Accepted: 2 March 2018
DOI: 10.1111/jac.12279



WILEY Journal of Agronomy and Crop Science

HEAT STRESS

# Thresholds, sensitive stages and genetic variability of finger millet to high temperature stress

R. A. Opole[1,2] | P. V. V. Prasad[1] | M. Djanaguiraman[1,3] | K. Vimala[1] | M. B. Kirkham[1] | H. D. Upadhyaya[1,4]

[1]Department of Agronomy, 2004 Throckmorton Plant Sciences Center, Kansas State University, Manhattan, KS, USA

[2]Kenya Agricultural and Livestock Research Organization, Kakamega, Kenya

[3]Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore, India

[4]International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Telangana, India

**Correspondence**
P. V. Vara Prasad, Department of Agronomy, 2004 Throckmorton Plant Science Center, Manhattan, KS, USA.
Email: vara@ksu.edu

**Funding information**
Department of Agronomy, Kansas State University; United States Agency for International Development, Grant/Award Number: AID-OAA-L-14-00006; The United States Department of Agriculture–Agricultural Research Service

## Abstract

Finger millet [*Eleusine coracana* (L.) Gaertn.] is an important coarse cereal crop grown in the arid and semi-arid regions and often experiences high temperature (HT) stress. The objectives of this research were (i) to quantify effects of season-long HT stress on physiological and yield traits, (ii) to identify the developmental stages most sensitive to HT stress and (iii) to quantify the genetic variability for HT stress tolerance in finger millet. Research was conducted in controlled environment conditions. HT stress decreased the chlorophyll index, photosystem II activity, grain yield and harvest index. Maximum decrease in number of seeds per panicle and grain yield per plant was observed when stress was imposed during booting, panicle emergence or flowering stages. Maximum genotypic variation was explained by panicle width and number of seeds per panicle at optimum temperature (OT) and grain yield per plant at HT and number of seeds at HT. Based on the stress response and grain yield, tolerant or susceptible genotypes were identified. Finger millet is sensitive to HT stress during reproductive stages, and there was genotypic variability among the finger millet genotypes for number of seeds per panicle and grain yield under HT, which can be exploited to enhance stress tolerance.

**KEYWORDS**
abiotic stress, finger millet, genetic variability, high temperature stress, season-long, sensitive stage

## 1 | INTRODUCTION

Finger millet [*Eleusine coracana* (L.) Gaertn.] is an important small millet cultivated in arid and semi-arid regions of the world for food and nutritional security at minimal cost compared with major cereals (Gupta et al., 2017; Satish, Ceasar, & Ramesh, 2017). Finger millet occupies ~12% of the global millet area, and the major producers are Uganda, India, Nepal and China. Finger millet annual world production is 4.5 million tons of grain, of which Africa produces 2 million tons (Upadhyaya, Gowda, Pundir, Reddy, & Singh, 2006). Finger millet needs very little water for their production and can be cultivated under non-irrigated conditions or in very low rainfall regimes (200–500 mm). The optimal day and night temperature for finger millet growth and development is 27–32 and 22°C, respectively. The critical daytime and night-time temperature is 18–32 and 18°C, respectively. Temperature >32°C inhibits flowering in finger millet (Board on Science and Technology for International Development, 1996; Directorate of Millets Development, 2014; Krishna, 2014). Temperatures close to or >32/22°C are common in the semi-arid regions of the world (Prasad, Boote, & Allen, 2006), where finger

**Research highlight:** We quantified impact of high temperature (HT) stress to determine thresholds, sensitive stages and genetic variability of finger millet. HT stress decreased number of seeds per panicle and seed yield per panicle. The periods of gametogenesis and anthesis were most sensitive to HT stress affecting seed yield. There was genetic variability for HT stress tolerance in finger millet that can be exploited to develop HT stress tolerant genotypes.

  

millet is an important food crop. With the anticipated global warming, these regions will be subjected to even higher temperatures. Therefore, quantifying the impacts of high temperatures on reproductive growth and yield processes of finger millet is needed.

Climate models predict that the arid and semi-arid regions of the world are highly vulnerable to climate change, and in future, the frequency of extreme events such as drought and high temperature (HT) will be greater (Challinor, Wheeler, Garforth, Craufurd, & Kassam, 2007; Lobell, Schlenker, & Costa-Roberts, 2011; Sivakumar & Stefanski, 2011; Zeng, Neelin, Lau, & Tucker, 1999). Global mean surface air temperatures have increased by 0.5°C in the 20th century, and it is predicted to increase further by 1.4–3.1°C at the end of 21st century (IPCC, 2013). The increase in temperature is brought by differential changes in daytime maximum and night-time minimum temperatures. Most climate models predict that, in future, the increase in night-time minimum temperature will be higher than the daytime maximum temperature (Dai, Wigley, Boville, Kiehl, & Buja, 2001). In addition to rising mean annual temperatures, the frequency, duration and severity of periods with extreme HT will also increase (Easterling, Meehl, & Parmesan, 2000; Tripathi, Tripathi, Chauhan, Kumar, & Singh, 2016). Increases of temperature may cause yield declines between 2.5% and 10% across a number of agronomic crop species (Hatfield et al., 2011). The climate models predict that the global crop yields will reduce by roughly 1.5% per decade without effective climate change adaptation measure (Lobell & Gourdji, 2012). Temperature projections for sub-Saharan Africa (SSA) for all seasons have indicated that, the average temperature will increase by 0.3–4°C by end of this century (Boko et al., 2007). In many parts of SSA, increased both frequency and intensity of extreme weather events are projected (IPCC, 2013). The temperature projections for South Asia indicated an increase of 3.3°C by the end of this century. The increase in temperature will be more pronounced during winter than in summer (IPCC, 2007).

In crop plants, HT stress tolerance is a complex phenomenon involving an array of biochemical and physiological processes happening at organelle, cellular and whole plant level (Bita & Gerats, 2013; Bokszczanin & Fragkostefanakis, 2013; Mathur, Agrawal, & Jajoo, 2014; Prasad, Bheemanahalli, & Jagadish, 2017; Wahid, Gelani, Ashraf, & Foolad, 2007). HT stress decreases crop yields by (i) faster crop development leading to shorter crop duration, (ii) impacting rates of photosynthesis, respiration and grain filling rate and duration, (iii) an increase in the saturation vapour pressure of air leading to reduced water use efficiency and (iv) damaging the cell ultrastructure (Lobell & Gourdji, 2012; Ray, Gesch, Sinclair, & Allen, 2002; Stone, 2001; Ziska, Blumenthal, Runion, Hunt, & Diaz-Soltero, 2011). Studies have shown that when plants are subjected to mild HT stress (1–4°C above optimal growth temperature), there were moderate decreases in yield (Sato, 2006; Tesfaendrias, McDonald, & Warland, 2010; Timlin et al., 2006; Wagstaffe & Battey, 2006). However, exposure to a more intense HT stress (>4°C above optimum) results in severe yield loss and even complete crop failure (Gote & Padghan, 2009; Kadir, Sidhu, & Al-Khatib, 2006; Sato, Peet, & Thomas, 2000; Tesfaendrias et al., 2010). The impacts of HT stress on yield were quantified for major field crops [rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), sorghum (*Sorghum bicolor* L., Moench), pearl millet (*Pennisetum glaucum* L. R.Br.), dry bean (*Phaseolus vulgaris* L.), peanut (*Arachis hypogea* L.) and soybean (*Glycine max* L.) (reviewed in Prasad et al., 2017). However, little information is available on effect of HT stress on finger millet yield and its components.

Research on various cereals revealed that HT stress decreased chlorophyll content, photosystem II quantum yield, photosynthetic rate and economic yield (Djanaguiraman, Prasad, Murugan, Perumal, & Umesh, 2014; Narayanan, Prasad, Fritz, Boyle, & Gill, 2015; Sunoj, Shroyer, Jagadish, & Prasad, 2016). Studies on rice, wheat, maize (*Zea mays* L.), sorghum, pearl millet, peanut, cowpea (*Vigna unguiculata* L.) and common bean indicated that reproductive stage appears to be more vulnerable to HT than vegetative stages of crop development (reviewed in Hatfield et al., 2008, 2011; Prasad & Djanaguiraman, 2014; Prasad et al., 2017). Studies on maize (Schoper, Lambert, Vasilas, & Westgate, 1987), wheat (Ferris, Ellis, Wheeler, & Hadley, 1998; Prasad, Pisipati, Ristic, Bukovnik, & Fritz, 2008), rice (Matsui, Omasa, & Horie, 2001; Prasad, Boote, Allen, Sheehy, & Thomas, 2006; Prasad et al., 2017) and sorghum (Djanaguiraman et al., 2014; Prasad, Djanaguiraman, Perumal, & Ciampitti, 2015) indicated that HT stress during reproductive stages decreased the number of seeds per panicle and individual seed weight, resulting in lower grain yields. Grain numbers are a result of successful fertilization (seed set), which mainly depends on the functionality of male (pollen) and female (ovule) gametes. Adverse environmental conditions during floral development and anthesis can negatively influence gametes viability and its functions leading to decrease in floret fertility, consequently, seed set (Djanaguiraman, Perumal, Ciampitti, Gupta, & Prasad, 2017; Djanaguiraman et al., 2014; Prasad, Boote, Allen, Sheehy et al., 2006). HT stress during the grain filling period decreases individual grain size due to shorter grain filling duration (Prasad, Pisipati, Mutava, & Tuinstra, 2008) and/or grain filling rate (Dias & Lidon, 2009; Prasad, Boote, & Allen, 2006, Prasad, Pisipati, Ristic et al., 2008). The impacts of HT stress during the reproductive stage of finger millet are not known. Improved knowledge on how finger millet responds to HT stress and quantifying the response will help to develop crop, soil, nutrient and water management practices that can enhance resilience to changing environments.

Existence of genetic variability for HT stress tolerance is a critical factor for the development of more HT-tolerant cultivars. Genetic diversity among germplasm with varied degree of HT stress tolerance has been well documented in cereals such as rice, wheat, sorghum and pearl millet (Djanaguiraman et al., 2014, 2017; Nguyen et al., 2013; Pradhan, Prasad, Fritz, Kirkham, & Gill, 2012; Prasad, Boote, Allen, Sheehy et al., 2006). In cereals, the HT-tolerant genotypes are defined by maintenance of photosynthesis, chlorophyll content and stomatal conductance under HT stress, while the yield of these genotypes is maintained through higher seed set, grain number and individual grain weight at HT (Djanaguiraman et al., 2014, 2017; Nguyen et al., 2013; Pradhan et al., 2012; Prasad, Boote, Allen, Sheehy et al., 2006; Prasad et al., 2017; Singh et al.,

2015; Yang, Sears, Gill, & Paulsen, 2002). However, research on quantifying genetic variability for HT stress in finger millet is limited. Hence, the objectives of this research were (i) to quantify effects of HT stress on physiological and yield traits, (ii) to identify the developmental stages of finger millet most sensitive to HT stress and (iii) to quantify the genetic variability for HT stress tolerance in finger millet.

## 2 | MATERIALS AND METHODS

Studies were conducted in controlled environmental facilities in the Department of Agronomy at Kansas State University, Manhattan, Kansas, USA.

### 2.1 | Effects of season-long HT stress

To determine the season-long HT stress effects on growth, physiology and yield, ten seeds of the finger millet genotype, 27116701 SD, were sown at the 2-cm depth in 3.8 L PVC pots containing Metro Mix 350 (Hummert International, Topeka, KS, USA). A controlled release fertilizer, Osmocote Classic 90551 (19-6-12, N-P-K) (Scotts, Marysville, OH, USA), was incorporated into the rooting medium at the manufacturer's recommended rate of 1.8 kg/m$^3$ before sowing. Three indoor growth chambers (Conviron Model CMP 3244, Winnipeg, Manitoba, Canada) were used to impose various temperature treatments. Each growth chamber was 75 cm wide, 180 cm long and 185 cm high. After emergence, the plants were thinned to three per pot.

All the three growth chambers were maintained at daytime maximum/night-time minimum temperatures of 32/22°C from sowing until 10 days after emergence. Then, the three temperature treatments were imposed by changing the temperature of growth chambers to 32/22°C (OT), 36/26°C ($HT_1$) and 38/28°C ($HT_2$) representing three temperature regimes until maturity. Daytime and night-time temperatures were held for 12 hr (6 hr each) with a 6-hr transition period between each daytime maximum and night-time minimum temperatures. The photoperiod was 12 hr, and photon flux density (400–700 nm) provided by cool fluorescent lamps was 940 μmol m$^{-2}$ s$^{-1}$ measured at canopy level. Relative humidity in the chambers was uniformly set at 85%. The relative humidity was maintained inside the growth chamber by automated spray of water as fine mist by the growth chamber inbuilt program. Air temperature and relative humidity were continuously monitored at 20-min intervals in all growth chambers until maturity. The pots had drainage holes and were watered daily to pot capacity to keep adequate soil moisture to avoid water stress. Pots (50 in number) were randomly moved within each growth chamber to eliminate any positional bias with reference to treatment effects (temperature).

