Sorghum is an important grain crop in semiarid regions of the world. The mean optimum temperature range for sorghum is 21 to 35°C for seed germination, 26 to 34°C for vegetative growth and development, and 25 to 28°C for reproductive growth (Maiti, 1996). Recent synthesis and analyses of data on past and future climates suggest that, at the present rates of greenhouse gas emissions and population growth, the global mean surface temperatures will increase by 1.4 to 5.8°C (IPCC, 2007). In addition, we will experience greater climate variability characterized by increased frequency of short episodes of extreme temperatures events, including short periods of temperature stress (IPCC, 2007). These changes could have significant influence on productivity of grain crops, including sorghum. Therefore, it is important to understand impacts of both seasonlong and short episodes of high-temperature (HT) stress on physiology, growth and yield of grain sorghum.

Sorghum-producing regions often experience daytime/nighttime temperatures of >32/22°C (Prasad et al., 2006a). High-temperature stress can cause significant decreases in sorghum grain yields (Prasad et al., 2006a). Dry matter and seed yields of grain sorghum were maximum at 27/22°C (daytime/nighttime temperature). Temperatures above 33/28°C during early stages of seed development decreased seed yield, with a larger reduction at early stages of seed development.

**ABSTRACT**

Sorghum (*Sorghum bicolor* L. Moench) grown in semiarid regions is often exposed to short periods of high-temperature (HT) stress during reproductive development. Objectives of this research were (i) to quantify the effects of short episodes of HT stress during reproductive development on physiological, growth, and yield processes of grain sorghum and (ii) to identify the stage(s) most sensitive during the reproductive development phase to HT stress. Plants of hybrid DK-28 E were grown in growth chambers at daytime maximum/nighttime minimum optimum temperature (OT) of 32/22°C until 29 d after sowing. Thereafter, plants were exposed to OT or HT (40/30°C) or were reciprocally transferred at 10-d intervals (10 d before flowering, 0, 10, 20, and 30 d after flowering [DAF]) from OT to HT and vice versa. Transferred plants remained in the new temperature regime for 10 d before being returned to their original temperature regime. Continuous HT stress delayed panicle emergence and decreased plant height, seed set, seed numbers, seed yield, seed size, and harvest indices but did not influence leaf photosynthesis. Exposure to short (10-d) periods of HT stress at flowering and 10 d before flowering caused maximum decreases in seed set and seed yield, and HT stress during postflowering stages (10, 20, and 30 DAF) decreased seed yield, with a larger reduction at early stages of seed development.

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**Abbreviations**: DAF, days after flowering; DAS, days after sowing; HT, high temperature; OT, optimum temperature.

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development induce floret and embryo abortion (Downes, 1972). High temperatures also decrease seed-filling duration, resulting in smaller seed size and lower seed yields (Chowdhury and Wardlaw, 1978; Kiniry and Musser, 1988). In a recent study, seasonlong (from emergence to maturity) effects of a range of HT >35/25°C on physiology, growth, and yield of grain sorghum hybrid DK-28E were quantified (Prasad et al., 2006a). This research suggested that there were no significant influences of seasonlong growth temperatures in the range of 36/26 to 44/34°C on leaf photosynthetic rates. However, HT (≥36/26°C) significantly decreased seed set, seed number, seed size, seed-filling duration, and seed yields when compared with optimum temperature (OT) (32/22°C). Growth temperature of 40/30°C delayed panicle exsertion by about 30 d, while panicle exsertion was completely inhibited at growth temperatures of 44/34°C (Prasad et al., 2006a).

