Heat impact on yield components of fertile primary tillers in wheat can inform crop modelling for future climates

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Abstract

In recent decades, rising temperatures have increasingly affected wheat crops in major producing regions around the world. Climate models predict further increases in mean temperature and in the frequency of temperature extremes for the near to mid-future.

The impact of heat on wheat at different periods of the crop cycle was studied in two experiments conducted with finely controlled temperatures in a glasshouse. While heat shocks affected the main stem and primary tillers of a plant differently, a common response to heat was found for all stems (irrespective of their rank), when considering the timing of the stress relative to stem anthesis. The greatest impact on grain number was observed for stress applied ~10 days before stem anthesis. The impact of pre-anthesis stress on grain set were slightly compensated by an increase in individual grain weight. Overall, grain yield was substantially affected for early pre-flowering stress and early-to-mid post-flowering stress. The results of this study have been used to improve estimations of heat impact in crop modelling and thus improve the accuracy of crop simulations for future climate scenarios.

Key Words

Heat stress, heat shock, global warming, wheat, grain number, grain size.

Introduction

With global warming, wheat crops are experiencing higher temperatures that affect productivity in many producing regions around the world, including Australia (IPCC 2014; Zheng et al., 2012; Lobell et al., 2015; Asseng et al., 2015). In the Australian wheatbelt, seasonal temperatures (August-November) have increased on average by 0.33ºC per decade since 1985 (Ababaei and Chenu, submitted). This temperature increase, together with changes in water limitation, have caused a yield loss of ~240 kg ha^{-1} per decade for a mid-maturing variety (Janz) sown at a typical date (15 May; Ababaei and Chenu, submitted).

Heat stress can affect wheat crops at each stage of the crop cycle (e.g. Farooq et al., 2011; Hunt et al., 2018). However, heat events mostly impact grain yield of an established crop when they occur (i) pre-anthesis and affect grain number (e.g. Ugarte et al., 2007), or (ii) during grain filling and reduce the size of individual grains (e.g. Tashiro and Wardlaw, 1990). Overall, the impact of heat stress depends on the timing, severity and duration of heat events, as well as genotypic characteristics (e.g. Prasad et al., 2014).

This study investigated the impact of pre- and post-anthesis heat on yield and its components for wheat plants and their fertile tillers.

Material and Methods

Two experiments with continuous heat stress (from sowing to maturity) and short episodes of heat (7-d stress) were conducted in a glasshouse at Gatton, Australia, with the heat-tolerant wheat recombinant inbred line (RIL) SB062 from the Seri x Babax population (Olivares-Villegas et al., 2007). Four seeds were sown per pot at 2 cm depth after 4 to 6 weeks of vernalisation at 4ºC. Plants were thinned to two plants per pot at the seedling stage. All plants were grown under 16 h photoperiod, in unlimited water and nutrient conditions, at a density of ~100 plants m^{-2} (a density similar to local field practices).

In both experiments, plants were either grown for the whole-plant cycle with the same temperature regime (control or heat treatments), or they were moved for 7 days from the 'control bay' to the 'hot bay', before returning in the control bay. The temperature was finely controlled and mimicked a daily pattern, with the temperature raising over 4 h from a constant minimum at night, to a maximum around the middle of the day (for 6 h), before decreasing slowly over 4 h to the minimum temperature, which was kept constant for 10 h.

In the first experiment ('Exp 1'), the glasshouse bays were at 26.4/12.7ºC (max/min temperatures for the control; 18.3ºC on average) and 33.3/21.3ºC (26.3ºC on average; heat). In the second experiment ('Exp 2'), they were grown at 25.3/13.1ºC (18.3ºC on average; control) and 35.6/23.7ºC (28.7 ºC on average; heat).

Each treatment consisted of six pots, all surrounded by border pots to avoid edge effects. Phenological stages were followed on one or two plants per pot in both experiments, and anthesis of each of their stems was recorded in Exp 2. These plants were harvested at maturity. Grain number, individual grain size and yield per plant (in Exp 1 and 2) and per stem (in Exp 2) were measured after 5 days at 70°C.

Analyses were performed in R (R Core Team, 2018). Statistical differences were tested with student's t-tests at a 5% level.

Results and Discussion

Impact of continuous heat on wheat

Wheat plants survived the extremely high temperature that were imposed on them from sowing to maturity (33.3/21.3°C and 35.6/23.7°C; Figures 1 and 2). In these extreme conditions, they set a few grains in all primary tillers and filled in priority those grains from the main stem (9.4 grains of 30.1 mg in the main stem compared to ~15 grains of less than 20 mg each in tillers; Figure 1). By contrast, control plants set significantly more grains ($P < 0.05$) in the main stem than in their tillers, but all stems had grains of similar size on average (~50 mg). Stressed plants also had significantly less tillers (2±0) compared to control plants (4±1.3). Overall, continuously stressed plants yielded 0.6 g plt^{-1} in the hottest treatment (35.6/23.7°C) compared to 6.0 g plt^{-1} in the control treatment (25.3/13.1°C).

