



Sorghum genotypes differ in high temperature responses for seed set



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ABSTRACT

Significant genotypic differences in tolerance of pollen germination and seed set to high temperatures have been shown in sorghum. However, it is unclear whether differences were associated with variation in either the threshold temperature above which reproductive processes are affected, or in the tolerance to increased temperature above that threshold. The objectives of this study were to (a) dissect known differences in heat tolerance for a range of sorghum genotypes into differences in the threshold temperature and tolerance to increased temperatures, (b) determine whether poor seed set under high temperatures can be compensated by increased seed mass, and (c) identify whether genotypic differences in heat tolerance in a controlled environment facility (CEF) can be reproduced in field conditions. Twenty genotypes were grown in a CEF under four day/night temperatures (31.9/21.0 °C, 32.8/21.0 °C, 36.1/21.0 °C, and 38.0/21.0 °C), and a subset of six genotypes was grown in the field under four different temperature regimes around anthesis. The novelty of the findings in this study related to differences in responsiveness to high temperature—genotypic differences in seed set percentage were found for both the threshold temperature and the tolerance to increased maximum temperature above that threshold. Further, the response of seed set to high temperature in the field study was well correlated to that in the CEF ($R^2 = 0.69$), although the slope was significantly less than unity, indicating that heat stress effects may have been diluted under the variable field conditions. Poor seed set was not compensated by increased seed mass in either CEF or field environments. Grain yield was thus closely related to seed set percentage. This result demonstrates the potential for development of a low-cost field screening method to identify high-temperature tolerant varieties that could deliver sustainable yields under future warmer climates.

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1. Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is a major dryland summer grain crop grown in semi-arid, subtropical areas where short episodes of high temperature stress can adversely affect crop growth and development. Maximum temperatures in many sorghum growing areas are around or exceed 32 °C for both vegetative and reproductive stages (Prasad et al., 2006a). High temperature stress is expected to become more frequent under future climate scenarios, as average temperatures are likely to rise by 0.5°–2.5 °C (IPPC, 2007). This includes the sorghum-belt of eastern Australia, where climate predictions indicate an increase in the number of days with maximum temperature above 35 °C

(Hennessy et al., 2010). This predicted increase in temperature can have a negative impact on plant growth and development, and could lead to a decline in crop productivity (Muchow et al., 1994). Therefore, identifying and developing high temperature stress tolerant sorghum lines is important to minimize the negative effect of future climate change.

The adverse effects of high temperature are generally more pronounced on reproductive than on vegetative processes (Prasad et al., 2006a; Nguyen et al., 2013). Hence, even though high temperature stress events can delay phenology because of changes in leaf growth patterns (Prasad et al., 2006b, 2008; Craufurd and Wheeler, 2009), pollen germination and seed set are amongst the processes that are most sensitive to heat stress (Saini and Aspinall, 1982; Ferris et al., 1998; Prasad et al., 2006a; Devasirvatham et al., 2010; Nguyen et al., 2013). Previous studies found that high temperature stress around anthesis can decrease pollen germination and seed set in cereals (Barnabas et al., 2008), including rice (*Oryza sativa*

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Table 1

List of genotypes used in this study, ranked from most (top) to least (bottom) tolerant based on seed set percentage under high temperature (38 °C) (Nguyen et al., 2013). Genotypes in bold were included in the field study.

Genotype	Characteristics ^a
R9403463-2-1	Elite male parent line, DAFF ^b breeding program
IS 8525 ^b	Landrace with excellent pollen quality in low temperature, Ethiopia
CCH1 ^c	Commercial hybrid, Australia
AQL33/QL36^c	Hybrid, Australia
BTx623	Elite female parent line, USA
PI609489 ^b	Breeding line, Mali
PI563516 ^b	Breeding line, Mali
R9188	Derivative of sweet sorghum line, USA
Tx7000	Early flowering male parent line, USA
Ai4 ^b	Photoperiod insensitive, possibly cold tolerant line, China
KS4	Ancestral female parent line, USA
CCH2 ^c	Commercial hybrid, Australia
QL33	Elite parent line, DAFF breeding program
B963676	Elite female parent line, Australia
Tx642 (B35)	Partially converted durra landrace, Ethiopia
R931945-2-2	Male parent with low pollen quality at low temperatures, DAFF breeding program
SC170-6-8	Partly converted caudatum line, Ethiopia
B923296	Elite heat sensitive female parent line, DAFF breeding program
Not ranked	
QL12^d	Male parent line, Australia
QL36^d	Elite male parent line, DAFF breeding program

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^b Double dwarf genotype.

^c Hybrid genotype.