At the vegetative stage (5th visible leaf stage), one plant in each pot (about 3–5 pots) was tagged for measuring leaf physiological traits. A self-calibrating chlorophyll meter (SPAD, Model 502; Spectrum Technologies, Plainfield, IL, USA) was used for measuring chlorophyll index. Photosystem II quantum yield (Fv/Fm ratio) was measured using a pulse-modulated chlorophyll fluorometer (OS5p; Spectrum Technologies, Plainfield, NH, USA). Leaf level photosynthesis, stomatal conductance, transpiration and leaf temperature were measured on individual, attached, top most fully expanded leaves in the top 2nd internode from tagged plants in different pots using a LI-6400XT Portable Photosynthesis System (LI-COR; Lincoln, NE, USA). Gas exchange measurements were taken at growth temperature and ambient $CO_2$ (400 μmol m$^{-2}$ s$^{-1}$) conditions. The internal LED light source in the LI-6400XT was set at 1,600 μmol m$^{-2}$ s$^{-1}$, and gas exchange was recorded during vegetative, booting, 50% flowering and 50% grain fill stages.

At maturity, one plant from each pot was removed carefully, washed in tap water and data on plant height (the maximum height from the base of the stem to tip of the plant), number of leaves per plant, number of tillers per plant and internode length (cm) were recorded. Internode length was determined by taking an average of 3 internodes in the middle of the canopy (6th through 8th internode). The leaves were removed, and the area was measured using a portable leaf area meter (LI-3000, LI-COR; Lincoln, NE, USA) and expressed as cm$^2$ per plant. The leaves and stems were dried at 65°C for 7 days and weighed.

To record the yield and its components, plants in five different pots were chosen and tagged at the heading stage. At physiological maturity, the number of panicles per plant was recorded and the tagged panicle was harvested and dried at 40°C for 10 days. The number of fingers per panicle, length of finger (cm), number of seeds per panicle and seed dry weight (g) were recorded from the tagged panicle. All the panicles were dried and hand-threshed to determine grain yield (g) per plant, 100-seed weight (g) and harvest index (ratio of grain yield to total above ground biomass). The 100-seed weight (g) was estimated as the ratio of total seed dry weight to total number of seeds and multiplied by 100.

### 2.2 | Effects of short episodes of HT stress

To identify the HT sensitive stages of finger millet, ten seeds of the finger millet genotype, 27116701 SD, were sown in the greenhouse maintained at 27/18°C (daytime maximum and night-time minimum temperature) and 50% RH as mentioned earlier. The photon flux density (400-700 nm) provided by natural sunlight was around 400–900 μmol m$^{-2}$ s$^{-1}$ during the crop growing season. All the plants (30 pots) were maintained in the greenhouse until the start of the booting stage then moved to a growth chamber maintained at 27/18°C (OT: daytime maximum/night-time minimum temperature). At the designated stage [booting, panicle emergence, flowering, 10, 20, 30 and 40 days after flowering (DAF)], three pots (3 plants/pot) were transferred to growth chambers maintained at 38/28°C (HT: daytime maximum/night-time minimum temperature) for short periods (10 days) and returned back to the greenhouse. Uniform plants at similar developmental stages were selected based on plant height and number of leaves to impose the HT stress. A set of three pots were continuously maintained from booting to 40 DAF at OT and

HT to serve as controls. The RH was set and maintained at 85%. The other growth conditions were the same as season-long HT stress experiment. At maturity, data on plant height (cm), number of leaves per plant, leaf area ($cm^2$) per plant, number of panicles per plant, number of fingers per panicle and finger length (cm) were recorded on the tagged plants/panicles as mentioned earlier. Plants were separated into component parts (leaf and stem) and dried at 65°C for 7 days. Panicles were dried at 40°C for 10 days, hand-threshed, and number of seeds per panicle, 100-seed weight (g) and grain yield per plant were recorded.

## 2.3 | Genetic variability for HT stress tolerance

Fifty-one finger millet germplasm lines of the minicore collection were obtained from ICRISAT, Hyderabad, Telangana, India and sown at 2-cm depth in 1.8 L pots (pot diameter at the top and bottom was 21 and 16 cm, respectively, pot depth was 20 cm) containing commercial Sun Grow Metro Mix 200 potting soil (Hummert International, Topeka, KS, USA). The seedlings were grown in four large growth chambers at optimum temperature (OT; 30/20°C, daytime maximum and night-time minimum). The pots were randomly arranged within each growth chamber to avoid positional effects within the chamber. The crop husbandry and growth chamber conditions were similar to those mentioned in previous sections. Finger millet plants were grown under OT from seedling emergence until booting. Thereafter, a set of five pots were transferred from the OT to HT stress conditions (38/28°C daytime maximum/night-time minimum) at booting stage. The duration of stress was 14 days. After the stress period, the plants were returned to OT, where it remained until final harvest at maturity. Control plants (five pots) remained under OT from seedling emergence to final harvest at maturity.

The chlorophyll content and thylakoid membrane damage were recorded in all the genotypes on 14th day of temperature treatment using SPAD meter and OS30p chlorophyll fluorometer, respectively. In each pot, the panicle from main tiller was tagged with cotton thread. At maturity, the tagged panicle was hand-harvested and dried at 40°C for 7 days. The number of fingers per panicle, panicle length, panicle width, finger length, finger width was measured in

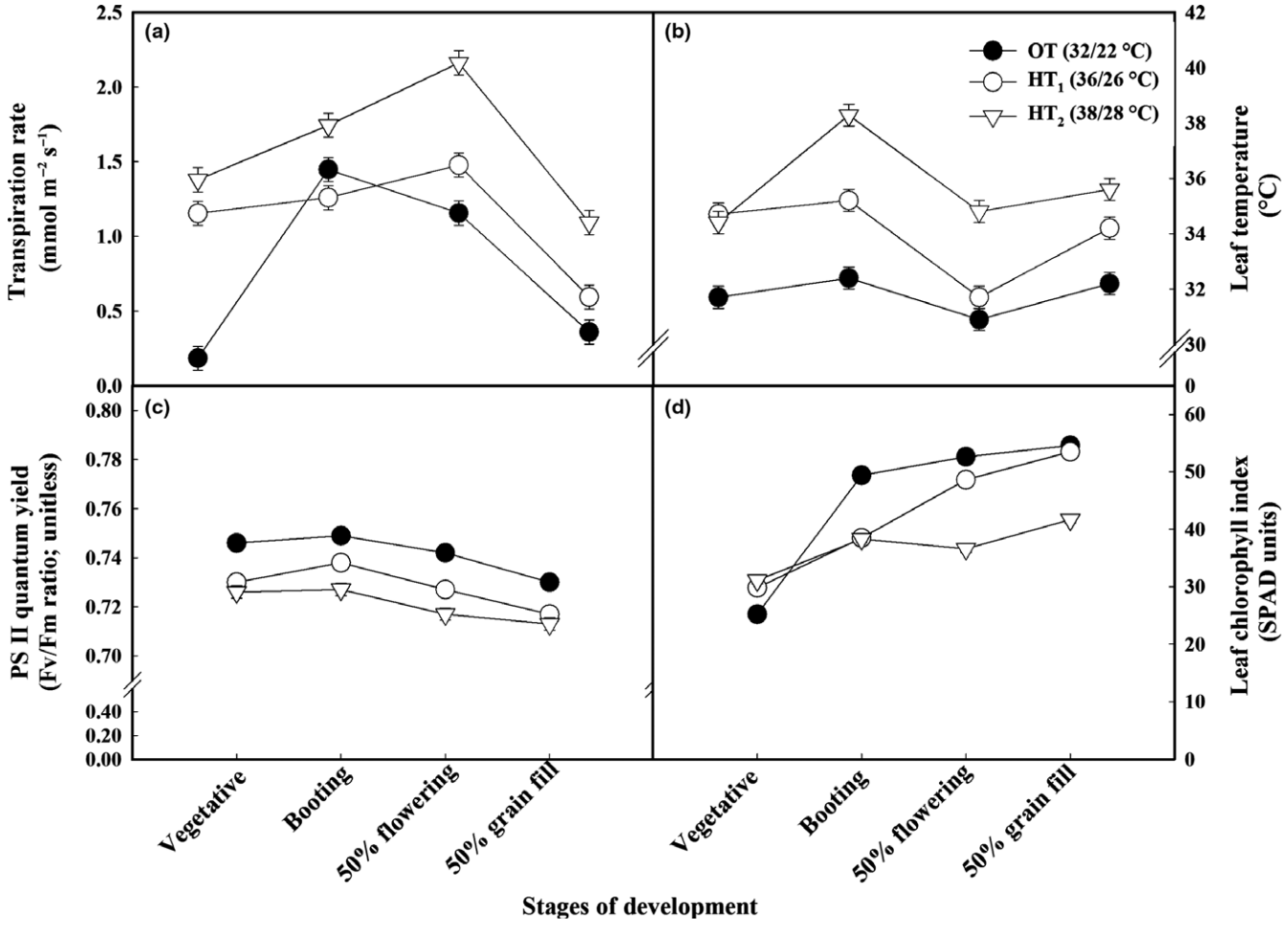


**FIGURE 1** Effects of season-long HT temperature treatments [optimum (OT, 32/22°C), high temperature stress ($HT_1$, 36/26°C) and ($HT_2$, 38/28°C)], on (a) leaf transpiration (mmol $m^{-2}$ $s^{-1}$); (b) leaf temperature (°C); (c) PS II quantum yield (Fv/Fm ratio; unitless); and (d) chlorophyll index (SPAD units) of finger millet at different growth stages. Vertical bars denote ± *SE* of means. Means with the same letter are not significantly different at $p < .05$

the tagged panicles. The tagged panicles were hand-threshed, and the seeds were counted and weighted. The 100-seed weight (g) was estimated as the ratio of total seed dry weight per panicle to total number of seeds per panicle and multiplied by 100.

## 2.4 | Data analyses

The experimental design for season-long, short episode and genetic variability was a randomized block design. Temperature treatment was randomly assigned to the growth chambers. Statistical analyses were performed using SAS 9.1.3 (SAS Institute, 2003). The PROC GLM procedures were used, and the least square difference was used to separate the treatment means. Standard error bars are shown as an estimate of variability. The classification of finger miller genotypes for HT stress tolerance was performed using principal component analysis (PCA) as described by Kakani et al. (2005) by considering the reproductive trait variability under OT and HT stress. Eigenvectors generated by PCA were used to identify parameters that differentiated finger millet genotypes for HT stress tolerance. The factor loading values of variables and genotypes in PC1 and PC2 were used to classify the variables and genotypes. Genotypes that had +PC1 and +PC2 scores were classified as tolerant (quadrant I). Those with +PC1 and −PC2 scores were classified as moderately tolerant (quadrant II). Those with −PC1 and +PC2 scores were classified as moderately susceptible (quadrant III), and those with −PC1 and −PC2 scores were classified as susceptible (quadrant IV).

# 3 | RESULTS

## 3.1 | Quality control of growth chambers

The temperatures of the growth chamber for the OT treatment during the season-long HT stress experiment were 31.7 ± 0.5°C daytime maximum and 21.6 ± 0.5°C night-time minimum, respectively. In $HT_1$, they were 35.5 ± 0.5°C and 25.8 ± 0.5°C; and in $HT_2$, they were 37.9 ± 0.5°C and 27.6 ± 0.5°C. For the short-term HT stress and genetic variability experiment, temperatures were also with ±0.4°C of the target temperatures. In all the experiments, relative humidity was similar across all temperature regimes at about 85 ± 5%. Quality of the temperature control and growth chamber performance was previously published (Pradhan et al., 2012).