Short episodes of HT stress can also cause significant yield reductions. Yield variability of grain crops is often related to environmental conditions during the most sensitive stages of crop development (Wheeler et al., 2000). Short periods (1 to 6 d) of HT stress at flowering can cause significant decreases in seed numbers and seed yield in rice (Oryza sativa L.) (Jagadish et al., 2007) and peanut (Arachis hypogaea L.) (Prasad et al., 2001). In studies on peanut and rice, microsporogenesis (about 3 to 5 d before flowering) and flowering (at anthesis) were relatively more sensitive to HT compared with postflowering stages (Prasad et al., 1999; Matsui et al., 2001). Previous studies reported strong negative linear relationship between spikelet fertility and cumulative temperature >34°C in rice (Jagadish et al., 2007) and between pollen production and cumulative temperature >33°C in peanut (Prasad et al., 1999). Short episodes of HT (≥37°C) can occur in sorghum-producing regions during reproductive periods, for example, in Kansas (Fig. 1). Effects of short episodes of temperatures >33/28°C on phenology, growth, yield, and yield components of grain sorghum are not well understood and need to be researched further. A few studies (Downes, 1972; Craufurd et al., 1998; Hammer and Broad, 2003; Prasad et al., 2006a) compared the effects of HT stress during vegetative and reproductive development of grain sorghum and suggested that reproductive processes (e.g., panicle initiation, seed growth, and seed size) were more sensitive to HT than were vegetative processes (e.g., leaf appearance, photosynthesis). Most studies on sorghum have investigated seasonlong effects of HT stress from sowing to maturity or for the entire vegetative or reproductive phase. When plants are exposed to seasonlong or longer periods of HT, they have opportunity to acclimate, and such responses would be different than that of short, sudden episodes of HT stress. In addition, comparison of stage sensitivity at various growth phases are often made from different experiments conducted at different locations. Comparison of stage sensitivity from different experiments may often be confounded by variety, soil type, and environment. There are no systematic studies describing relative sensitivities of different stages within the reproductive development phase of grain sorghum to short episodes of HT in a single experiment. Such knowledge will improve our understanding of response of grain sorghum to HT stress and development crop management strategies to minimize risk.

The objectives of our research were (i) to quantify the effects of short episodes of HT stress during reproductive development on physiological, growth, and yield process of grain sorghum and (ii) to identify the stage(s) during the reproductive development phase (starting from 10 d before panicle emergence through maturity) most sensitive to HT. We hypothesize that short periods of HT stress during flowering stages of reproductive development will cause maximum decreases in yield and yield components.

**MATERIALS AND METHODS**

This research was conducted in controlled environment facilities at the Department of Agronomy at Kansas State University in Manhattan, KS. Two independent experiments were conducted to determine the impact of HT stress during reproductive development on physiology, growth, and yield of one sorghum hybrid, DK-28E. Experiments involved reciprocal transfers (Prasad et al., 1999), that is, moving plants reciprocally between OT and HT regimes at different stages for fixed periods of time before returning them to their original temperature regime.

**Plant Husbandry and Growth Conditions**

Seeds of photoperiod-insensitive sorghum hybrid DK-28E were treated with fungicide (Captan, Hummert International, Earth City, MO) as a precautionary measure against seedborne diseases. Five seeds per pot were sown at 4 cm depth in 15-L pots (top and bottom pot diameters were 27.5 and 26 cm, respectively; pot depth was 25 cm). Rooting medium was potting soil (Metro Mix 350, Hummert Int., Topeka, KS). Four large indoor growth chambers (Conviron Model CMP 3244, Winnipeg, Manitoba, Canada) were used for this research; two chambers were used for each experiment. Each growth chamber was 136 cm wide, 246 cm long, and 180 cm high. There were 48 pots per growth chamber. After emergence, plants were thinned to three plants per pot until maturity. All four growth chambers were maintained at a daytime maximum/nighttime minimum temperature regime of 32/22°C from sowing until 10 d before panicle emergence (29 d after sowing, DAS). Starting from 30 DAS, plants were grown at either 32/22°C (OT) or at 40/30°C (HT) or were reciprocally transferred at 10-d interval between OT and HT treatments and vice versa until 80 DAS. Daytime and nighttime temperature regimes were held for 12 h with a 6-h transition period between the daytime maximum and nighttime minimum temperatures. The photoperiod was 12 h, and photon flux density (400 to 700 nm) provided by cool fluorescent lamps was 667 μmol m⁻² s⁻¹ measured at canopy level. Relative humidity in the chambers was set at 85%. Air temperature, relative humidity, and light level were continuously monitored at 20-min intervals in all growth chambers throughout the experiments. Pots were watered daily to keep the soil moisture at field capacity to avoid any water stress.
Reciprocal Transfer Treatments

