

High night temperatures during grain number determination reduce wheat and barley grain yield: a field study

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Abstract

Warm nights are a widespread predicted feature of climate change. This study investigated the impact of high night temperatures during the critical period for grain yield determination in wheat and barley crops under field conditions, assessing the effects on development, growth and partitioning crop-level processes driving grain number per unit area (GN). Experiments combined: (i) two contrasting radiation and temperature environments: late sowing in 2011 and early sowing in 2013, (ii) two well-adapted crops with similar phenology: bread wheat and two-row malting barley and (iii) two temperature regimes: ambient and high night temperatures. The night temperature increase (ca. 3.9 °C in both crops and growing seasons) was achieved using purpose-built heating chambers placed on the crop at 19:00 hours and removed at 7:00 hours every day from the third detectable stem node to 10 days post-flowering. Across growing seasons and crops, the average minimum temperature during the critical period ranged from 11.2 to 17.2 °C. Wheat and barley grain yield were similarly reduced under warm nights (ca. 7% °C⁻¹), due to GN reductions (ca. 6% °C⁻¹) linked to a lower number of spikes per m². An accelerated development under high night temperatures led to a shorter critical period duration, reducing solar radiation capture with negative consequences for biomass production, GN and therefore, grain yield. The information generated could be used as a starting point to design management and/or breeding strategies to improve crop adaptation facing climate change.

Keywords: climate change, crop development, crop growth, grain number, *Hordeum vulgare* L., minimum temperature, *Triticum aestivum* L.

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Introduction

Climate variations represent an ever present challenge for agriculture and world food security and are magnified by climate change (IPCC, 2014). Cereals are of primary importance to ensure food security (Hall & Richards, 2013), as they are adapted to a wide range of environments. Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) are the two major temperate cereals produced in the world, resulting in a significant source of food and animal feed (FAO, 2015). Understanding the response of wheat and barley to the most likely climate change scenarios is required in order to develop adaptation strategies to guarantee sustainable food production for a growing global population (Howden *et al.*, 2007).

A highlighted characteristic of climate change is global warming, featuring night temperature increases. Current scientific knowledge on climate change highlights that temperature will be the most affected and predictable variable (IPCC, 2014). Global temperature is projected to rise under all assessed emission scenarios, increasing between 1 and 3.7 °C to the end of this century (IPCC, 2014). Retrospective analysis has shown that minimum (i.e. night) temperatures increased at a faster rate than the maximum (i.e. day) ones during the last decades (Alexander *et al.*, 2006; Sillmann *et al.*, 2013a). As multi-model ensembles project higher increases in the frequency of warm nights compared to warm days, asymmetric warming across the day is expected to continue in the future (Sillmann *et al.*, 2013b). Warm nights have been observed in large, mostly temperate, cropping areas both in the Southern Hemisphere, such as the Argentinean Pampas (Fernández-Long *et al.*, 2013) and the Australian wheat belt (Alexander *et al.*, 2007), but also in the

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Northern Hemisphere, such as the North American wheat belt (Vincent & Mekis, 2006) and Central and South Asia (Klein Tank *et al.*, 2006). Therefore, wheat and barley crops are currently exposed, and likely to continue to be exposed, to warm nights during their growing seasons.

The design of adaptation strategies to high night temperatures in terms of crop breeding and management will rely on knowledge on the key processes or traits affected and the magnitude of the impact (Asseng *et al.*, 2009; Fischer *et al.*, 2014). Although the temperature response of growth and developmental processes at the organ level has been studied (e.g. leaf photosynthesis or spikelet initiation rate), they can only be cautiously scaled up at crop level (Sadras & Richards, 2014), taking into account canopy structure and the energy balance. In wheat, there have been studies of associating grain yield loss to high night temperatures amongst other variables (Magrin *et al.*, 2005; Lobell & Ortiz-Monasterio, 2007). Data collected at the canopy level are scarcer, but gradually becoming more available (Fischer & Maurer, 1976; Ottman *et al.*, 2012; Lizana & Calderini, 2013) because of its far relevance to the real world. The impact of warm nights has not been thoroughly tested comparatively in wheat and barley at the crop level.

Environmental conditions around flowering have a large influence on grain yield determination in wheat and barley because grain number per unit area (GN) (Fischer, 1985; Arisnabarreta & Miralles, 2008) and potential grain weight (Calderini *et al.*, 1999; Bingham *et al.*, 2007) are defined during that period. In both species, the critical period for grain yield determination coincides with the spike growth and grain-setting period, linked to tiller per plant (Alzueta *et al.*, 2012) and floret per spike survival (Miralles *et al.*, 2000). That phase occurs approximately from the beginning of penultimate leaf appearance to the beginning of active grain filling period, that is from DC33 (the third detectable stem node) to 10 days after DC65 (10 days after anthesis) according to Zadoks *et al.* (1974) decimal code. GN determination in both crops can be analysed in terms of the availability, utilization of and partitioning of assimilates to the spike during the critical period, which is also influenced by temperature effects on development as the period is shorter under higher temperatures (Fischer, 1984). In Eqn (1), GN is a function of the critical period duration (CPD, d) and crop growth rate during that period, described as the product of the average daily incident photosynthetically active radiation (PAR, MJ m⁻² d⁻¹), the fraction of this radiation that is intercepted by the crop canopy (F_{PAR}) and the biomass produced per unit PAR intercepted or radiation use efficiency (RUE, g MJ⁻¹). In

addition, a proportion of the biomass produced during this period is partitioned to the spike (BPS, fraction), and an amount of the spike biomass will sustain a grain, described by the fruiting efficiency (FE, grains g⁻¹ spike weight at anthesis), which integrates intra-spike partitioning, floret development and grain set.

