

Can stay-green help to increase heat tolerance in wheat?

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Abstract

In Australian production systems, high temperatures during early grain-filling are particularly detrimental to grain development and yield of wheat crops. In a two-year field study, we explored the impact of post-flowering heat on stay-green and grain development in wheat crops. At two locations in south-east Queensland, 28 wheat genotypes were planted at different sowing dates in irrigated trials. Significant variations in grain weight were observed between environments. Tolerance to post-flowering heat was associated with stay-green phenotypes. Significant correlations were observed between individual grain weight and leaf greenness at mid-grain fill in environments affected by post-flowering heat shocks. A weaker correlation was found in the milder environment. The results suggest that wheat genotypes with delayed leaf senescence could be selected to sustain grain yields in hot environments.

Keywords

Heat, senescence, grain filling, weight, adaptation.

Introduction

Wheat is highly sensitive to heat before anthesis and during the early grain filling stages (Bergkamp et al. 2018). Recent increases in average temperatures due to global warming have shortened the wheat crop cycle in the Australian Wheatbelt (Ababaei and Chenu 2020). In Australian production systems, heat stress primarily affects grain filling rather than the pre-anthesis period (Ababaei and Chenu 2020). Post-anthesis heat stress affects individual grain weight partly due to heat-induced leaf senescence (Bergkamp et al. 2018; Farooq et al. 2011; Ullah and Chenu 2019). A brief episode of post-flowering heat (i.e. 5 days above 32 °C for 6 h d⁻¹) can reduce individual grain weight by 15% compared to plants grown in the absence of heat stress (Nuttall et al. 2018). Wheat genotypes with a capacity to retain green canopy for longer during grain filling (i.e. stay-green phenotype) are likely to contribute to yield stability by sustaining assimilates supply to developing grains (Gregersen et al. 2008; Abdelrahman et al. 2019).

This study aimed to assess the impact of post-flowering heat stress on crop senescence and examine any association between stay-green phenotype and individual grain weight in a set of 28 genotypes subjected to heat stress.

Materials and Methods

Field experiments were conducted in 2018 and 2019 at two locations in southern Queensland, Australia (Table 1). Twenty-eight wheat genotypes (see details in Ullah N et al. 2021) with varying heat tolerance were planted at Gatton (27°34'50"S, 152°19'28"E) in early July (sowing 1, GAT18s1) and late August (sowing 2, GAT18s2) in 2018 and at Tosari near Tummaville (27°49'09.1"S 151°26'14.9"E) in mid-July in 2019 (TOS19). Plots (2×6 m) were arrayed in a randomised block design with four replicates. Trials were established for each planting time in irrigated field conditions, except at Tosari where crops experience a mild drought stress during grain fill. Standard crop management practices included non-limiting fertilizer application as well as control of weeds, diseases, and pests at all trials.

In 2018, SPAD values of the flag leaf from a subset of eight genotypes (Seri-M82, Hartog, SB062, Janz, Sokoll, Suntop, Suntop_1, Yitpi) were measured 14 days after anthesis using a SPAD-502 chlorophyll meter (SPAD-502, Konica Minolta, Japan). For this purpose, individual spikes were tagged at anthesis when at least 50% of their spikelets were flowering. In addition, normalized difference vegetative index

