Claudio and Provinciale) was selected on the basis of their performance across water × N conditions in the first experiment and their good yielding behaviour under the GENVCE network. The irrigation treatments included the extreme cases of the previous experiment (rainfed throughout, with an accumulated rainfall of 95 and 326 mm, and well irrigated from jointing onwards, with a total irrigation of 162 and 316 mm; for exp. 2 and 3, respectively) plus two treatments in which irrigation was only applied either before (107 and 228 mm, for the exp. 2 and 3, respectively) or after anthesis (55 and 88 mm, for the exp. 2 and 3, respectively).

In all the experiments, for the fertilization treatment, each plot assigned to a high-N level had ammonium nitrate broadcasted at a rate of 200 kgN ha^{-1} *c.* 7 weeks after sowing (before the onset of active growth at the end of winter).

From jointing to maturity each experimental unit was sampled weekly (samples taken from areas labelled soon after seedling emergence, to warrant exact targeted density of uniformly distributed plants in all cases; the size of each sample was 50 cm of a central row in all cases except at maturity when it was doubled) and weighed after being oven-dried for 3 d at 60 °C. After determining dry weight, N content was determined in the samples at anthesis and maturity by a Kjeldahl procedure. At maturity yield components were determined.

Daily incident radiation was taken from a public Meteorological Station next to the experimental zone, and the photosynthetically active radiation (PAR) was estimated as 0.5 of the total solar radiation (McCree, 1972). Incident and transmitted radiation were measured using a 1 m long linear sensor (LI 191 S, Licor Inc., Lincoln NE, USA). To measure transmitted radiation, the line sensor was placed at ground level across the rows until anthesis and from anthesis until maturity the sensor was placed leveled over the senesced leaves. The amount of radiation intercepted by the crop was calculated weekly as the ratio between the difference of incident and transmitted radiation to incident radiation; measurements were made from the appearance of the first node to maturity at noon only on clear days, which has been shown to be a representative assessment of the canopy interception during the whole day (Hipps, 1983; Thorne et al., 1988). In addition, the Normalized Difference Vegetation Index (NDVI) was measured from weekly readings of the canopy reflectance using a portable spectroradiometer (Greenseeker Hand HeldTM optical sensor unit, model 505; NTech Industries, Inc., Ukiah, CA, USA). The amount of radiation captured by the crop, the accumulated fraction of absorbed photosynthetically active radiation (fAPAR), was calculated on a daily basis and summed for a given period. Radiation Use Efficiency (RUE) was calculated by dividing the accumulated biomass by the accumulated fAPAR.

The raw data of the variables measured weekly were adjusted for each experimental unit by non-linear regression to a logistic curve against accumulated thermal time, calculated as the sum of daily average temperature [(Tmax + Tmin)/2] with a base temperature of 0 °C. The NLIN procedure (SAS Institute, 2004) was used and all relationships were highly significant ($R^2 > 0.90$; $P < 0.001$). For the grain filling analysis, the procedure described in Darroch and Backer (1990) was followed to analyse the parameters of the logis-