

Grain weight responses to post-anthesis spikelet-trimming in an old and a modern wheat under Mediterranean conditions

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Abstract

Average grain weight is a major yield component contributing to its variation, especially in Mediterranean regions where grain weight is frequently exposed to terminal stresses affecting grain growth. Most of the literature agrees that wheat grain growth is hardly limited by the source. However, no source–sink ratios studies seem to have been conducted in the Mediterranean region to determine to what degree wheat grain growth is actually limited by the source in these particular regions. We conducted two field experiments in Catalonia (north-eastern Spain), where an old cultivar (Anza) and a more recently released one (Soissons) were sown in a range of different nitrogen and water availabilities and sowing dates. This was to analyse the degree of source limitation for grain growth. Sink size was modified by removing half of the spikelets *c.* 10 days after anthesis, virtually doubling the availability of assimilates per grain effectively growing.

Trimming the spikes did not produce significant changes in grain growth rate or duration of grain filling. Consequently, grain weight did not respond noticeably to the reduction in sink demand and any eventual response has been far from representing a strong competition among grains during grain filling.

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1. Introduction

It is well known that grain number per unit area is the yield component most strongly related to yield variations in wheat (e.g. Frederick and Bauer, 1999), as well as in most other grain-crops (Slafer, 1994; Egli, 1998). Despite this strong and consistent relationship, the average grain weight can be an important source of variation of grain yield (Calderini *et al.*, 2001), particularly so in cereal growing regions characterised by terminal stresses, such as those of the Mediterranean basin (Acevedo *et al.*, 1999). Therefore, understanding the causes of grain weight determination could be critical to plant breeders and agronomists aimed to increase yield or yield stability, particularly in the Mediterranean region.

In addition, number of grains per unit land area and the averaged grain weight are frequently negatively correlated (Slafer and Andrade, 1993); a fact often interpreted as a sign of the com-

petition among grains for an insufficient assimilate availability during grain filling (i.e. whenever grain number is increased each grain can access less assimilates than those needed to maximise growth). If grains compete for limited growth resources during grain filling reducing sink size and, as a consequence, improving the source–sink ratio after anthesis would be important in general and critical in Mediterranean conditions. On the other hand, if grain weight is determined largely independently of post-anthesis source strength it would be critical to improve potential grain size.

A direct approach to determine whether (and to what degree) final grain size is consequence of competition among grains during grain filling has been to modify the source–sink relationship (i.e. defoliation, shading, degrading treatments imposed soon after anthesis before the onset of the effective grain filling period). In general, individual studies may have found some inconsistencies, but analysing them together clearly reveals that wheat grains do not or slightly respond to these kind of source–sink manipulations (e.g. Slafer and Savin, 1994; Borrás *et al.*, 2004). In other words, that the capacity of the wheat canopy to provide assimilates to the growing grains is

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generally adequate to allow the grains to completely fill (Savin and Slafer, 1991; Richards, 1996).

Despite the fact that this generalised behaviour included some analyses of wheat grain size responses to post-anthesis source–sink ratios under stress (e.g. Slafer and Miralles, 1992), and the review by Slafer and Savin (1994); later updated and expanded by Borrás et al. (2004) were comprehensive, virtually no studies were conducted in the Mediterranean region.

In Mediterranean conditions grain size is recognised to be a yield component particularly vulnerable due to the frequent stresses to which grain growth is exposed in cereal production. Thus, results might not be straightforwardly extrapolated from other regions.

We are not aware of any study in Mediterranean countries with wheat. However, with barley under rain-fed Mediterranean conditions in north-eastern Spain, Voltas et al. (1997) have found average increments of *c.* 20% on barley grain size when degrading half of the spikes. Moreover, the greatest increments were found in those trials with the smallest control grain size, suggesting a major degree of source limitation in low-yielding environments, indicating that the stronger the stress in post-anthesis the more limited by the source was grain growth. However, Voltas et al. (1997) had imposed the treatments at anthesis and it was clearly shown a few years later, that removing florets or grains before the onset of grain growth may alter the potential size of grains (Calderini et al., 2001). Then the reported increase in grain size may be the reflection of a sink-limitation rather than a source-limitation during grain filling (i.e. removing competitors during flowering and the very few days following may have contributed to an increase in grain weight potential rather than an increase in assimilate availability per grain as the driving force for the observed increase in final grain weight due to the treatment). Clearly further studies on the grain size responsiveness to source–sink manipulations, exclusively during the actual grain growth period, in Mediterranean conditions are needed before concluding on likely differences in these environments compared with other, less stressful grain filling conditions.