^d Not ranked, because of poor seed establishment in the 38 °C treatment.

and *Oryza glaberrima*) (Prasad et al., 2006b) and sorghum (Prasad et al., 2008; Nguyen et al., 2013). Studies on sorghum and rice with a range of temperatures around anthesis found genotypic differences in the response of pollen viability and seed set to high temperatures (Prasad et al., 2006b; Nguyen et al., 2013). However, it is unclear whether these differences were associated with differences in the threshold temperature, defined as the temperature above which a detectable reduction in a physiological process occurs (Wahid et al., 2007), or in the tolerance to increased temperature above that threshold. Identification of temperature thresholds provides a basis for climate risk assessment on crop growth and development due to future climate change (Wahid et al., 2007; Luo, 2011), as genotypes with a high temperature threshold are less likely to be affected by temperature increase in the short term than genotypes with a lower threshold.

Selection for improved seed set under high temperatures will only be useful if increased seed set is not offset by a reduction in individual seed mass. Under optimum growing conditions, a reduction in seed number can increase individual seed mass of sorghum as a consequence of increased assimilate availability per grain (Gambín and Borrás, 2007; Yang et al., 2009). Although grain yield compensation was only partial when half the spikelets were removed at anthesis (Gambín and Borrás, 2007; Yang et al., 2009), more complete yield compensation could potentially occur in case of a more moderate reduction in seed set percentage following mild heat stress. This would potentially mitigate adverse effects of heat stress on grain yield.

A prerequisite to the development by breeding programs of high-temperature tolerant germplasm is the availability of a fast and reliable screening platform under field conditions. The development of such a phenotyping system may be hampered by the daily fluctuations in maximum temperature, which influence the precision of individual trials and repeatability across trials (Wahid et al., 2007; Cottee et al., 2012). Ehlers and Hall (1998) suggested screening of plants for high temperature stress in hot

environments, provided a threshold temperature is reached around the critical growth stage, and lines with greater yield could be selected. Field based high temperature tents have been used to screen for temperature tolerance in cotton (*Gossypium hirsutum* L.) (Cottee et al., 2010). Although reliability and repeatability can be poor because of interactions with other environmental factors under field conditions, controlled environment experiments are likely to be much more expensive. Application of a field-based phenotyping platform in a breeding program therefore requires a screening system that is representative of results from controlled environments.

In a recent study in a controlled environment facility (CEF) with two maximum temperatures (optimum 32 °C and high 38 °C), sorghum genotypes differed in both pollen germination and seed set under high temperature. The two traits were highly correlated across genotypes and temperature regimes, suggesting that the decrease in seed set was a consequence of a reduction in pollen germination (Nguyen et al., 2013). These findings indicated that seed set percentage could be a useful screen to identify germplasm that is tolerant to high temperatures. Thus, the objectives of this study were to (a) dissect known differences in heat tolerance for a range of sorghum genotypes into differences in the threshold temperature and tolerance to increased temperatures, (b) determine whether poor seed set under high temperatures can be compensated by increased seed mass, and (c) verify whether genotypic differences in heat tolerance in a CEF can be reproduced in field conditions.

2. Materials and methods

2.1. Genetic material

Twenty sorghum genotypes, including 17 inbred lines and three hybrids, were used in the CEF study (Table 1). The genotypes represented a diverse range of germplasm used by the sorghum pre-breeding program in Queensland, Australia (Jordan et al., 2011). Previous analyses indicated a wide variation in pollen germination and seed set percentage under high temperatures for 18 of the 20 genotypes (Nguyen et al., 2013). A subset of six of these sorghum genotypes with comparable phenology, but contrasting levels of heat tolerance, was selected for the field experiment (Table 1).

2.2. Controlled environment experiment

Procedural details for the experiments conducted in the CSIRO CEF, St. Lucia, Queensland, Australia, have been described in detail by Nguyen et al. (2013). In this study, an additional two intermediate temperature regimes were added to those reported by Nguyen et al. (2013). Briefly, plants were grown at four different temperatures in four chambers that were each 3 m long, 2.7 m wide, and 3.6 m high, and had fully automated control of temperature, photoperiod, and relative humidity (RH). Photoperiod was set at 14 h and the light level (350–850 nm) to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at canopy height. The target maximum and minimum temperatures for each chamber were 30/22 °C, 33/22 °C, 36/22 °C and 38/22 °C, but actual temperatures were 31.9/21.0 °C, 32.8/21.0 °C, 36.1/21.0 °C and 38.0/21.0 °C. The minimum temperature was maintained throughout the 10 h dark period. Around 1 h after the onset of the light period, temperature was gradually increased at a rate of around 3 °C h⁻¹, until the pre-set maximum temperature was reached (Fig. 1). The temperature was maintained at its maximum and then gradually dropped at a rate of 3 °C h⁻¹, until the minimum temperature was reached just before the end of the light period. Hence, all treatments experienced similar temperatures, except during the middle of the light period, when maximum

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