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The relationship between grain and ovary size in wheat: An analysis of contrasting grain weight cultivars under different growing conditions

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ABSTRACT

Grain size correlates with ovary size at anthesis, across cultivars, spike position, temperature changes, and source-sink manipulations, and it has been suggested that this correlation may be a functional (i.e. causal) one. To investigate possible causality, this relationship was studied across different agronomical/environmental conditions, such as nitrogen fertilization levels, plant densities, and growing seasons (i.e. 2014 and 2015), in two wheat cultivars with different grain size. Grain volume correlated with ovary volume within cultivars, across the whole dataset. However, ovary volume varied more than 10-fold, while grain volume varied only about 0.5-fold. In 2014, grains were only slightly smaller or, in the most fertilized treatments, not statistically different than in 2015, despite 3–4-fold smaller ovaries. Even within 2015 data, the various treatments resulted in large variations in ovary volume, but grain volume was unaffected. The results indicated that ovary size varies significantly with agronomical/environmental conditions (i.e., nitrogen and density treatments, and season), while grain size is more conservative within cultivars. The cultivar's typical grain size can be achieved, if resources are not limiting, independent of large variations in ovary size.

1. Introduction

Wheat is one of the most important food crops in the world, providing more than 20% of both calories and proteins consumed by the world population (Braun et al., 2010). Increasing wheat yield is therefore important to feed the increasing world population. Yield increases have been generally achieved by increasing grain number (GN) (Foulkes et al., 2009; Bustos et al., 2013) while grain weight (GW) has not been modified much (Austin et al., 1980; Waddington et al., 1986). Further increases in yield are possible by increasing both GW (Foulkes et al., 2009; Bustos et al., 2013) and GN (Sadras and Lawson, 2011; Wu et al., 2014). Understanding the mechanisms regulating grain weight is therefore of utmost importance and the relationship between grain weight and floret traits is important to understand the determination of grain weight potential (Calderini et al., 2001).

In many species, fruit weight is correlated with ovary weight or size at anthesis, and both fruit and ovary size are usually related to cell number rather than to cell size (Cruz-Castillo et al., 2002; Rosati et al., 2009). Fruit size correlates with ovary size also in grain crops (Cantagallo et al., 2004; Yang et al., 2009; Hasan et al., 2011; Xie et al., 2015). In grain crops, this relationship has been shown to hold across cultivars (Calderini et al., 2001; Yang et al., 2009; Hasan et al., 2011; Xie et al., 2015) spike position (Calderini et al., 1999; Hasan et al., 2011), temperature changes (Calderini et al., 1999; Calderini et al., 2001), and source-sink manipulations (i.e. shading or de-graining) prior to anthesis (Cantagallo et al., 2004). Because of this relationship, it has been proposed that grain size may be functionally related to ovary size (Calderini et al., 1999; Cantagallo et al., 2004; Yang et al., 2009). In fact, the ovary wall turns into the fruit pericarp and could potentially impose a physical restriction to the growing fruit (Ugarte et al., 2007; Hasan et al., 2011).

However, correlation does not prove causality and whether ovary and fruit size are functionally related remains unclear. It is possible that the correlation between grain and ovary size results from both the ovary and then the grain responding in a similar way to the variable studied, without implying causality. If the condition tested is uniform during both the formation of the ovaries and the following grain filling period, then both ovaries and grains could respond in a similar way. In

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fact, cultivar differences as well as spike positions are factors that do not change during the cycle.

The fruit vs. ovary size correlation has not been studied under varying agronomical conditions, such as N fertilization and plant density. In a previous paper (Reale et al., 2017), we found that ovary size was affected by contrasting conditions, including cultivar, nitrogen availabilities and plant densities, in two cultivars (i.e. one large and one small grained cultivar). We additionally found that ovary size differences were due to differences in cell number, not cell size. However, in Reale et al. (2017) only data on ovary size, and only for one season, were reported. No data on grain size, and therefore on the relationship between ovary and grain size, were shown.

The aim of the present work was to test whether the fruit vs. ovary size relationship holds across different combinations of contrasting conditions, including nitrogen (N) availabilities, plant densities (D) and seasons, across two cultivars (i.e. one large and one small grained cultivar). Our hypothesis is that this relationship may not be a functional one and that, by manipulating agronomical/environmental factors, it is possible to decouple grain size from ovary size.

2. Materials and methods

2.1. Plant material and growing conditions

Common wheat (*Triticum aestivum* L.) was grown in 2013-14 and in 2014-15 at the experimental station of the Department of Agricultural, Food and Environmental Sciences of the University of Perugia, located in Papiano (43°N, 12.3°E, 165 m a.s.l.), in the middle Tiber Valley, Central Italy. The field was flat, with uniform cropping history and soil characteristics, 1.2% organic matter and high contents of extractable P and exchangeable K. In both years, the previous crop was sunflower. The mineral N available after sunflower was not measured, but several experiments carried out in the same soil in previous years revealed that the amount of N available after sunflower may amount to 30–40 kg N ha^{-1} (see for example Tosti et al., 2014).

