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The importance of the period immediately preceding anthesis for grain weight determination in wheat

D.F. Calderini[1], R. Savin[1], L.G. Abeledo[1], M.P. Reynolds[2] & G.A. Slafer[1]
[1]*Departamento de Produccion Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martin 4453 (C1417DSE), Capital Federal, Argentina;* [2]*CIMMYT (International Centre for Maize and Wheat Improvement), 06600 Mexico, D.F., Mexico*

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Abstract

Although individual grain weight is an important source of variation for grain yield, there is still poor understanding of the causes determining final grain weight. Almost all studies conducted for understanding the determinants of grain weight have been focused on the post-anthesis period. However, there is important evidence that pre-anthesis conditions could also modify final grain weight. Three experiments including different sowing dates, genotypes and temperature regimes between booting and anthesis, were carried out in Argentina and Mexico to analyse the effect of temperature and associated traits during the pre- and post-anthesis periods on grain weight under field conditions. In these experiments final grain weight could not be explained by average or maximum temperature during the post-anthesis period. However, average temperature between booting and anthesis was closely related to the observed grain weight differences, probably as a consequence of the effects of this factor on carpel growth. Differences in grain weight between genotypes and grain position were successfully explained by differences in carpel weight at anthesis. These results suggest that our knowledge to determine grain weight could improve if the immediately pre-anthesis period conditions were taken into account.

Introduction

Most of the research aimed to identify physiological mechanisms of grain weight determination has been focused on the period when the grains actually grow (Egli, 1998). However, recently published studies (Wardlaw, 1994; Calderini et al., 1999a,b; Calderini & Reynolds, 2000) have shown that the period immediately preceding anthesis, when the carpels (that will become the external structures of the grain) grow, also seems to be important for grain weight. For example, the analysis of the effect of temperature, probably the most conspicuous environmental factor affecting grain weight and quality (Egli, 1998), has been frequently restricted to changes in this factor during the grain filling period. Several of such studies have shown that the higher the temperature the lighter the grains at maturity. This has been shown to be true for cases in which the higher temperatures were imposed either throughout grain filling (e.g. Sofield et al., 1977; Chowdhury & Wardlaw, 1978) or as brief periods (3–6 days) of high temperatures interrupting a rather cool grain filling condition (e.g. Stone & Nicolas, 1994; Wardlaw & Wrigley, 1994; Savin et al., 1996) However, differences in grain weight between genotypes and in some cases even between sowing dates (e.g. Stone & Nicolas, 1995; Calderini et al., 1999b) could hardly be explained by differences in environmental conditions between anthesis and physiological maturity. Wardlaw (1994) showed that pre-anthesis temperatures could also modify grain weight in wheat, and recent studies (Calderini et al., 1999b) demonstrated that high temperatures between heading and anthesis could affect grain weight in a similar magnitude to that produced by brief events (ca. 6 days) of high temperatures during the grain filling period. The objective of the present study was to analyse the effect of temperature and associated traits during the pre- and post-anthesis periods on grain weight under field conditions.

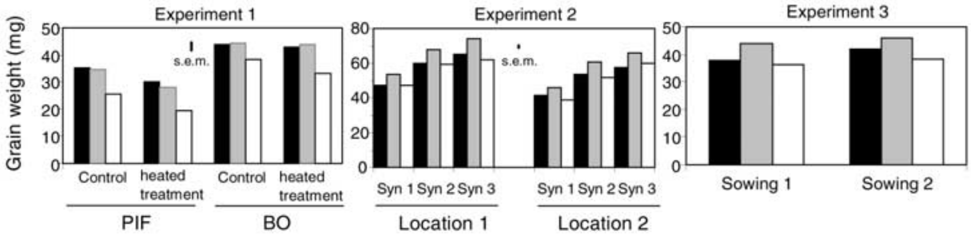

Figure 1. Grain weight of grain positions 1 (closed bars), 2 (dotted bars) and 3 (open bars) of control and heated treatment in cultivars Pro INTA Federal (PIF) and Buck Ombú (BO) in Experiment 1; synthetic lines 1, (Syn 1), 2 (Syn 2), and 3 (Syn 3) in Ciudad Obregón (location 1) and El Batán (location 2) in Experiment 2, and sowing date 1 (Sowing 1) and 2 (Sowing 2) in Experiment 3. Bars represent standard error of the means. In Experiment 3 standard error was 0.5mg.