$$\text{GN} = \text{CPD} * \text{PAR} * F_{\text{PAR}} * \text{RUE} * \text{BPS} * \text{FE} \quad (1)$$

Based on process knowledge and evidence from other crops, CPD and RUE are likely traits to be negatively affected by high night temperatures. As was shown in maize crops, warm nights accelerate development shortening the CPD and thereby reducing the accumulated intercepted solar radiation during that period with a negative impact on GN (Cantarero *et al.*, 1999). The fraction of PAR intercepted by the crop during the critical period should not be affected by high night temperatures in crops without water, nutritional or biotic constraints whose sowing date and rate are adequately managed (Richards, 2000). RUE integrates effects of photosynthesis within the canopy and loss of assimilates through photorespiration, dark respiration and senescence, being a robust integrative trait of growth processes at crop level (Monteith, 1977; Sinclair & Muchow, 1999). As dark respiration increases with temperature (Penning De Vries *et al.*, 1979), a negative impact of high night temperatures on RUE could be expected. However, evidence from maize (Cantarero *et al.*, 1999) and rice (Peraudeau *et al.*, 2015) suggests that the effect of warm nights on respiration could be negligible at crop level. Finally, both biomass partitioning to spike and/or fruiting efficiency could be unaffected under high night temperatures. In fact, higher FE was observed at high daytime temperatures (Dreccer *et al.*, 2014), but the opposite effect could be expected whether temperature exceeds 30 °C leading to floret or grain abortion (Saini & Aspinall, 1982). We therefore hypothesize that high night temperatures during the critical period will reduce GN largely due to impact on crop development.

The main objective of this study was to investigate the impact of high night temperatures during the critical period on grain yield in well-adapted wheat and barley cultivars, assessing the above effects on GN and its drivers: crop development, growth and biomass partitioning. Equation (1) describes the main approach used to test our work hypothesis. The study was focused on comparative crop physiology using field experiments, so that the information could be used as a starting point to design management and/or breeding strategies to improve crop adaptation facing climate change.

Material and methods

Experimental conditions and crop management

Two field experiments were carried out at Facultad de Agronomía, Universidad de Buenos Aires (34°35'S, 58°29'W, 26 masl) in 2011 and 2013. The soil was a silty clay loam, classified as Vertic Argiudoll, 3.8% of organic matter content and pH 6.7. A commercial cultivar of bread wheat ('Baguette 13 Premium') and one of two-row malting barley ('Scarlett') were evaluated in both experiments. These cultivars were chosen because of their similar phenology, particularly flowering date, high yield potential and wide adoption by farmers in the Rolling Pampas Region. Sowing dates were different between years to explore contrasting solar radiation and temperature conditions during the critical period. Crops were sown late (August 6th 2011) and early (June 6th 2013), and sowing rates were adjusted accordingly to ca. 400 and 300 plants m⁻² in 2011 and 2013, respectively. Throughout the paper, the combination of year and sowing date is referred to as 'growing season'. Plots were 4 m long and 1.25 m wide (7 rows 0.175 m apart). Both field trials 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). One week before sowing, soil samples were extracted at the top 0.2 and 0.6 m soil layer to determine P and N availability, respectively. Urea was applied at tillering to reach a soil N availability of 180 kg N ha⁻¹, and triple superphosphate was applied at sowing aiming at more than 20 ppm of available P. Plant pathogens, pests and weeds were prevented or controlled with recommended chemical treatments.

Experiments were a combination of two crops (i.e. wheat and barley) and two night temperature regimes during the critical period: ambient (i.e. unheated crops) and high night temperatures (i.e. heated crops) in both growing season (2011-late sowing and 2013-early sowing). Each experiment was arranged in a randomized split plot design with 3 replicates; crops were considered as main plots and night temperature regimes as sub-plots. The night temperature increase was achieved using purpose-built heating chambers, which were placed on the crop at 19:00 hours and removed at 7:00 hours every day during the treatment period. The timing was chosen as minimum temperature largely occurs before 7:00 hours during the period of interest. The heating treatment was applied from the third detectable stem node (DC33, Zadoks *et al.*, 1974) to 10 days post-flowering (DC65 + 10 days, Zadoks *et al.*, 1974) to coincide with the critical period of both wheat and barley crops. Portable chambers (see Fig. 2) 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) with a gabled roof for preventing rainfall accumulation. Chambers were equipped with two portable electric fan heaters connected to two temperature sensors and monitored by an automated control unit (Cavadevices, Buenos Aires, Argentina). One of the temperature sensors was placed in the heated canopy and the other one in the unheated control canopy (i.e. nearest plot), and 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). This value was chosen as representative night temperature increase for mid to late century in Southern South America, taking into account projections of mean temperature increments of 1–4.5 °C (Magrin *et al.*, 2007). The heater stopped each time that the programmed temperature difference was reached, but the fan was permanently operating to reduce spatial temperature variation within the chamber. Unheated control crops were not covered by a chamber based on a test with a chamber on, without heaters and fans, which revealed that inside temperature was not significantly different to outside one.

Crop measurements and analysis

Crop phenology was evaluated every 2–3 days, using the decimal code of Zadoks *et al.* (1974). Dates of emergence (DC11), third detectable stem node (DC33) and anthesis (DC65) were recorded. DC11 was recorded when 50% of the plants in the plots reached that stage, while DC33 was determined over 20 main shoots randomly chosen. In wheat, DC65 was defined as 50% of the spike population with anthers extruded. In barley, as anthesis normally occurs before heading, 20 or more spikes were manually inspected after flag leaf appearance (opening the flag leaf sheath) and DC65 was reached when 50% of the spikes had anthers extruded. Physiological maturity (DC95) was determined by monitoring grain dry matter accumulation by destructive harvest (twice per week starting at 10 days after DC65). Time to anthesis (i.e. DC11 to DC65), CPD (i.e. DC33 to 10 days after DC65) and the whole cycle duration (i.e. DC11 to DC95) were calculated.

