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Relationship between fruiting efficiency and grain weight in durum wheat

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ABSTRACT

Future increases in grain number may be achieved through improving fruiting efficiency (FE; grains set per unit spike dry weight at anthesis). In recent experiments it was found a negative relationship between the average weight of the grains and FE. The objective of this paper was to determine whether this negative relationship was constitutive (i.e. the increased FE caused all grains to be smaller) or resulted from the increased proportion of grains of smaller potential size. Four experiments, involving 8 different environmental conditions, were carried out during two consecutive growing seasons (2008–2009 and 2009–2010) in which two durum wheat cultivars contrasting in FE and average grain weight were compared. In these conditions we determined FE and carried out a comprehensive study analysing in detail the weights of each individual grain along each of the spikelets. Averaging all experimental conditions, there was a negative relationship between average grain weight (GW) and fruiting efficiency (FE). Donduro with low FE produced in average heavier grains than Vitron. However, when considering individual grains there were, in general, no differences in GW. Therefore, the negative relationship between average grain weight and FE would not be constitutive, and would mostly represent the increase in the proportion of distal grains within the spikelets or of grains from apical spikelets as a consequence of an increased FE, reducing the average size of the grain but mostly unaffecting the size of particular grains. This provides further and stronger support to the idea of using FE as a criterion to further raise yield potential in wheat breeding programmes.

1. Introduction

Both evolutionary and breeding reasons explain that the number of grain per m^2 is more plastic than grain weight (Peltonen-Sainio et al., 2007; Sadras, 2007; Sadras and Slafer, 2012). Therefore, grain number is commonly more responsive than grain weight not only to environmental but also to genetic factors (Slafer et al., 2014). Although both components are frequently negatively related, this relationship may not reflect a strong competition among grains for assimilates during the effective period of grain growth (Miralles and Slafer, 1995; Acreche and Slafer, 2006). In fact, grain growth is most frequently limited by the sink- than by the source-strength during post anthesis (Borrás et al., 2004; González et al., 2014). As yield seems to be mechanistically related to grain number per m^2 in most grain crops (Slafer et al., 2006) and particularly in bread (Reynolds et al., 2009; Sadras and Slafer, 2012; Serrago et al., 2013) and durum wheat (Giunta et al., 2007; Pedro et al., 2011; Ferrante et al., 2012), understanding the mechanisms controlling grain number determination may be relevant to further raising yield (Fischer, 2011; Foulkes et al., 2011; and referenced quoted therein).

Before and during the green revolution, there was a continuous shift of partitioning of assimilates towards an improved growth of the juvenile spikes during pre-anthesis period. This led to an increased spike dry weight at anthesis (Siddique et al., 1989; Slafer and Andrade, 1993), and it was paramount for increasing grain number associated with plant height reduction (Fischer, 2007). As in modern cultivars partitioning to reproductive organs is close to its optimum and plant height has been optimised, alternative traits to ensure future breeding further increases grain number must be envisaged (Reynolds et al., 2012; Fischer et al., 2014 and referenced quoted therein).

Recent studies showed that a diminished rate of floret primordia abortion in wheat during the last part of the stem elongation phase was associated with an increased number of fertile florets at

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anthesis (Ferrante et al., 2010; González et al., 2011a; González et al., 2015), with an increased likelihood of particular fertile florets to set grains, or with both (Ferrante et al., 2013a). In turn, comprehensive studies analysing in detail floret development as affected by changes in environmental conditions (both signals and resources), showed that the onset of floret death was not a purely developmental feature (González et al., 2011a; Ferrante et al., 2013b), supporting the model relating floret death with the initiation of active growth of the juvenile spike (Slafer et al., 2005), in which florets are developing.

Alternatively, increases in grain number per m^2 could be achieved by improving the efficiency with which a certain growth of the juvenile spike before anthesis may be used to set grains, or fruiting efficiency (FE; i.e. the number of grains set per unit of spike dry weight at anthesis), as shown when comparing either cultivars released at different eras (Acreche et al., 2008), modern cultivars (Abbate et al., 1998; González et al., 2011b; Foulkes et al., 2011; Ferrante et al., 2012), or promising lines (Pedro et al., 2011; García et al., 2014). Thus, it seems possible to achieve genetic gains in grain number by increasing FE (Pedro et al., 2012). However, a concomitant reduction in grain weight may be expected if the increased FE is a consequence of a reduction in size of the carpels of the fertile florets, as grain weight potential is related to the size of the ovaries (Calderini et al., 1999, 2001; Ugarte et al., 2007; Hasan et al., 2011). For instance, in a previous study on physiological bases for yield differences among modern durum wheats it was found a negative relationship between average grain weight and FE (Ferrante et al., 2012), being clear that differences in FE were associated with differences in grain per spike and per spikelet (Ferrante et al., 2013a). This negative relationship between average grain weight and FE was in line with a positive relationship between grain weight and crop growth rate per grain during the grain set period (which would be a proxy to the reciprocal of FE) shown by Gambín and Borrás (2010) when comparing different species. These evidences open room to two alternative hypotheses (Fig. 1) on the nature of the negative relationship between grain weight and FE (Fig. 1a):