Materials and methods

Experiments

To deal with the objective, 3 experiments (Experiments 1, 2 and 3) were carried out under field conditions. Experiment 1 was conducted during 1996 at the experimental field of the Faculty of Agronomy, University of Buenos Aires (34 ° 35′S, 58 ° 29′W, altitude 25 m). Treatments consisted of the combination of two high-yielding wheat cultivars (Pro INTA Federal, PIF and Buck Ombú, BO) and two temperature regimes for the growing spikes (control or heated spikes) during the period from ear emergence (at 50% of ear emergence) to anthesis. Sowing date was 27 March 1996. Experimental plots of 7 rows, 0.20 m apart and 3 m long were arranged in a split-plot design with three replications. Main plots were assigned to cultivars and subplots to the pre-anthesis thermal regime. Sowing density was 350 plants m^{-2}. To increase spike temperature during the heading-anthesis period, transparent acrylic boxes (50 cm length, 20 cm height and 6.5 cm wide) were installed covering only the spikes after their emergence until anthesis in the heated treatment.

Experiment 2 was sown at the International Maize and Wheat Improvement Center (CIMMYT), Mexico, in two locations during the 1997-1998 growing season. Location 1 was Ciudad Obregón (27 ° 20′N, 105 ° 55′W altitude 39 m) and Location 2 was El Batán (19 ° 31′N, 98 ° 50′W altitude 2249 m). Dates of sowing were 15 November 1997 and 22 May 1998 for location 1 and 2, respectively. In each location, the study involved three synthetic hexaploid lines of wheat in three replicates. Synthetic lines for the experiment were 68.111/RGB-4//WARD/3/FGO/4/RABI/5/Ae. Sq. (878), ROK/KML/ /Ae. Sq. (214), and CPI/GEDIZ/3/G00//J069 /CRA/4/Ae. Sq. (629). Hereafter, they will be called: Syn 1, Syn 2 and Syn 3, respectively. These lines were chosen for differing in grain weight potential.

In both locations, synthetic lines were sown on raised beds spaced at a frequency of 80 cm. In Ciudad Obregón the plots consisted of two beds, 5 m long with 4 rows 10 cm apart per bed, seed rate was 50 seeds per row meter. In El Batán the plots consisted of two beds, 5 m long with 2 rows 20 cm apart per bed, with 1 seed sowed every 3cm in each row.

Experiment 3 consisted of one synthetic hexaploid line (Syn 1) sown in two dates (with three repetitions each) in El Batán during 1998. Sowing dates were 22 May and 17 June. Plots consisted of two beds, 5 m long with 2 rows 20 cm apart per bed, seed rate on the row was one seed per 3 cm.

In all these experiments mineral nitrogen was applied at sowing at least at a rate of 150 kg N ha^{-1}. Plots were irrigated from planting to maturity and the experiments were maintained free of biotic stresses.

Measurements

Dry weight of the carpels of each of the three most proximal florets (those closest to the rachis) in the four central spikelets of four main-shoot spikes per experimental unit were measured at booting, heading and anthesis in Experiments 1 and 2. The only exception was Syn 2 in El Batán (Experiment 2) where carpel weight was not recorded. At anthesis the carpels of heated spikes were also dried and weighed in Experiment 1.