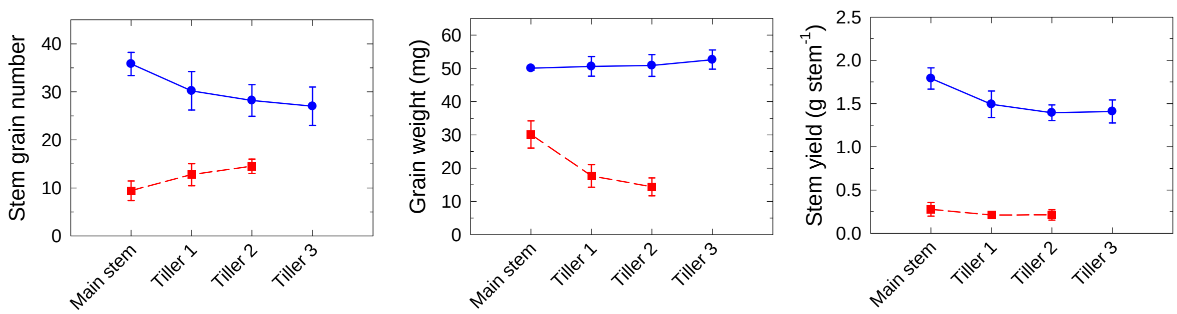

Fig. 1: Impact of heat stress on stem grain number, individual grain weight and yield in wheat line SB062. Data from Exp 2, where plants were grown under 25.3/13.1°C (blue) or 35.6/23.7°C (red) from sowing to harvest. Error bars correspond to standard errors (n=6).

Heat-shock effects on wheat plants

In Exp 1, plants were submitted to 7-d heat during either pre- or post-anthesis (Figure 2). In the tested conditions, the earlier the stress, the fewer grains set, so much so that plants stressed for only 7 days at ~20 d before anthesis had a similar grain number to plants continuously stressed from sowing to harvest. Post-anthesis stresses applied between 0 and 28 days after anthesis significantly affected grain weight ($P < 0.05$), with individual grain weight on average not significantly different ($P = 0.05$) from those of continuously stressed plants (~40 mg). Overall, a 7-d heat stress affected yield the most for early pre-flowering stress (~20 d before anthesis) and early post-flowering stress (~0-20 d after anthesis).

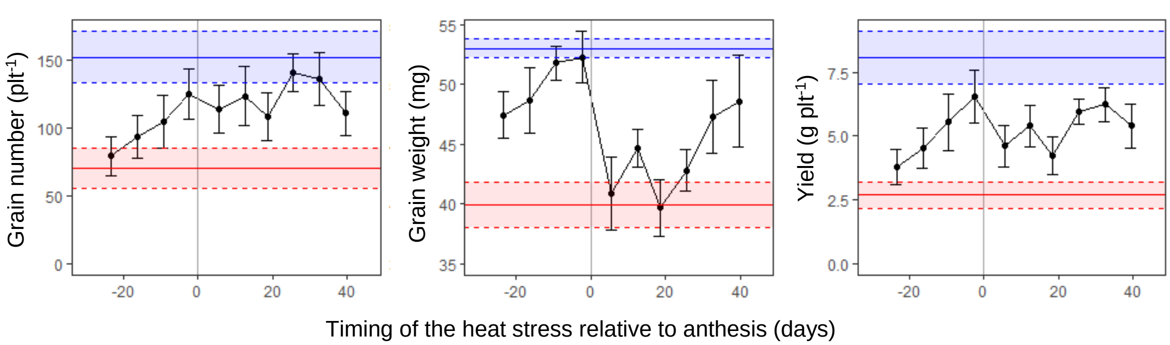

Fig. 2: Impact of pre- and post-anthesis stress on grain number, averaged individual grain weight and yield in wheat line SB062 in Exp 1. Each point corresponds to a 7-d heat stress (33.3/21°C) submitted at different times relative anthesis (day 0). The blue and red lines correspond to averaged values for the control, and plants submitted to heat throughout the plant cycle, respectively. Error bars and shading areas correspond to standard errors (n=6).

Heat-shock effects on different tillers

Pre-anthesis heat shocks affected the grain number of all stems, irrespective of the stem rank (Figure 3). While the intensity of the response varied with the timing of the stress when expressed relative to plant anthesis (Figure 3, left), a more consistent response was found for all stem types when considering phenology of stems relative to their own anthesis (Figure 3, right). For both the main stem and primary tillers, grain number was most affected by heat around 10 days before stem anthesis. Conversely, individual grain weight was greatest around this time with grain weight slightly larger than in the control. However, the increase in grain weight only partly compensated the decrease in grain number, and overall, stem yield was most impacted by heat stress ~10 days before stem anthesis.

