



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

Abbreviations: PAR, photosynthetic active radiation; GW, grain weight; GFR, grain filling rate; GFD, grain filling duration; EGFP, effective grain filling period; $\text{midday}F_{\text{PAR}}$, 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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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.,

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 (Rathey 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 Premium') and a two-row malting barley ('Scarletti') 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 seasons (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

(i.e. high night temperature) with respect to outside (i.e. ambient night temperature).

2.2. Measurements and analysis

Crop phenology was evaluated every 2–3 days, using the decimal code of Zadoks et al. (1974). Dates of emergence (DC11), defined when 50% of the plants in the plots reached that stage, and anthesis (DC65), defined as 50% of the spike population with anthers extruded, were recorded. In barley, as anthesis normally occurs before heading, 20 or more spikes were manually examined after flag leaf appearance (opening the flag leaf sheath) and DC65 was reached when 50% of the spikes had anthers extruded. Physiological maturity (DC90) was determined by monitoring grain dry matter accumulation in specific grains at set positions in the spike (see below).

Two spikes of the first cohort shoots (main stems and first tillers) were sampled from each plot twice a week from 10 days after DC65 onwards. Grains of apical, central and basal spikelet positions in the spike were removed, oven dried (60 °C, 72 h) and weighed every time. In wheat, as each spikelet can have more than one grain, only the two more proximal grains to the rachis (i.e. the first and second one) were considered in apical, central and basal spikelets. In central spikelets, the third grain (called distal) was also considered separately. The dynamics of grain growth at different spikelet positions were characterised by fitting the data to the following bilinear model:

$$GW = a + bx \text{ if } (x \leq c) \text{ and } \quad (1)$$

$$GW = a + bc \text{ if } (x > c)$$

The model considers grain weight (GW, mg) in relation to days from DC65 (x) as a bilinear relationship, with a plateau after parameter c is reached. Parameter b is the grain filling rate (GFR, mg d^{-1}) and c indicates the time when DC90 stage is reached (i.e. the time when grain weight stops growing). Thus, the period between DC65 and DC90 corresponds to the grain filling duration (GFD, d). As during the lag phase, there is no important increase in grain weight (Egli, 2006), the effective grain filling period (EGFP, d) was calculated as:

$$EGFP = GFD - (a/GFR) \quad (2)$$

DC90 at crop level was determined following the bilinear model (Eq. (1)). Each input point corresponded to the average of all different grain positions. Time (d) from DC11 to 10 days after DC65, from 10 days after DC65 to DC90 and the whole cycle duration (i.e. DC11 to DC90) were calculated. The duration of post-anthesis phases was also calculated in thermal time units (°Cd) using daily mean temperature (natural or including the night heating) and assuming a base temperature of 8.2 °C for wheat (Slafer and Savin, 1991) and 7.5 °C for barley (Gualano and Benez-Arnold, 2009).

Daily temperature and global solar radiation were recorded at the experimental field (Vantage Pro 2, Davis Instruments Co. Inc.; San Francisco, USA), and 50% of this incident solar radiation was considered incident photosynthetic active radiation (PAR) (Sinclair and Muchow, 1999). In order to determine the fraction of solar radiation intercepted by the crop before night heating period beginning (i.e. 10 days after DC65), this trait was measured every two or three days during the two weeks after DC65 with a linear ceptometer (BAR-RAD 100, Cavadevices.com, Buenos Aires, Argentina) on clear days between 12 and 14 h. Incident radiation with the ceptometer placed immediately above the canopy and transmitted radiation with this device placed at the base of the crop (crossing central rows at 45°) were recorded in each plot. From these measurements, the fraction of solar radiation intercepted by the crop at

midday (${}_{\text{midday}}F_{\text{PAR}}$) was calculated as the ratio between the difference of incident and transmitted radiation to incident radiation, and the daily fraction of solar radiation intercepted by the crop (F_{PAR}) was estimated according to the methodology (Eq. (3)) proposed by Charles-Edwards and Lawn (1984). The F_{PAR} 10 days after DC65 was obtained by interpolation between measurements around the treatment beginning date when they did not exactly coincided with that crop stage.

$$F_{\text{PAR}} = 2 * {}_{\text{midday}}F_{\text{PAR}} / (1 + {}_{\text{midday}}F_{\text{PAR}}) \quad (3)$$

Quadrat harvests for biomass (0.5 m of the 5 central rows, i.e. 0.44 m²) were carried out 10 days after DC65 and one week after the DC90 stage. A representative sub-sample of ca. 20% fresh weight was separated into spikes, which were counted to determine spike number per m², stem (including sheaths), and green and/or yellow leaf blades. These sub-samples and the rest of the sample were oven dried (60 °C, 72 h) and weighed. Leaf area index was calculated 10 days after DC65 from area measurements in the sampled leaf blades, prior to oven drying, using an optical leaf area meter (LI-3100C Area Meter, LI-COR Inc., USA). Water soluble carbohydrates content was determined on stems (including sheaths) in each sub-sample taken (i.e. 10 days after DC65 and ca. one week after DC90), after oven dried (60 °C, 72 h), by sequential extractions in ethanol and water followed by determination using the anthrone method of Yemm and Willis (1954).

