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A field and controlled environment evaluation of wheat (*Triticum aestivum*) adaptation to heat stress

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ABSTRACT

Heat stress is a major constraint on wheat (*Triticum aestivum* L.) production in many regions of the world. While research into heat stress tolerance has been conducted across many crop species, there are still significant gaps in our understanding of the impacts of heat stress on production, the level of genetic variation for heat stress tolerance in the field and the varying phenotypic responses to various yield components. Here, we report on the heat stress tolerance for 24 bread wheat (*Triticum aestivum* L.) genotypes which were evaluated across 13-environments over two growing seasons in the Mediterranean-type climate of southern Australia. Numerous climatic co-variates were measured to further understand interactions of temperature stress on crop performance. Not surprisingly, heat stress was found to have significant negative impacts on grain yield in field conditions, with reductions of 302 kg ha^{-1} $°C^{-1}$ for each day with maximum temperature in excess of 30°C during anthesis and a reduction of 161 kg ha^{-1} $°C^{-1}$ for each day with maximum temperature in excess of 30°C during grain fill. Genotype by environment interactions for grain yield performance under varying levels of heat stress were also observed in the field, suggesting that plant breeding selection strategies could be used to improve adaptation to heat stress. Additionally, all genotypes were phenotyped using a controlled environment assay (plants exposed to an air temperature of 36°C and a wind speed of 40 km h^{-1} for three consecutive, eight-hour days, 10 days post the end of anthesis). Significant differences in genotype performance for leaf senescence and leaf chlorophyll content in response to heat stress were identified under the controlled environment conditions. Further evaluation showed that some of the field genotype by environment interaction for heat stress tolerance could be explained by performance under controlled environment conditions. This suggests that detailed physiological studies in controlled environment conditions do relate to performance in field conditions.

1. Introduction

Abiotic constraints to bread wheat (*Triticum aestivum* L.) production, such as heat, drought and frost have negative effects on grain yield (Collins et al., 2008; Dolferus et al., 2011). Abiotic stresses are common throughout the Australian grain belt, particularly in southern Australia, where high temperatures at critical developmental stages significantly reduce grain yield potential (Zheng et al., 2012). Compounding this is the frequent co-occurrence of multiple types of abiotic stress particularly hot, windy and terminal-drought conditions (Machado and Paulsen, 2001; Shah and Paulsen, 2003). To minimise the effect of abiotic stress on crop production, winter cereals grown in environments with a Mediterranean-type climate are typically sown so that plants develop during the cooler winter months. Generally this results in anthesis occurring before the characteristic warmer and drier conditions of late spring and early summer. Mediterranean-type climates are typically prone to brief periods of high temperatures during late spring with maximum daily temperatures of 35°C or greater, accompanied by winds in excess of 40 km h^{-1} (Alexander et al., 2010; Talukder et al., 2013). Additionally, climate change predictions suggest that such events may become more frequent (Hayman et al., 2012).

Accumulated thermal units, are fundamental to plant growth and an important driver of plant growth and productivity. As discussed by Porter and Gawith (1999), there are optimal temperatures for plant growth and function that vary depending on the developmental stage of the plant. Associated with this are minimum temperatures and

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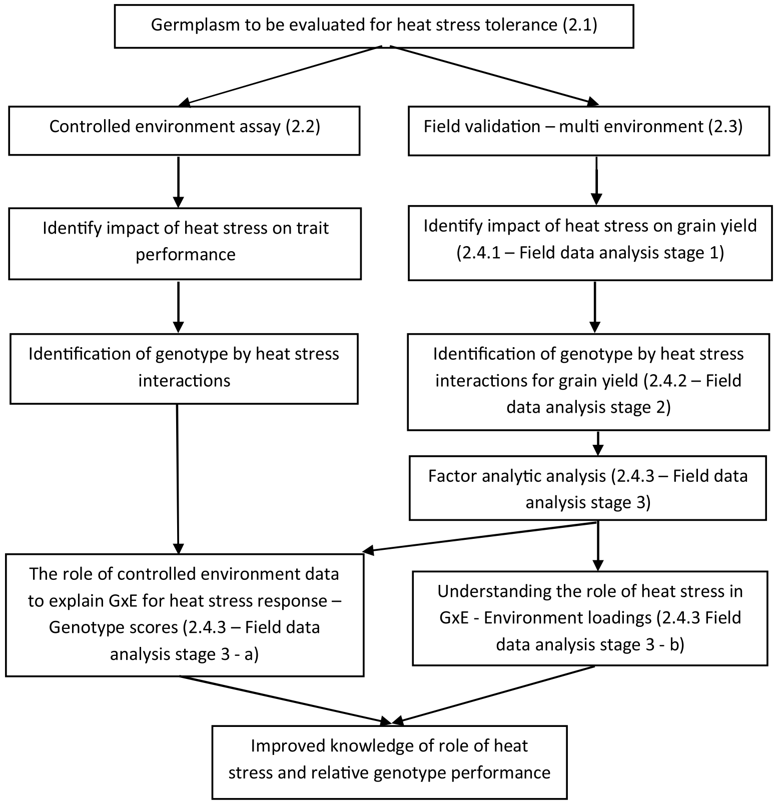