From anthesis onwards, one main-shoot spike from each replication was harvested at least twice weekly and the dry weight of grains corresponding to the three most proximal florets (subsequently referred to as G_1, G_2 and G_3) of central spikelet was recorded in Experiments 1 and 2. In Experiment 3, 10 main-shoot spikes were harvested from each replication at maturity, and

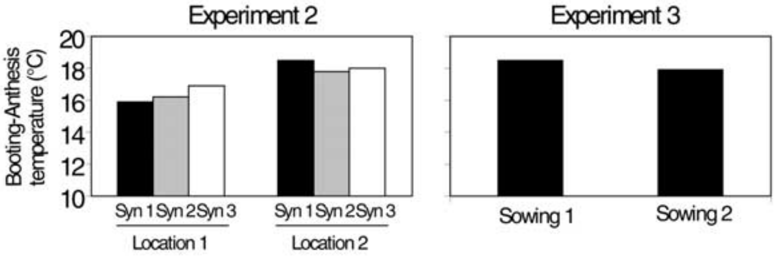

Figure 2. Average temperature during the booting-anthesis period for synthetic lines 1 (closed bars), 2 (dotted bars), and 3 (open bars) in Ciudad Obregón (location 1) and El Batán (location 2) in Experiment 2, and sowing dates 1 (Sowing 1) and 2 (Sowing 2) in Experiment 3

dry weight of grains corresponding to G_1, G_2 and G_3 from the 5 central spikelets were recorded.

In all trials, air temperature was recorded at the meteorological station situated near the experiment (ca. 100 m). Data were subjected to analysis of variance for split-plot or split-split-plot according to the experiment. For more details see Calderini et al., (1999a) and Calderini and Reynolds (2000).

Results and discussion

Grain weight and temperature during the pre- and post-anthesis periods

In experiments 1, 2 and 3 grain weight was modified by experimental site, sowing date, genotype and grain position (Figure 1). The differences between cultivars PIF and BO in Experiment 1 could not be related to differences in grain-filling conditions as both reached anthesis virtually simultaneously. In Experiment 2, grain weight (as average of genotypes and grain positions) was 15% higher in C. Obregón than in El Batán (Figure 1). However, average temperature during grain filling was higher in C. Obregón (18.6, 18.8, and 19.0 °C in Syn 1, Syn 2 and Syn 3 respectively) than in El Batán (18.0, 17.7, and 17.6 °C in Syn 1, Syn 2 and Syn 3 respectively). In Experiment 3, grain weight (averaged across grain positions) was significantly ($p < 0.01$) higher (7%) in sowing 2 than in sowing 1 (Figure 1). Average (as well as daily mean and maximum) grain filling temperatures were similar between sowing 1 (18 °C) and sowing 2 (17.9 °C).

Therefore, in all experiments post-anthesis temperatures seemed not to be the cause of grain weight differences between cultivars, sites or sowing dates. In Experiment 1, it was clear that high temperatures between heading and anthesis reduced final grain weight (Figure 1). Taking into account that the period between booting and anthesis (i.e. when carpels grow) has been proposed as critical for grain weight determination (data in Figure 1 and see also Calderini et al., 1999b), average temperatures for pre-anthesis were analysed in Experiments 2 and 3. In both Experiments the lower the average temperature between booting and anthesis the higher the final grain weight (see Figures 1 and 2).

Although Experiment 1 has shown clear evidence that artificially increasing spike temperature immediately before anthesis decreased grain weight (Figure 1), the analysis of the other experiments supported the hypothesis with data from open field conditions. However, the different impact of higher temperatures between grain positions (see G_1 and G_3 in Figure 1) in Experiment 1 was not found in Experiments 2 and 3 (Figure 1). Possibly, this difference between experiments could be related to the timing at which the high temperature treatment was imposed in Experiment 1 (between heading and anthesis), and the different developmental stage of florets from different grain positions that has been reported for wheat at heading (see Miralles et al., 1998).

Carpel growth

Following previous findings in barley and wheat, it is hypothesised that the effect of high temperature immediately before anthesis on grain weight described above could be the consequence of the effects of this factor on carpel growth (Scott et al., 1983; Calderini et al., 1999a; Calderini & Reynolds, 2000), In Experiment 1, BO, the cultivar with the heaviest grains (Figure 1), reached the highest carpel weight at anthesis both in control and heated treatments within each grain position (Figures 3a, b, c). At the same time, carpels corresponding to heated spikes reached lower weight ($p < 0.001$) than controls (Figures 3a, b, c) and this difference between treatments could be explained by a shortening of the period between head-