In 2013, the change of percentage green area, individually for the three uppermost leaves, and water soluble carbohydrates concentration in stems (including sheaths) were measured on the first cohort shoots sampled for grain weight dynamics (see above). Therefore, shoots sampled (twice a week from 10 days after DC65 onwards) were separated in spike (for grain weight determination), stem with sheaths (for reserves determination) and leaf blades (for green area analysis). Sampled leaf blades containing at least a minimal portion of green tissue were grouped according to their canopy leaf layer position (i.e. flag leaf and two positions down), pasted on white paper sheets, digitalized with a scanner at 300 dpi and then the total and green leaf area were determined with Assess (Lamari, 2002), an image analysis software (Serrago et al., 2009).

At commercial maturity (ca. two weeks after DC90 stage), 1 m of the 5 central rows (i.e. 0.88 m²) was cut in each plot and threshed in a stationary thresher. Grain yield per unit area (corrected to 0% of moisture content) and grain weight (through a sub-samples of 200 oven dried grains) were determined from this sample. Grain number per m² was calculated as the quotient between grain yield and grain weight, and the grain number per spike as the quotient between grain number per m² and spike number per m².

Statistical analyses were carried out with InfoStat (Di Rienzo et al., 2010). All data were analyzed by ANOVA to evaluate the main effects of growing season, crop, night temperature regime and their interactions. A Tukey test was used to detect significant differences between means. Relationships between traits and their response to temperature were analyzed by linear regressions, Model II, to estimate intercepts and slopes with the lmodel2 procedure in R (Legendre, 2013). In order to compare crops (avoiding innate differences between wheat and barley) or grains from different positions in the spike (which have differences in potential grain weight; Miralles and Slafer, 1995), each trait value was calculated as a value relative to the average of each crop across all environments (i.e. ambient and higher night temperature during 2011 and 2013 growing seasons). After that, slope test was used to compare trait or crop responses to temperature.

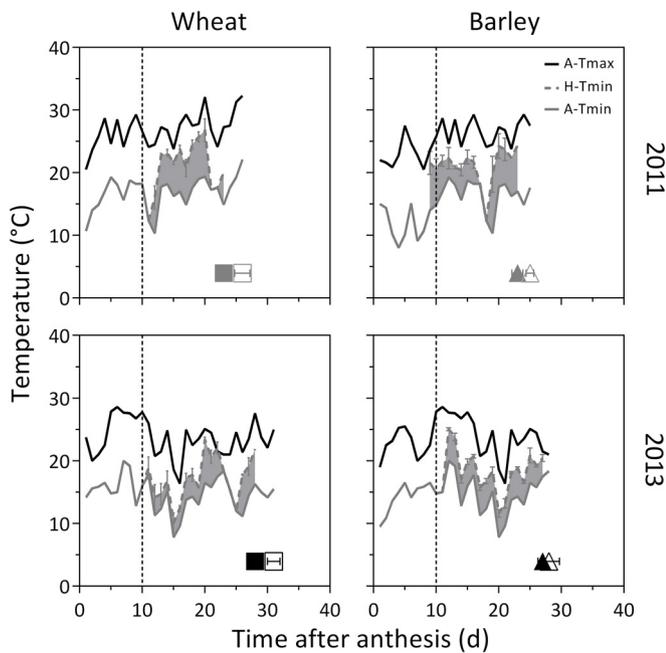


Fig. 1. Dynamics of daily ambient minimum (A-Tmin) and maximum (A-Tmax) temperatures, and high (H-Tmin) minimum temperature during post-anthesis for wheat (left panel) and barley (right panel) crops during 2011 (late sowing date, top panel) and 2013 (early sowing date, bottom panel) growing seasons. H-Tmin was calculated as A-Tmin plus the night temperature increase reached each treatment day. Vertical dashed lines indicate the beginning of night heating period, i.e. 10 days after anthesis (DC65 + 10d; Zadoks et al., 1974). Physiological maturity (DC90; Zadoks et al., 1974) is indicated in heated (close symbols) and unheated (open symbols) wheat (squares) and barley (triangles) crops (average of 3 replications and its standard error) during 2011 (grey symbols) and 2013 (black symbols) growing seasons.

3. Results

3.1. Environmental and growing conditions before and during heating treatments

The main crop characteristics at the time of imposing the night heating (i.e. 10 days after DC65), as well as environmental conditions prior to the treatment period (i.e. from DC11 to 10 days after DC65) were described in Table 1. Detailed information of ambient conditions during experiments can be found in García et al. (2015). Briefly, wheat and barley crops were exposed to different photothermal environments between years largely due to the contrasting sowing dates, characterized by higher incident solar radiation and mean temperature leading to a shorter time between DC11 and 10 days after DC65 in 2011 compared to 2013. In both growing seasons, barley had a shorter cycle than wheat, but the difference was 5 days or less. Biomass accumulated before the night heating period was significantly higher in barley than wheat in 2011 (ca. 19%), but similar in 2013. At 10 days after DC65, barley had significantly more fertile spikes per m² (ca. 129 and 88% in 2011 and 2013, respectively), leaf area index (ca. 57 and 7% in 2011 and 2013, respectively) and spike dry weight per m² (ca. 17% in both growing seasons) than wheat (Table 1). Differences in leaf area index were not completely reflected in the fraction of PAR intercepted by the crops at 10 days after DC65. At this stage, barley tended to intercept more PAR than wheat (ca. 5%) in 2011, but both crops showed values of PAR interception of at least 90% in the two growing seasons (Table 1).