## 3.2 | Effects of season-long HT stress

Overall, there was no effect of HT on photosynthesis (Figure S1). However, transpiration rate (mmol $m^{-2}$ $s^{-1}$), PS II quantum yield (Fv/Fm ratio; unitless) and leaf temperature (°C) were significantly ($p < .05$) affected by HT stress (Figure 1). Transpiration rate was higher at the 50% flowering stage than at vegetative, booting or grain filling stages (Figure 1a). Transpiration rate, stomatal conductance (Figure S1) and leaf temperature were higher in the 36/26 and 38/28°C treatments compared with the 32/22°C treatment. Lower values for PS II quantum yield were observed at 38/28°C compared with 32/

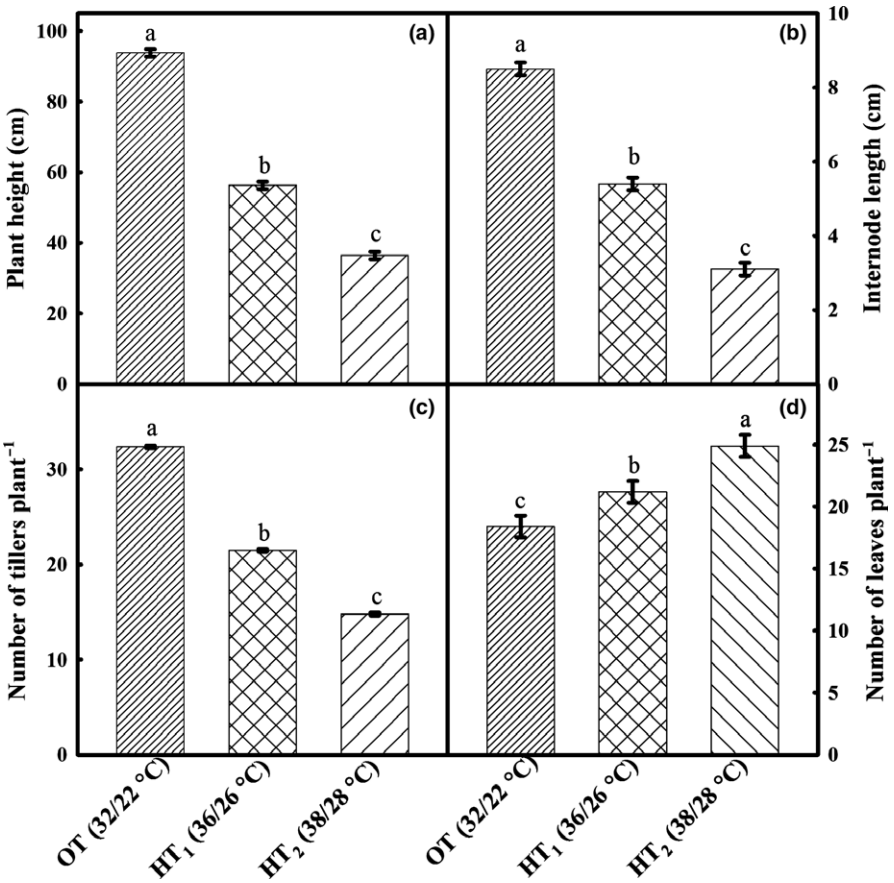


**FIGURE 2** Effects of season-long HT temperature treatments [optimum (OT, 32/22°C), high temperature stress ($HT_1$, 36/26°C and $HT_2$, 38/28°C)] on (a) plant height (cm); (b) internode length (cm); (c) number of tillers per plant; and (d) total number of leaves per plant at maturity of finger millet. Vertical bars denote ± *SE* of means. Means with the same letter are not significantly different at $p < .05$

22 and 36/26°C (Figure 1c). Leaf chlorophyll index (SPAD units) was higher at 32/22°C compared with 36/26 and 38/28°C (Figure 1d).

Significant interactions were observed between temperature and stage of measurement for morphological and growth traits. Panicle emergence was delayed by 16 days, flowering by 21 days and physiological maturity by 28 days at 36/26°C compared to the control. While at 38/28°C, panicle emergence, flowering and physiological maturity were delayed by 19, 27 and 38 days, respectively, compared to 32/22°C. HT stress decreased plant height, internode length, number of tillers per plant and increased total number of leaves per plant (Figure 2). Yield and yield components were significantly ($p < .05$) influenced by temperature treatments (Figure 3). Number of fingers per panicle was decreased (on average ~1–1.5 fingers) with increasing temperature from 32/22 to 36/26 or 38/28°C (Figure 3a). Compared with 36/26 and 38/28°C, plants at 32/22°C had more seeds per panicle (Figure 3c) and heavier seeds (Figure 3d). The leaf and stem dry weights were decreased by HT stress (Figure S2). Grain yield decreased by 75% under 36/26°C and by 84% at 38/28°C compared with 32/22°C (Figure 3e), and harvest index decreased by 54% under 36/26°C and by 62% under 38/28°C compared with 32/22°C (Figure 3f).

### 3.3 | Effects of short episode of HT stress

Finger millet growth traits such as plant height (cm per plant), number of leaves per plant, leaf area per plant ($cm^2$) and leaf dry weight (g per plant) were not influenced by short episodes of HT stress (Table 1). However, stem dry weight per plant (g) was significantly ($p < .05$) decreased by HT stress. At continuous HT stress, stem dry weight decreased 51% compared with the OT control.

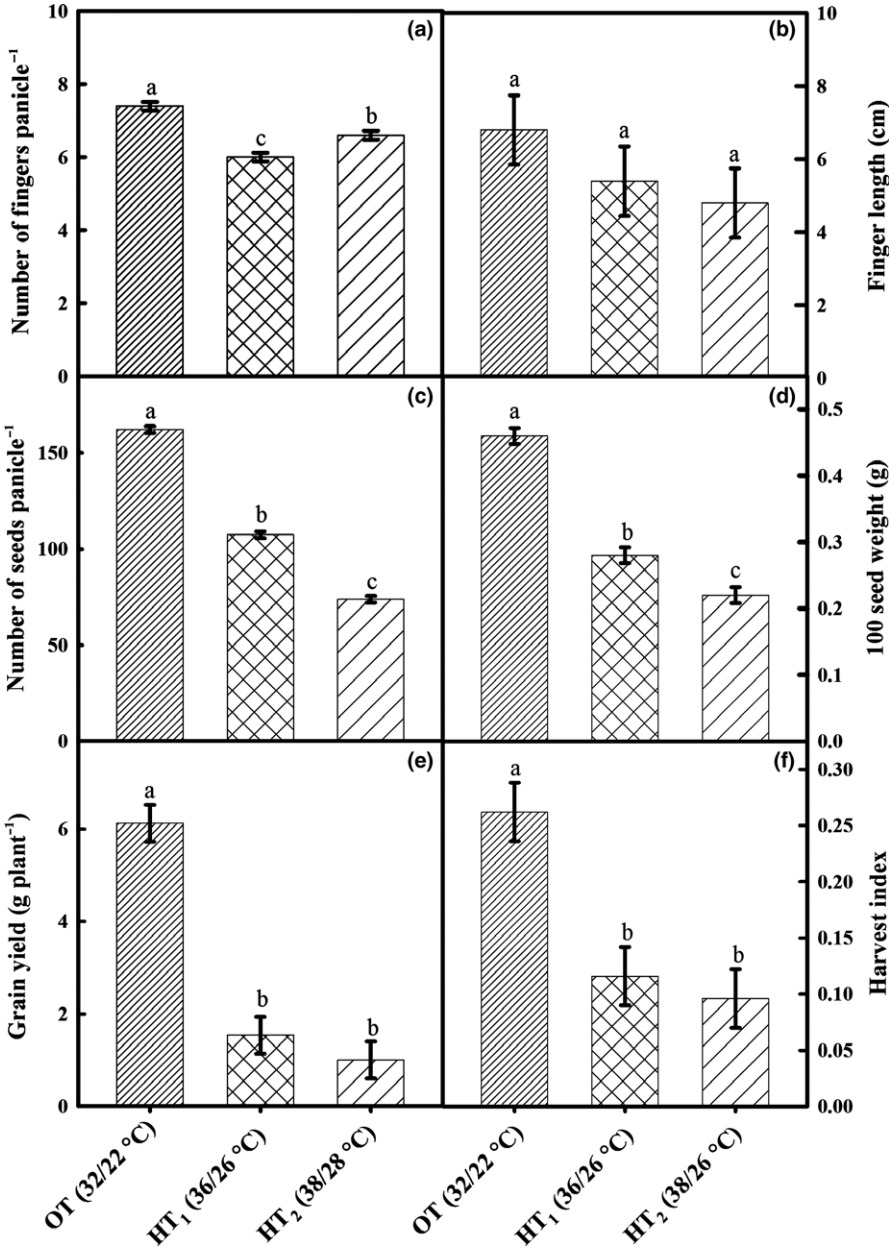


**FIGURE 3** Effects of season-long HT temperature treatments [optimum (OT, 32/22°C), high temperature stress ($HT_1$, 36/26°C and $HT_2$, 38/28°C)] on (a) number of fingers per panicle; (b) finger length (cm); (c) number of seeds per panicle; (d) 100-seed weight (g); (e) grain yield (g per plant); and (f) harvest index at maturity. Vertical bars denote ± *SE* of means. Means with the same letter are not significantly different at $p < .05$

**TABLE 1** Effects of short episode of HT stress imposed during different stages of development on finger millet growth and yield traits

| | Stages of high temperature stress imposition | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Trait** | **1[a]** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **LSD** |
| Plant height (cm) | 127.5 | 129.0 | 124.5 | 137.5 | 125.3 | 131.0 | 134.3 | 138.5 | 124.3 | NS |
| Number of leaves per plant | 34 | 47.3 | 36.8 | 50.0 | 64.0 | 46.8 | 27.5 | 27.0 | 47.3 | NS |
| Leaf area ($cm^2$ per plant) | 267 | 391.5 | 178.8 | 318.0 | 451.5 | 437.3 | 432.0 | 231.8 | 194.0 | NS |
| Leaf dry weight (g per plant) | 24.4 | 22.3 | 23.7 | 22.9 | 25.5 | 22.7 | 19.6 | 23.2 | 20.3 | NS |
| Stem dry weight (g per plant) | 40.5 | 29.5 | 30.5 | 29.6 | 28.1 | 29.5 | 28.1 | 31.8 | 19.9 | 7.4* |
| Panicle dry weight (g) | 38.1 | 24.6 | 28.7 | 27.2 | 28.8 | 27.0 | 34.4 | 35.5 | 34.4 | 8.7* |
| Number of panicles per plant | 2.8 | 1.8 | 4.0 | 4.0 | 6.5 | 4.5 | 2.8 | 3.5 | 2.8 | NS |
| Number of fingers per panicle | 7.8 | 6.8 | 5.8 | 5.5 | 7.3 | 7.0 | 7.5 | 6.8 | 7.3 | NS |
| Finger length (cm) | 9.8 | 9.5 | 7.5 | 7.0 | 8.5 | 8.3 | 8.5 | 7.3 | 11.0 | NS |

*Significant at the .05 probability level; NS—non-significant at the .05 probability level.
[a]Developmental stages of high temperature stress imposition: 1, continuous OT (control); 2, booting; 3, panicle emergence; 4, flowering; 5, 10 days after flowering (DAF); 6, 20 DAF; 7, 30 DAF; 8, 40 DAF; 9, continuous high temperature (HT).

Yield and yield components (panicle dry weight, number of seeds per panicle, 100-seed weight and grain yield per plant) were significantly ($p < .05$) decreased by short episode of HT stress imposed at various stages, but there were no significant differences for number of panicles per plant, number of fingers per panicle and finger length (Table 1). The highest percentage decrease (~70–75%) in number of seeds per panicle occurred when short episode of HT stress was imposed at booting or panicle emergence, compared to plants grown at continuous OT. While short episode of HT stress during flowering or 10 days after flowering caused similar decreases (~60%) in number of seeds per panicle. There was no significant effect of short episode of HT stress on 100-seed weight (Figure 4b). Only continuous HT stress decreased 100-seed weight by 52% compared with the control. Grain yield significant decreased by 36% at booting, 72% at panicle emergence, 57% at flowering, 36% at 40 DAF and 79% at continuous HT compared with the control (Figure 4c).

## 3.4 | Genetic variability for HT stress tolerance

Across all genotypes, HT stress decreased the chlorophyll index (SPAD units; 6.6%) and increased the O/P ratio of chlorophyll *a* fluorescence by 70.5% (Table 2). Finger millet genotypes varied significantly ($p < .05$) for chlorophyll index (SPAD units), O/P ratio of chlorophyll *a* fluorescence and canopy temperature (Table 3). Among the genotypes, the O/P ratio of chlorophyll *a* fluorescence at HT ranged between 0.309 (relative units; IE2312) and 0.371 (relative units; IE4734) (Table 3). Similarly, the chlorophyll index ranged from 44.8 (SPAD units; IE2437) to 52.9 (SPAD units; IE3973) and canopy temperature at HT ranged between 37.6°C (IE4734) and 42°C (IE4497) (Table 3). The interaction of genotype and temperature showed that the highest increase in O/P ratio of chlorophyll *a* fluorescence was observed in genotype IE6154 (108%) and IE3952 (105%) due to HT stress and maximum decrease in chlorophyll index (SPAD units) was observed in the genotype IE4734 (14%; Table 3).