From sowing to 29 DAS (panicle initiation), all plants in all four growth chambers were grown at OT. At 30 DAS, plants in two growth chambers were exposed to HT. Thereafter, plants were transferred at 10-d intervals from OT to HT and from HT to OT until 80 DAS, giving a total of nine treatments (eight reciprocal transfer treatments and two controls). Plants remained in the new temperature regime for 10 d before being returned to their original temperature regimes, where they remained until final harvest at maturity. Some plants were kept at 32/22°C and 40/30°C environment from 30 DAS to harvest maturity (125 DAS) to serve as OT and HT controls, respectively. Plants were randomly selected for transfers, and treatments were arranged randomly within each growth chamber.

Data Collection

Data on phenology (i.e., days from sowing to boot leaf emergence, anthesis, and physiological maturity) were recorded for plants from all treatments. All physiological traits were measured on attached, fully expanded flag leaves of four tagged plants from each treatment. Chlorophyll content and stability of photosynthetic (thylakoid) membranes were measured at the beginning and end of each transfer treatment. A self-calibrating chlorophyll meter (SPAD, Model 502, Spectrum Technologies, Plainfield, IL) was used for chlorophyll measurements. Thylakoid membrane stability was assessed by measuring chlorophyll $a$ fluorescence using a fluorometer (OS 30, OptiScience, Hudson, NH) after 30 min of dark adaptation of leaves and by determining the ratio of variable fluorescence (the difference between maximum and minimum fluorescence) to maximum fluorescence. Decrease in this ratio indicates stress and damage to thylakoid membranes. In addition, leaf level gas exchange measurements (photosynthesis, stomatal conductance, and transpiration) and leaf temperatures from three plants from OT and HT treatments were measured at the end of each transfer using a LI-COR 6400 portable photosynthesis system (LI-COR, Lincoln, NE). Gas exchange measurements were taken on fully expanded flag leaves at midday at growth temperature and ambient CO2 conditions. The internal LED light source in the LI-COR 6400 was set at 1600 μmol m−2 s−1 to have a constant and uniform light across all measurements.

Relative water content was determined on fully expanded leaves of two plants (one leaf per plant). From each leaf, 2.5-cm-long square pieces were collected, excluding midribs. Fresh weight of leaf discs was measured, and discs were then floated immediately on deionized water in a petri dish kept in the dark at 4°C for 24 h; turgid weight was obtained after removing the superficial droplets of water. Thereafter, leaves were oven dried at 65°C for 7 d. Relative water content (%) was calculated as [(fresh weight − dry weight)/(turgid weight − dry weight)] × 100.

At maturity (125 DAS), data on plant height (base to tip of the plant), tiller numbers, and leaf area were measured using a LI-3100 (LI-COR, Lincoln, NE). Plants were separated into component parts (leaf, stem, panicle, and seed), and dry weights were recorded. Leaves and stems were dried at 65°C for 7 d. Panicles were dried at 40°C for 10 d and hand threshed, and seed numbers and seed dry weights were measured. Harvest index was estimated as ratio of seed yield to total aboveground biomass. In addition, data on panicle length, branches, total number of reproductive sites, and number of filled and unfilled seeds also were estimated. Individual spikelets were checked for seed by pressing the floret between the thumb and the index finger. Seed set was estimated as the ratio of spikelets with seed to the total number of reproductive sites and expressed as percentage. Individual seed weight (seed size) was estimated as the ratio of total seed dry weight and total number of seeds.