Ambient post-anthesis mean temperatures were in the 13–27 °C range (Fig. 1). Daily maximum temperature only reached 32 °C twice at the end of 2011 growing season when only wheat had not reached DC90. As a consequence of barley flowering earlier

(Table 1), ambient post-anthesis temperatures tended to be slightly higher in wheat, particularly in 2011 (ca. 2 °C on average). The daily post-anthesis night heating treatment was described as the average increase over the minimum temperature (Fig. 1). Night temperature increase was similar between crops ($p=0.61$), but different between growing seasons ($p=0.01$). The heating treatment increased night air temperature by 4.9 ± 0.2 °C in 2011 and 3.4 ± 0.3 °C in 2013. As a consequence of the night heating mainly, but also from growing season and slight phenology differences, average minimum temperature during the night heating period (i.e. from 10 days after DC65 to DC90) ranged from 14.3 ± 0.1 °C (unheated wheat in 2013) to 21.9 ± 0.1 °C (heated wheat in 2011), while the average mean temperature during that period ranged from 18.6 ± 0.1 °C to 24.7 ± 0.2 °C. On the other hand, the average maximum temperature during the treatment period was affected only by growing season and slight phenology differences, ranging from 22.8 ± 0.1 °C to 27.5 ± 0.3 °C.

3.2. Response of grain yield and grain weight to post-anthesis warm nights

Night heating from 10 days after DC65 significantly reduced ($p < 0.01$) wheat and barley grain yield, thousand grain weight and the effective grain filling period, with no effect on grain number per m², its components (spike number per m² and grain number per spike) or grain filling rate (Table 2). There were no interactions between night temperature regime and growing seasons or crops (Table 2). Under ambient night temperature, barley out-yielded wheat in both growing seasons due to more and heavier grains (Table 2). Those crop differences in thousand grain weight were not associated with intrinsic differences in the effective grain filling period or the grain filling rate, although barley tended to have a higher filling rate for a shorter duration mainly in 2013. As the lag phase was not affected by night temperature regime ($p=0.91$), differences in the effective grain filling period were reflected in the time to DC90 (Fig. 1). The lag phase was similar between crops ($p=0.55$) and longer in 2013 than 2011 (7 and 6 days, respectively, $p=0.02$). Grain filling rate was not affected by the night temperature regime (Table 2).

Thousand grain weight was reduced ca. 3% per °C of night temperature increase from 10 days after DC65 to DC90, similarly for wheat and barley (Fig. 2a). This was consistent with a reduction of ca. 4% per °C in the effective grain filling period, while no significant effects were observed on the grain filling rate (Fig. 2b,c). In fact, thousand grain weight and the effective grain filling period had similar temperature response ($p=0.32$). In line with the grain weight reduction, grain yield was decreased ca. 4% per °C of night temperature increase (inset Fig. 2a). A small grain number reduction, mainly in wheat (ca. 1% per °C, data not shown), possibly associated to lower grain set in younger spikes cohorts (Table 2) can explain why grain yield decrease per °C increase was slightly higher than grain weight. However both traits (grain yield and grain weight) showed similar response to warm nights ($p=0.07$). Variations in grain yield were indeed linearly associated to thousand grain weight changes ($r^2 > 0.95$, $p < 0.01$ both for wheat and barley). In line with crop differences in the best environment (i.e. ambient night temperature during 2013, Table 2), the effect of higher night temperature on thousand grain weight tended to be higher in barley than wheat in absolute terms (ca. 1.3 vs. 0.8 mg of reduction per °C in barley and wheat, respectively), while that of the effective grain filling period had the opposite trend (ca. 0.6 and 1 d of shortening per °C in barley and wheat, respectively).

The effect of post-anthesis higher night temperature on individual grain weight of different positions along wheat and barley spikes (Fig. 3) was similar to the observed by thousand grain weight (Fig. 2a). As the spike structure is different, comparisons between

Table 1
Growing conditions, phenology and climate, from emergence to 10 days after anthesis (i.e. from DC11 to DC65 + 10d; Zadoks et al., 1974), and wheat and barley performance before night heating period beginning (i.e. DC65 + 10d). Summary ANOVA (bottom of the table) shows significance levels for main effects, growing season (GS) and crop (C), and their interaction. Detailed information of ambient conditions during experiments can be found in García et al. (2015).

GS	C	Emergence – 10 days after anthesis			10 days after anthesis				
		Time (d)	Mean temperature (°C)	Incident PAR (MJ m ⁻² d ⁻¹)	Biomass (g m ⁻²)	Spike number (spikes m ⁻²)	Leaf area index	PAR intercepted	Spike dry weight (g m ⁻²)
2011	Wheat	83	16.2	8.3	971	488	2.4	0.90	227
	Barley	80	15.5	8.0	1153	1120	3.8	0.96	267
2013	Wheat	125	13.5	5.7	1115	521	3.2	0.96	248
	Barley	120	13.2	5.6	1054	982	3.4	0.97	290
ANOVA	**	**	**	**	ns	ns	ns	*	ns
	C	**	**	**	ns	**	**	**	*
	GS*C	ns	**	**	**	*	*	ns	ns

ANOVA results: **: $p < 0.01$, *: $p < 0.05$, ns: not significant ($p > 0.05$). PAR: photosynthetic active radiation; LAI: leaf area index.