Across all genotypes, HT stress significantly decreased ($p < .05$) panicle width (15%), finger width (19%), number of seeds per panicle (95%), seed yield per panicle (97%) and seed size (31%) over OT (Table 2). Irrespective of temperature, finger millet genotypes varied significantly ($p < .05$) for number of seeds per panicle, panicle length (cm), panicle width (cm), finger length (cm), finger width (cm), number of seeds per panicle, seed yield per panicle and seed size (g per 100 seed) (Table 4). The panicle length ranged from 19.8 cm (IE3392) to 4.5 cm (IE4570), and finger length ranged between 17.2 cm (IE3392) and 3.4 cm (IE4570) (Table 4). The panicle width and finger width ranged between 5.8 cm (IE6337) and 1.3 cm (IE4570) and 1.1 cm (IE3973) and 0.4 cm (IE4570) cm, respectively (Table 4). Averaged across temperatures, the highest number of seeds per panicle was observed in genotype IE2957 (1377.9) and the lowest in genotype IE4757 (180.4) (Table 5). The seed yield per panicle ranged from 3.4 g per panicle (IE5066) to 0.29 g per panicle (IE4757) (Table 5). The 100-seed weight was the highest in the genotype IE2296 (0.375 g) and the lowest in genotype IE2871 (0.079 g) (Table 5).

The interaction of genotype and temperature showed that the highest panicle width decrease was observed in genotype IE4570 (50.6%) due to HT stress; however, the genotype IE2710 had increased (3%) panicle width due to HT stress (Table 4). The data on finger width indicate that in most of the genotypes, the finger width was decreased by HT (Table 4). Number of seeds per panicle and seed yield per panicle showed a decrease in the range of 71%–100% and 80%–100%, respectively. The genotype IE2312 had a decrease of 71% in number of seeds per panicle; however, the genotypes IE4673, IE4734 and IE6154 had a decrease of 100% due to HT stress (Table 5). HT stress decreased the 100-seed weight in all the genotypes, except in IE2589, IE4545, IE4673, IE 4757, IE5201, IE5367 and IE6473 (Table 5).

## 3.5 | Principal component analysis

The principal component analysis indicated that the first two principal component vectors (PC1 and PC2) accounted for 45.4% of the total variation (Figure 5a). Among the various traits in PC1, maximum variation was explained by panicle width OT at HT (17%) and

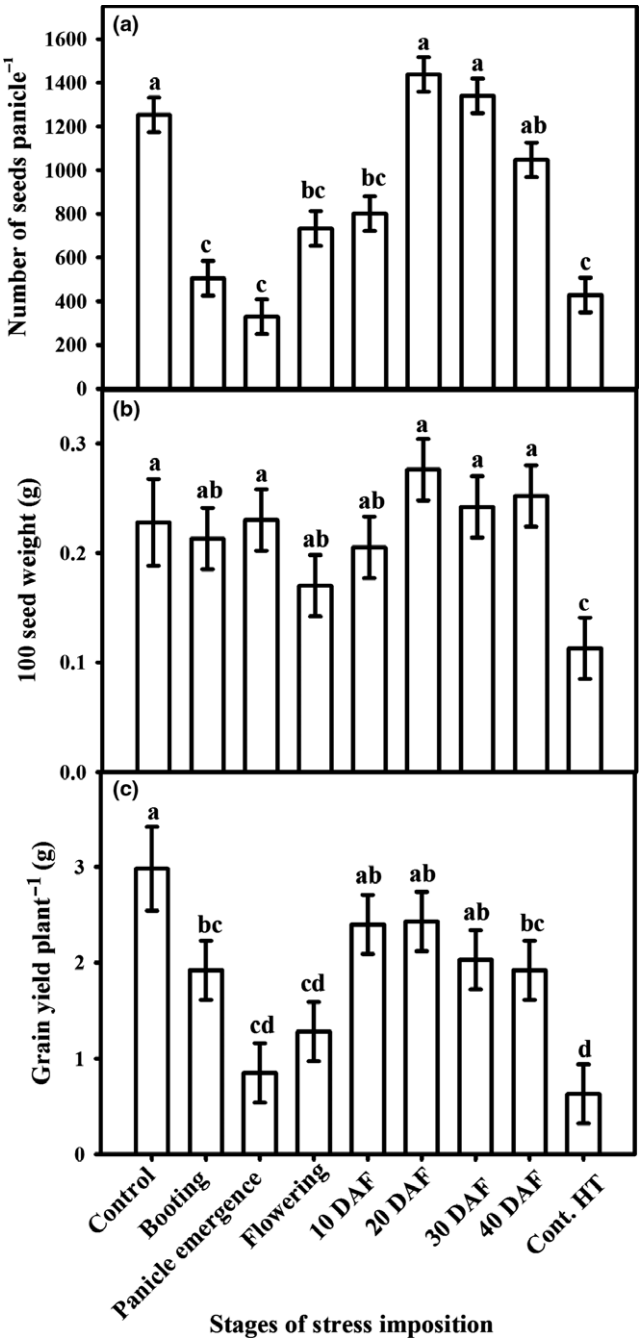


**FIGURE 4** Effects of short episode of HT temperature [optimum (OT, 27/18°C), high temperature stress (HT, 38/28°C)] at different growth stages of finger millet on (a) number of seeds per panicle; (b) 100-seed weight; and (c) and grain yield per plant (g). Vertical bars denote ± *SE* of means. Means with the same letter are not significantly different at $p < .05$. Abbreviations: control—continuous optimum temperature (27/18°C); DAF—days after flowering; Cont. HT—continuous high temperature (38/28°C)

grain yield per panicle at OT (14%) (Figure 5a). In PC2, maximum variability was observed for number of seeds per panicle at HT (26%) followed by grain yield per panicle at HT (24%) (Figure 5a). Among the finger millet germplasm, 13 genotypes (top four as IE2312, IE2957, IE5201 and IE2430; +PC1 and +PC2 scores; quadrant I, Figure 5b) were classified as HT tolerant. Fifteen genotypes were classified as moderately tolerant to HT (e.g., IE4028, IE4497, IE2437 and IE2710; +PC1 and -PC2 scores; quadrant II; Figure 5b). The 10 genotypes under −PC1 and +PC2 group were classified as moderately susceptible to HT (e.g., IE2911, IE6082, IE6421 and IE3391; quadrant III, Figure 5b), and 13 genotypes under −PC1 and -PC2 group were classified as susceptible to HT (e.g., IE4797, IE4757, IE4570 and IE4734; quadrant IV; Figure 5b).

**TABLE 2** Main effect of temperatures [optimum temperature (OT, 30/20°C: daytime maximum/night-time minimum temperature) and high temperature (HT, 38/28°C)] during booting stage for 14 days on physiological and yield traits

| Trait | Optimum temperature | High temperature | LSD |
|---|---|---|---|
| Chlorophyll index (SPAD units) | 52.3 | 48.8 | 0.161*** |
| O/P ratio (relative units) | 0.200 | 0.341 | 0.001*** |
| Leaf temperature (°C) | 30.4 | 40.3 | 0.115*** |
| Number of fingers per panicle | 6.42 | 6.33 | 0.198 |
| Panicle length (cm) | 9.54 | 9.48 | 0.187 |
| Panicle width (cm) | 3.48 | 2.94 | 0.077*** |
| Finger length (cm) | 6.57 | 6.61 | 0.141 |
| Finger width (cm) | 0.797 | 0.649 | 0.019*** |
| Number of seeds per panicle | 1,467 | 67 | 18*** |
| Seed yield (g per panicle) | 3.79 | 0.13 | 0.041*** |
| Seed size (g per 100 seed) | 0.265 | 0.183 | 0.012*** |

***Significant at the 0.001 probability level.

## 4 | DISCUSSION

This research showed evidence that (i) season-long HT (≥36/26°C) stress decreased leaf physiological traits, yield and yield components, (ii) short episode of HT (10 days of 38/28°C) stress decreased stem and panicle dry weight, number of seeds per panicle, 100-seed weight and grain yield per plant, (iii) booting, panicle emergence and flowering stages were the most sensitive to HT stress and (iv) there exists a good genetic variability for HT stress response in finger millet.

HT stress (38/28°C) decreased chlorophyll index compared to OT (32/22°C; Figure 1d). Lesser accumulation of chlorophyll molecule in HT-stressed plants may be attributed to impaired chlorophyll synthesis or its accelerated degradation or a combination of both (Ashraf & Harris, 2013). HT stress (≥36/26°C) increased O/P ratio of chlorophyll *a* fluorescence compared to OT (32/22°C; Figure 1c; Table 2), which indicates structural and functional alterations in chloroplast namely damages to thylakoid membranes (Ahmad, Diwan, & Abrol, 2010; Allakhverdiev et al., 2008). HT stress decreased PSII

**TABLE 3** Interaction of genotype (G) and temperature [T, optimum temperature (OT, 30/20°C: daytime maximum/night-time minimum temperature) and high temperature (HT, 38/28°C)] during booting stage for 14 days on physiological traits

