Field Crops Research 150 (2013) 42–51

Contents lists available at SciVerse ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Understanding grain yield responses to source–sink ratios during grain filling in wheat and barley under contrasting environments

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ARTICLE INFO

Article history:
Received 11 December 2012
Received in revised form 15 May 2013
Accepted 17 May 2013

Keywords:
Triticum aestivum
Hordeum vulgare
Grain number
Grain weight
Spike photosynthesis
Stem reserves

ABSTRACT

A better understanding of the effects of different source–sink ratio during the grain filling period on grain growth may be relevant in order to further increase cereal grain yield. The main objective of the present work was to determine the effect of different manipulations of the source–sink ratios in wheat and barley grown at four different environmental conditions on responsiveness of sinks (grain growth and yield) and sources (spike photosynthesis and water soluble carbohydrates in the stems). Four treatments were imposed 7 days after anthesis in two contrasting locations with low- and high-inputs conditions in wheat (cv. Soissons) and barley (cv. Sunrise): they were a control, a treatment removing all the spikelets from the upper half of the spikes (T_S), and shadings decreasing incident radiation by 75% on the whole canopy (S_W) or only on the leaves (having the top area of the meshes individual holes for each spike to be exposed to solar radiation, S_L). As expected grain yield was closely related to grain number per m^2. Average grain weight was reduced by shading treatments far more markedly in S_w than in S_L. Interestingly, significant amounts of water soluble carbohydrates in the stems remained at maturity in S_L and S_w treatments and spike photosynthesis in S_L was consistently higher than in the unshaded controls in both species. These results may be an indication that wheat and barley are not source-limited during grain filling and that only when subjected to an extremely severe stress, grain size would be reduced due to lack of enough assimilates available to fill them.

1. Introduction

Grain yield increases during the last century were almost fully (Slafer et al., 1990; Calderini et al., 1999; Fischer, 2007b), or at least mainly (Calderini et al., 1995; Sadras and Lawson, 2011), related to increases in grain number per m^2. This is in line with the fact that grain growth is frequently sink-limited both in wheat (Jenner, 1979; Savin and Slafer, 1991; Slafer and Savin, 1994; Miralles and Slafer, 1995; Kruk et al., 1997; Borrás et al., 2004; Calderini et al., 2006) and barley (Dreccer et al., 1997; Savin et al., 2006; Bingham et al., 2007). This is seemingly true even in environments characterized by terminal stress (Cartelle et al., 2006; Pedro et al., 2011). In other words, post-flowering source-strength is commonly in excess to meet the demands of growing grains in cereals (Richards, 1996; Bingham et al., 2007). However, some reports disagree with this conclusion, and examples in the literature with grain weight responding to source–sink manipulations during grain filling can be also found in wheat (Bremner and Rawson, 1978; Fischer and HilleRisLambers, 1978; Bindraban, 1996; Sandaña et al., 2009) and barley (Grashoff and d'Antuono, 1997; Voltas et al., 1997). Differences among experiments could be related to the timing at which the treatments were imposed. In the experiments made by Fischer and HilleRisLambers (1978) and Voltas et al. (1997) the source–sink manipulations treatments were imposed at anthesis. Then, the responses found in these experiments could be due to increases in grain weight potential, more than due to alleviation of source limitations during grain filling, as potential size of the grains is determined up to few days after anthesis (Brocklehurst, 1977). Having a clearer picture of the expected responsiveness of grain growth to source strength is relevant for identifying prospective alternatives for further increasing yields. Further increases in grain number could be critically relevant if grain growth is mainly sink-limited or totally ineffective if it were compensated by proportional grain weight reductions if grain growth were source-limited (Slafer et al., 2005; Reynolds et al., 2009; Foulkes et al., 2011). To determine whether there is a negative association between the number of grains per m^2 and their average weight could be of

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0378-4290/$ – see front matter
http://dx.doi.org/10.1016/j.fcr.2013.05.016

little help for clarifying the issue as such inverse relationship may be caused by competitive or non-competitive reasons (Miralles and Slafer, 1995; Acreche and Slafer, 2006). Therefore, direct determination of the degree of source- or sink-limitations to grain growth is critical. The most common approach to determine whether there is source- or sink-limitation has been the imposition of treatments in which either, source or sink strengths are manipulated ca. 7–10 days after flowering. Commonly, source manipulations are defoliations or shadings while sink manipulations are removals of grains (e.g. partially trimming the spikes), determining reductions or increases in the source–sink relationship, respectively.

During the grain filling period, the assimilate supply to fill the grains is the current canopy photosynthesis, of which spike photosynthesis may be a major contributor (Evans and Rawson, 1970; Araus et al., 1993; Tambussi et al., 2007), plus the translocation of non-structural reserves stored before the onset of grain filling (Ehdaie et al., 2008; Bingham et al., 2009). Commonly research reporting on whether grain growth is source- or sink-limited has been exclusively focused on grain weight responsiveness to treatments, disregarding to what degree changes in grain weight were explained by opposite changes in source-strength (either increased-reduced photosynthetic activity or accumulation-depletion of non-structural carbohydrate reserves). For instance, as the capacity of cereals to compensate for reductions in source–sink ratios is based on using stored assimilates in stems during grain filling (Setter et al., 1998; Richards et al., 2002; Borrás et al., 2004; Serrago et al., 2011), grain weight reductions in treated plants should be accompanied by a depletion of carbohydrate reserves to conclude that grain growth in the non-manipulated control was source-limited.