Quadrant harvests (0.5 m of the 5 central rows, i.e. 0.44 m²) for biomass were carried out at DC33, 10 days after DC65 and 1 week after the DC95 stage. A representative sub-sample of ca. 20% fresh weight was separated into spikes, stem (including sheaths), and green and/or yellow leaves. Spikes were counted. These sub-samples and the rest of the sample were oven-dried (60 °C, 72 h) and weighed. In the last cut (i.e. 1 week after DC95 stage), spikes were threshed and grain weighed to calculate harvest index. At commercial maturity (ca. 2 weeks after DC95 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 average grain weight (through a sub-samples of 200 oven-dried grains) were determined from this sample. GN was calculated as the quotient between grain yield and average grain weight, and the grain number per spike as the quotient between GN and spike number per m².

The fraction of solar radiation intercepted by the crop was measured twice a week during the critical period with a linear ceptometer (BAR-RAD 100, Cavadevices.com, Buenos Aires, Argentina) on clear days between 12 and 14 h. Two measurements were recorded per plot each time, 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°). From these measurements, the fraction of solar radiation intercepted by the crop at midday ($f_{\text{midday}}F_{\text{PAR}}$) 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 (Equation 2) proposed by Charles-Edwards & Lawn (1984).

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

The F_{PAR} between two measurement dates was obtained by interpolation. Daily temperatures 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 IPAR (Sinclair & Muchow, 1999). RUE was calculated as the quotient between biomass accumulated during the critical period and accumulated intercepted PAR during this period, and biomass partitioning to spike (BPS) as the ratio between spike dry weight and biomass accumulated during the critical period. Finally, fruiting efficiency (FE) was calculated as the quotient between GN and spike dry weight at 10 days after DC65.

Statistical analyses were carried out with InfoStat (Di Rienzo *et al.*, 2010). All data were analysed 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 temperature were analysed by linear regressions, Model II, to estimate intercepts and slopes with the lmodel2 procedure in R (Legendre, 2013).

Results

Photothermal environments and night temperature increase

Crops were exposed to different photothermal environments between years, largely due to the contrasting sowing dates, which spanned the recommended sowing

window for temperate cereals in the region (Fig. 1). The 2011 growing season (late sowing date) was characterised by a higher mean temperature for the whole cycle (ca. 16.8 vs. 14.1 °C), a longer average photoperiod from emergence to anthesis (ca. 13.5 vs. 12.3 h) and higher average daily incident PAR for the whole cycle (ca. 8.8 vs. 6.1 MJ m⁻²), compared to 2013 growing season. The combination of longer photoperiod and higher ambient temperature resulted in a shorter time to anthesis in 2011 than 2013, which was also reflected in the whole cycle of both wheat and barley (Fig. 1 and Table 1). Under ambient night temperature, duration between crop emergence (DC11) and physiological maturity (DC95) were 100 ± 1.0 y 146 ± 1.2 days for wheat and 96 ± 1.2 and 137 ± 1.9 days for barley during 2011 and 2013 growing season, respectively.

The heater system and night temperature regimes are presented in Fig. 2. High night temperatures effect across the critical period can be appreciated through the dynamics of ambient and higher minimum temperatures (i.e. ambient plus night temperature increase of each particular day). Night temperature increase was similar across crops ($P = 0.35$) and growing seasons ($P = 0.29$). On average, heating increased night air temperature at spike height by ca. 3.9 °C. Average minimum temperature during the critical period ranged from 11.2 ± 0.1 °C (unheated barley in 2013) to 17.2 ± 0.4 °C (heated wheat in 2011), while the average mean temperature ranged from 15.4 ± 0.1 to 20.1 ± 0.2 °C. These ranges were originated from the heating treatment mainly, but also from growing season differences and slightly by crop phenology ones. No frost events were registered during this phase as minimum temperatures were always higher than 5 °C

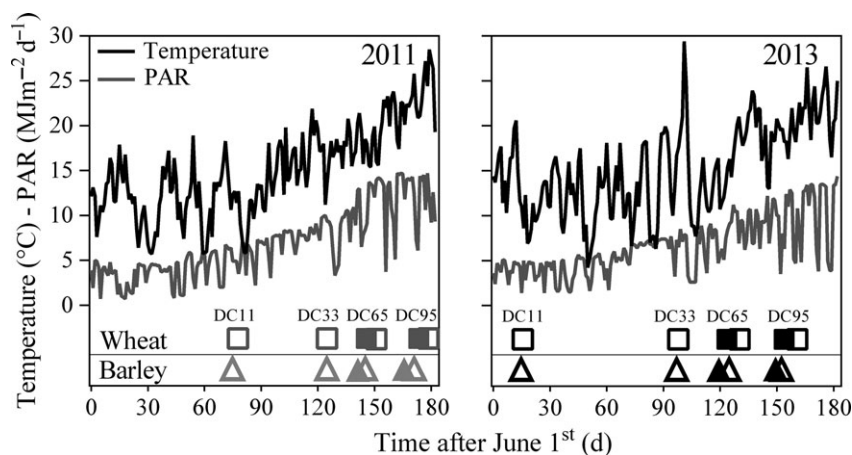


Fig. 1 Daily mean temperature and incident photosynthetically active radiation (PAR) for the 2011 (late sowing date) and 2013 (early sowing date) growing seasons at Buenos Aires, Argentina. Wheat (squares) and barley (triangles) phenological events (averaged date) for the heated (closed symbols) and the unheated (open symbols) crops during the critical period are indicated. Phenological events (Zadoks *et al.*, 1974): DC11 (emergence), DC33 (third detectable stem node), DC65 (anthesis) and DC95 (physiological maturity).

both in heated and natural crops (Fig. 2). Regarding heat shock events, maximum temperatures were lower than 29 °C during the critical period in both crops and growing seasons, excepting 1 day that reached 35.3 °C in 2013 on the 5th day of heating treatment (Fig. 2). At that point, there were no phenological differences between heated and unheated crops, which were all at DC34 stage. The event occurred before the pollen meiosis stage, no sterility was observed in either treatment.