| Genotype ID | Traits | | | | | |
|---|---|---|---|---|---|---|
| | O/P ratio of Chlorophyll *a* fluorescence (relative units) | | Chlorophyll index (SPAD units) | | Canopy temperature (°C) | |
| | OT | HT | OT | HT | OT | HT |
| IE2296 | 0.210 | 0.346 | 53.1 | 49.8 | 30.4 | 40.7 |
| IE2312 | 0.209 | 0.309 | 53.6 | 51.0 | 30.5 | 40.6 |
| IE2430 | 0.209 | 0.324 | 53.3 | 50.4 | 30.7 | 40.7 |
| IE2437 | 0.207 | 0.350 | 49.4 | 44.8 | 30.8 | 40.6 |
| IE2589 | 0.188 | 0.320 | 51.8 | 48.6 | 30.5 | 40.6 |
| IE2606 | 0.206 | 0.339 | 53.6 | 50.4 | 30.9 | 41.2 |
| IE2619 | 0.199 | 0.331 | 52.2 | 47.2 | 30.3 | 41.4 |
| IE2710 | 0.202 | 0.337 | 52.5 | 49.4 | 30.8 | 41.2 |
| IE2821 | 0.192 | 0.344 | 53.7 | 49.1 | 30.8 | 40.9 |
| IE2871 | 0.197 | 0.341 | 49.9 | 46.7 | 31.1 | 40.4 |
| IE2911 | 0.205 | 0.316 | 53.3 | 50.5 | 30.5 | 40.5 |
| IE2957 | 0.204 | 0.334 | 53.6 | 50.2 | 30.3 | 40.8 |
| IE3104 | 0.206 | 0.339 | 55.2 | 52.8 | 30.9 | 40.8 |
| IE3391 | 0.213 | 0.328 | 50.6 | 47.2 | 30.7 | 40.5 |
| IE3392 | 0.209 | 0.352 | 52.0 | 48.1 | 30.7 | 40.9 |
| IE3470 | 0.194 | 0.349 | 52.9 | 48.5 | 31.1 | 40.6 |
| IE3475 | 0.195 | 0.329 | 51.7 | 48.2 | 30.4 | 40.5 |
| IE3618 | 0.209 | 0.341 | 53.4 | 49.1 | 30.7 | 40.4 |
| IE3721 | 0.209 | 0.346 | 52.3 | 47.1 | 29.7 | 40.4 |
| IE3945 | 0.210 | 0.340 | 54.4 | 50.4 | 30.8 | 40.3 |
| IE3952 | 0.177 | 0.362 | 48.4 | 45.4 | 29.5 | 38.0 |
| IE3973 | 0.210 | 0.344 | 56.4 | 52.9 | 30.5 | 41.6 |
| IE4028 | 0.208 | 0.345 | 53.4 | 49.8 | 30.8 | 40.7 |
| IE4057 | 0.215 | 0.340 | 50.9 | 47.1 | 30.9 | 41.2 |
| IE4121 | 0.203 | 0.337 | 52.0 | 49.8 | 31.0 | 40.5 |
| IE4491 | 0.201 | 0.346 | 52.2 | 49.5 | 30.6 | 40.6 |
| IE4497 | 0.211 | 0.335 | 48.5 | 45.2 | 31.2 | 42.0 |
| IE4545 | 0.210 | 0.322 | 51.2 | 47.9 | 30.7 | 41.0 |
| IE4565 | 0.199 | 0.349 | 51.3 | 48.5 | 30.3 | 40.2 |
| IE4570 | 0.175 | 0.357 | 50.2 | 47.2 | 29.0 | 38.2 |
| IE4622 | 0.214 | 0.355 | 51.4 | 48.9 | 30.9 | 40.6 |
| IE4646 | 0.204 | 0.346 | 52.7 | 50.0 | 30.6 | 41.1 |
| IE4673 | 0.179 | 0.353 | 48.3 | 45.5 | 29.5 | 37.7 |
| IE4734 | 0.189 | 0.371 | 54.8 | 47.0 | 30.4 | 37.6 |
| IE4757 | 0.207 | 0.348 | 53.1 | 49.8 | 29.9 | 39.7 |
| IE4795 | 0.177 | 0.353 | 52.8 | 48.3 | 30.3 | 39.2 |
| IE4797 | 0.201 | 0.351 | 55.4 | 52.4 | 29.5 | 39.0 |
| IE4816 | 0.207 | 0.329 | 52.8 | 50.2 | 30.5 | 41.9 |
| IE5066 | 0.203 | 0.342 | 50.7 | 47.9 | 30.2 | 40.4 |
| IE5091 | 0.211 | 0.330 | 48.8 | 47.1 | 29.5 | 40.0 |
| IE5106 | 0.195 | 0.342 | 51.6 | 47.1 | 30.2 | 40.2 |
| IE5201 | 0.207 | 0.322 | 51.1 | 47.4 | 30.0 | 39.2 |
| IE5367 | 0.198 | 0.342 | 53.7 | 50.0 | 30.3 | 41.1 |
| IE6082 | 0.210 | 0.326 | 53.6 | 49.7 | 30.5 | 40.8 |
| IE6154 | 0.176 | 0.366 | 51.7 | 48.4 | 30.0 | 37.9 |
| IE6221 | 0.182 | 0.353 | 54.7 | 51.0 | 30.2 | 40.0 |
| IE6240 | 0.190 | 0.337 | 51.3 | 49.0 | 30.4 | 40.5 |
| IE6294 | 0.202 | 0.350 | 53.0 | 50.5 | 31.2 | 41.6 |
| IE6337 | 0.203 | 0.351 | 51.4 | 48.5 | 30.5 | 40.7 |
| IE6421 | 0.195 | 0.322 | 53.2 | 49.9 | 30.6 | 40.4 |
| IE6473 | 0.206 | 0.346 | 52.6 | 49.1 | 30.8 | 41.1 |
| Mean | 0.200 | 0.341 | 52.3 | 48.8 | 30.4 | 40.3 |
| LSD (G) | | 0.006 | | 0.818 | | 0.39 |
| LSD (T) | | 0.001 | | 0.162 | | 0.58 |
| LSD (G x T) | | 0.006 | | 0.818 | | 0.58 |

quantum yield compared to OT which can lead to changes in energy allocation to the photosystems (Wahid & Shabbir, 2005). Similar changes were observed in other cereals (wheat; Prasad, Pisipati, Ristic et al., 2008; sorghum; Djanaguiraman et al., 2014). Photosynthesis has been long recognized as sensitive to environment stresses. In the present study, the photosynthetic rate was not affected by HT stress (38/28°C; Figure S1). The absence of a clear effect of HT on photosynthesis is consistent with previous reports for sorghum (Jain, Prasad, Boote, Allen, & Chourey, 2007; Prasad, Pisipati, Mutava et al., 2008) and rice (Prasad, Boote, Allen, Sheehy et al., 2006). This indicates that the overall electron transport may remain almost unaltered regardless of substantial PS II photodamage. The increase in overexcitation of PS II might have exacerbated damage to PS II (Behrenfeld, Prasil, Kolber, Babin, & Falkowski, 1998). The other possible mechanism involved in PS II photodamage could be that the excess energy that cannot be used to drive photosynthesis can enhance the production of reactive oxygen species, which can induce photooxidative damage to PS II (Roach & Krieger-Liszkay, 2014). Compared to OT, the transpiration rate (Figure 1a) and the stomatal conductance (Figure S1) were enhanced under HT stress. When temperature increases, the viscosity of water declines and mesophyll conductance increases, which may improve the supply of water to sites of evaporation and thus increase the stomatal aperture (von Caemmerer & Evans, 2015). The higher transpiration rate in the HT might have resulted in better leaf cooling which might have served as a self-protection mechanism to dissipate the harmful heat leading to no change in photosynthesis (Yan, Chen, Shao, Zhang, & Xu, 2011).

**TABLE 4** Interaction of genotype (G) and temperature [T, optimum temperature (OT, 30/20°C: daytime maximum/night-time minimum temperature) and high temperature (HT, 38/28°C)] during booting stage for 14 days on yield traits

| | Traits | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Number of fingers per panicle | | Panicle length (cm) | | Panicle width (cm) | | Finger length (cm) | |
| Genotype ID | OT | HT | OT | HT | OT | HT | OT | HT |
| IE2296 | 7.67 | 7.50 | 10.00 | 9.42 | 4.37 | 3.40 | 5.27 | 5.53 |
| IE2312 | 7.50 | 6.50 | 7.90 | 7.15 | 3.08 | 3.15 | 6.35 | 6.70 |
| IE2430 | 7.50 | 7.33 | 9.55 | 9.57 | 3.57 | 3.00 | 7.95 | 7.73 |
| IE2437 | 8.50 | 7.83 | 13.73 | 13.43 | 3.87 | 3.08 | 6.53 | 6.45 |
| IE2589 | 6.17 | 6.67 | 12.30 | 12.13 | 3.55 | 3.48 | 8.20 | 8.43 |
| IE2606 | 5.33 | 4.83 | 12.15 | 11.33 | 3.88 | 3.05 | 6.17 | 5.83 |
| IE2619 | 5.50 | 5.50 | 9.98 | 9.72 | 2.78 | 2.83 | 6.83 | 6.75 |
| IE2710 | 10.33 | 10.50 | 15.22 | 14.40 | 4.08 | 4.22 | 11.27 | 11.45 |
| IE2821 | 6.83 | 6.17 | 5.98 | 6.07 | 3.10 | 3.07 | 5.17 | 5.17 |
| IE2871 | 5.83 | 5.50 | 12.17 | 12.92 | 2.80 | 2.77 | 10.22 | 10.52 |
| IE2911 | 4.33 | 4.50 | 9.53 | 9.15 | 2.95 | 2.72 | 3.48 | 3.63 |
| IE2957 | 4.50 | 4.50 | 9.55 | 9.62 | 2.90 | 2.96 | 8.37 | 8.22 |
| IE3104 | 5.50 | 5.33 | 11.10 | 11.55 | 3.50 | 3.20 | 9.28 | 9.00 |
| IE3391 | 5.83 | 5.50 | 8.25 | 8.35 | 3.25 | 2.80 | 4.55 | 4.68 |
| IE3392 | 6.17 | 6.17 | 20.00 | 19.65 | 3.42 | 3.38 | 17.18 | 17.87 |
| IE3470 | 6.17 | 6.50 | 8.70 | 8.92 | 3.58 | 2.17 | 5.82 | 5.73 |
| IE3475 | 6.33 | 5.50 | 9.00 | 8.73 | 2.20 | 2.13 | 5.82 | 5.43 |
| IE3618 | 4.17 | 4.50 | 7.83 | 7.97 | 3.28 | 2.73 | 5.53 | 5.85 |
| IE3721 | 6.17 | 6.33 | 8.60 | 8.58 | 2.93 | 2.93 | 7.37 | 7.35 |
| IE3945 | 7.33 | 7.83 | 8.38 | 8.37 | 2.37 | 2.17 | 4.17 | 4.35 |
| IE3952 | 9.33 | 9.50 | 7.60 | 7.52 | 4.50 | 3.55 | 4.17 | 4.33 |
| IE3973 | 6.00 | 5.50 | 9.33 | 9.38 | 4.15 | 3.25 | 6.98 | 7.17 |
| IE4028 | 7.17 | 7.17 | 6.63 | 6.33 | 3.32 | 3.07 | 4.23 | 4.60 |
| IE4057 | 6.00 | 5.67 | 6.77 | 6.60 | 3.30 | 3.15 | 4.65 | 4.85 |
| IE4121 | 5.33 | 5.50 | 9.45 | 9.43 | 4.35 | 2.40 | 8.32 | 8.58 |
| IE4491 | 7.33 | 7.17 | 9.52 | 9.60 | 3.50 | 3.08 | 7.50 | 7.32 |
| IE4497 | 8.50 | 8.17 | 9.65 | 9.28 | 3.42 | 2.78 | 5.45 | 5.45 |
| IE4545 | 6.50 | 6.67 | 10.17 | 9.40 | 3.55 | 3.50 | 6.53 | 6.77 |
| IE4565 | 7.00 | 6.83 | 7.33 | 7.48 | 3.33 | 2.35 | 4.40 | 4.65 |
| IE4570 | 4.67 | 4.83 | 4.63 | 4.45 | 2.57 | 1.27 | 3.72 | 3.42 |
| IE4622 | 5.33 | 5.00 | 8.73 | 8.37 | 2.48 | 1.73 | 5.17 | 5.43 |
| IE4646 | 5.50 | 5.83 | 8.88 | 8.47 | 3.82 | 2.95 | 6.53 | 6.80 |
| IE4673 | 8.00 | 7.50 | 10.07 | 10.52 | 3.58 | 2.52 | 6.13 | 6.42 |
| IE4734 | 5.33 | 5.50 | 9.57 | 9.27 | 3.20 | 2.22 | 8.33 | 8.33 |
| IE4757 | 5.67 | 5.50 | 8.45 | 8.45 | 2.78 | 2.38 | 5.32 | 5.42 |
| IE4795 | 7.17 | 7.50 | 10.28 | 10.42 | 3.55 | 3.20 | 6.65 | 6.45 |
| IE4797 | 4.17 | 4.17 | 6.65 | 6.78 | 2.33 | 1.98 | 4.80 | 4.83 |
| IE4816 | 6.50 | 6.33 | 8.77 | 8.80 | 3.42 | 2.52 | 5.85 | 5.42 |
| IE5066 | 6.50 | 6.17 | 11.57 | 12.03 | 3.02 | 2.42 | 6.57 | 6.52 |
| IE5091 | 6.50 | 6.67 | 10.78 | 10.65 | 3.95 | 3.35 | 5.55 | 5.45 |
| IE5106 | 6.50 | 6.17 | 6.43 | 6.67 | 4.87 | 4.80 | 4.43 | 4.45 |
| IE5201 | 7.50 | 7.50 | 6.70 | 6.90 | 3.62 | 3.37 | 5.32 | 5.32 |

(Continues)

**TABLE 4** (Continued)

| | Traits | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Number of fingers per panicle | | Panicle length (cm) | | Panicle width (cm) | | Finger length (cm) | |
| Genotype ID | OT | HT | OT | HT | OT | HT | OT | HT |
| IE5367 | 5.50 | 5.50 | 9.68 | 9.30 | 3.78 | 2.32 | 6.07 | 6.15 |
| IE6082 | 5.67 | 5.50 | 9.60 | 9.73 | 3.20 | 2.75 | 7.57 | 7.35 |
| IE6154 | 7.33 | 7.17 | 8.58 | 8.27 | 3.18 | 2.82 | 5.87 | 5.77 |
| IE6221 | 7.83 | 7.83 | 8.35 | 8.27 | 5.33 | 4.58 | 6.45 | 6.55 |
| IE6240 | 5.50 | 5.17 | 9.82 | 9.55 | 3.32 | 2.77 | 6.32 | 6.30 |
| IE6294 | 6.17 | 6.33 | 8.43 | 8.70 | 3.60 | 3.03 | 6.05 | 5.97 |
| IE6337 | 6.67 | 6.17 | 14.87 | 15.30 | 5.78 | 4.83 | 11.45 | 11.02 |
| IE6421 | 6.67 | 6.83 | 9.60 | 9.65 | 3.45 | 2.53 | 6.20 | 6.32 |
| IE6473 | 6.17 | 6.17 | 9.95 | 10.33 | 3.87 | 3.25 | 7.38 | 7.37 |
| Mean | 6.42 | 6.32 | 9.54 | 9.47 | 3.48 | 2.94 | 6.58 | 6.62 |
| LSD (G) | 1.00 | | | 0.94 | | 0.39 | | 0.71 |
| LSD (T) | 0.19 | | | 0.18 | | 0.07 | | 0.14 |
| LSD (G x T) | 0.19 | | | 0.18 | | 0.07 | | 0.14 |

Season-long HT stress decreased growth traits (e.g., plant height, internode length and total dry matter) leading to lower grain yield. The decreased plant height under $HT_1$ and $HT_2$ was attributed to decreased internode length (Figure 2b). In grain sorghum, season-long HT stress resulted in significant increases in leaf numbers, particularly when reproductive development was arrested without any decrease in leaf photosynthetic rates (Prasad, Boote, & Allen, 2006). Exposure of plants to severe HT stress (>36/26°C) decreased the stem growth resulting in decreased plant height. High temperatures caused decreases in vegetative dry matter of other $C_4$ cereals [maize, Sunoj et al. (2016) and pearl millet (*Pennisetum glaucum* (L.), Ashraf and Hafeez (2004)]. Increased respiration rate under HT stress can also contribute to lower dry matter production under HT stress (Djanaguiraman, Prasad, & Schapaugh, 2013; Sunoj et al., 2016). Season-long HT stress had adverse effects on yield and yield components compared with OT (Figure 3). Lower seed yield at HT stress compared to OT was due to lower seed numbers per panicle and 100-seed weight. In sorghum, temperatures >36/26°C decreased seed set, seed yield and harvest index compared with 32/22°C (Prasad, Boote, & Allen, 2006). Similarly, exposure to longer duration HT stress during panicle development or grain filling also decreased grain yield due to decreases in seed numbers and/or individual seed weight of grain sorghum under field conditions (Prasad et al., 2015). The decrease in harvest index under HT stress is due to decreased grain yield and stem and leaf dry matter accumulation (Figure S2).