For interpreting the effects of different source–sink ratios on grain yield it is important to consider the background environmental conditions in which the responsiveness to the treatments is assessed (Borrás et al., 2004). Thus, differences in the environmental background in which source–sink ratios were manipulated could be responsible for the conflicting results mentioned above. Then, for conclusions of any study to be extrapolated, manipulations of source–sink ratios should be done under contrasting growing conditions. Therefore, the main objective of this study was to determine responsiveness of sinks (grain growth and yield) and sources (photosynthesis and non-structural reserves) to manipulations of source–sink ratio (trimming the spikes and fully or partially shading the canopy at the onset of grain growth) in wheat and barley grown at four different environmental conditions.

2. Materials and methods

2.1. General conditions, treatments and experimental design

Two field experiments were conducted on normal sowing dates and sowing densities for wheat and barley crops in Catalonia, NE Spain (Table 1). The experiments were conducted in two different locations within the province of Lleida during the 2009/10 growing season. One of the experiments was conducted at Agramunt (41°84′70″ N, 01°80′60″ E, 330 masl, within a region characterized by rainfed cereal production systems) and the other was conducted at Gimenells (41°83′60″ N, 00°81′30″ E, 258 m, a region with most agriculture conducted under irrigation). The experiment at Agramunt was sown in a farmer's field, selected because of its low nitrogen fertility, with a soil classified as Typic xerorthtent; while experiment at Gimenells was sown in a more fertile soil, classified as Petrocalcic calcixerept.

Treatments in both experiments consisted in the factorial combination of (i) two species, bread wheat and two-rowed barley; (ii) two levels of inputs, "low" and "high", and (iii) four different source–sink ratios imposed during grain filling. Treatments were arranged in a split-plot design with three replicates. In each replicate there were four main plots (6 rows 0.20 m apart and 6 m long) assigned to the combinations of barley and wheat under high and low inputs, and the sub-plots (6 rows 1.5 m long) were the source–sink manipulations.

The genotypes selected for wheat (cv. Soissons) and barley (cv. Sunrise) were chosen carefully to be well adapted cultivars representing those commonly sown in the region, and also used as standard controls by the GENVCE (group for the evaluation of the new cereals varieties in Spain) (Cossani et al., 2009). Thus results may be regarded to be safely extrapolable to "average" modern well-adapted cultivars of each of these species in the region. The water regimes were either rainfed or with supplementary irrigation in low and high inputs levels, respectively; while nitrogen (N) availability was that available in the soil in the low inputs treatment or with the additional supply from N fertiliser at sowing in high input treatments (Table 1).

Treatments modifying the source–sink ratios consisted of a control, a treatment increasing the ratio, and two treatments decreasing the ratio (Fig. 1). In all cases, the treatments were imposed 7 days after flowering. The flowering time was determined in both species when pollen liberation occurred inside the spike (Waddington et al., 1983). To increase source–sink ratios, all spikes in the central 4 rows of the corresponding sub-plots were hand trimmed, removing all the spikelets from the upper half of the spikes of every single shoot (T_S), to have an homogeneous treatment comprising the whole canopy (Acreche and Slafer, 2009) rather than manipulating isolated spikes within unmanipulated canopy (Fig. 1b). The two treatments to reduce the source–sink ratio consisted in heavily shading the sub-plots through installing black meshes (covering the experimental unit decreasing incident radiation by 75%) of the whole canopy (producing a "total shading" of leaves and spikes; S_W) (Fig. 1c) or making holes in the upper surface of the mesh enclosure so that spikes were exposed to solar radiation while the rest of the crop canopy (leaves, sheaths, stem) remained shaded (leaf shading treatment, SL) (Fig. 1a and c). The three source–sink manipulation treatments were performed in the four environmental conditions (location × input level, which represented not only different conditions for grain filling but also different conditions of the crops at the time of imposition of treatments) and in both species; with the exception of the high-input treatment of barley growing at Agramunt, in which the shadings could not be installed (there were emergence failures in part of these main plots).

2.2. Measurements and analysis

The developmental stages of seedling emergence, jointing, booting, anthesis, and maturity were recorded when 50% of the plants in each plot reached them. Samples of 1 m of a central row of each sub-plot were taken at flowering and at maturity. In these samples above-ground biomass was determined after oven-drying the samples for 72 h at 60 °C. The samples were partitioned into the different organs (stems plus leaf sheaths, leaf lamina and spikes at flowering; and stems, leaves, chaff and grains at maturity) and counted the number of stems and fertile spikes at flowering and the number of spikes and grains at maturity. The yield and its components were also determined. The content of non-structural reserves was determined on stems (plus sheaths), by sequential extractions in ethanol and water followed by determination using the anthrone method (Galicia et al., 2009).

As the treatment T_S changed the normal distribution of grains (all spikelets of the upper half of the spikes were removed), in order to determine the effects of treatments on grain growth dynamics and on final grain weight, individual grains of the central spikelets