- (i) the trade-off (negative reciprocal causal relationships in net benefits between trait magnitudes; Saeki et al., 2014) reflects that the higher FE would have been achieved through a reduction in size of fertile florets and then the improved number of grains is associated to smaller florets, determining a concomitant reduction of individual grain size (Fig. 1b). It means that the increased FE would reflect a maternal adjustment of the size of the offspring (Sadras and Denison, 2009) allowing more – but smaller – florets to become fertile for a certain amount of resources available for floret primordia growth. This hypothesis implies that the reduction in average grain weight due to an increased FE would reflect a reduction in size of each of the grains (Fig. 1c). If this alternative hypothesis proves right the improvement in grain number through increases in FE would be disappointingly vain, as it would bring about no yield gain (Fig. 1d).
- (ii) the reduction in grain weight associated with an increase in FE does not produce a compensation annulling yield gains. This alternative implies that increases in fruiting efficiency would not be the consequence of a reduction in floret size but likely due to an improvement in partitioning towards florets of the total spike growth. As the increased FE would bring about an increase in the proportion of grains set in more distal florets; and the more distal the grain position the lower its weight potential (Fig. 1e). Thus the increase in FE would allow more distal florets to become fertile florets and it would increase the proportion of distal grains, which would reduce average grain weight independently of changes in the size of particular grains with increases in FE (Fig. 1f). This alternative hypothesis implies that improvement in grain number through increases in FE would effectively bring about yield gains (Fig. 1g), despite of the negative relationship between average grain weight and FE.

The objective of this study was to quantitatively determine whether the reduction in average grain weight, associated with an increased FE, between two modern durum wheats, was a constitutive consequence of a generalised reduction in size of all grains when FE was higher or resulted from the increased proportion of grains of smaller grain size potential which would also be a consequence of increasing FE.

2. Materials and methods

2.1. General conditions and treatments

Details of the four experiments carried out through two growing seasons are available in Ferrante et al. (2012). To recap briefly, two experiments (exps. 1 and 4) were carried out outdoors in microcrops in large cubic containers (1 m height and 1 m^2 surface; details of the containers are available in Ferrante et al., 2010) at the School of Agronomy, University of Lleida, Spain (41°37′50″N, 0°35′27″E; altitude 180 m) while the other two (exps. 2 and 3) were field experiments conducted at Gimenells (41°39′11″N, 0°23′28″E; altitude 258 m) (Table 1).

All experiments were sown within the common sowing dates and densities of the region. Diseases and insects were prevented or controlled by spraying recommended fungicides and insecticides while weeds were removed by hand throughout the growing seasons.

Two contrasting modern durum wheat cultivars, Vitron and Donduro, were grown in all experiments. Vitron was characterised for having consistently higher FE than Donduro, while the latter had grains consistently heavier (Ferrante et al., 2012). Experiment 1 included, in factorial combination with the cultivars, two treatment of nitrogen (N) availability: a low N control with an initial soil N content equivalent to 50 kgN ha^{-1} (N50) produced by broadcasting 30 kgN ha^{-1} to the natural soil N availability of 20 kgN ha^{-1}; and a high N treatment which received 230 kgN ha^{-1}, resulting in an initial availability of 250 kgN ha^{-1} (N250) (Table 1). Experiment 4 did also include, in factorial combination with N and cultivars, two water treatments: a rain-fed (RF) and a treatment irrigated periodically from once weekly in winter to practically daily during grain filing (Table 1). Thus, all in all, we have compared these contrasting cultivars over 8 environmental conditions (ranging in yield from less than 3 to more than 10 Mg ha^{-1}; Ferrante et al., 2012).

2.2. Measurements and analyses

For this study we measured spike dry weight at anthesis and at maturity we determined grain number at each spikelet and grain weight individually (i.e. grain by grain from each spikelet at each position of the spike). Samples were taken at anthesis ($1_{(2008–2009)}$ or $0.5_{(2009–2010)}$ linear meter of each experimental unit) and at maturity (from $2_{(2008–2009)}$ or $1_{(2009–2010)}$ linear meters of each experimental unit) and in the lab we separated main shoots and tillers. For spike dry weight determinations at anthesis, all spikes were cut from the samples and then were weighed separately (after oven drying them). At maturity, grain number were counted and weighed separately for main shoot and tillers. Then, we calculated the efficiency with which the available resources in the reproductive organs at anthesis were used to set grains; the fruiting efficiency (FE; the ratio between grain number and spike dry weight at anthesis), as well as the average grain weight of the main shoot spikes.