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Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat

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ABSTRACT

Short periods of heat stress in spring under Mediterranean climate can have large effects on crop yields. Most studies on heat stress have focused on crop responses to extended periods of high temperature under controlled environment conditions. There is limited information on the effects of short periods of heat stress on the yield of wheat. Therefore, field and controlled environment studies were undertaken to determine the effects of short-term heat stress on flag leaf senescence, as well as grain yield and its components. Wheat genotypes were exposed to heat stress for a single-day at two different stages: (H1) near flowering or green anther stage and (H2) early grain set or 7–10 days after anthesis (DAA) in 2009 and 2010. Heat treatment was applied in the field in a portable purpose-built heat chamber in which the temperature was steadily increased to a maximum of 35 °C, which was maintained for 3 h before being allowed to steadily decrease to the ambient temperature, like a typical spring heat event. Similar to the field studies, wheat genotypes were also exposed to a single-day heat event (35 °C maximum) in the controlled environment (CE) study. This single-day heat stress event caused a significant reduction in grain yield and yield components in both years. Heat stress (H1 or H2) accelerated the rate of loss of flag leaf chlorophyll content. A higher rate of senescence in 2009, which was warmer and drier than 2010, was associated with greater yield loss. Reduction in grain yield among the genotypes was negatively correlated ($r = -0.79$; $p < 0.001$) with the rate of flag leaf senescence. Heat stress reduced post-heading duration and grain yield across genotypes and heat stress treatments was strongly correlated ($r = 0.80$; $p < 0.001$ in 2009 and $r = 0.82$; $p < 0.001$ in 2010) with post-heading duration. There was also a significant ($p < 0.001$) positive correlation between wheat grain yield and grain number m^{-2} (2009: $r = 0.79$ and 2010: $r = 0.70$) and wheat grain yield and individual grain mass (IGM) at harvest ($r = 0.70$ in 2009 and $r = 0.82$ in 2010). Standardized partial regression coefficient (b) showed that of the two yield components the contribution of grain number ($b = 0.786$) to the grain yield was higher than IGM ($b = 0.435$) in 2009. In contrast, IGM ($b = 0.665$) appeared to be a stronger contributor to the grain yield than grain number ($b = 0.443$) in 2010. Grain yield loss of different wheat genotypes was strongly correlated ($r = 0.91$; $p < 0.001$) between the field and CE. The results of these studies showed that under field and CE conditions, Janz was consistently the most sensitive genotype to heat stress. In contrast, CM9-6Y, CM9-4Y and Krichauff appeared to be most tolerant to heat stress. Averaged over the two growing seasons and heat stress treatments, the reduction in grain yield was greater in Janz (25%) than in CM9-6Y and CM9-4Y (13% each), followed by Krichauff (16%) and Excalibur (18%). It could be suggested that early headed wheat genotypes with slower rate of leaf senescence after heat exposure and longer post-heading duration could be more tolerant to heat stress.

1. Introduction

Ambient temperatures have steadily increased since the beginning of this century and are predicted to continue rising because of climate change (IPCC, 2007). The frequency of extreme events such as the number of hot days is also anticipated to increase due to global warming (Pittock, 2003). This ongoing warming trend may increase the frequency and severity of heat stress and under such a scenario, crop production would benefit from strategies that improve tolerance of field crops to heat stress.

Wheat (*Triticum aestivum* L.) is usually exposed to short periods of high temperatures (33–40 °C) when crops are approaching flowering and grain filling (Stone and Nicolas, 1994; Dhadhwal, 1989). Such heat events are common in Mediterranean climates like that of the southern and western grains belt of Australia. Wheat crops worldwide experience heat stress to varying degrees at different

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phenological stages, but heat stress during the reproductive phase is more harmful than during the vegetative phase due to its direct effect on grain number and grain mass (Wollenweber et al., 2003). Photosynthesis is the most sensitive physiological process affected by high temperature in plants (Wahid et al., 2007) and a reduction in photosynthesis from heat stress is associated with a reduction in growth and grain yield in wheat (Al-Khatib and Paulsen, 1990; Wang et al., 2011). Heat stress reduces photosynthesis through disruption in the structure and function of chloroplasts, and reductions in chlorophyll content (Xu et al., 1995), which accelerates leaf senescence (Tewari and Tripathy, 1998). Leaf senescence is the progressive loss of green leaf area that occurs during reproductive development of a crop (Nooden, 1988), and is negatively associated with grain yield in wheat (Reynolds et al., 1994; Wang et al., 2011).

Heat stress during the few days immediately preceding anthesis can reduce grain number and grain yield of wheat (Calderini et al., 1999a,b; Calderini and Reynolds, 2000). Reduction in grain set was also observed when plants were exposed to a single day heat stress (30 °C) between booting and anthesis (Saini and Aspinall, 1982). Heat stress accelerates the rate of grain filling but grain filling duration is shortened (Tewolde et al., 2006; Dias and Lidon, 2009). However, reduction in the duration of grain filling under heat stress may not be fully compensated by increased grain filling rates (Stone et al., 1995). It has been reported that under heat stress conditions, the supply of photoassimilates may limit grain filling (Calderini et al., 2006; Talukder et al., 2013) and reduce the activity of key enzymes involved in starch accumulation in wheat grains (Zhao et al., 2008). Even a short period of episodic temperature over 30 °C slows starch accumulation and reduces grain growth in wheat due to heat induced denaturation of soluble starch synthase enzyme (Jenner, 1994).