Different stages of finger millet development responded differently to a short episode (10 days) of HT stress (Figure 4). Maximum decreases in seed numbers and/or grain yield were observed when short episode of HT stress was imposed at booting, panicle emergence, flowering and 10 days after flowering (Figure 4). These results concur with those of Prasad, Pisipati, Mutava et al. (2008), Prasad et al. (2015), Prasad and Djanaguiraman (2014), and Djanaguiraman et al. (2017) who reported that maximum decreases in yield of grain sorghum, wheat and pearl millet, respectively, occurred when HT stress was imposed at gametogenesis and flowering. Similar results were also reported by Wollenweber, Porter, and Schellberg (2003), where grain number of wheat was decreased by 41% and individual grain weight decreased by 45% when short episode (8 days) of HT stress (35/25°C) was imposed at anthesis. The adverse effects of short episodes of HT stress on yield of finger millet could be explained by a decrease in seed numbers and seed weight. Decreased seed numbers are generally attributed to decreased percent seed set caused by injury to microsporogenesis (pollen development) and mega-sporogenesis (ovule development) process under HT stress (Cross, McKay, McHughens, & Bonham-Smith, 2003; Prasad, Craufurd, Kakani, & Boote, 2001; Prasad, Pisipati, Mutava et al., 2008; Young, Wilen, & Bonham-Smith, 2004; Djanaguiraman and Prasad, 2014). According to Jain et al. (2007), loss of pollen viability under HT stress is associated with altered carbohydrate metabolism and starch deficiency in developing pollen grains. Other mechanism associated with loss of viability of gametes includes increased production of reactive oxygen species, alterations in lipid composition, anatomical abnormalities and decreased antioxidants (Prasad et al., 2017).

The finger millet genotypes varied for panicle length, finger length, number of seeds per panicle at HT and O/P ratio for chlorophyll *a* fluorescence at HT (Figure 5a). Under HT stress, seed yield is positively correlated with number of seeds per panicle and negatively correlated with O/P ratio for chlorophyll *a* fluorescence. In sorghum, under HT stress, the seed set percentage (number of seeds per panicle) is strongly correlated with seed yield (Nguyen et al., 2013; Singh et al., 2015). The number of seeds per panicle and seed yield per panicle was ranged between <1 – 360 and <0.01 – 0.73 g, respectively, suggesting that ample genetic variation is available in finger millet that could be

**TABLE 5** Interaction of genotype (G) and temperature [T, optimum temperature (OT, 30/20°C: daytime maximum/night-time minimum temperature) and high temperature (HT, 38/28°C)] during booting stage for 14 days on yield traits

| | Traits | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Finger width (cm) | | Number of seeds per panicle | | Seed yield (g per panicle) | | Seed size (g per 100 seed) | |
| Genotype ID | OT | HT | OT | HT | OT | HT | OT | HT |
| IE2296 | 0.80 | 0.63 | 666 | 30 | 4.10 | 0.04 | 0.62 | 0.13 |
| IE2312 | 0.97 | 0.95 | 1,236 | 354 | 3.01 | 0.61 | 0.25 | 0.17 |
| IE2430 | 0.95 | 0.52 | 1,252 | 189 | 3.33 | 0.35 | 0.27 | 0.18 |
| IE2437 | 0.97 | 0.68 | 1,329 | 32 | 3.66 | 0.02 | 0.28 | 0.07 |
| IE2589 | 0.80 | 0.77 | 1,567 | 133 | 1.98 | 0.33 | 0.13 | 0.25 |
| IE2606 | 0.87 | 0.58 | 2,233 | 41 | 5.10 | 0.06 | 0.23 | 0.14 |
| IE2619 | 0.88 | 0.58 | 861 | 13 | 1.78 | 0.02 | 0.21 | 0.13 |
| IE2710 | 0.75 | 0.52 | 2,482 | 24 | 4.40 | 0.02 | 0.18 | 0.09 |
| IE2821 | 0.53 | 0.52 | 1,380 | 13 | 3.12 | 0.02 | 0.23 | 0.14 |
| IE2871 | 0.73 | 0.77 | 1,968 | 10 | 2.68 | 0.00 | 0.14 | 0.02 |
| IE2911 | 0.65 | 0.62 | 1,395 | 360 | 2.37 | 0.40 | 0.17 | 0.11 |
| IE2957 | 0.97 | 0.95 | 2,533 | 223 | 4.81 | 0.34 | 0.19 | 0.15 |
| IE3104 | 0.93 | 0.90 | 1,709 | 105 | 4.02 | 0.15 | 0.24 | 0.14 |
| IE3391 | 0.52 | 0.58 | 1,367 | 139 | 3.50 | 0.32 | 0.26 | 0.23 |
| IE3392 | 0.53 | 0.55 | 1,159 | 57 | 4.15 | 0.02 | 0.36 | 0.03 |
| IE3470 | 0.65 | 0.62 | 1,364 | 19 | 5.16 | 0.02 | 0.38 | 0.11 |
| IE3475 | 0.58 | 0.55 | 1,310 | 78 | 3.01 | 0.13 | 0.23 | 0.18 |
| IE3618 | 0.72 | 0.78 | 1,662 | 69 | 4.07 | 0.16 | 0.25 | 0.24 |
| IE3721 | 0.80 | 0.72 | 1,264 | 86 | 2.14 | 0.09 | 0.17 | 0.11 |
| IE3945 | 0.72 | 0.57 | 1,436 | 16 | 4.06 | 0.02 | 0.29 | 0.15 |
| IE3952 | 0.55 | 0.52 | 2,190 | 4 | 5.70 | 0.00 | 0.26 | 0.05 |
| IE3973 | 1.15 | 1.10 | 1,509 | 151 | 4.82 | 0.17 | 0.32 | 0.12 |
| IE4028 | 0.83 | 0.62 | 1,417 | 29 | 5.17 | 0.06 | 0.37 | 0.21 |
| IE4057 | 0.83 | 0.75 | 1,407 | 42 | 3.97 | 0.10 | 0.28 | 0.25 |
| IE4121 | 1.03 | 0.72 | 1,247 | 7 | 4.70 | 0.01 | 0.38 | 0.15 |
| IE4491 | 0.95 | 0.53 | 954 | 7 | 2.58 | 0.01 | 0.27 | 0.16 |
| IE4497 | 0.62 | 0.58 | 2,343 | 19 | 5.53 | 0.04 | 0.24 | 0.23 |
| IE4545 | 0.58 | 0.55 | 929 | 86 | 2.49 | 0.26 | 0.27 | 0.31 |
| IE4565 | 0.55 | 0.42 | 1,455 | 2 | 2.46 | 0.00 | 0.17 | 0.16 |
| IE4570 | 0.48 | 0.35 | 658 | 1 | 1.04 | 0.00 | 0.16 | 0.05 |
| IE4622 | 0.85 | 0.85 | 1,191 | 15 | 3.81 | 0.03 | 0.33 | 0.21 |
| IE4646 | 0.93 | 0.82 | 2,422 | 145 | 4.32 | 0.18 | 0.18 | 0.13 |
| IE4673 | 0.93 | 0.67 | 1,711 | 1 | 5.34 | 0.00 | 0.31 | 0.33 |
| IE4734 | 0.63 | 0.45 | 844 | 0 | 1.50 | 0.00 | 0.18 | 0.07 |
| IE4757 | 0.57 | 0.42 | 358 | 3 | 0.58 | 0.00 | 0.16 | 0.24 |
| IE4795 | 0.95 | 0.65 | 562 | 1 | 1.48 | 0.00 | 0.27 | 0.14 |
| IE4797 | 0.49 | 0.48 | 559 | 1 | 1.31 | 0.00 | 0.24 | 0.13 |
| IE4816 | 0.88 | 0.58 | 1,631 | 137 | 3.95 | 0.28 | 0.24 | 0.21 |
| IE5066 | 0.65 | 0.62 | 2,220 | 4 | 6.86 | 0.01 | 0.31 | 0.30 |
| IE5091 | 0.97 | 0.62 | 900 | 84 | 3.20 | 0.25 | 0.36 | 0.30 |
| IE5106 | 0.98 | 1.02 | 1,752 | 14 | 5.04 | 0.04 | 0.29 | 0.28 |
| IE5201 | 0.87 | 0.65 | 1,391 | 209 | 4.55 | 0.73 | 0.33 | 0.35 |
| IE5367 | 0.88 | 0.73 | 889 | 16 | 2.31 | 0.04 | 0.26 | 0.28 |
| IE6082 | 0.75 | 0.55 | 1,463 | 236 | 3.85 | 0.55 | 0.26 | 0.23 |
| IE6154 | 0.92 | 0.75 | 1,780 | 1 | 5.75 | 0.00 | 0.32 | 0.16 |
| IE6221 | 0.92 | 0.72 | 2,160 | 3 | 6.10 | 0.01 | 0.28 | 0.23 |
| IE6240 | 0.92 | 0.68 | 2,499 | 10 | 6.77 | 0.03 | 0.27 | 0.25 |
| IE6294 | 0.97 | 0.63 | 1,200 | 2 | 3.32 | 0.00 | 0.28 | 0.21 |
| IE6337 | 1.10 | 0.58 | 2,060 | 12 | 6.24 | 0.03 | 0.30 | 0.28 |
| IE6421 | 0.78 | 0.62 | 850 | 156 | 2.54 | 0.42 | 0.30 | 0.27 |
| IE6473 | 0.82 | 0.55 | 2,128 | 79 | 6.06 | 0.24 | 0.29 | 0.31 |
| Mean | 0.80 | 0.65 | 1,468 | 68 | 3.80 | 0.13 | 0.27 | 0.18 |
| LSD (G) | | 0.09 | | 92 | | 0.20 | | 0.06 |
| LSD (T) | | 0.01 | | 18 | | 0.04 | | 0.01 |
| LSD (G x T) | | 0.01 | | 18 | | 0.04 | | 0.01 |

exploited in breeding programmes. Even under such extreme HT stress, some finger millet genotypes (e.g., IE2301 and IE5201) had relatively higher seed yield at HT stress through increased number of seeds per panicle and decreased O/P ratio for chlorophyll *a* fluorescence at HT. Chlorophyll fluorescence analysis, a non-intrusive method, can detect the effects of environment stress in plants and give insights into the ability of a plant to tolerate environment stresses (Maxwell & Johnson, 2000). Climate predictions indicate that finger millet growing areas are likely to get warmer. Our results indicate such an increase in temperature may have serious implications for finger millet productivity. The HT stress in our experiments may be too extreme and harsh for finger millet. The presence of genotypic variation even under extreme HT stress suggests opportunities for genetic improvement. Targeted plant breeding programmes for enhancing HT tolerance are possible and can help crop plants to adapt to HT stress and other associated biotic and abiotic stresses. Further evaluation of HT tolerance of the selected lines across locations and under field conditions is essential before initiating large-scale targeted HT stress tolerance breeding programmes.