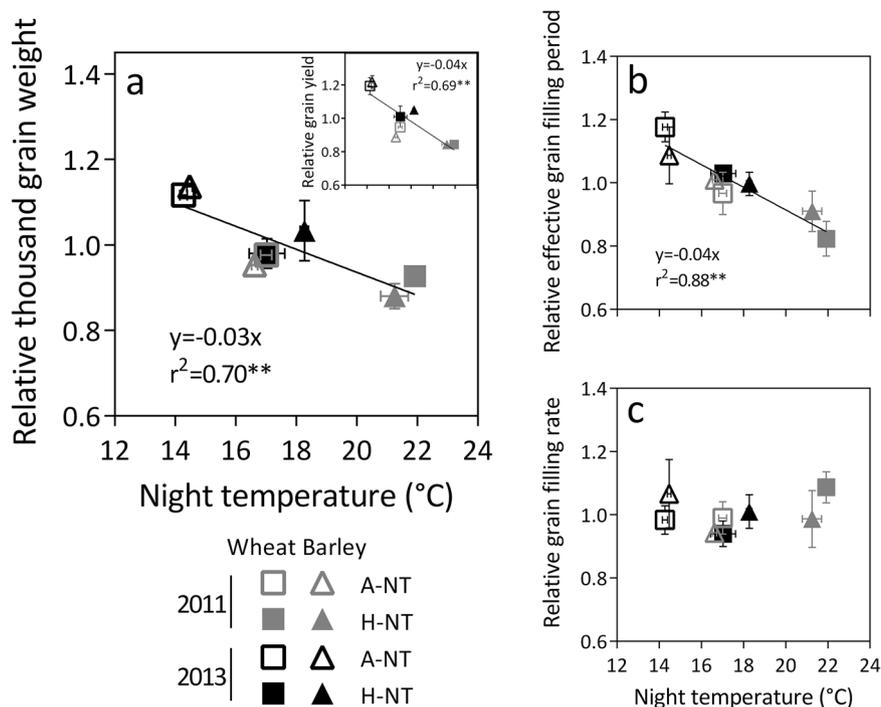


Fig. 2. (a) Thousand grain weight, (b) effective grain filling period and (c) grain filling rate responses to average night temperature from 10 days after anthesis to physiological maturity (i.e. from DC65 + 10d to DC90; Zadoks et al., 1974). Grain yield response to night temperature is also included (inset in a). In order to make crops comparison possible, each trait value was calculated as a value relative to the average of each crop across all environments. Each point (average of 3 replications and its standard error) corresponds to wheat (squares) and barley (triangles) crops under different night temperature regime, i.e. ambient (A-NT, open symbols) and high (H-NT, close symbols) night temperatures, during 2011 (grey symbols) and 2013 (black symbols) growing seasons. Trait sensitivity (i.e. slope), regression coefficient (model II) and probability (**: $p < 0.01$, *: $p < 0.05$, ns: not significant) are indicated. In all cases wheat and barley did not show responses significantly different, therefore a common regression was used for both crops.

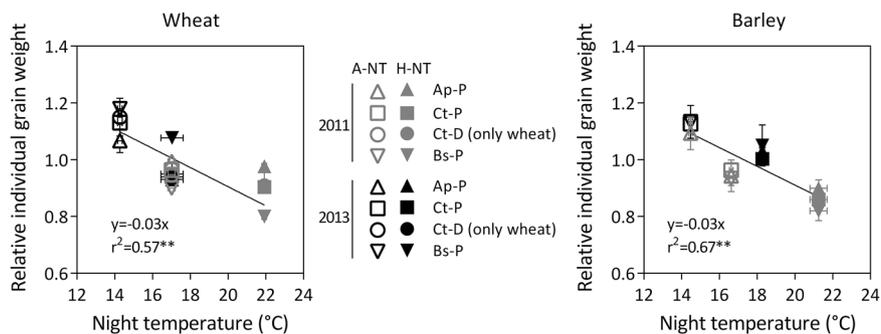


Fig. 3. Individual grain weight from different positions along wheat (left) and barley (right) spikes responses to average night temperature from 10 days after anthesis to physiological maturity (i.e. from DC65 + 10d to DC90; Zadoks et al., 1974). In order to make comparison from different spike position possible, each grain weight value was calculated as a value relative to the average of each crop across all environments. Each point (average of 3 replications and its standard error) corresponds to proximal grains of apical (Ap-P, triangles), central (Ct-P, squares) or basal (Bs-P, inverted triangles) spikelets, or (only in wheat) distal grains of central spikelets (Ct-D, circles), in crops under different night temperature regime, i.e. ambient (A-NT, open symbols) and high (H-NT, close symbols) night temperatures, during 2011 (grey symbols) and 2013 (black symbols) growing seasons. Individual grain weight sensitivity (i.e. slope), regression coefficient (model II) and probability (**: $p < 0.01$, *: $p < 0.05$, ns: not significant) are indicated. In both crops, grains of different spike positions did not show responses significantly different, therefore a common regression was used for all grain positions. Wheat Ap-P grains were excluded of the analysis as they did not have a significant response to night temperature increase.