Impact of warm nights on grain yield, phenology and yield components

Under ambient night temperature, crops yielded more (ca. 32% on average for both crops) in 2013 than in 2011, and barley out-yielded wheat (ca. 20% on average for both growing seasons) (Table 1). On average for wheat and barley, grain yield differences between growing seasons were associated with longer time to anthesis (ca. 57%) and more (ca. 13%) and heavier grains (ca. 17%) in 2013 than in 2011. In the same way, crops produced more biomass in 2013 than in 2011 (ca. 24% on average for wheat and barley). On the other hand, grain yield differences between crops across both growing seasons were mainly related to a higher GN in barley than in wheat (ca. 14%), due to more spikes per unit area (ca. 85%), albeit the reduced grain number per spike of barley with respect to wheat (ca. -38%). Biomass produced during the whole cycle was similar between crops, but barley had higher harvest index than wheat (ca. 19% on average for 2011 and 2013). Differences in phenology between wheat and barley were small in both growing seasons, up to 5 days for time to anthesis and less than a week for the whole cycle (Table 1 and Fig. 1).

High night temperatures during the critical period significantly reduced grain yield (ca. 17% across growing seasons and crops, $P < 0.01$) (Table 1). In line with grain yield reductions, a significant effect of high night temperatures was detected on time to anthesis ($P < 0.01$), GN ($P < 0.01$) and spike number per unit area ($P < 0.01$) (Table 1). Interactions between night temperature, crop and growing season were not significant. High night temperatures during the critical period reduced the time to anthesis by ca. 6% while GN was reduced by ca. 17% across growing seasons and crops. Warm nights differentially affected grain number components, as spike number per m² was significantly reduced (ca. 12% across growing seasons and crops), while grain number per spike was not affected by night temperature regime ($P = 0.17$). This reduction in spike number under high night temperatures could be a consequence of higher tiller mortality, as no significant differences between night temperatures regimes were

detected ($P = 0.26$) on the stem number per unit area at the beginning of the critical period. At DC33, only significant differences in stem number per unit area between growing seasons ($P = 0.02$) or crops ($P < 0.01$) were detected. At this crop stage, wheat had 1143 ± 42 and 911 ± 112 stems m⁻² in 2011 and 2013, respectively; while barley had 1600 ± 71 and 1286 ± 81 stems m⁻² in 2011 and 2013, respectively. Grain weight was not significantly affected by night temperature regime ($P = 0.51$). However, the interaction between growing season and night temperature was statistically significant ($P = 0.02$). Grain weight tended to be heavier (ca. 5%) in heated crops in 2011 (late sowing date) and lighter (ca. 3%) in 2013 (early sowing date). On the other hand, crops exposed to high night temperatures during the critical period produced a significantly lower biomass during the whole cycle (ca. 18% across growing seasons and crops, $P < 0.01$), while the harvest index (i.e. proportion of this biomass that was partitioned to grain) was unaffected by night temperature regime ($P = 0.37$) (Table 1). Similarly to grain weight, the interaction between growing season and night temperature regime was statistically significant ($P = 0.03$) for harvest index. Under high night temperatures, biomass partitioned to grain tended to be higher (ca. 7%) in 2011 and minor (ca. 3%) in 2013, in wheat mainly.

Impact of warm nights on grain number determinants during the critical period

Under ambient night temperature, wheat accumulated more intercepted PAR than barley (ca. 16% across growing seasons) as a consequence of longer CPD (ca. 16% across growing seasons) (Table 2). Although the average PAR and the fraction of that PAR intercepted by the crops during the critical period were significantly different between crops (Table 2), the magnitudes were small (ca. 2 and 3%, respectively). Most of the crops intercepted 95% of PAR during the critical period (Table 2) and average PAR differences were associated with crop phenology one. Considering that PAR is steadily increasing with the day of the year, as shorter the CPD, minor is the average PAR during the phase. In spite of the differences in PAR capture, biomass produced during the critical period was similar between crops (Table 2) as a consequence of the higher RUE observed in barley (ca. 20% higher than in wheat across growing seasons). Barley had also a higher biomass partitioning to spike than wheat (ca. 10% across growing seasons) (Table 2) leading into GN differences between crops (Table 1).