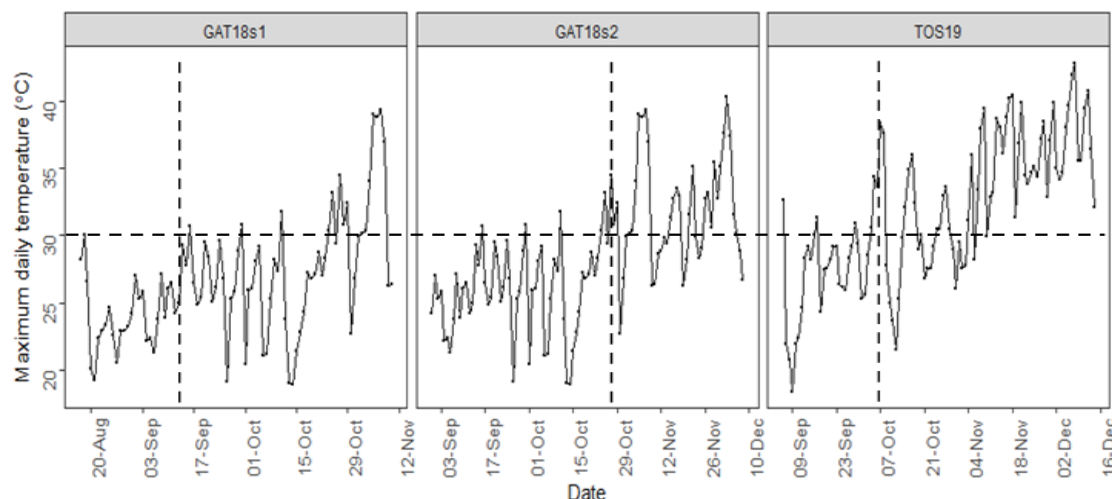
(NDVI) values were measured 14 days after anthesis (plots were considered at anthesis when at least 50% of plants had flowered) for each plot of the 28 genotypes at GAT18s2 and TOS19 using a handheld Green-seeker (Trimble Navigation Limited, Sunnyvale, CA, USA). As the focus was on comparing genotypic performance under environments experiencing heat stress, NDVI was not measured for the first sowing of GAT18s1. Plots were harvested with a combine harvester and individual grain weight of each plot was estimated from 2 or 3 sub-samples of 100 grains. For individual spikes, individual grain weight was estimated from all grains of the tagged spikes. Linear regression and statistical analyses were performed with R (R Core Team, 2018).

Table 1. Field trial characteristics including sowing dates, post-flowering mean temperature and post-flowering average daily max temperature, number of post-flowering hot days ($T_{\max} > 30^{\circ}\text{C}$), trial-mean for days from sowing to flowering or to harvest, as well as trial-mean grain yield.

Trial	Site	Sowing date	Post-flow. mean temp. ($^{\circ}\text{C}$)	Post-flow. max temp. ($^{\circ}\text{C}$)	Hot days after flow.	Days to flow.	Days to harvest	Grain yield (t/ha)
GAT18s1	Gatton	03/07/2018	19.6	26.2	1	73	116	5.12±32
GAT18s2	Gatton	31/08/2018	23.3	31.7	11	53	92	2.19±16
TOS19	Tosari	16/07/2019	21.5	30.7	12	75	109	2.71±29

Results and Discussion

The GAT18s2 and TOS19 trials experienced high temperatures more frequently ($T_{\max} > 30^{\circ}\text{C}$) from early to mid-grain filling (i.e. 7-20 DAA). At both locations, later sowings (GAT18s2 and TOS19) produced significantly lower yield than the mildest GAT18s1 trial ($P < 0.001$), which mainly received heat events



late during the grain filling (Figure 1; Table 1).

Figure 1. Variation in maximum daily temperature from sowing to harvest in GAT18s1, GAT18s2 and TOS19. Dashed vertical lines correspond to the trial-mean anthesis dates, while dashed horizontal line corresponds to a threshold temperature (30°C). GAT18s1 experienced only one hot day ($T_{\max} > 30^{\circ}\text{C}$) compared to GAT18s2 and TOS19, where crops received 11 and 12 hot days after flowering, respectively.

In 2018, a significant correlation ($R^2 = 0.67$, $P = 0.013$) was found between the greenness of the flag leaf 14 days after anthesis and individual grain weight in GAT18s2 (Figure 2), where crops were subjected to frequent heat events ($T > 30^{\circ}\text{C}$; Figure 1 and Table 1). In contrast, in GAT18s1, where heat events mostly occurred towards the end of the grain filling period, flag leaf greenness was not significantly correlated with individual grain weight for the tested genotypes ($R^2 = 0.46$, $P = 0.065$, Figure 2).

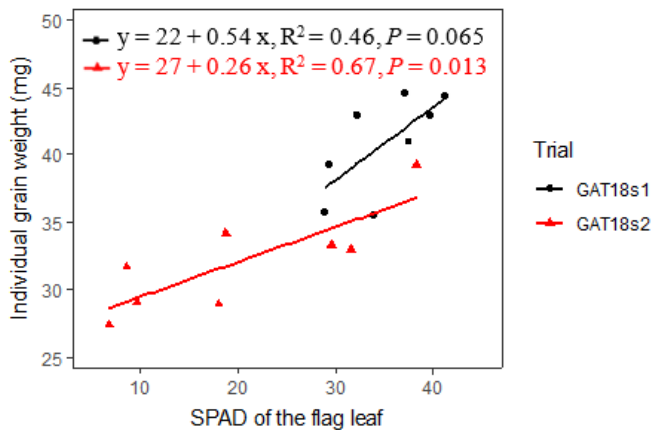


Figure 2. Relationships between individual grain weight and flag leaf greenness measured 14 days after anthesis for eight wheat genotypes in GAT18s1 (black) and GAT18s2 (red).