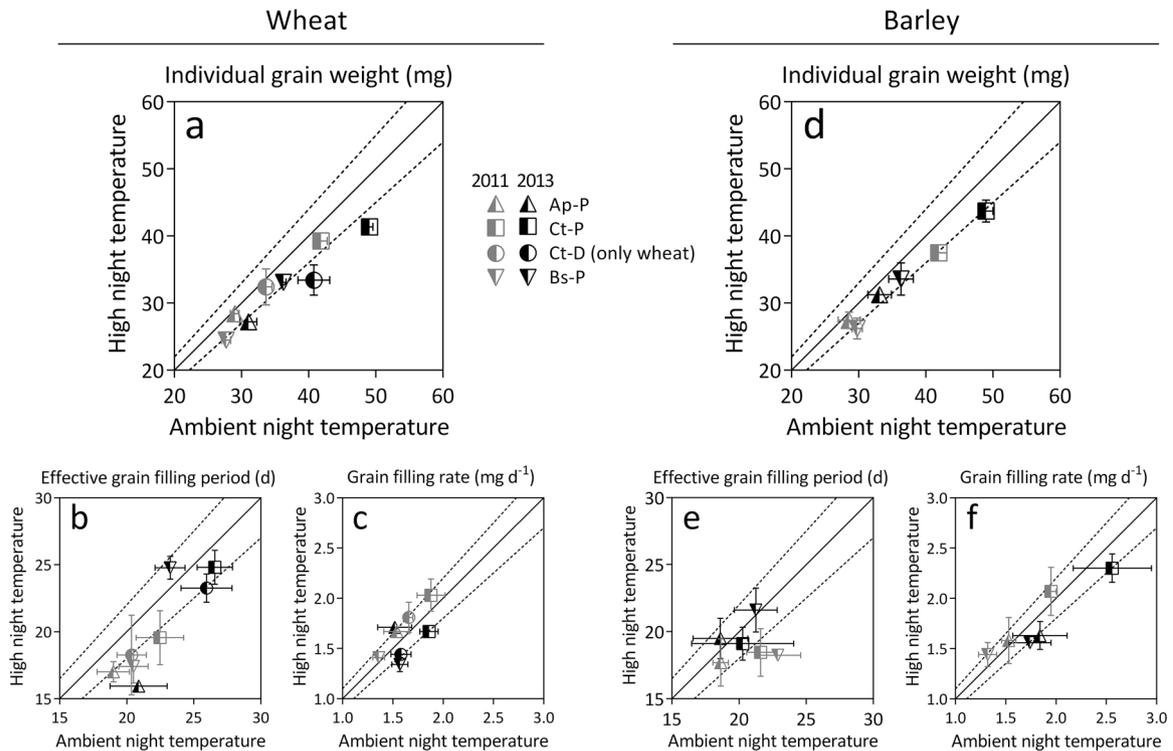


Fig. 4. Contrast between crops under different night temperature regime from 10 days after anthesis to physiological maturity (i.e. from DC65 + 10d to DC90; Zadoks et al., 1974), i.e. ambient and high night temperatures, in terms of (a,d) individual grain weight and its main determinants, (b,e) effective grain filling period and (c,f) grain filling rate, for different grain positions along the spike. Each point (average of 3 replications and its standard error) corresponds to proximal grains of apical (Ap-P, triangles), central (Ct-P, squares) or basal (Bs-P, inverted triangles) distal grains of central spikelets (Ct-D, circles), in wheat (a–c) and barley (d–f) crops during 2011 (grey symbols) and 2013 (black symbols) growing seasons. 1:1 relationship (continuous line) and a variation of $\pm 10\%$ (dashed lines) are indicated in each sub-figure.

crops for a particular grain position are not possible. In wheat, warm nights reduced the grain weight ca. 3% per °C of night temperature increase, similarly in grains of the basal and central (both proximal and distal positions) spikelets ($p = 0.15$), but temperature increases had no effect on grains in the apical spikelet (not significant regression, $p = 0.20$). In barley, grain weight of all spikelet was similarly reduced ($p = 0.51$) by night temperature increase, ca. 3% per °C as well. In spite of the differences in absolute grain weight between grains of different positions along the spike, heated crops always showed lower absolute values, both in wheat (Fig. 4a) and barley

(Fig. 4d). In wheat, the individual grain weight reduction tended to be higher in 2013 (ca. 14%) than 2011 (ca. 6%) mainly in grains of central spikelets, while in barley a similar reduction (ca. 8%) was observed in both growing seasons. In line to what was described for thousand grain weight (at canopy level), individual grain weight reductions observed at different positions along the spike, due to night temperature increases, were associated with a shorter effective grain filling period (Fig. 4b,e), while changes in grain filling rate were less obvious (Fig. 4c,f). However, it is clear that in wheat in 2013 there was a trend towards a reduction in both duration and

Table 2

Growing season (GS), crop (C) and night temperature regime (NT) from 10 days after anthesis to physiological maturity (i.e. from DC65 + 10d to DC90; Zadoks et al., 1974) effect on wheat and barley grain yield and its determinants. Summary ANOVA (bottom of the table) shows significance levels for main effects and their interaction.

GS	C	NT	Grain yield (g m ⁻²)	Grain number (grains m ⁻²)	Spike number (spike m ⁻²)	Grain number spike ⁻¹ (grains spike ⁻¹)	Thousand grain weight (g)	Grain filling	
								Effective period (d)	Rate (mg d ⁻¹)
2011	Wheat	A-NT	481	15111	485	31.2	31.9	21	1.59
		H-NT	428	14149	470	30.2	30.2	18	1.74
	Barley	A-NT	550	16788	864	19.5	32.8	21	1.61
		H-NT	523	17336	937	18.7	30.2	18	1.69
2013	Wheat	A-NT	607	16635	552	30.2	36.4	25	1.57
		H-NT	514	15986	521	30.7	32	22	1.51
	Barley	A-NT	753	19363	1050	18.4	39	22	1.82
		H-NT	650	18530	1003	18.5	35.6	20	1.72
ANOVA	GS	**	**	*	ns	**	*	ns	ns
	C	**	**	**	**	**	ns	ns	ns
	NT	**	ns	ns	ns	**	**	ns	ns
	GS*C	*	ns	ns	ns	**	ns	ns	ns
	GS*NT	ns	ns	ns	ns	ns	ns	ns	ns
	C*NT	ns	ns	ns	ns	ns	ns	ns	ns
	GS*C*NT	ns	ns	ns	ns	ns	ns	ns	ns

Ambient (A-NT) and high (H-NT) night temperatures. ANOVA results: **: $p < 0.01$, *: $p < 0.05$, ns: not significant ($p > 0.05$).