Following the components of eqn (1), a significant effect of high night temperatures during the critical

Table 1 Growing season (GS), crop (C) and night temperature regime during the critical period (NT) effect on wheat and barley grain yield (GY), time to anthesis (DC11-65), grain number per unit area (GN), average grain weight (GW), spike number per unit area (SN), grain number per spike (GNS), above ground dry matter accumulated during the whole cycle (AGDM) and harvest index (HI). Summary ANOVA (bottom of the table) shows significance levels for main effects and their interaction

GS	C	NT	GY, g m ⁻²	DC11-65, days	GN, grains m ⁻²	GW, mg	SN, spikes m ⁻²	GNS, grains spike ⁻¹	AGDM, g m ⁻²	HI
2011	Wheat	ANT	481	73	15 111	31.9	485	31	1229	0.39
		HNT	428	68	12 444	34.4	413	30	984	0.44
	Barley	ANT	550	70	16 788	32.8	864	20	1206	0.46
		HNT	452	66	13 435	33.7	730	18	954	0.47
2013	Wheat	ANT	607	115	16 635	36.4	552	30	1498	0.41
		HNT	445	108	12 933	34.6	457	28	1192	0.38
	Barley	ANT	753	110	19 363	39.0	1050	18	1524	0.49
		HNT	670	105	17 367	38.6	997	17	1350	0.50
ANOVA	GS		**	**	*	**	*	*	**	ns
	C		**	*	**	*	**	**	ns	**
	NT		**	**	**	ns	**	ns	**	ns
	GS*C		**	ns	ns	*	*	ns	ns	ns
	GS*NT		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 (ANT) and high (HNT) night temperatures.

ANOVA results: ** $P < 0.01$, * $P < 0.05$, ns: not significant ($P \geq 0.05$).

period was observed on CPD ($P < 0.01$), PAR ($P < 0.01$) and fraction of PAR intercepted by the crop ($P = 0.04$) with a consequent minor accumulated intercepted PAR in that phase (ca. 18% across growing seasons and crops, $P < 0.01$) (Table 2). However, the magnitude of the impact was higher on CPD (reduction of ca. 14% across growing seasons and crops) than over PAR or fraction of PAR intercepted (reductions of ca. 3% and 2%, respectively). Fraction of radiation intercepted by the crops during the critical period was close to 95% both in unheated and heated crops (Table 2). RUE was not affected ($P = 0.87$) by the night temperature regime (Table 2). Therefore, the lower radiation capture under high night temperatures was translated into a minor biomass accumulated during the critical period (ca. 20% across growing seasons and crops, $P < 0.01$). As neither BPS ($P = 0.79$) nor FE ($P = 0.43$) were affected by the night temperature regime (Table 2), observed differences in GN (Table 1) were associated with lower above ground dry matter under warm nights during the critical period in both crops.

GN was reduced ca. 6% per °C of night temperature increase, similarly for wheat and barley, observing a similar response in the CPD but not in RUE (Fig. 3). To compare crops (avoiding innate differences between wheat and barley), each GN, CPD or RUE value was calculated as a value relative to the average of each

crop across all environments. Comparing among traits, a similar ($P = 0.97$) negative impact of high night temperatures on both GN and CPD (ca. 6% per °C) was found, for the explored range. Grain number was linearly associated with grain yield ($r^2=0.91$, $P < 0.01$). The impact of night temperature was such that grain yield decreased by 7% (ca. 76 g m⁻²) per degree of night temperature increase during the critical period (Fig. 4). This sensitivity was higher if average mean temperature during the critical period is considered; wheat and barley grain yield was reduced ca. 10% per degree of mean temperature increase (data not shown).

Discussion

Crop yield adaptation to climate change represents a continuous challenge for food security and environmental sustainability (Howden *et al.*, 2007). In this context, the understanding of crop response to environmental variations is valuable information to design adaptation strategies (Evans, 1993; Fischer *et al.*, 2014). The present study evaluated wheat and barley response to high night temperatures during grain number determination and quantified functional processes affected at crop level. Grain yield in well-adapted wheat and barley cultivars was reduced ca. 7% per degree of night temperature increase during the critical period. An accelerated development under high night temperatures led to a shorter phase, reducing resource

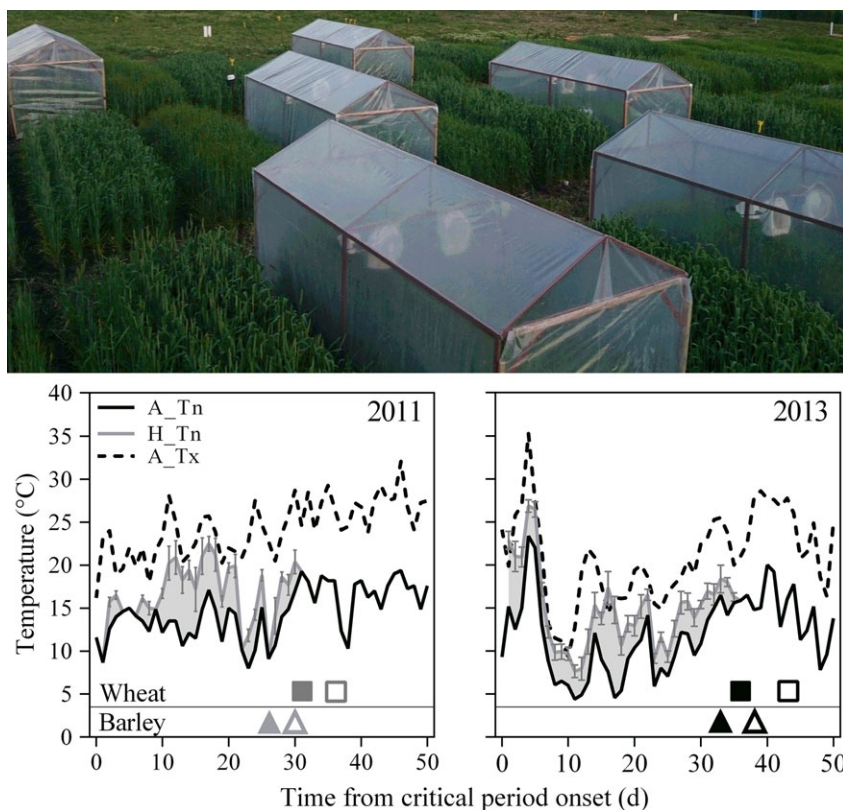


Fig. 2 Photograph of the purpose-built heating chambers used to increase night temperatures in wheat and barley crops, and dynamics of daily ambient minimum (A_Tn) and maximum (A_Tx) temperatures, and high (H_Tn) minimum temperature during the critical period for 2011 (late sowing date) and 2013 (early sowing date) growing seasons. H_Tn was calculated as A_Tn plus the night temperature increase reached each treatment day. The critical period was considered as the time from the third stem node stage to 10 days after anthesis (i.e. from DC33 to 10 days after DC65; Zadoks *et al.*, 1974) for both crops. The end of that period (averaged date) in heated (close symbols) and unheated (open symbols) wheat (squares) and barley (triangles) crops is indicated.

