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Grain number and grain filling of two-row malting barley in response to variation in post-anthesis radiation: Analysis by grain position on the ear and its implications for yield improvement and quality

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ABSTRACT

Grain weight is reported to be a relatively well conserved characteristic across spring barley (*Hordeum vulgare* L.) crops that vary in grain number m^{-2}. Understanding the mechanisms that promote stability in grain weight is important to ensure that efforts to increase grain number beyond current high levels successfully increase yield without compromising grain quality. The aims of this study were to establish 1) whether post-anthesis grain abortion contributes to the stability of grain weight by helping match grain numbers to post-anthesis assimilate supply and 2) whether variations in post-anthesis assimilation per unit grain number affect the heterogeneity of grain weight. Field experiments were conducted in a high-yield potential environment for spring barley in 2011 and 2012. Crops were either shaded post anthesis (a 59% reduction in radiation incident on the crop) to reduce net carbon assimilation or grown unshaded. Grain growth was measured at different spikelet locations on the ear and on different shoots (main shoot and tillers) of the same plant. Shading crops from 14 days after anthesis until harvest maturity reduced yield by 19–20%, mean grain weight (MGW) by 12–16% and harvest index by 5–6%, but did not significantly affect grain number in either year. The magnitudes of these effects were considerably lower than the reduction in radiation imposed by shading suggesting some compensatory adjustment in radiation use efficiency or dry matter partitioning to grain after shading. The rate of grain filling was higher for grains in central spikelets than grains at distal or basal locations on the ear. Shading reduced the rate of grain filling to a similar extent (23–27%) at most locations evaluated on the ear, but had no effect on the duration of grain filling. In spite of the comparable effects of shading on grain growth across different spikelet positions and hierarchy of shoots, crops harvested after shading tended to have a more variable individual grain weight (larger interquartile range and coefficient of variation) than crops that were unshaded. The results show that post-anthesis grain abortion does not contribute to the stability of MGW in spring barley. Moreover, low levels of post-anthesis radiation in crops of large grain number m^{-2} (sink capacity) can increase heterogeneity of grain weight, which may have negative consequences for grain quality.

1. Introduction

Understanding the relationships between grain number formation, grain development and grain filling is fundamental to our efforts to increase cereal yields through plant breeding and improved crop management. Grain yield of barley, as with other cereals, is the product of two components, the number of grains produced per unit ground area and the mean grain weight (MGW; Gallagher et al., 1975). While grain number in barley varies widely with location and season and typically accounts for the majority of the variation in yield across environments (Gallagher et al., 1975; Baethgen et al., 1995; Abeledo et al., 2003; del Moral et al., 2003; Bingham et al., 2007; Peltonen-Sainio et al., 2007; Serrago et al., 2013; Kennedy et al., 2017), grain weight tends to be less variable and is poorly correlated with yield (Gallagher et al., 1975; Bulman et al., 1993; Baethgen et al., 1995; Abeledo et al., 2003; Sadras and Slafer, 2012). The smaller variability in MGW may be a consequence of evolutionary and/or breeding selection for increased grain size, as larger seed with larger embryos and storage reserves have a greater chance of producing seedlings that establish successfully, are able to compete with neighbouring plants and tolerate damage from herbivores (Sadras, 2007). At present, the physiological mechanisms that underlie this apparent conservation of MGW are not

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fully understood, especially in the context of the large variations in grain number. A relatively stable MGW implies that the number of grains set is in some way matched to the potential of the crop to supply assimilates for grain filling (i.e. the sink capacity is set lower than the source capacity or that the sink and source capacities are maintained in relatively close balance) and that only in circumstances where post-anthesis assimilation is reduced significantly, for example by drought or disease, will grains fail to fill adequately.

There are several possible mechanisms through which this might be achieved. Firstly, grain numbers and grain storage capacity (potential grain size) may be determined concomitantly prior to fertilization according to some common measure of overall assimilate availability (Sinclair and Jamieson, 2006; Sadras and Denison, 2009; Slafer et al., 2014). In this way an upper limit may be set on grain size and the numbers of grains adjusted in concert. There is ample evidence to suggest that the number of tillers and florets that survive to produce ears and grains respectively is regulated by assimilate availability or organ and crop growth rate during late stem extension (Gallagher et al., 1976; Hay and Kirby, 1991; Prystupa et al., 2004; Slafer et al., 2009; Sadras and Slafer, 2012). Similarly, potential grain size has been correlated with carpel size at anthesis which, in turn, is sensitive to treatments that vary carbon assimilation and crop growth prior to ear emergence (Calderini et al., 2001, 2006).