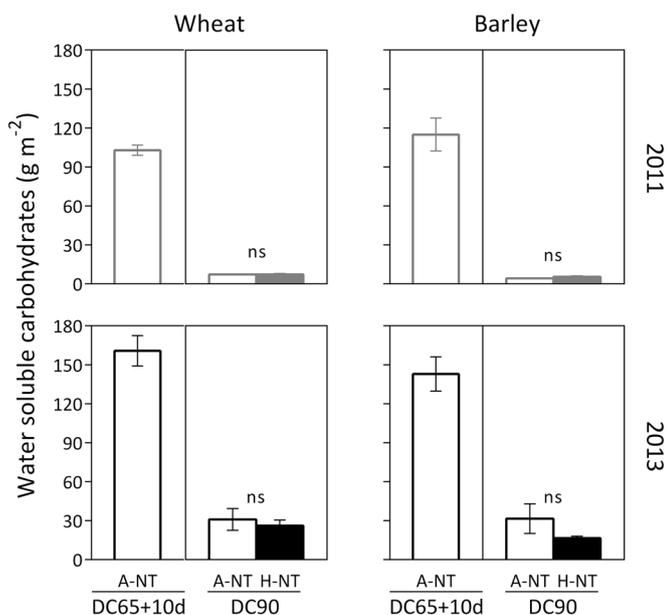


Fig. 5. Water soluble carbohydrates at the beginning, i.e. 10 days after anthesis (DC65 + 10d; Zadoks et al., 1974), and at the end, i.e. physiological maturity (DC90; Zadoks et al., 1974), of night heating period for wheat (left panel) and barley (right panel) crops under different night temperature regime from DC65 + 10d to DC90, i.e. ambient (A-NT) and high (H-NT) night temperatures, during 2011 (grey bars) and 2013 (black bars) growing seasons. Crossed vertical lines indicate standard error. Night temperature regime effect at DC90 (ANOVA result) is also indicated (**: $p < 0.01$, *: $p < 0.05$, ns: not significant).

rate, while in 2011 the increase in rate did not compensate for the reduction.

Stem reserves levels, measured as water soluble carbohydrates, were similar at DC90 ($p = 0.21$) between heated and unheated crops (Fig. 5). Since (i) crops under different night temperature regime had similar water soluble carbohydrates levels at 10 days after DC65 and (ii) heated crops reached DC90 many days in advance (Fig. 1), the amount of stem reserves mobilized per day was higher in crops under higher than ambient night temperature. Wheat and barley showed similar results, while the amount of water soluble carbohydrates was higher in 2013 (earlier sowing date) than 2011 ($p < 0.01$). During 2013, the dynamics of green leaf area (expressed as percentage of the value reached at the beginning of night heating period) and water soluble carbohydrates concentration, were evaluated in first cohort shoots (Fig. 6). As flag leaf and two positions down showed similar senescence patterns (data not shown), the average green leaf area of these three top leaves is presented. Higher night temperatures tended to hasten senescence, as relative green leaf area vs. calendar days, especially in barley. A similar trend was observed for the dynamics of water soluble carbohydrate concentration (i.e. higher decline under warm nights). When both dynamics, green leaf area and water soluble carbohydrates, were plotted vs. thermal time units, most of the differences between crops under different night temperature regimes disappeared. However, in barley, the decline in water soluble carbohydrates concentration was faster under higher than ambient night temperature (Fig. 6h).

4. Discussion

The understanding and quantification of responses of key crops, such as wheat and barley, to observed and predicted warming scenarios is essential to design climate change adaptation strategies (Howden et al., 2007; Fischer et al., 2014). Following this premise, field-grown well-adapted wheat and barley cultivars were exposed

to post-anthesis high night temperatures and their responses were comparatively evaluated. Thousand grain weight was reduced by 3% per °C of night temperature increase, similarly for wheat and barley, being the main cause of a grain yield reduction of 4% per °C. The main change associated with grain weight reduction was an accelerated development under high night temperatures. This led to a shorter effective grain filling period in both crops while source availability did not seem to be a limiting factor under the conditions tested, i.e. crops without water, nutritional or biotic constraints exposed to night temperature increase along the moderately high temperatures range (Wardlaw and Wrigley, 1994; Stone et al., 1995; Savin et al., 1997). Grain number per unit area tended to be lower (although not significant in statistical terms, $p = 0.54$) under high night temperatures, mainly in wheat (ca. 1% per °C of night temperature increase), probably due to lower grain set in the younger spikes cohorts.

