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Post-anthesis warm nights reduce grain weight in field-grown wheat and barley

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ABSTRACT

Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) crops are exposed to warm nights during their growing seasons and this trend is unlikely to change. The aim of this work was to evaluate the effect of higher post-anthesis night temperatures on field-grown crop yield, focusing on final grain weight determination. Experiments combined: (i) two well-adapted crops with similar phenology: bread wheat and two-row malting barley, under (ii) two temperature regimes: ambient and high night temperatures from 10 days after anthesis to physiological maturity during (iii) two contrasting growing seasons in terms of radiation and temperature: late sowing in 2011 and early sowing in 2013. The night temperature increase (ca. 4.1 °C) was achieved using purpose-built heating chambers placed on the crop at 7 pm and removed at 7 am every day during the heating period. Across growing seasons and crops, the average minimum temperature during that period ranged from 14.3 °C to 21.9 °C. Thousand grain weight was reduced by ca. 3% per °C of night temperature increase, similarly for wheat and barley, causing a grain yield reduction of ca. 4% per °C. An accelerated development under high night temperatures led to a shorter effective grain filling period, reducing the final grain weight. The lack of consistent impact on source availability between crops and seasons, measured as senescence and stem water soluble carbohydrates, as well as a similar impact in magnitude and direction on individual grain weight for different grain positions along wheat or barley spikes, suggest that the negative effects of warm nights on grain weight were directly related to processes within the grain itself.

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1. Introduction

Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) crops are exposed to warm nights during their growing seasons and this trend is unlikely to change. These crops are highly relevant as source of calories for human and animal feed (FAO, 2015a), thus, adaptation strategies need to be designed to maintain and increase cereal production under future climate scenarios (Howden et al., 2007). Temperature is the most affected and predictable variable under climate change scenarios (IPCC, 2014) and rising minimum temperatures are projected to continue (Alexander et al., 2006; Sillmann et al., 2013a; Sillmann et al., 2013b). Empirical regressions between observed or simulated crop yield (mainly wheat) and historical temperature data have shown that temperate cereals grain yield is strongly correlated to minimum temperature (Lobell and Ortiz-Monasterio, 2007; Magrin et al., 2009; Peltonen-Sainio et al., 2010). Although variations across cropping regions exist, the trend is that the higher the minimum temperatures are, the lower the grain yield is. In general, the lower the latitude, the higher the grain yield losses due to night temperature increase. Understanding and quantifying the response of main crop processes to growing environments is, therefore, required to design management and breeding adaptation strategies (Fischer et al., 2014).

Wheat and barley grain yield is largely determined by grain number and potential grain weight establishment around flowering, which has been defined as the critical period for yield determination in both species (Fischer, 1985; Calderini et al.,

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Abbreviations: PAR, photosynthetic active radiation; GW, grain weight; GFR, grain filling rate; GFD, grain filling duration; EGFP, effective grain filling period; $_{\mathrm{midday}}F_{\mathrm{PAR}}$, fraction of solar radiation intercepted by the crop at midday; F_{PAR}, daily fraction of solar radiation intercepted by the crop.

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1999a; Bingham et al., 2007; Arisnabarreta and Miralles, 2008). In fact, a recent study showed the impact of higher night temperatures during that critical period. A 7% grain yield loss per °C was reported both in spring wheat and barley as a consequence of an accelerated development that shortened the period duration, reducing resource capture with negative consequences for biomass production and grain number setting (García et al., 2015). Although grain number is the main yield component, variations in grain weight are quantitatively important (Borrás et al., 2004; Slafer et al., 2014). Final grain weight is defined by potential grain weight (sink) and the availability of assimilates per grain (source) during the grain filling period (Fischer, 1984). Assimilates supply and contributions from reserves (non-structural carbohydrates previously stored in stems) are frequently reported to be enough to deal with sink demand during grain filling (Borrás et al., 2004; Dreccer et al., 2009; Serrago et al., 2013). However, frequent adverse conditions such as biotic constraints (Bingham et al., 2009; Serrago et al., 2011) or higher temperatures (Slafer and Miralles, 1992; Savin et al., 1997) can modify source-sink ratio generating a source limitation that reduces the final grain weight (Fischer and Maurer, 1976; Serrago and Miralles, 2014) and, in turn, temperate cereals grain yield (Chowdhury and Wardlaw, 1978; Wardlaw et al., 1980). Industry penalties due to the down-grade of commercial quality (Rattey et al., 2009) or poor seedling establishment in stressed environments (Grieve and Francois, 1992) can also be linked with smaller grains.