Data Analyses

Two independent experiments were conducted simultaneously in four different growth chambers. Each experiment was designed as a randomized block design with added controls in two growth chambers. There were four replications of each transfer and control treatments in each experiment. Plants were randomly selected for transfer treatments and were randomly arranged within the growth chambers. All data were statistically analyzed using SAS PROC ANOVA procedures (SAS Institute, 2003) software. Initial data analyses were conducted separately for each experiment (Exp. 1 and Exp. 2) and in combination. Results of both experiments, separately or in combination, had similar responses and significance levels for all traits with no interaction effects. Therefore, mean responses across two experiments (eight replicated pots, four in each experiment) are presented and described below. Standard errors are shown as an estimate of variability, and LSD were used to compare and test the significance of transfer treatments compared with respective controls.

RESULTS

The mean daytime and nighttime temperature (± SD) in the OT treatment were 32.4°C (± 0.5) and 22.7°C (± 0.7), respectively. The corresponding temperatures in HT treatment were 40.2°C (± 0.3) and 30.1°C (± 0.5), respectively.
Relative humidity during daytime and nighttime were similar across both temperature regimes at 72 ± 7% in Exp. 1. Temperatures were ± 0.4°C of the target temperatures, and relative humidity was within ± 10% in Exp. 2.

**Effects of Growth Temperature**

There were significant effects ($P < 0.001$) of HT on phenology, physiological, growth, and yield traits (Table 1). Compared with OT (32/22°C), continuous exposure to HT (40/30°C) during the reproductive phase delayed time to panicle emergence by 28 d and flowering by 20 d. However, duration from panicle emergence to flowering was shorter at HT (4 d) compared with OT (12 d). There was no effect of HT on relative water content or leaf photosynthetic rates when averaged across the season (Table 1) or at various stages of crop development (Fig. 2). Chlorophyll content and chlorophyll $a$ fluorescence were not significantly different at various times of crop development (Fig. 2). However, when averaged across the entire season, chlorophyll content and chlorophyll $a$ fluorescence at HT were significantly lower than at OT (Table 1).

High-temperature stress significantly ($P < 0.001$) decreased plant height at maturity, percentage seed set, seed numbers, and seed size but had no significant influence on leaf area, leaf dry weights, or total potential reproductive sites (Table 1). In contrast, HT stress significantly increased leaf numbers. Stem dry weights were slightly ($P = 0.05$) higher under HT stress, whereas seed yields were significantly ($P < 0.001$) lower. Thus, total dry weights were significantly ($P < 0.001$) higher at OT compared with HT, which led to significantly ($P < 0.001$) smaller harvest indices at HT compared with OT (Table 1).

**Effect of Reciprocal Transfers**

Transferring plants from OT to HT (exposure to 10 d of HT) significantly influenced most growth (Fig. 3) and yield traits (Fig. 4). Plant height at maturity was significantly ($P = 0.05$) decreased when plants were exposed to HT at 10 d before flowering and at flowering but not at other stages of development (Fig. 3a). Leaf numbers decreased with exposure to OT at 10 d before flowering and at flowering, whereas exposure at later stages of crop development increased leaf numbers (Fig. 3b). There was no consistent trend in leaf area (Fig. 3c) and vegetative dry weight (Fig. 3d) in response to temperature stress.

Exposures to 10 d of HT stress significantly decreased seed set (percentage of reproductive sites forming seeds) only at 10 d before flowering and at flowering (Fig. 4a). Maximum decreases in seed set of plants under HT stress occurred at flowering (54%) and 10 d before flowering (22%); control plants at OT had about 81% seed set. There was no significant influence of HT at later stages of reproductive development in which seed set was close to 79%.

Transfers from HT to OT (exposure to OT) slightly (about 6%) but significantly increased seed set at most stages, with maximum increases occurring when plants were exposed to OT at 10 d before flowering, at flowering, and at 10 d after flowering (DAF).

Transfers from OT to HT (exposure to HT) significantly ($P < 0.05$) decreased seed yield across all stages of reproductive development, except at 40 DAF (Fig. 4b). Maximum decreases in seed yield occurred when plants were exposed to HT at flowering or 10 d before flowering. Decreases were less pronounced at 10, 20, and 30 DAF. In contrast, transfers from HT to OT (exposure to OT) did not influence seed yield across all stages of reproductive development.