4.1. Crop development was influenced by warm nights

As studies focused on night temperature during the grain filling period are scarce, comparisons can only be made with studies that analyzed mean temperature obtained by variations in both minimum and moderately high (up to 32 °C) maximum temperatures (or only the last ones), as explored in our study. In this field, data are more abundant for wheat than for barley. Two decades ago, Wardlaw and Wrigley (1994) reviewed the estimated wheat grain weight reduction under moderately high temperature post-anthesis and reported to be in the range from 1.4 to 7.5% per °C of mean temperature increase both under field and controlled conditions. More recently, Ottman et al. (2012) reported a grain weight reduction of ca. 3% per °C of post-anthesis mean temperature increase in a field study where a spring wheat was exposed to both day and night warming through variations in sowing date and supplemental infrared heating. In barley, Savin et al. (1997) found a grain weight reduction of ca. 1% per °C of mean temperature increase in single plants grown under controlled conditions. This lower sensitivity compared to our study could be associated with the later time of heating imposition (from 20 days after DC65), or to genotypic differences found in barley (Passarella et al., 2005; Hakala et al., 2012). Both aspects, a lower grain weight loss when heating treatment was applied late during grain filling and genotypic differences, were also observed in wheat by Lizana and Calderini (2013) under field conditions where the mean temperature increase was mainly achieved by night heating. Thus, Lizana and Calderini (2013) showed that grain weight of the most sensitive cultivar was reduced by ca. 1.5% or 1% per °C of mean temperature increase from 3 to 15 days or from 20 to 32 days after DC65, respectively; meanwhile grain weight of the less sensitive cultivar was reduced by ca. 1% per °C only due to heating at the beginning of grain filling. Considering a longer night heating period from booting (DC45; Zadoks et al., 1974) to DC90, Prasad et al. (2008) reported a wheat grain weight reduction of ca. 3% per °C of night temperature increase, whilst grain number per spike was reduced by ca. 5% per °C in single plants grown under controlled conditions. In spite of the experimental differences, all these studies show that grain weight reductions due to increase of moderately high temperatures are strongly associated with shortened grain filling durations, which was confirmed by our study.

As stated above, wheat and barley grain weight had a similar response to post-anthesis warm nights, strongly driven by the developmental rate. Heating was applied from 10 days after DC65 to minimise effects on potential grain weight (Serrago et al., 2013). Lower grain weight under high night temperatures was the result of shortening effective grain filling period without compensations in grain filling rate. At this point, it is important to clarify whether the negative impact of high night temperature on grain dry weight is a

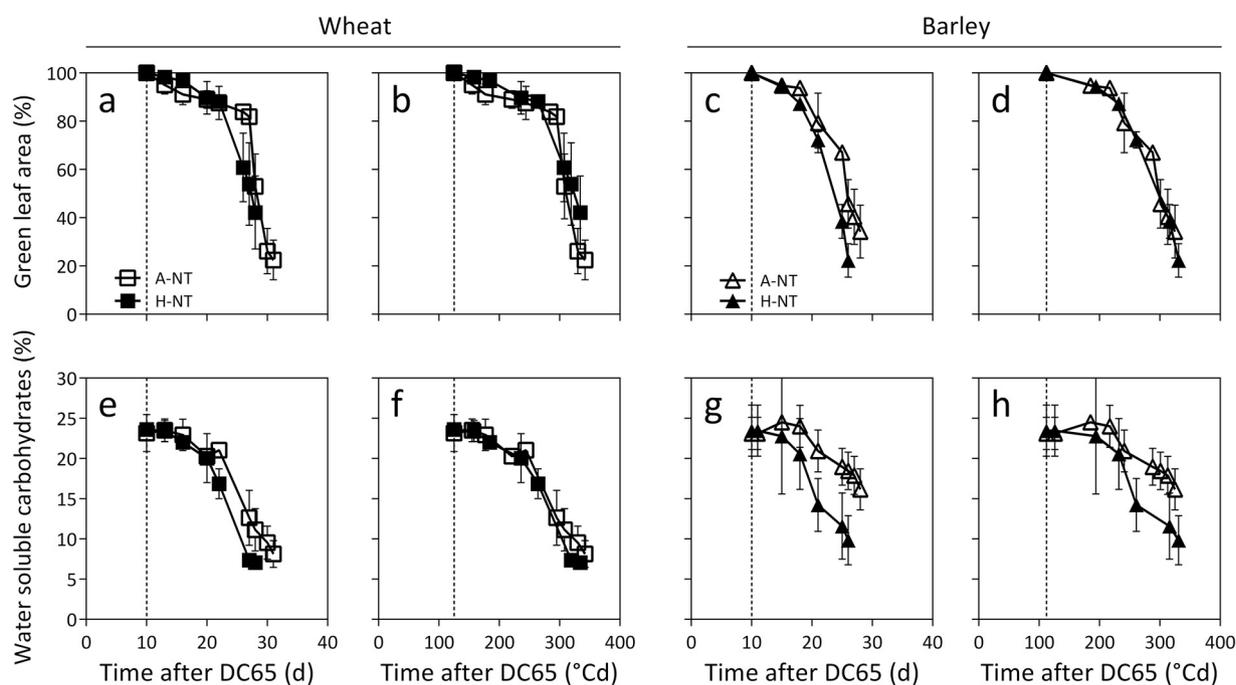


Fig. 6. Dynamics of green leaf area (average of three top leaves) percentage (top panel) and water soluble carbohydrates concentration (bottom panel) during the night heating period, i.e. from 10 days after anthesis (vertical dashed line) to physiological maturity (i.e. from DC65 + 10d to DC90; Zadoks et al., 1974) in wheat (squares) and barley (triangles) crops under different night temperature regime, i.e. ambient (A-NT, open symbols) and high (H-NT, close symbols) night temperatures, during 2013 growing season. Each point is the average of 3 replications and its standard error. Trait evolutions are represented in (a,c,e,g) calendar days and (b,d,f,h) thermal time units after DC65 in order to evaluate them with and without temperature impact on grain development, respectively. Base temperature of 8.2 °C for wheat (Slafer and Savin, 1991) and 7.5 °C for barley (Gualano and Benech-Arnold, 2009) were assumed.