At the crop level, a positive and significant correlation between post-anthesis leaf greenness (measured with NDVI) and individual grain weight was found in GAT18s2, which experienced frequent heat events (Figures 1 and 3, Table 1). This correlation was also positive but not significant for crops in TOS19, which experienced heat and drought conditions during late grain filling (Figures 1 and 3, Table 1). At 14 days after anthesis, genotypic variations were observed in the two trials for both (i) NDVI, with variations from 0.35 to 0.65, and (ii) individual grain weight, with variations of over 10 mg per grain in both trials for the most contrasting lines ($P < 0.001$) (see details in Ullah et al. 2021).

It has been reported that genotypes with stay-green phenotype have an improved ability to fill grain and have better yield stability (Gregersen et al. 2008). Previous studies also showed positive relationships between stay-green and yield in standard conditions (in wheat, Christopher et al. 2016; in rice, Liu et al. 2017), and under heat stress (in wheat, Hazratkulova et al. 2012) or drought (in wheat, Christopher et al. 2016 and 2018; in sorghum, Borrell et al. 2000). Given the current trends in increased frequency of post-flowering heat stress (Ababaei and Chenu 2020) and the projected impact of post-flowering heat events in the future (Collins and Chenu 2021), breeding for genotypes with increased stay-green appears a promising way to sustain or improve wheat productivity.

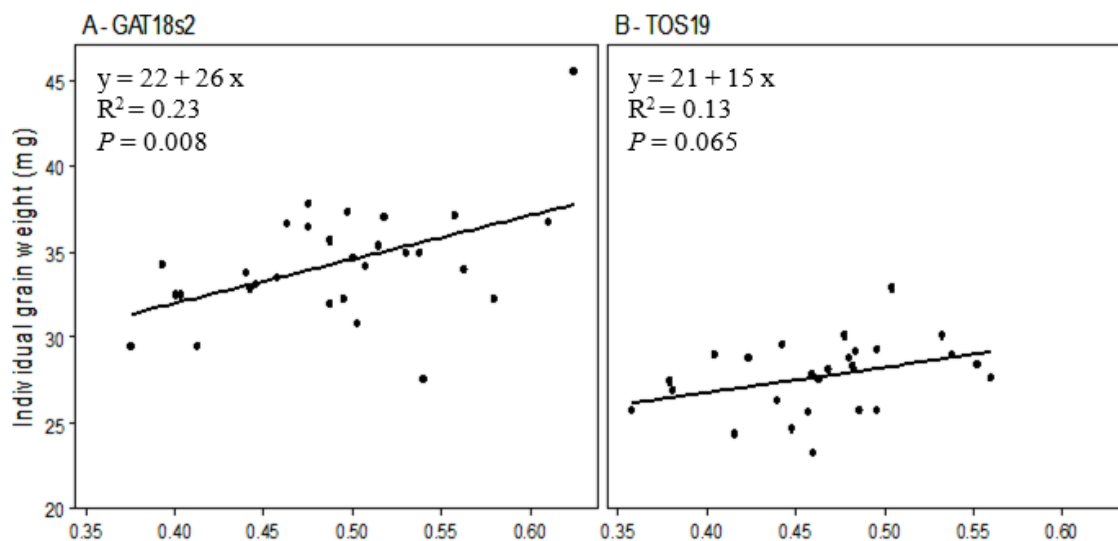


Figure 3. Relationships between individual grain weight and NDVI 14 days after anthesis for 28 wheat genotypes in GAT18s2 (A) and TOS19 (B).

Conclusion

In wheat, the grain filling period is highly sensitive to short episodes of heat stress that can accelerate senescence and adversely affect yield. Stay-green phenotypes with greater SPAD and NDVI 14 days after anthesis appeared to have superior ability to sustain individual grain weight and yield in the face of heat stress. However, this association was observed to weaken under extreme high temperatures associated with drought conditions. Overall, the results likely indicate that stay-green genotypes have improved photo-assimilates supply under warm conditions compared to more senescent types. The study suggests that stay-green is a promising trait to improve heat tolerance to post-flowering heat stress in wheat.

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