Grain weight is generally analysed and modelled in terms of two temperature dependent traits: grain filling rate and grain filling duration (Wardlaw and Wrigley, 1994; Egli, 2006). Mean temperatures ranging between 15 and 18 °C are considered as optimum for maximum grain weight (Chowdhury and Wardlaw, 1978; Calderini et al., 1999b). When temperatures rise above that range, temperate cereals response during grain filling is commonly divided in two ranges: (i) moderately high temperatures, i.e. mean temperature between 15 and 25–30 °C with maximum temperatures up to 32 °C, and (ii) very high temperatures, often referred to as “heat shock”, i.e. maximum daily temperature ranging from 35 to 40 °C for at least a few days (Wardlaw and Wrigley, 1994; Stone et al., 1995; Savin et al., 1997). Taking into account current and projected warming scenarios for temperate cereals (Alexander et al., 2006; Sillmann et al., 2013a; Sillmann et al., 2013b), night temperature increases are expected to vary in the first of these ranges. The crop response to this temperature range is largely characterized by changes in rate and duration of existing processes. As temperature gets warmer, final grain weight is reduced as a consequence of the grain filling duration shortening which is not completely compensated by the increase in grain filling rate (Tashiro and Wardlaw, 1989).

Temperature affects grain filling duration directly through its universal impact on developmental rate, while grain filling rate can be affected both directly and indirectly as a consequence of temperature impact on assimilate availability (Wardlaw et al., 1980; Egli, 2006). The contribution of reserves to the final grain weight is higher when crop photosynthesis, the main source of assimilates for grain filling, is limited (Blum, 1998; Asseng and van Herwaarden, 2003). Accelerated crop senescence due to higher temperatures is frequently reported as the cause of an elevated stem reserves remobilization (Blum et al., 1994). Higher dark respiration rates is also suggested as a process contributing to yield loss when asymmetric warming (minimum temperature increase is higher than that of maximum temperature) is considered (Grant et al., 2011). At this point, it is important to highlight that processes’ response observed at the organ or, for some traits, plant level, such as leaf gas exchange rate, have been shown to differ when scaled up at canopy level (Sadras and Richards, 2014; Peraudeau et al., 2015), emphasizing the relevance of field studies. Experiments under controlled conditions are useful in understanding the detailed responses of plants to specific environmental factors; however they can differ considerably from field conditions and cannot be simply extrapolated to interpret grain yield variations observed in the field (Savin et al., 1996).

Despite their strategic relevance, surprisingly little or no information is available for field experiments regarding the comparative response of wheat and barley to warm nights during the grain filling period. Therefore, this work aimed to evaluate the effect of higher post-anthesis night temperatures on grain yield in well-adapted wheat and barley cultivars grown under field conditions, focusing on final grain weight determination.

2. Materials and methods

2.1. Experiments, environments and crop management

Commercial cultivars of a bread wheat (‘Baguette 13 Premiumí) and a two-row malting barley (‘Scarlettí) were evaluated in the field under two night temperature regimes during the grain filling period: ambient (i.e. unheated crops) and high night temperatures (i.e. heated crops) in two contrasting environments (given by year and sowing date). Throughout the manuscript the combination of year and sowing date is referred to as “growing season”. Cultivars were chosen because of their similar phenology (particularly flowering date), high yield potential, and wide adoption by farmers in the Rolling Pampas, one of the most productive areas in Argentina (Hall et al., 1992; Andrade et al., 2015). Experiments were carried out at Facultad de Agronomía, Universidad de Buenos Aires, Argentina (34°35′S, 58°29′W, 26 masl) on a silty clay loam soil, classified as Vertic Argiudoll, with 3.8% of organic matter content and pH 6.7. The two growing seasons consisted of a late sowing (August 6th) in 2011, and an early sowing (June 6th) in 2013. Sowing rates were adjusted accordingly to the sowing dates, ca. 400 and 300 plants m^{-2} in 2011 and 2013, respectively. Plots were 4 m long and 1.25 m wide (7 rows 0.175 m apart). Crops were managed without water, nutritional or biotic constraints. They were drip irrigated to supplement natural rainfall during the growing season (water availability of the uppermost 1 m of soil was kept near field capacity). Based on soil sampling up to 0.2 m and 0.6 m depth a week before sowing, triple superphosphate was applied at sowing aiming at more than 20 ppm of available P and urea was applied at tillering to reach a soil N availability of 180 kg N ha^{-1}, respectively. Plant pathogens, pests and weeds were prevented or controlled with recommended chemical treatments.

Each experiment was arranged in a randomized split plot design with 3 replicates; crops were main plots and night temperature regimes sub-plots. The night temperature increase was achieved using purpose-built heating chambers placed on the crop at 7 pm and removed at 7 am every day during the treatment period. The timing was chosen as minimum temperature largely occurs before 7 am during the period of interest. The heating treatment was applied from 10 days after anthesis (DC65 + 10d, Zadoks et al., 1974) to physiological maturity (DC95, Zadoks et al., 1974) in order to modify night temperature after the lag phase (period when endosperm cells division takes place), avoiding some impact on grain set and potential grain weight determination (Serrago et al., 2013). A detailed description of the portable chambers used to increase night temperature can be found in García et al. (2015). Briefly, chambers consisted of an iron frame (3 m length, 1.3 m width and 1.3 m height) covered with a transparent polyethylene (200 μm thickness) and equipped with two portable electric fan heaters connected to two temperature sensors and monitored by an automated control unit (Cavadevices, Buenos Aires, Argentina). The system was programmed to increase temperature by 4 °C inside

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