direct effect on grain development and/or is partially mediated by effects on the canopy as source of assimilates (Wardlaw et al., 1980; Slafer and Miralles, 1992), as dark respiration is known to increase exponentially with temperature (Penning de Vries et al., 1979). Interception of green leaf area and availability and consumption (i.e. depletion between the beginning of night heating and maturity) of water soluble carbohydrates did not seem to be affected by an increase in night temperature within each crop. There were no significant differences in PAR interception at the beginning of heating treatment, despite barley having more green leaf area, or on the dynamics of green leaf area loss during grain filling. In the growing season with the lower ambient temperature and higher yield potential (2013) only the heated barley treatment consumed more water soluble carbohydrates when the impact of night warming on grain development was discarded (i.e. analysis in thermal time units). However, it did not imply a different grain weight response to night temperature increase from the one observed when sowing late (i.e. warmer and lower yield potential) or in wheat. In the unheated crops in 2013, barley apparently required less water soluble carbohydrates (in concentration terms) for grain filling than wheat as reserves depletion was lower for the similar green leaf area loss, possibly due to its higher leaf area index and biomass at 10 days after DC65. Thus, even if respiration losses increased with warm nights (no differences were detected measuring at the leaf level on a single date at the middle of grain filling period; data not shown), the impact of assimilates availability for grain filling was negligible in both wheat and barley. Measurements on carbon exchange at canopy level are necessary in future studies.

The lack of consistent impact on source availability as well as a similar impact on individual grain weight for different grains 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 (Wardlaw et al., 1980; Slafer and Miralles, 1992). As grains in central spikelets or proximal grains

inside one particular spikelet within the spike have priority for assimilates supply (Bremner and Rawson, 1978), a source limitation due to warm nights should have been detected in grains placed in unfavourable positions such as apical/basal spikelets and/or eventually in distal grains within the central spikelets (Miralles and Slafer, 1995); however, those effects were not detected. Therefore, in wheat and barley crops, an accelerated development under warm nights was the main cause of grain weight reduction as a consequence of reductions of the effective grain filling period. High temperature during grain filling can lead to important quantitative losses due to a direct effect on grain development, which could be particularly aggravating at high yield levels where temperate crops have been reported as sink-limited (Wardlaw et al., 1980; Slafer and Miralles, 1992; Borrás et al., 2004; Serrago et al., 2013).

4.2. Final considerations and challenges ahead

The present study complements a previous one that showed that warm nights during the grain number determination period led to a 7% grain yield reduction per °C increase (García et al., 2015). Although the impact of night temperature on grain yield during post-anthesis period was lower than that observed during the critical earlier period, it is relevant in terms of grain production and trade. Linking the impact of only post-anthesis night warming and the worldwide wheat and barley production in 2013, 716 and 164 Mt respectively (FAO, 2015a), if no crop adaptation strategies are adopted, ca. 29 Mt of wheat and 7 Mt of barley could be lost per °C of post-anthesis night temperature increase. To put this in perspective, these amounts represent 20% and 25% of the global wheat and barley exports, which reached 144 and 28 Mt, respectively in 2012 (FAO, 2015b).

The relevance of crop development to explain grain weight and, in turn, grain yield response to post-anthesis warm nights becomes important in the quantification of the impact of climate change sce-

narios on wheat and barley production. In the present study, the grain filling duration calculated in thermal time units, considering a base temperatures of 8.2 °C for wheat (Slafer and Savin, 1991) and 7.5 °C for barley (Gualano and Benesch-Arnold, 2009), did not differ between night temperature regimes ($p=0.89$) or growing season ($p=0.88$) and both crops had similar grain filling duration ($p=0.14$), ca. 330 °Cd. This lack of influence of the asymmetric warming on the thermal time approach is in line with other studies that reported no effect of thermal amplitude in a temperature range similar to that explored in the present study (Slafer and Rawson, 1996). In cooler regions where warming could even produce benefits for winter wheat performance, differences between warming timing (night vs. night and day) were not found (Fang et al., 2015).

Since wheat and barley grain weight and, in turn, grain yield reduction under high night temperatures during grain filling appear to be driven by crop development, one obvious question is whether there is useful genetic variability in the response of developmental rate to night warming, which would imply genetic variability in the cardinal temperatures (Fischer et al., 2014; Sadras and Dreccer, 2015). In general, cardinal temperatures vary along the crop cycle and some genotypic variability within a phase can be found among wheat genotypes (Slafer and Rawson, 1995; Porter and Gawith, 1999). On the other hand, Parent and Tardieu (2012), in a meta-analysis including wheat and barley and 15 other crops, did not find genotypic variability in the sensitivity of developmental rate to temperature. At this point, analysis methodology may either help or hinder the search of genetic variability in the response of developmental rates to temperature. Slafer and Rawson (1994), using absolute values of developmental rate (d^{-1}) and assuming a lineal-type response, found genetic variation in the sensitivity of wheat developmental rate to temperature during grain filling. Parent and Tardieu (2012) normalized the developmental rate absolute values at a standard temperature (20 °C) and used an Arrhenius-type response curve, which may mask smaller but quantitative important genotypic differences. As absolute and not relative impacts are ultimately important at the paddock level, more information about variability in developmental rate responsiveness to temperature is required to develop breeding strategies for higher night temperature scenarios. Compared to the pre-anthesis phases, where length can be manipulated via photoperiod and vernalisation sensitivity in addition to temperature, only temperature modulates the duration of grain filling period (Slafer and Rawson, 1994). This is a clear challenge for plant breeding efforts. Our results suggest that post-anthesis warm nights have a direct effect on grain weight mediated by developmental rate responsiveness to temperature. Breeding and management adaptation strategies should be mainly focused on crop development when warm nights are a feature of the target environment.

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