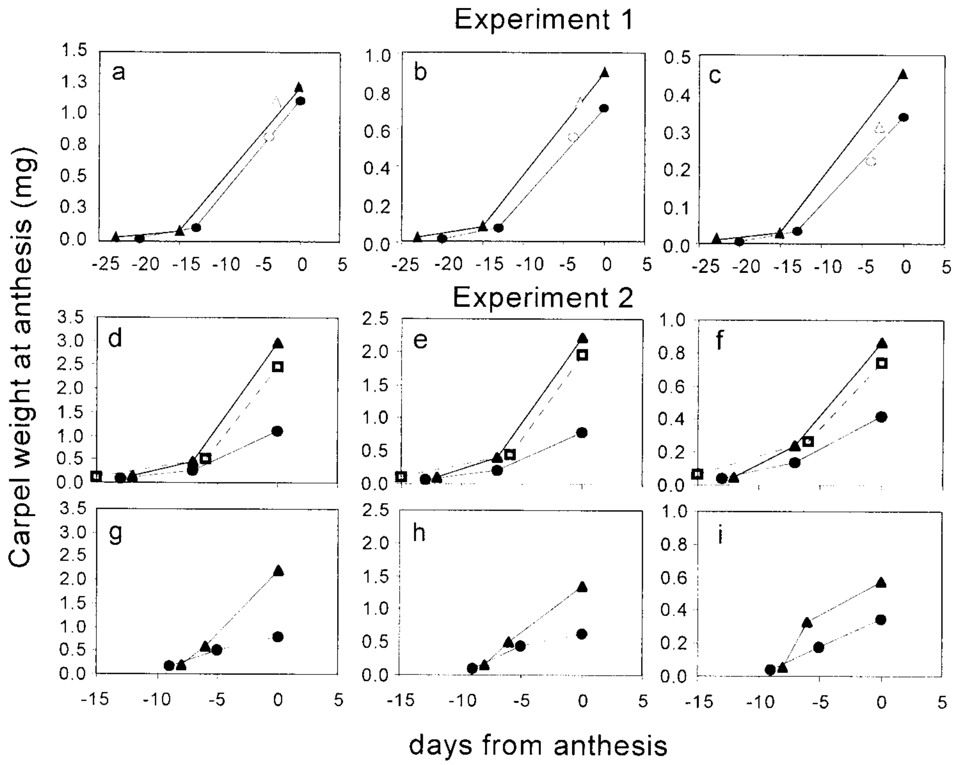

Figure 3. Relationship between carpel weight and days from anthesis for grain positions G_1 (a, d and g), G_2 (b, e and h) and G_3 (c, f and i) in Experiments 1 (a, b and c) and 2 (d, e, f, g, h, and i). In Experiment 1, data correspond to control (closed symbols) and heated (open symbols) treatments of cultivars Pro INTA Federal (circles) and Buck Ombú (triangles). In Experiment 2; data correspond to synthetic line 1 (circles), 2 (squares), and 3 (triangles) in location 1, Ciudad Obregón (d, e and f) and location 2, El Batán (g, h and i).

ing and anthesis in heated spikes (see Figures 3a, b, c). The distal G_3 was more affected by the heated treatment than G_1 and G_2. Carpel weight at anthesis decreased by 17, 20 and 34% in G_1, G_2 and G_3, respectively as average of both cultivars, and P. Federal was more affected than B. Ombu (Figures 3a, b, c). In Experiment 2, and in agreement with Experiment 1, genotypes differed in carpel weight at anthesis ($p < 0.05$), and the higher the carpel weight at anthesis the higher the grain weight at harvest within each grain position (Figures 3d, e, f, g, h, i, and Figure 1). In addition, carpel weight at anthesis was higher in sowing 1 (in which grain weight was higher as well) than in sowing 2 (Figures 3d, e, f, g, h, i).

In Experiments 2 and 3 there was not a differential effect of immediately pre-anthesis temperatures on grain weight for different grain positions (Figure 1). As was suggested above, the higher effect found in G_3 in Experiment 1 could be related with the timing of the heated treatment. This speculation could be supported by considering the effect of temperature on carpel growth dynamics between Experiments 1 and 2. In Experiment 2 no particular timing of higher temperatures was found.