Identifying genetic variation in tolerance to heat stress among wheat genotypes could play an important role in developing management strategies to cope with sustained increase in temperature associated with global climate change. Some differences among wheat genotypes in response to increasing temperatures have been reported previously (Al-Khatib and Paulsen, 1990; Bukovnik et al., 2009). Progress in selecting heat tolerant wheat genotypes in plant breeding programs could be accelerated if a suitable technique could be developed to simulate heat stress events in the field.

Previous information on the effects of heat stress on yield and its components has been mainly derived from pot-grown plants under controlled environment conditions (Stone and Nicolas, 1994, 1995a,b, 1998). Others have investigated heat stress by manipulating sowing dates (McDonald et al., 1983; Reynolds et al., 1994) or undertaking research at different locations (Reynolds et al., 1994; Lopes et al., 2012) due to difficulties in applying heat stress in the field. Only a few attempts have modified crop canopy temperature under field conditions (Fischer and Maurer, 1976; Ferris et al., 1998; Ugarte et al., 2007). Most studies have focused on crop responses to extended periods of high temperature. Therefore, there is relatively little data on the effects of short periods of heat stress near flowering and early grain set on the yield of wheat. The aim of this study was to examine the effect of a single-day heat stress event on flag leaf senescence, as well as grain yield and its components. This study also aims to compare the response of wheat genotypes exposed to heat stress in the field with those exposed to heat in a controlled environment chamber.

2. Materials and methods

2.1. Genotypes

Four Australian commercial bread wheat genotypes (Excalibur, Gladius, Janz and Krichauff) were grown in the field in 2009. Two additional CIMMYT breeding lines [TURACO/CHIL-CM92354-33M-OY-OM-6Y-OB-OBGD (abbreviated to CM9-6Y), TURACO/CHIL-CM92354-33M-OY-OM-4Y-OB (abbreviated to CM9-4Y) were also included in the field study in 2010. The CIMMYT lines were received from Australian Cereal Collection Centre. Wheat genotypes were selected on the basis of previous reports of sensitivity to heat stress. There is some evidence that Excalibur has superior heat tolerance than other wheat genotypes (Bukovnik et al., 2009); CM9-6Y was released as a heat tolerant cultivar in Bangladesh (BARI, 2011). The same set of six bread wheat genotypes were also evaluated for heat stress tolerance under controlled environment conditions in 2010.

2.2. Experimental design and conditions

2.2.1. Field study

The experimental setup has been detailed in Talukder et al. (2013). Briefly, field experiments were sown in a red chromosol soil according to the McKenzie et al. (2001) soil classification system at the Waite Campus of the University of Adelaide on June 26, 2009 and June 24, 2010. Each plot consisted of four rows, 1.5 m long × 0.5 m wide row spacing. Nitrogen (62 kg ha^{-1}) and phosphorus (20 kg ha^{-1}) fertilizers were applied as urea and di-ammonium phosphate (DAP) in three equal applications 30, 45 and 60 days after seeding. One manual weeding was done at the maximum tillering stage (Zadoks growth scale – ZGS = 24–27) (Zadoks et al., 1974) to control weeds. The experiments were sprayed with a fungicide to control leaf rust during the heading stage. The experiments were not irrigated in both years. Heat stress was applied to the middle two rows of designated plots as per treatments described below. The experiments were laid out in a split plot design with four replications. Wheat genotypes were placed in the main plots and heat stress treatments in the subplots.

During the wheat growing seasons in 2009 (June to November) and 2010 (June to December), the experimental site received 416 and 495 mm total rainfall, of which about 24% fell during the grain filling period (September to October). The average maximum temperature during September–October was 19.4° in 2009 and 17.1 °C in 2010. Furthermore, the mean maximum temperature during heading to physiological maturity was 25.0 °C in 2009 and 21.8 °C in 2010. In 2009, there were 8 consecutive days during grain filling with maximum temperature above 35 °C at later grain filling stage. In contrast, daily maximum temperature during grain filling did not exceed 35 °C in 2010. The long-term (1970–2013) daily average of maximum air temperatures during the grain filling period of wheat was 23 °C, whereas it was 28 °C in 2009 and 21 °C in 2010 (Fig. 1). However, there was a large variation in daily temperature in both seasons and experimental weather data can be found in Talukder et al. (2013).

Wheat genotypes were exposed to a single-day heat event (35 °C maximum) either near flowering when anthers were still green (H1 – green anther stage, ZGS 57–59), or at the early grain set stage at 7–10 days after anthesis (DAA) (H2 – ZGS 71–73) using heat chambers with dimensions of 1.5 m × 0.5 m × 1.2 m (L × W × H) and some plots were maintained as unheated control. The chambers were made from standard-Clear-Greca polycarbonate sheet. A 1200 W electric fan heater used in each chamber was connected to a thermostat and a power generator for providing heat. Heat chambers were placed over the crop rows during the heat treatment. Temperature and relative humidity inside the chambers were monitored by using a Tinytag logger (Gemini Data Loggers UK Ltd) placed at canopy height. The temperature inside the chamber was increased gradually as a step function to a maximum of 35 °C, which was maintained for 3 h. Thereafter the temperature was allowed to decrease steadily down to the ambient temperature by 5 pm (Talukder et al., 2013). This temperature regime was similar to the pattern of temperature that occurs during a spring heat event in