The responses observed in the present investigations are from tagged panicles that were exposed to HT stress under controlled environment conditions. However, under field conditions, it will be different due to day to day variation in timing, intensity and duration of stress events. Hence, further research is warranted under field conditions for quantifying the impact of season-long and short episodes of HT stress on finger millet yield on multiple genotypes and quantifying genetic variability. In both of our experiments (season-long and short HT stress), the relative humidity in the growth chambers was kept constant at 85% under all the temperatures regimes;

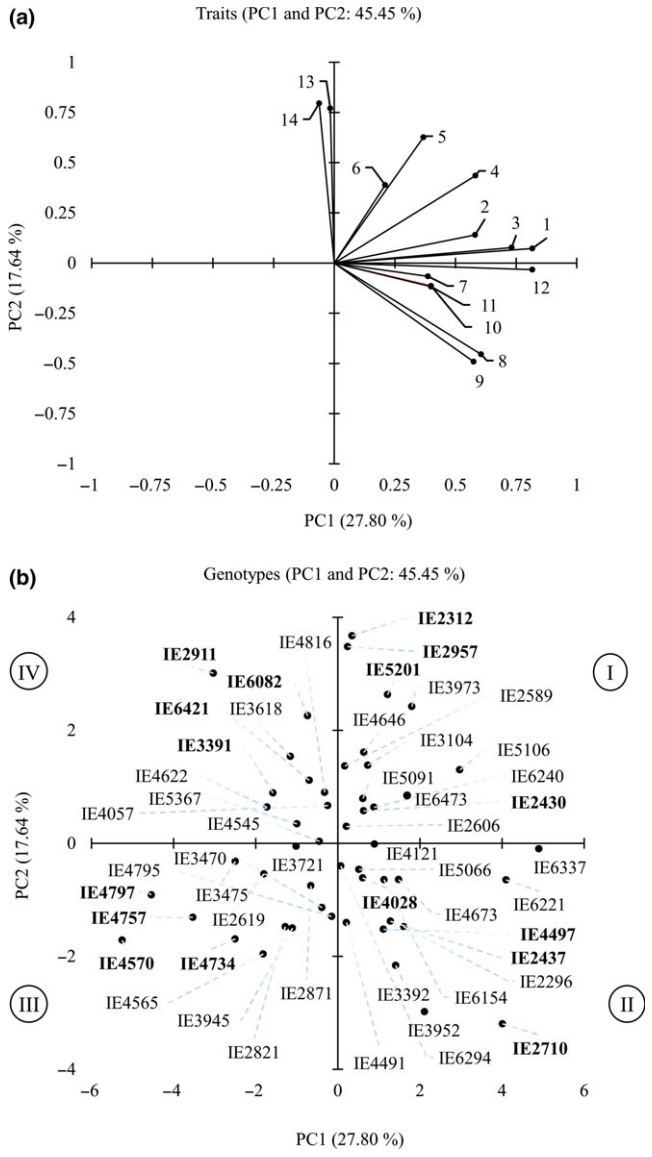


**FIGURE 5** First and second principal component scores (PC1 and PC2) for identifying traits conferring high temperature stress tolerance: (a) the factor loading value for variables is indicated by thick lines radiating from the centre showing the direction (angle) and magnitude (length) and (b) classification of 51 finger millet genotypes based on the factor scores of first and second principal components. 1- panicle width (HT), 2- number of seeds (OT), 3- seed yield (OT), 4- finger width (OT), 5- finger width (HT), 6- seed size (HT), 7- seed size (OT), 8- number of fingers (OT), 9- number of fingers (HT), seed size (HT), 9- finger length (HT), 10- finger length (OT), 11- finger length (HT), 12- panicle width (OT), 13- seed yield (HT) and 14- number of seeds (OT)

this resulted in different vapour pressure deficits (VPDs) in different temperature regimes. In future, it is predicted that increased temperature will be observed; however, the relative humidity will remain constant (Rind, 1998), resulting in different VPD under different temperature regimes. Thus, treatment conditions of our experiments are expected to occur in future climates. However, the direct effects of different VPD (at same temperatures) on finger millet are not known and require further investigation.

## 5 | CONCLUSIONS

Season-long HT stress (36/26 or 38/28°C) compared to 32/22°C decreased chlorophyll index, seed number, 100-seed weight, grain yield and harvest index. The stages of finger millet most sensitive to short episode of HT stress were booting, panicle emergence and flowering, leading to decreased number of seeds per panicle and lower grain yield. There was differential response of genotypes to HT stress, with some genotypes showing tolerance with respect to chlorophyll *a* fluorescence, with number of seeds per panicle and seed yield per panicle under HT stress. To achieve optimum productivity of finger millet, a desirable crop management strategy would be to prevent HT stress during the most vulnerable reproductive stages, by choosing appropriate genotypes (phenology and duration) and planting dates. In addition, development of finger millet genotypes with improved tolerance to HT stress can provide greater yield stability and resilience in current and future climates.

## ACKNOWLEDGEMENTS

This research was supported by the Department of Agronomy, Kansas State University; Feed the Future Innovation Lab for Collaborative Research on Sorghum and Millet; Feed the Future Innovation Lab for Collaborative Research on Sustainable Intensification (Grant no. AID-OAA-L-14-00006) funded by the United States Agency for International Development and the Ogallala Initiative funded by The United States Department of Agriculture–Agricultural Research Service. We thank Dr. Yared Assefa for assistance with statistical analysis. The technical support of Dr. Gautam P. Pradhan is greatly appreciated. This is contribution number 13-313-J from the Kansas Agricultural Experiment Station.

## CONFLICT OF INTEREST STATEMENT

Authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## ORCID

*P. V. V. Prasad* http://orcid.org/0000-0001-6632-3361

## REFERENCES

Ahmad, A., Diwan, H., & Abrol, Y. P. (2010). Global climate change, stress and plant productivity. In A. Pareek, S. K. Sopory, H. J. Bohnert & Govindjee (Eds.), *Abiotic stress adaptation in plants: Physiological, molecular and genome foundation* (pp. 503–521). Dordrecht: Springer Science and Business Media.

Allakhverdiev, S. I., Kreslavski, V. D., Klimov, V. V., Los, D. A., Carpentier, R., & Mohanty, P. (2008). Heat stress: An overview of molecular responses in photosynthesis. *Photosynthesis Research*, *98*, 541–550. https://doi.org/10.1007/s11120-008-9331-0

Ashraf, M., & Hafeez, M. (2004). Thermotolerance of pearl millet and maize at early growth stages: Growth and nutrient relations. *Biologia*

*Plantarum*, *48*, 81–86. https://doi.org/10.1023/B:BIOP.0000024279.44013.61

Ashraf, M., & Harris, P. J. C. (2013). Photosynthesis under stressful environments: An overview. *Photosynthetica*, *51*, 163–190. https://doi.org/10.1007/s11099-013-0021-6

Behrenfeld, M. J., Prasil, O., Kolber, Z. S., Babin, M., & Falkowski, P. G. (1998). Compensatory changes in Photosystem II electron turnover rates protect photosynthesis from photoinhibition. *Photosynthesis Research*, *58*, 259–268. https://doi.org/10.1023/A:1006138630573

Bita, C. E., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science*, *4*, 273.

Board on Science and Technology for International Development (1996). *Lost crops of Africa, volume I. Grains* (pp. 39–58). Washington, DC: National Research Council, National academy press.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Osman-Elasha, B., … Yanda, P. (2007). Africa. In: M. L. Parry, O. F. Canziani & J. P. Palutikof et al. (Eds.), *Climate change 2007: impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change*. (pp. 433–467). Cambridge, UK: Cambridge University Press.

Bokszczanin, K. L., & Fragkostefanakis, S. (2013). Perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance. *Frontiers in Plant Science*, *4*, 315.

Challinor, A., Wheeler, T. R., Garforth, C., Craufurd, P. Q., & Kassam, A. (2007). Assessing the vulnerability of food crop systems in Africa to climate change. *Climatic Change*, *83*, 381–399. https://doi.org/10.1007/s10584-007-9249-0

Cross, R. H., McKay, S. A. B., McHughens, A. G., & Bonham-Smith, P. C. (2003). Heat stress effects on reproduction and seed-set in *Linum usitatissimum* L. (flax). *Plant Cell & Environment*, *26*, 1013–1020. https://doi.org/10.1046/j.1365-3040.2003.01006.x

Dai, A., Wigley, T. M. L., Boville, B. A., Kiehl, J. T., & Buja, L. E. (2001). Climates of the twentieth and twenty-first centuries simulated by the NCAR climate system model. *Journal of Climate*, *14*, 485–519. https://doi.org/10.1175/1520-0442(2001)014<0485:COTTAT>2.0.CO;2

Dias, A. S., & Lidon, F. C. (2009). Evaluation of grain filling rate and duration in bread and durum wheat, under heat stress after anthesis. *Journal of Agronomy & Crop Science*, *195*, 137–147. https://doi.org/10.1111/j.1439-037X.2008.00347.x

Directorate of Millets Development (2014). *Status paper on coarse cereals (Soghum, pearl millet, finger millet, small millets, maize and barley)* (pp. 87–99). Hyderabad, India: Department of Agriculture and Cooperation, Ministry of Agriculture, Government of India.

Djanaguiraman, M., Perumal, R., Ciampitti, I. A., Gupta, S. K., & Prasad, P. V. V. (2017). Quantifying pearl millet response to high temperature stress: Thresholds, sensitive stages, genetic variability and relative sensitivity of pollen and pistil. *Plant Cell & Environment*, https://doi.org/10.1111/pce.12931. [Epub ahead of print].

Djanaguiraman, M., & Prasad, P. V. V. (2014). High temperature stress. In M. Jackson, B. Ford-Lloyd & M. Parry (Eds.), *Plant genetic resources and climate change* (pp. 201–220). Wallingford, UK: CABI Publishers.

Djanaguiraman, M., Prasad, P. V. V., Murugan, M., Perumal, R., & Umesh, U. K. (2014). Physiological differences among sorghum (*Sorghum bicolor* L. Moench) genotypes under high temperature stress. *Environmental & Experimental Botany*, *100*, 43–54. https://doi.org/10.1016/j.envexpbot.2013.11.013

Djanaguiraman, M., Prasad, P. V. V., & Schapaugh, W. T. (2013). High day- or nighttime temperature alters leaf assimilation, reproductive success, and phosphatidic acid of pollen grain in soybean [*Glycine max* (L.) Merr.]. *Crop Science*, *53*, 1594–1604. https://doi.org/10.2135/cropsci2012.07.0441

Easterling, D. R., Meehl, G. A., & Parmesan, C. (2000). Climate extremes: Observations, modeling, and impacts. *Science*, *289*, 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Ferris, R., Ellis, R. H., Wheeler, T. R., & Hadley, P. (1998). Effect of high temperature stress at anthesis on grain yield and biomass of field grown crops of wheat. *Plant Cell & Environment*, *34*, 67–78.

Gote, G. N., & Padghan, P. R. (2009). Studies on different thermal regimes and thermal sensitivity analysis of tomato genotypes. *Asian Journal of Environmental Science*, *3*, 158–161.

Gupta, S. M., Arora, S., Mirza, N., Pande, A., Lata, C., Puranik, S., … Kumar, A. (2017). Finger Millet: A "Certain" Crop for an "Uncertain" future and a solution to food insecurity and hidden hunger under stressful environments. *Frontiers in Plant Science*, *8*, 643. https://doi.org/10.3389/fpls.2017.00643

Hatfield, J. L., Boote, K. J., Fay, P., Hahn, L., Izaurralde, R. C., Kimball, B. A., … Wolfe, D. (2008). Agriculture. In M.K. Walsh, G. Guibert, & R. Hauser et al. (Eds.), *The effects of climate change on agriculture, land resources, water resources, and biodiversity in the United States* (pp. 21–74). Washington, DC: U.S. Department of Agriculture.

Hatfield, J. L., Boote, K. J., Kimball, B. A., Ziska, L. H., Izaurralde, R. C., Ort, D., … Wolfe, D. W. (2011). Climate impacts on agriculture: Implications for crop production. *Agronomy Journal*, *103*, 351–370. https://doi.org/10.2134/agronj2010.0303

IPCC (2007). Climate change 2007: The physical science basis. In S. Solomon, D. Quin, M. Manning, X. Chen, M. Marquis, K. B. Averyt, H. L. Tignor & M. Miller (Eds.), *Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (pp. 1–996). Cambridge, UK: Cambridge University Press.