As it has been shown that the degree of sink-limitation for yield during grain filling might have tended to be reduced with breeding (Kruk et al., 1997; Shearman et al., 2005), if there is a source-limited grain growth this limitation would be more clearly evidenced in modern than in traditional cultivars, as modern cultivars normally overyield their predecessors by increasing the number of grains per m^2 (Calderini et al., 1999).

The aim of this study was to determine whether wheat grain growth under Mediterranean conditions is actually source-limited and if so whether an old and a modern cultivar would differ in their responsiveness.

2. Materials and methods

2.1. Location

Two field experiments were carried out in the 2003–2004 growing season. Experiment 1 was conducted at Agramunt (latitude $41^{\circ}47'17''N$, longitude $1^{\circ}5'59''E$, altitude 337 m) in a Xerorthent soil. Experiment 2 was conducted at the experi-

mental facilities of the Centre UdL-IRTA in Gimènells (latitude $41^{\circ}39'11''E$, longitude $0^{\circ}23'28''$, altitude 258 m) in a Calcixerupt petrocalcic soil.

Both locations are some 80 km apart within the province of Lleida (Catalonia, north-eastern Spain). Agramunt is within the rainfed agricultural system while Gimènells is within an irrigated area.

Experiment 2 was also fertilised with nitrogen to avoid its deficiencies and irrigated (345 mm along the growing season). Weeds, insects and diseases were controlled or prevented using conventional commercial pesticides applied following the recommendations from their manufacturers. Experiment 1 was sown on 21 November 2003 at a rate of 390 seeds m^{-2} . Experiment 2 was sown at different dates increasing seed rate accordingly (see below).

2.2. Treatments

The common treatments in both experiments, needed to achieve the objective of the study, were a factorial combination of two cultivars and two levels of sink manipulation. The background under which these treatments were imposed included a range of environmental conditions that differed in each experiment. This range was produced by a factorial combination of two nitrogen fertilisation levels and two irrigation levels in experiment 1; and by four different sowing dates in experiment 2.

The two genotypes chosen were the old cultivar Anza (released in 1969 and very widely grown in the past and still grown by many farmers) and the more recently released French cultivar Soissons (released in 1992).

Sink size was modified by manipulating the number of spikelets per spike. For this purpose, at anthesis (50% of spikes extruded anthers in each experimental unit) 40 main-shoot spikes (having similar number of spikelets per spike), from the central rows of each plot, were tagged randomly. Ten days later all the spikelets from one side of 20 spikes, chosen randomly from the 40 spikes labelled before, were removed by hand (trimmed spikes); while the other 20 spikes remained unaltered as controls.

In experiment 1, environmental treatments consisted of a combination of two levels of nitrogen fertiliser, 0 kg N ha^{-1} (N_0) and 200 kg N ha^{-1} (N_{200}) applied at tillering (DC 2.0, Zadoks et al., 1974) as urea, with rain-fed (R) or irrigated conditions (I), the latter consisted of a twice-weekly irrigation of *c.* 10 mm each starting at the beginning of stem elongation (DC 3.1). In this experiment, the treatments were arranged in a split-block split-split-plot design with three replicates. Main plots consisted of the two cultivars, sown in strips across the two water regimes in the entire replication. The sub-plots consisted of the two nitrogen levels; while the source–sink manipulation treatment was assigned to sub-sub-plots. Sub-plots consisted of 22 rows, 0.135 m apart and 5 m long.

In experiment 2, environmental treatments consisted of four sowing dates: 17 December (S_1); 15 January (S_2); 16 February (S_3) and 15 March (S_4). The sowing densities increased with the delay in sowing (380, 410, 440 and 470 seeds m^{-2} for S_1 , S_2 , S_3 and S_4 , respectively) in order to ensure a dense canopy capable of maximise radiation interception during stem elongation. The

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