capture and increasing tiller death with negative consequences for biomass production, GN and therefore, grain yield.

Grain yield sensitivity to warm nights: crop development prevailing over growth

As expected, in wheat and barley crops, GN was the main yield component responding to environmental conditions around flowering, in agreement with the literature (Fischer, 1985; Arisnabarreta & Miralles, 2008). The wheat and barley cultivars evaluated showed differences in GN determination. Under ambient night temperature, barley set more grains than wheat due to its higher spikes establishment, which was not compensated by the higher grain number per spike observed in wheat. On the other hand, wheat had a longer CPD (ca. 16%) than barley with lower RUE (ca. 17%). These consistent trait differences compensated each other, as similar biomass produced during the critical period was observed in both crops. In this case, the higher GN in

barley than in wheat was associated with a higher biomass partitioning to spike. However, both crops had a similar and robust GN sensitivity to high night temperatures (ca. -6% per degree of warming) characterized by lower spikes and accelerated development that reduced biomass production. Potential grain weight could be also affected during that period (Calderini *et al.*, 1999; Bingham *et al.*, 2007); however, a consistent effect of night temperature regime was not detected on grain weight.

Wheat and barley GN variations across environments are mainly driven by spikes per unit area (Sadras & Rebetzke, 2013; Slafer *et al.*, 2014). When a two-row malting barley cultivar was exposed to different environments (e.g. sowing dates, N levels), changes in GN were associated with those in spike number per m^2 (García Del Moral & García Del Moral, 1995), probably because the spike structure (only one potential grain per spikelet) limits the grain number that each spike can set (Arisnabarreta & Miralles, 2006). In wheat, an alternative GN regulation can be expected for grain

Table 2 Growing season (GS), crop (C) and night temperature regime during the critical period (NT) effect on critical period duration (CPD), and daily average incident photosynthetically active radiation (PAR), fraction of PAR intercepted by the crop (F_{PAR}), radiation use efficiency (RUE), biomass partitioning to spike (BPS), fruiting efficiency (FE), accumulated intercepted PAR (AIPAR_{CP}) and above ground dry matter produced (AGDM_{CP}) during that phase. Summary ANOVA (bottom of the table) shows significance levels for main effects and their interaction

GS	C	NT	CPD, days	PAR, MJ m ⁻² d ⁻¹	F_{PAR}	RUE, g MJ ⁻¹	BPS	FE, grains g ⁻¹	AIPAR _{CP} , MJ m ⁻²	AGDM _{CP} , g m ⁻²
2011	Wheat	ANT	36	10.0	0.93	2.2	0.32	63	336	760
		HNT	31	10.0	0.91	2.4	0.26	70	282	689
	Barley	ANT	30	9.8	0.96	3.0	0.33	61	284	836
		HNT	26	9.5	0.94	2.8	0.40	53	231	635
2013	Wheat	ANT	43	7.3	0.96	2.7	0.29	71	300	810
		HNT	36	7.0	0.95	2.6	0.26	81	241	629
	Barley	ANT	38	7.1	0.98	3.0	0.35	72	263	788
		HNT	33	6.9	0.95	3.0	0.36	82	216	612
ANOVA		GS	**	**	*	ns	ns	*	*	ns
		C	**	*	*	*	*	ns	**	ns
		NT	**	**	*	ns	ns	ns	**	**
		GS*C	ns	ns	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
		GS*C*NT	ns	*	ns	ns	ns	ns	ns	ns

Ambient (ANT) and high (HNT) night temperatures.

ANOVA results: ** $P < 0.01$, * $P < 0.05$, ns: not significant ($P \geq 0.05$).

number per spike (Slafer *et al.*, 2014), as it has the potential to differentiate more floret primordia and set 3–5 grains per spikelet (Langer & Hanif, 1973). In the present study, spike number per m² was the main GN component in both crops, highlighting the importance of this yield component when expecting environmental changes (Slafer *et al.*, 2014). No significant high night temperatures effect on grain number per spike was observed in wheat with respect to barley. Considering that heating treatment was imposed (DC33) after the maximum number of tillers per plant was reached (Alzueta *et al.*, 2012), the lower spike establishment under warm nights observed in wheat and barley would be a consequence of a higher tiller mortality linked to less biomass produced during the critical period.