Grain weight and associated traits during the post-anthesis period

Grain weight was significantly ($p < 0.05$) associated with grain filling rate (mg/°Cday) in Experiments 1 and 2 (the experiments where grain filling rate and duration were measured).

Grain filling rate, but not grain filling duration (°Cday), was the post-anthesis trait that better explained final grain weight (data not shown). This agrees with previous studies focused on the analysis of physiological determinants of grain weight when grain filling rate and grain filling duration were measured in thermal time units (e.g. Simmons et al., 1982; Loss et al., 1989; Miralles & Slafer, 1995). In addition, grain filling rate was positively and significantly associated with carpel weight at anthesis in experiments 1 and 2 (see Calderini et al., 1999b; Calderini & Reynolds, 2000). It seems from preliminary results

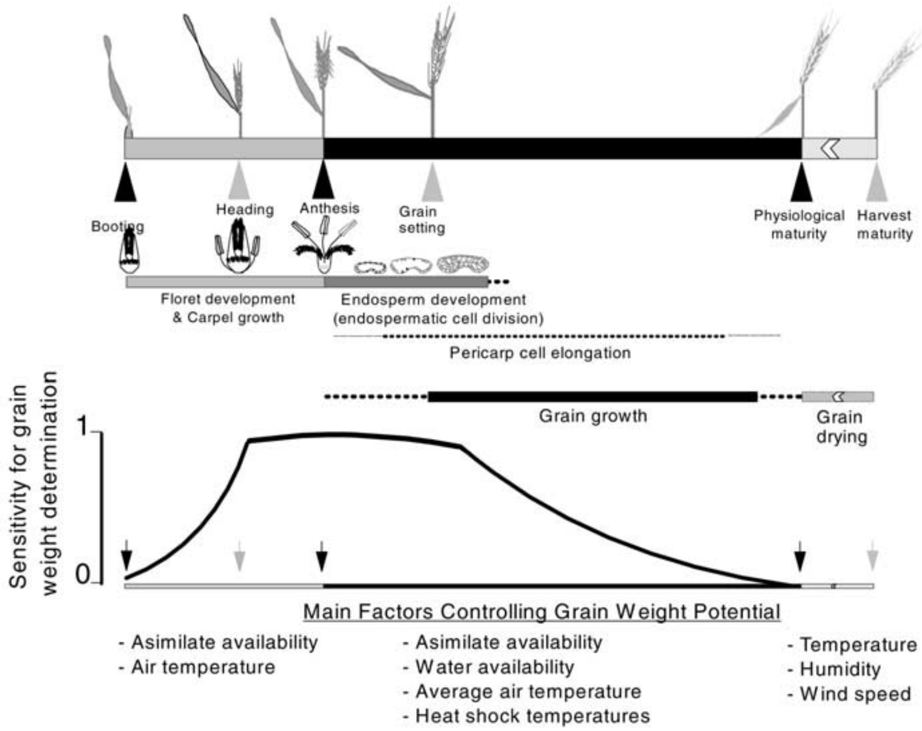

Figure 4. Schematic diagram of grain weight determination in wheat from booting to harvest maturity. This diagram considers relevant floret and grain processes (e.g. carpel growth and endospermatic cell division) and includes a hypothesised grain weight sensitivity to plant and environmental factors from booting to harvest maturity.

that pericarp cell elongation during post-anthesis may be responsible for differences in final grain weight between wheats with different carpel weight at anthesis (Calderini & Reynolds, unpublished).

These results suggest that the knowledge of grain weight determination in wheat (and the accuracy of simulation models) could be significantly improved if future studies considered the conditions during the period of carpel growth, the few days immediately preceding anthesis. A simple, schematic model would suggest that grain weight determination is particularly sensitive to genetic and environmental factors during both the frequently recognised phase of endosperm cell division and growth, but also during the mostly disregarded phase when the carpels, that will become the pericarp of the grain, grow (Figure 4). Although this simple model is in its infancy it could be useful for generating hypotheses aimed to study grain weight determination in wheat.

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