Secondly, the same outcome (a relatively conserved MGW) might be achieved if there was some mechanism for reducing the number of grains after anthesis if conditions during grain development and filling restrict the assimilation capacity. Adjustments in the grain number of barley and other small grain crops have been observed in studies evaluating post-anthesis treatments such as shading, temperature modification, and drought (Habgood and Uddin, 1983; Nicolas et al., 1985; Grashoff and d'Antuono, 1997; Zinselmeier et al., 1999; Boyer and Westgate, 2004; Boyer and McLaughlin, 2007; Estrada-Campuzano et al., 2008; Sanchez-Bragado et al., 2016). In many cases the mechanisms responsible for these losses have not been elucidated, although grain abortion has been reported for several species (Zinselmeier et al., 1999; Estrada-Campuzano et al., 2008). In maize, the abortion of grains induced by crop water stress can be prevented by the exogenous supply of sugars, suggesting that a limited carbohydrate supply may be responsible for the abortion (Zinselmeier et al., 1999). Not only are grain numbers sensitive to reductions in assimilation, but the growth of surviving grains can also be affected differentially depending on their location on the ear. In wheat grain growth was reduced by post-anthesis shading to a smaller extent in florets located closest to the base of the rachilla compared to those further away, thereby increasing the variation in individual grain weight (Bremner and Rawson, 1978). Similarly grains in florets closest to the rachilla were least sensitive to increases in assimilate availability induced by partial degraining (Xie et al., 2015). Comparable data on the response of grains at different positions on barley ears are lacking.

The mechanisms by which grain numbers are matched to the potential supply of assimilate during grain filling and the way in which assimilate is allocated between grains, both within and between ears, has implications for how plant breeding might increase yield without compromising grain quality. Currently yield of barley is generally considered to be sink limited (Bingham et al., 2007; Kennedy et al., 2017). A route to increase the yield of sink limited crops is, therefore, to increase grain numbers (Pedro et al., 2012; Reynolds et al., 2012; Miralles et al., 2000; Gonzalez et al., 2003). However, if the sink capacity is expanded so that source and sink are brought into closer balance at the start of grain filling, the crop may be at greater risk of source limitation should environmental conditions subsequently deteriorate. Significant grain abortion in the face of increased source limitation could help maintain grain quality, but restrict yield improvement. Alternatively, if post-anthesis grain abortion is not an important mechanism in barley, the result of increased source limitation might be a reduction in grain quality associated with lower mean grain weight and possibly greater heterogeneity of individual grain weight. In spring barley heterogeneity of grain weight is undesirable for maltsters, because variable grain are more difficult to process (Passarella et al., 2003).

Questions about the regulation of grain numbers in response to post-anthesis assimilation and its potential consequences for yield and quality are best answered thorough a detailed analysis of grain formation and growth at specific spikelet positions on the ear as this provides a greater resolution than standard yield component analysis. The aim of the research reported here was to investigate the effects of varying post-anthesis assimilation, through shading, on grain growth of spring barley at discrete positions on ears of main shoots and primary tillers. The specific objectives were to 1) establish whether there is any evidence of grain abortion in response to a reduction in post-anthesis incident radiation and hence assimilation and 2) determine the effects of variations in radiation per unit grain number on heterogeneity of grain weight.

2. Materials and methods

2.1. Site characteristics and experimental design

Field experiments were conducted on spring barley (*Hordeum vulgare* L., cv Quench) at Teagasc, Oak Park, Carlow, Ireland in 2011 and 2012. Quench is a two-row malting variety selected because of its popularity amongst growers at the time of the study. Its yield and grain quality characteristics were representative of other recommended varieties. In each year the fields were sheltered, relatively flat and located 52° 51′ N, 6° 54′ W at an altitude of 57 m. The top soil texture (determined by hand texture analysis) was loam (USDA, Rowell, 1994) with a moderate moisture holding capacity. The site was characterised by continuous arable production and the experiments occupied a position in the rotation that is standard practice for commercial spring barley production in the region. In 2011 the previous crop was winter barley and in 2012 it was winter wheat.

Crops were sown on 10th March 2011 and 14th March 2012 at a seed rate of 330 viable seeds m^{-2}. Shading and unshaded control treatments were allocated at random to plots to give a randomised block design with six replicates in 2011 and four replicates in 2012. Plot size in 2011 was 6 m^2 (2 m wide × 3 m long) with 2 m wide discard plots between shaded and control plots to avoid overshadowing. Shading treatments were applied to entire plots in 2011. Plot size in 2012 was 96 m^2 (4 m wide × 24 m long) and shades were erected over sub-plots of 2 × 3 m; here the shades were located alongside discard areas *within* plots to avoid overshadowing. Shaded and unshaded plots were further sub-divided into two sampling areas; one for destructive sampling of ears for grain growth assessment during the treatment period and one for final grain number, biomass and yield determination at harvest. These are referred to as the frequent and final sampling areas respectively.

2.2. General husbandry and imposition of shading

Crops were managed for high yield potential with the aim of keeping the crop well supplied with mineral nutrients and free of pests and disease. Nitrogen applications of 132 (2011) and 154 kg N ha^{-1} (2012) were split (50:50) between early post-emergence when tramlines became visible and during tillering. Maintenance applications of P and K were made after sowing based on soil chemical analysis. Fungicides were applied shortly before stem extension and at ear emergence. Applications of aphicide and herbicide were as required.

Shading treatments were imposed 14 days after Zadoks growth stage (GS) 55 (50% ear emergence; Tottman and Broad, 1987). As anthesis in spring barley tends to occur before the ear is fully emerged this timing also corresponded to approximately 14 days after anthesis (GS 61). The timing of shading was selected to avoid potential interference