An accelerated development rate and a lower C assimilation rate due to higher dark respiration are the processes commonly suggested to explain biomass and then grain yield reductions under high night temperatures (Lobell & Ortiz-Monasterio, 2007; Grant *et al.*, 2011). Taking RUE as an integrative crop-growth trait (Monteith, 1977; Sinclair & Muchow, 1999) and the CPD as a crop-development indicative one (Fischer, 1984), our study showed a higher relative importance of development on wheat and barley GN under high night temperatures during the critical period than growth or biomass partitioning. In fact, the CPD sensi-

tivity to high night temperatures was similar to that of GN (ca. $-6\% \text{ } ^\circ\text{C}^{-1}$) both in wheat and barley. It is important to highlight that when CPD was calculated in thermal time units considering the two most widely used base temperatures, 0 (Kirby *et al.*, 1985) and 4.5 °C (Fischer, 1985), not significant differences were found between unheated and heated crops (data not shown). A comparable result was found in maize showing shorter CPD under high night temperatures without significant variation in RUE or leaf dark respiration (Cantarero *et al.*, 1999). In the present study, although dark respiration was not measured, a reduced RUE variation was observed in both wheat and barley. Therefore, if wheat and/or barley dark respiration was increased by warm nights, the impact on RUE was negligible. A recent study in rice showed that high night temperatures enhanced dark respiration without significant impact on biomass accumulation (Peraudeau *et al.*, 2015). Similar measurements would be required in wheat and barley crops to assess to what extent possible thermal acclimation of dark respiration could take place (Atkin *et al.*, 2005). On the other hand and taking into account that physiological processes respond differently to temperature (Porter & Gawith, 1999), it is important to highlight that growth processes (e.g. RUE) that were not significantly affected under the night temperature range explored in our study (ca. 11–17 °C) could become important under warmer ones, beyond

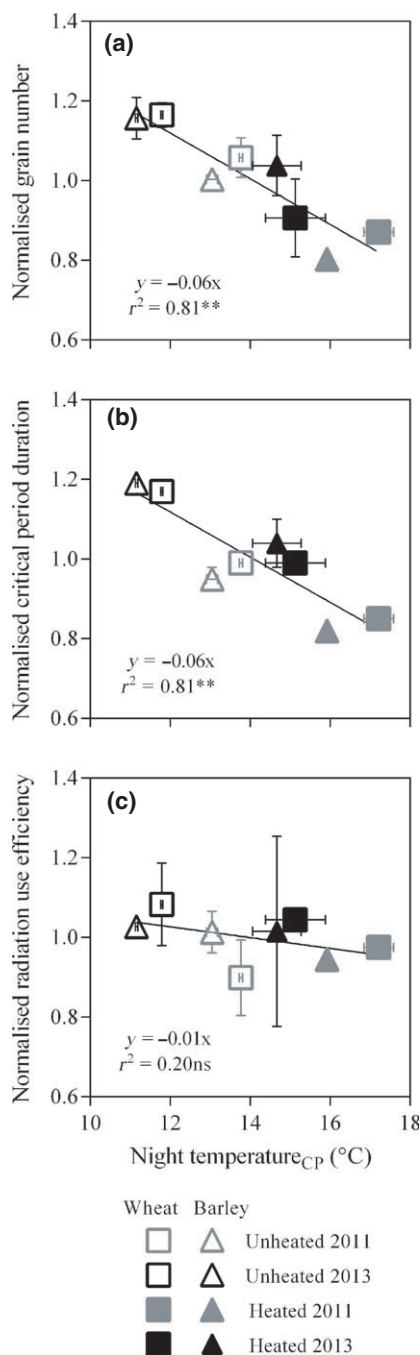


Fig. 3 (a) Grain number per unit area, (b) critical period duration, and (c) radiation use efficiency responses to average night temperature during the critical period. In order to make crops comparison possible, each trait value was normalised as a value relative to the average of each crop across all environments. Each point (average of 3 replications and its standard error) corresponds to heated (close symbols) or unheated (open symbols) wheat (squares) and barley (triangles) crops 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 $P \geq 0.05$) are included.

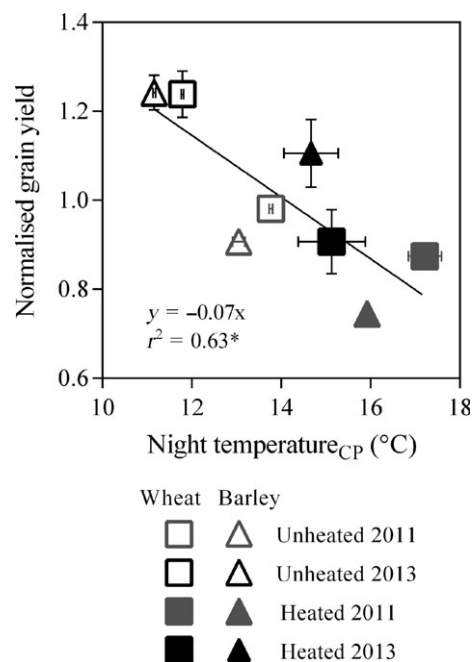


Fig. 4 Grain yield response to average night temperature during the critical period. In order to make crops comparison possible, each trait value was normalised as a value relative to the average of each crop across all environments. Each point (average of 3 replications and its standard error) corresponds to heated (close symbols) or unheated (open symbols) wheat (squares) and barley (triangles) crops 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 $P \geq 0.05$) are included.

the range of optimal temperatures. Importantly, the night temperature increase reported in the present study (ca. 3.9 °C) is in line with warming projections for the end of this century (IPCC, 2014).

Grain yield sensitivity to warm nights: importance of grain number determination period and possible adaptation strategies

Quantifications of the impact of warming on crop production based in regression analysis of past trends or crop simulations under future climate scenarios are generally focused on mean temperature during the whole growing season (Lobell *et al.*, 2011), although a few studies have separated the analysis in pre- and post-anthesis phases (Peltonen-Sainio *et al.*, 2010). Most of the evaluations under field conditions and/or canopy level consider warming across the whole wheat or barley crop cycle (Wheeler *et al.*, 1996), or the widely spread sowing dates (Ottman *et al.*, 2012) and locations (Gourdji *et al.*, 2013), instead of focusing on a particularly relevant phenological phases (Fischer & Maurer,

1976; Lizana & Calderini, 2013) to assess vulnerability, as is the case of the critical period in this study. Moreover, few studies have been specifically directed to evaluate the impact of high night temperatures, and they are restricted to winter wheat (Tian *et al.*, 2014; Fang *et al.*, 2015). To the best of our knowledge, our study is the first evaluation under field conditions of spring wheat and barley cultivars exposed to warm nights during GN determination.