IPCC (2013). Climate change 2013. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex & P. M. Midgley (Eds.), *The physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change* (p. 535). Cambridge, UK, and New York, NY: Cambridge University Press.

Jain, M., Prasad, P. V. V., Boote, K. J., Allen, L. H. Jr, & Chourey, P. S. (2007). Effects of season-long high temperature growth conditions on sugar-to-starch metabolism in developing microspores of grain sorghum (*Sorghum bicolor* L. Moench). *Planta*, *227*, 67–79. https://doi.org/10.1007/s00425-007-0595-y

Kadir, S., Sidhu, G., & Al-Khatib, K. (2006). Strawberry (Fragaria x ananassa duch.) growth and productivity as affected by temperature. *HortScience*, *41*, 1423–1430.

Kakani, V. G., Reddy, K. R., Koti, S., Wallace, T. P., Prasad, P. V. V., Reddy, V. R., & Zhao, D. (2005). Differences in *in-vitro* pollen germination and pollen tube growth of cotton cultivars in response to high temperature. *Annals of Botany*, *96*, 59–67. https://doi.org/10.1093/aob/mci149

Krishna, K. R. (2014). *Finger millet cropping zones of Asia and Africa. Agroecosystems: Soils, climate, crops, nutrient dynamics and productivity* (pp. 75–84). Oakville, ON: Apple Academic Press.

Lobell, D. B., & Gourdji, S. M. (2012). The influence of climate change on global crop productivity. *Plant Physiology*, *160*, 1686–1697. https://doi.org/10.1104/pp.112.208298

Lobell, D. B., Schlenker, W., & Costa-Roberts, J. (2011). Climate trends and global crop production since 1980. *Science*, *333*, 616–620. https://doi.org/10.1126/science.1204531

Mathur, S., Agrawal, D., & Jajoo, A. (2014). Photosynthesis: Response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology*, *137*, 116–126. https://doi.org/10.1016/j.jphotobiol.2014.01.010

Matsui, T., Omasa, K., & Horie, T. (2001). The difference in sterility due to high temperatures during the flowering period among japonica rice varieties. *Plant Production Science*, *1*, 90–93. https://doi.org/10.1626/pps.4.90

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence-a practical guide. *Journal of Experimental Botany*, *51*, 659–668. https://doi.org/10.1093/jexbot/51.345.659

Narayanan, S., Prasad, P. V. V., Fritz, A. K., Boyle, D. L., & Gill, B. S. (2015). Impact of high nighttime and high daytime temperature stress

on winter wheat. *Journal of Agronomy & Crop Science*, *201*, 206–218. https://doi.org/10.1111/jac.12101

Nguyen, C. T., Singh, V., van Oosterom, E. J., Chapman, S. C., Jordan, D. R., & Hammer, G. L. (2013). Genetic variability in high temperature effects on seed-set in sorghum. *Functional Plant Biology*, *40*, 439–448. https://doi.org/10.1071/FP12264

Pradhan, G. P., Prasad, P. V. V., Fritz, A. K., Kirkham, M. B., & Gill, B. S. (2012). High temperature tolerance in *Aegilops* species and its potential transfer to wheat. *Crop Science*, *52*, 292–304. https://doi.org/10.2135/cropsci2011.04.0186

Prasad, P. V. V., Bheemanahalli, R., & Jagadish, S. V. K. (2017). Field crops and the fear of heat stress - opportunities, challenges and future directions. *Field Crops Research*, *200*, 114–121. https://doi.org/10.1016/j.fcr.2016.09.024

Prasad, P. V. V., Boote, K. J., & Allen, L. H. Jr (2006). Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to high tissue temperature. *Agricultural and Forest Meteorology*, *139*, 237–251. https://doi.org/10.1016/j.agrformet.2006.07.003

Prasad, P. V. V., Boote, K. J., Allen, L. H. Jr, Sheehy, J. E., & Thomas, J. M. G. (2006). Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. *Field Crops Research*, *95*, 398–411. https://doi.org/10.1016/j.fcr.2005.04.008

Prasad, P. V. V., Craufurd, P. Q., Kakani, V. G., & Boote, K. J. (2001). Influence of high temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in peanut. *Australian Journal of Plant Physiology*, *28*, 233–240.

Prasad, P. V. V., & Djanaguiraman, M. (2014). Response of floret fertility and individual grain weight of wheat to high temperature stress: Sensitive stages and thresholds for temperature and duration. *Functional Plant Biology*, *41*, 1261–1269. https://doi.org/10.1071/FP14061

Prasad, P. V. V., Djanaguiraman, M., Perumal, R., & Ciampitti, I. A. (2015). Impact of high temperature stress on floret fertility and individual grain weight of grain sorghum: Sensitive stages and thresholds for temperature and duration. *Frontiers in Plant Science*, *6*, 820.

Prasad, P. V. V., Pisipati, S. R., Mutava, R. N., & Tuinstra, M. R. (2008). Sensitivity of grain sorghum to high temperature stress during reproductive development. *Crop Science*, *48*, 1911–1917. https://doi.org/10.2135/cropsci2008.01.0036

Prasad, P. V. V., Pisipati, S. R., Ristic, Z., Bukovnik, U., & Fritz, A. K. (2008). Impact of nighttime temperature on phenology and growth of spring wheat. *Crop Science*, *48*, 2372–5380. https://doi.org/10.2135/cropsci2007.12.0717

Ray, J. D., Gesch, R. W., Sinclair, T. R., & Allen, L. H. Jr (2002). The effect of vapor pressure deficit on maize transpiration response to a drying soil. *Plant and Soil*, *239*, 113–121. https://doi.org/10.1023/A:1014947422468

Rind, D. (1998). Climate change – just add water vapor. *Science*, *281*, 1152–1153. https://doi.org/10.1126/science.281.5380.1152

Roach, T., & Krieger-Liszkay, A. (2014). Regulation of photosynthetic electron transport and photoinhibition. *Current Protein & Peptide Science*, *15*, 351–362. https://doi.org/10.2174/1389203715666140327105143

SAS Institute (2003). *The SAS users guide, version 9.1.3*. Cary, NC: SAS Institute.

Satish, L., Ceasar, S. A., & Ramesh, M. (2017). Improved Agrobacterium-mediated transformation and direct plant regeneration in four cultivars of finger millet (*Eleusine coracana* (L.) Gaertn.). *Plant Cell, Tissue and Organ Culture*, *131*, 547–565. https://doi.org/10.1007/s11240-017-1305-5

Sato, S. (2006). The effects of moderately elevated temperature stress due to global warming on the yield and the male reproductive development of tomato (*Lycopersicon esculentum* mill.). *Horticulture Research*, *60*, 85–89.

Sato, S., Peet, M. M., & Thomas, J. F. (2000). Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic, mild heat stress. *Plant Cell & Environment*, *23*, 719–726. https://doi.org/10.1046/j.1365-3040.2000.00589.x

Schoper, J., Lambert, R., Vasilas, B., & Westgate, M. (1987). Plant factors controlling seed set in maize. *Plant Physiology*, *83*, 121–125. https://doi.org/10.1104/pp.83.1.121

Singh, V., Nguyen, C. T., van Oosterom, E. J., Chapman, S. C., Jordan, D. R., & Hammer, G. L. (2015). Sorghum genotypes differ in high temperature responses for seed set. *Field Crops Research*, *171*, 32–40. https://doi.org/10.1016/j.fcr.2014.11.003

Sivakumar, M. V. K., & Stefanski, R. (2011). Climate change in South Asia. In R. Lal, M. V. K. Sivakumar, M. A. Faiz, A. H. M. Mustafizur Rahman & K. R. Islam (Eds.), *Climate change and food security in South Asia* (pp. 13–30). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-90-481-9516-9

Stone, P. (2001). The effects of heat stress on cereal yield and quality. In A. S. Basra (Ed.), *Crop responses and adaptations to temperature stress* (pp. 243–291). Binghamton, NY: Crop. Food Products Press.

Sunoj, V. S. J., Shroyer, K. J., Jagadish, S. V. K., & Prasad, P. V. V. (2016). Diurnal temperature amplitude alters physiological and growth response of maize (*Zea mays* L.) during the vegetative stage. *Environmental Experimental Botany*, *130*, 113–121. https://doi.org/10.1016/j.envexpbot.2016.04.007

Tesfaendrias, M. T., McDonald, M. R., & Warland, J. (2010). Consistency of long-term marketable yield of carrot and onion cultivars in muck (organic) soil in relation to seasonal weather. *Canadian Journal of Plant Science*, *90*, 755–765. https://doi.org/10.4141/CJPS09175

Timlin, D., Rahman, S. M. L., Baker, J., Reddy, V. R., Fleisher, D., & Quebedeaux, B. (2006). Whole plant photosynthesis, development, and carbon partitioning in potato as a function of temperature. *Agronomy Journal*, *98*, 1195–1203. https://doi.org/10.2134/agronj2005.0260

Tripathi, A., Tripathi, D. K., Chauhan, D. K., Kumar, N., & Singh, G. S. (2016). Paradigms of climate change impacts on some major food sources of the world: A review on current knowledge and future prospects. *Agriculture, Ecosystems & Environment*, *216*, 356–373. https://doi.org/10.1016/j.agee.2015.09.034

Upadhyaya, H. D., Gowda, C. L. L., Pundir, R. P. S., Reddy, V. G., & Singh, S. (2006). Development of core subset of finger millet germplasm using geographical origin and data on 14 quantitative traits. *Genetic Resources and Crop Evolution*, *53*, 679–685. https://doi.org/10.1007/s10722-004-3228-3

von Caemmerer, S., & Evans, J. R. (2015). Temperature responses of mesophyll conductance differ greatly between species. *Plant Cell & Environment*, *38*, 629–637. https://doi.org/10.1111/pce.12449

Wagstaffe, A., & Battey, N. H. (2006). The optimum temperature for long-season cropping in the ever-bearing strawberry 'everest'. *Acta Horticulturae*, *708*, 45–50. https://doi.org/10.17660/ActaHortic.2006.708.2

Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. (2007). Heat tolerance in plants: An overview. *Environmental and Experimental Botany*, *61*, 199–223. https://doi.org/10.1016/j.envexpbot.2007.05.011

Wahid, A., & Shabbir, A. (2005). Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycine betaine. *Plant Growth Regulation*, *46*, 133–141. https://doi.org/10.1007/s10725-005-8379-5

Wollenweber, B., Porter, J. R., & Schellberg, J. (2003). Lack of interaction between extreme high temperature events at vegetative and reproductive growth stages in wheat. *Journal of Agronomy & Crop Science*, *189*, 142–150. https://doi.org/10.1046/j.1439-037X.2003.00025.x

Yan, K., Chen, P., Shao, H., Zhang, L., & Xu, G. (2011). Effects of short-term high temperature on photosynthesis and photosystem II performance in sorghum. *Journal of Agronomy & Crop Science*, *197*, 400–408. https://doi.org/10.1111/j.1439-037X.2011.00469.x

Yang, J., Sears, R. G., Gill, B. S., & Paulsen, G. M. (2002). Genotypic differences in utilization of assimilate sources during maturation of wheat under chronic heat and heat shock. *Euphytica*, *125*, 179–188. https://doi.org/10.1023/A:1015882825112

Young, L. W., Wilen, R. W., & Bonham-Smith, P. C. (2004). High temperature stress of *Brassica napus* during flowering reduces micro-and megagametophyte fertility, induces fruit abortion, and disrupts seed production. *Journal of Experimental Botany*, *55*, 485–495. https://doi.org/10.1093/jxb/erh038

Zeng, N., Neelin, J. D., Lau, K.-M., & Tucker, C. J. (1999). Enhancement of interdecadal climate variability in the Sahel by vegetation interaction. *Science*, *286*, 1537–1540. https://doi.org/10.1126/science.286.5444.1537

Ziska, L. H., Blumenthal, D. M., Runion, G. B., Hunt, E. R., & Diaz-Soltero, H. (2011). Invasive species and climate change: An agronomic perspective. *Climatic Change*, *105*, 13–42. https://doi.org/10.1007/s10584-010-9879-5

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Opole RA, Prasad PVV, Djanaguiraman M, Vimala K, Kirkham MB, Upadhyaya HD. Thresholds, sensitive stages and genetic variability of finger millet to high temperature stress. *J Agro Crop Sci*. 2018;00:1–16. https://doi.org/10.1111/jac.12279