Two hexaploid bread wheat cultivars with different grain size were used: Bora (Società Produttori Sementi, Italy; pedigree (H31 × 119 Trap1F2) × Enesco), which produces large grains (Thousand Grain Weight, TGW, of about 50 g) and Bologna (Società Italiana Sementi, Italy; pedigree (H89092 × H89136) × Soissons), which produces small grains (TGW of about 35 g).

The two cultivars were sown on November 7 in 2013 and on December 10 in 2014, and were grown either at different N availabilities (experiment one, both years) or at different plant densities (experiment two, both years). In the "N availability" experiment, the two cultivars, both sown at the usual density of 450 seeds m^{-2}, were grown at 0 or 240 kg N ha^{-2} (N0 and N240, respectively), the latter split into two applications of 120 kg ha^{-1} each, in mid-February and mid-March. Treatments were laid down according to a factorial combination with three replicates (randomized blocks). Each plot (12 m^2) consisted of 10 rows 0.15 m apart and 8 m long. Plots included two border rows on each side, and were spaced 0.30 cm apart. The first and last meter of the plots were also treated as borders and not included in measurements.

In the "plant density" experiment, the two cultivars were sown at 200 or 650 viable seeds m^{-2} (D200 and D650 respectively). A total of 160 kg N ha^{-1} was supplied, split into two applications of 80 kg ha^{-1} each, the first at tillering (mid-February) the second at initial stem elongation (mid-March). Experimental design and plots were arranged as in the N experiment.

In both experiments of both years, the crop was grown with standard crop management practices, including chemical control of weeds and diseases.

2.2. Morphometric analysis

At anthesis (Waddington stage 9.5), 24 main spikes (eight per replicate) from each N availability and plant density treatment were collected, for a total of 192 samples per each of the two years. Waddington stage 9.5 on the main spikes occurred on April 26 for Bora and April 28 for Bologna in 2014, and on May 4 for Bora and May 5 for Bologna in 2015, without differences between N rates and seeding densities. For each spike, the number of spikelets per spike was counted and ovary size was measured on the central flower of the eighth spikelet, i.e. the G2 position, where the largest grain tends to form (Hasan et al., 2011; Xie et al., 2015). This reduces the variability of the measurements because the largest grains are less variable in size than average grain size or "thousand grain weight". The latter, in fact, tends to decrease with increasing yield and grain number, due to increased fertility of more distal flowers, which tend to produce smaller ovaries and grains (Acreche and Slafer, 2006). Similarly, the eighth spikelet was chosen to standardize sampling at around the center of the spike in all treatments of both cultivars. Length and widths (both lateral and dorsal) of each ovary were measured using a Leica® DM 1000 light microscope equipped with a Leica® ICC50 HD camera and its image analyzer software Leica® LAS EZ.

Periodically after anthesis, up to physiological maturity, the same sampling procedure was applied, measuring grains in the same position. Grains were measured in length and width (both lateral and dorsal), this time using a Leica® MZ 125 stereomicroscope with an integrated Leica® IC A camera and the image analyzer software Leica® IM1000.

Ovary/grain volume throughout the grain filling period was assessed using the Piskunov (1978) equation:

$$\text{Ovary/grain volume} = 4/3\ \pi abc \qquad (1)$$

where $\pi = 3.1416$, $a = 0.5$ length, $b = 0.5$ width (lateral width) and $c = 0.5$ height (dorsal) of the grain.

Ovary and grain volumes were defined as individual ovary volume (IOV) and individual grain volume (IGV), to distinguish them from average values across the different positions.

2.3. Yield and yield components

In both years, just before harvesting the whole plot, a subsample of plants was harvested. This included all the plants along 1 m of row, in each of the 6 central rows of each plot. On this subsample, the total number of spikes was assessed, and the grain water content was measured (oven dry method). The total grain weight (with a standard 13% water content) and average grain weight (GW) (as the mean of three independent replicates of 100 grains) were determined. These data were used to calculate the nominal tillering index (i.e. n. of spikes m^{-2}/ n. viable seeds m^{-2} set at sowing), the total grain number (GN) and the number of grains per spike. The reminder of the plot was then harvested to determine the total grain yield.

2.4. Weather data

Weather data were taken from a weather station located at the same experimental field. The precipitation and temperature data are shown in Fig. 1A.

Precipitation during January and February, that is before and during the first N fertilization (mid-February), was more than twice as high in 2014 compared to both 2015 and the long-term average, and thus likely reduced the effectiveness of the 2014 first fertilization by leaching. Precipitation in March 2014, by contrast, was 69% of the average, thus probably making the second fertilization effective.

Average daily temperature differences between the two seasons varied, but temperature was consistently higher in spring 2015, from mid-April until mid-June, except for the last third of May, when it was