Wheat and barley grain yield loss due to warming calculated in the present study, 7% per degree of increase in night temperature or 10% per degree of mean temperature during the critical period was within the range reported in the literature from several approaches. Fischer *et al.* (2014) summarized literature reporting a wheat grain yield reduction of 5% per degree of mean temperature increase during the whole crop cycle. In agreement with this review, Asseng *et al.* (2015) showed wheat grain yield loss of 6% per degree of warming, based on predictions from 30 different wheat crop models validated against field experiments. Although it has been less evaluated, grain yield response of barley to warming has been estimated to be similar or higher than wheat (Lobell & Field, 2007; Peltonen-Sainio *et al.*, 2010). It is also possible that grain yield loss in response to warming could increase with higher mean growing season temperature (Ottman *et al.*, 2012; Gourdjji *et al.*, 2013), mostly due to more frequent extreme high temperatures that produce heat-shock effects on temperate crops (Saini & Aspinall, 1982; Zheng *et al.*, 2012). Focusing on night temperatures, regression analysis showed a higher sensitivity of wheat grain yield (and barley when it was included in the analysis) to minimum rather than maximum temperatures both in location specific (Magrin *et al.*, 2005, 2009; Lobell & Ortiz-Monasterio, 2007; Peltonen-Sainio *et al.*, 2010) as well as global-scale studies (Lobell & Field, 2007). In general, the lower the latitude, the higher the grain yield loss due to night temperature increase, that is from 1.5% °C⁻¹ in Finland (Peltonen-Sainio *et al.*, 2010) to 10.3% °C⁻¹ in the Yaqui Valley of Mexico (Lobell & Ortiz-Monasterio, 2007). Magrin *et al.* (2009), simulated a wheat yield potential reduction of 7% per degree of minimum temperature increase during October and November, that is the critical and grain filling period in the Rolling Pampas Region. Despite variations regarding the methodology to estimate grain yield sensitivity to temperature increase, all these studies suggest that warming reduces grain yield largely by an accelerated crop development (Fischer *et al.*, 2014; Asseng *et al.*, 2015). Only in high latitudes, where low temperatures limit growth, a positive effect of warming could be expected due to lengthening of the growing window (Peltonen-Sainio *et al.*, 2009).

The broadly documented relevance of the critical period for grain yield determination in wheat and barley crops (Fischer, 1985; Arisnabarreta & Miralles, 2008) suggests that the observed grain yield response to high night temperatures during that phase could dominate the response to warm nights during the whole cycle. Fischer & Maurer (1976) modified mean temperature (both heating and cooling) during tillering (GS21-GS31; Zadoks *et al.*, 1974), jointing (GS31-GS39; Zadoks *et al.*, 1974), flag leaf emergence to anthesis (GS39-GS65; Zadoks *et al.*, 1974) and grain filling (GS65-GS95; Zadoks *et al.*, 1974) in a spring wheat. The largest effects were detected in the second and third crop periods where grain yield was reduced 4% per degree of warming (Fischer & Maurer, 1976). Lizana & Calderini (2013) reported grain yield reductions of ca. 5%, 3% or 1% per degree of mean temperature increase from booting to anthesis (GS45-GS65; Zadoks *et al.*, 1974), from 3 to 15 days after anthesis or from 20 to 32 days after anthesis, respectively, in two spring wheat cultivars. In both studies, an accelerated development and reductions in GN were associated with grain yield reductions. Night temperature anomalies across different crop phases are likely to be correlated even though studies that analyze past and/or future trends in warm nights across different crop phases are scarce (Magrin *et al.*, 2005; Sadras & Monzon, 2006). It is important to highlight that warming during a certain phase can shift the development of the subsequent one to relatively cooler conditions, neutralizing the warming trend (Sadras & Monzon, 2006). Therefore, even though crop cycle can be shortened under warm nights by accelerated development of all crop phases, most of grain yield reductions probably originated from the reduced resource capture during the critical period.

As a practical outcome, our results suggest that agronomic and breeding decisions for wheat and barley crops under high night temperatures should have as an objective to maintain resource capture during the GN determination period and, consequently, biomass production to minimise grain yield losses. Screening for developmental rate responsiveness to temperature is only in its infancy, but likely to be urgently needed. In the meantime, early sowing and longer-season cultivars are considered as one readily available adaptation strategy in response to warming (Zheng *et al.*, 2012; Fischer *et al.*, 2014). Early sowing could avoid warming exploring relative cooler conditions and/or benefit from the performance of a double crop sequence as wheat(barley)/soya bean by an earlier sowing of the second crop (Calviño & Monzon, 2009). Additional frost tolerance could add on to the value of early sowing (Zheng *et al.*, 2015) as accelerated development will naturally result in crops flowering earlier, at higher frost risk. Although

the last frost date is predicted to be earlier under climate change, it is an event with high spatial variation and its occurrence in future climates cannot be discarded (Sillmann *et al.*, 2013b). Extended CPD by means of photoperiod sensitivity (Slafer *et al.*, 2001) could also be useful if the shortened vegetative phase duration due to both genetic and warming is complemented by management practices that maximise solar radiation interception at the beginning of the critical period and the formation of a large stand of spikes per unit area (e.g. higher N fertilizer or seed rates).

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