Fig. 1. Flowchart of the assays used to evaluate heat stress response and the analyses used to evaluate heat stress interactions and genotype performance (numbers in parentheses indicate the relevant section of the materials and methods).

maximum temperatures where it is understood that plant function virtually stops, with limited ability for plant function to recover. For wheat, Porter and Gawith (1999) reported this as being a minimum temperature of 9.5°C, optimal temperature of 21°C and maximum temperature of 31°C for anthesis. Minimum temperature of 9.2°C, optimal temperature of 20.7°C and maximum temperature of 35.4°C for grain fill. The focus of the current study is the impact of high temperatures (above optimum) on wheat productivity.

The interaction between high temperatures and wheat plants is complex with numerous physiological processes adversely affected (Wahid et al., 2007). Reproductive tissues in wheat are sensitive to heat stress as early as the young microspore stage of pollen development (Saini et al., 1999; Dolferus et al., 2011). However, in many environments (such as southern and western Australia), wheat is rarely exposed to heat stress at this growth stage but rather more frequently around anthesis and during grain fill (Alexander et al., 2010). During anthesis, heat stress reduces pollen viability and subsequently reduces fertilisation and seed set (Barnabas et al., 2008). During grain fill, temperature stress negatively effects starch and protein accumulation (Bhullar and Jenner, 1985; Zahedi et al., 2004). Plant development is accelerated by elevated temperatures, reducing grain fill duration and consequently grain size (Wardlaw, 1994; Stone and Nicolas, 1995b; Wollenweber et al., 2003; Sharma et al., 2008). Heat stress also accelerates leaf senescence, thus reducing plant photosynthetic capacity (Tewolde et al., 2006; Talukder et al., 2014). These factors all contribute to reduced grain yield. This has been demonstrated by Bennett et al. (2012a) and Kuchel et al. (2007a) who identified a reduction of up to 187 kg ha^{-1} for every one degree increase in average temperature during anthesis and grain fill in multi-year field experiments across southern Australia. However, genotypic variation for response to heat stress has been identified under controlled environment conditions (Stone and Nicolas, 1995a; Esten Mason et al., 2011), providing scope for improved performance under stress conditions.

Delayed sowing has commonly been used to identify heat stress tolerant phenotypes in the field in an effort to move sensitive reproductive stages to coincide with higher incidence of heat stress (Reynolds et al., 2007; Pinto et al., 2010; Bennett et al., 2012b; Esten Mason et al., 2013; Sadras et al., 2015). Although increased exposure to heat stress can be achieved, plants are also exposed to a range of abnormal environmental conditions during crop development including longer photoperiod and altered plant available water (Sadras et al., 2015). This can create an unrepresentative growing environment, particularly for a Mediterranean-type climate, so caution is required in comparing results from delayed-sowing experiments with those from agronomically recommended sowing dates. Alternative field methodologies, such as those used by Alexander et al. (2010) and Talukder et al. (2013), include using chambers in the field to limit confounding environmental factors while managing heat stress conditions. Such methods allow heat stress to be achieved within an agronomically representative environment. However, the physical encumbrance of handling chambers in field conditions limits capacity to screen large breeding populations to identify superior performing phenotypes.

Furthermore, identifying a true heat stress tolerant phenotype is difficult under field conditions due to other confounding abiotic stresses, such as drought and spring radiation frost occurring at similar developmental stages. The temperature, duration and timing of heat stress events can also differ across seasons, thus reducing the reliability and repeatability of the phenotypic screen. Variation in time-to-anthesis within the germplasm being evaluated may also mean that naturally occurring heat stress arises at different growth stages for each genotype studied. This may lead to selection for stress escape (through earlier/later maturity) rather than true genetic stress tolerance. To overcome these limitations, controlled environment phenotypic screens have been developed to manage these factors (Tashiro and Wardlaw, 1990; Stone and Nicolas, 1995a; Esten Mason et al., 2010, 2011; Maphosa et al., 2014). However, none of these reports have validated genotypic