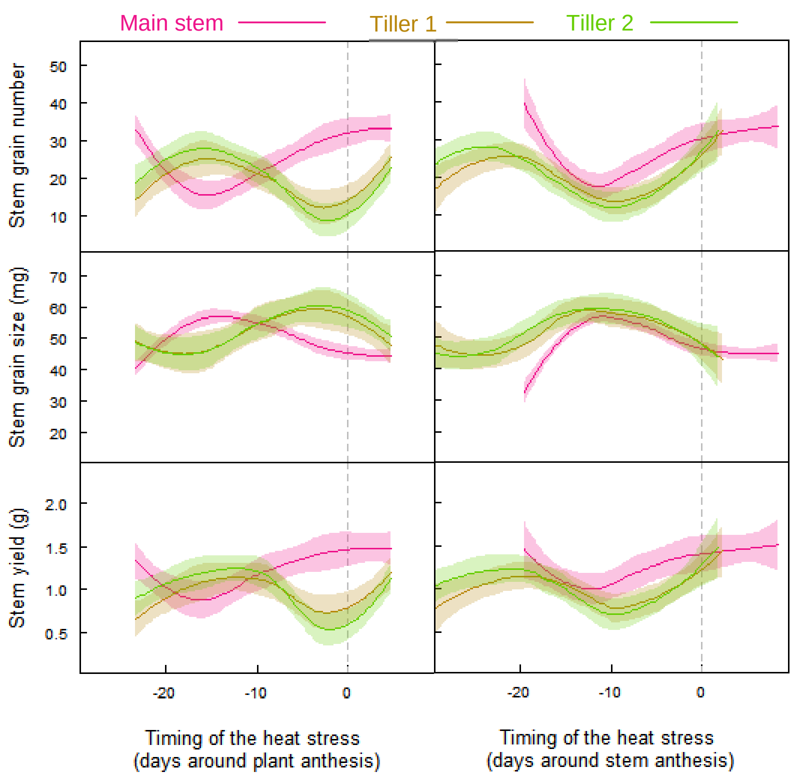

Fig. 3: Impact of 7-d heat on stem grain number, individual grain weight and yield applied from 28 days prior to anthesis to 8 days post anthesis in Exp 2. Results for the main stem (pink), first tiller (brown) and second tiller (green) are presented with a stress application expressed either relative to plant anthesis (left) or to the anthesis of the considered stem (right). For instance, a stress at 0 related to heat applied 3.5 days before and 3.5 days after the anthesis of the main stem (left) of the considered stem (right). Smoothing of the fitted line was performed with a loess fit. The shaded areas correspond to standard errors relative the fitted lines, at 0.05 level.

Discussion

For each fertile tiller, the greatest impact on grain number was observed for heat events about 10 days before anthesis of that stem, probably due to pollen sterility induced by heat at the time of meiosis (Saini and Aspinall, 1982; Zeng et al., 1985). This reduction in grain set resulted in a slight increase in grain weight, due to fewer sinks to fill during the post-anthesis period. Overall, grain yield of each stem remained most affected by heat occurring at this critical stage.

In the Australian production environments, heat shocks mostly impact established wheat crops after anthesis (Ababaei and Chenu, submitted). Greatest post-flowering heat impacts on both individual grain weight and yield were observed during early-to-mid grain filling, between 0-20 days after anthesis (Figure 1). Similar results were found for other treatments (e.g. Stone and Nicolas, 1995; Tashiro and Wardlow, 1990; Ullah and Chenu, 2019). In another study, a greater sensibility and a longer sensitive duration to post-anthesis heat were observed for a sister line of SB062 (SB003), which was also more sensitive for post-anthesis leaf senescence (i.e. less stay-green; Ullah and Chenu, 2019).

The results from this study have been used together with other data to add new modules to the APSIM-Wheat model (Holzworth et al., 2014), in which heat shocks affect grain set and grain filling depending on the timing and intensity of the stress (Lobell et al., 2015; Ababaei and Chenu, submitted). The model was used by these authors to assess the impact of heat in the Australian wheatbelt in current and projected future climate scenarios.

Conclusion

Short episodes of heat over the plant cycle affected different processes in wheat. Grain yield was most affected by heat events occurring pre-anthesis or during early-to-mid grain filling. For each fertile tiller, the greatest impact was observed ~10 days before its anthesis, likely due to heat-induced pollen sterility. The results from this study were used to improve the APSIM-Wheat crop model.

Given the frequency of post-flowering heat stress in the Australian wheatbelt, improving post-flowering adaptive traits appear promising to enhance wheat productivity in increasingly warm environments.

Acknowledgements

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