Total dry weights were decreased significantly ($P < 0.05$) when exposed to HT at 10 d before flowering or at flowering (Fig. 4c) but not at other stages of reproductive development. The response of harvest index to HT was similar to that of seed yield, with maximum decreases occurring at flowering, followed by lesser decreases at 10 d before flowering and 10 DAF (Fig. 4d). Transfers from OT to HT significantly decreased seed size (Fig. 5). The effects of HT during early stages of seed development were relatively larger than those at later stages of seed development. There were no significant increases in total dry weights or harvest indices when plants were transferred from HT to OT at different stages of reproductive development.

### Table 1. Influence of continuous optimum temperature (OT, 32/22°C) and high temperature (HT, 40/30°C) on various phenology and physiological, growth, and yield traits of grain sorghum.

<table>
<thead>
<tr>
<th>Trait</th>
<th>OT</th>
<th>HT</th>
<th>LSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to panicle emergence (d)</td>
<td>38</td>
<td>66</td>
<td>−1</td>
</tr>
<tr>
<td>Time to flowering (d)</td>
<td>50</td>
<td>70</td>
<td>−1</td>
</tr>
<tr>
<td>Relative water content (%)</td>
<td>92</td>
<td>89</td>
<td>NS†</td>
</tr>
<tr>
<td>Leaf photosynthesis (μmol m−2 s−1)</td>
<td>42</td>
<td>38</td>
<td>NS</td>
</tr>
<tr>
<td>Leaf chlorophyll (SPAD units)</td>
<td>44</td>
<td>38</td>
<td>2.8*</td>
</tr>
<tr>
<td>Chlorophyll a fluorescence</td>
<td>0.77</td>
<td>0.72</td>
<td>0.03*</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>136</td>
<td>71</td>
<td>16.1***</td>
</tr>
<tr>
<td>Leaf number (plant−1)</td>
<td>12</td>
<td>17</td>
<td>2.0***</td>
</tr>
<tr>
<td>Leaf area (cm² plant−1)</td>
<td>2111</td>
<td>2530</td>
<td>NS</td>
</tr>
<tr>
<td>Leaf dry weight (g plant−1)</td>
<td>10.6</td>
<td>13.9</td>
<td>NS</td>
</tr>
<tr>
<td>Stem dry weight (g plant−1)</td>
<td>21.8</td>
<td>15.1</td>
<td>6.6*</td>
</tr>
<tr>
<td>Total reproductive sites (panicle−1)</td>
<td>580</td>
<td>550</td>
<td>NS</td>
</tr>
<tr>
<td>Seed set (%)</td>
<td>80</td>
<td>7</td>
<td>20.5***</td>
</tr>
<tr>
<td>Seed number (panicle−1)</td>
<td>465</td>
<td>40</td>
<td>65***</td>
</tr>
<tr>
<td>Seed size (mg seed−1)</td>
<td>32.5</td>
<td>18.2</td>
<td>3.6***</td>
</tr>
<tr>
<td>Seed dry wt. (g plant−1)</td>
<td>19</td>
<td>1.5</td>
<td>5.64***</td>
</tr>
<tr>
<td>Total dry wt. (g plant−1)</td>
<td>56</td>
<td>30</td>
<td>13.0***</td>
</tr>
<tr>
<td>Harvest index</td>
<td>0.38</td>
<td>0.04</td>
<td>0.13***</td>
</tr>
</tbody>
</table>

*Significant at $P ≤ 0.05$.

***Significant at $P ≤ 0.001$.

†NS, nonsignificant ($P > 0.05$).
DISCUSSION

This research clearly demonstrates that short episodes (10 d) of HT stress (40/30°C, HT) during reproductive development of grain sorghum could be detrimental to yield and yield components. Preflowering (10 d before flowering), flowering, and postflowering stages were sensitive to HT stress; however, sensitivity varied by stage. Reciprocal transfers showed that maximum decreases in yield occurred when HT stress was imposed at flowering and 10 d before flowering. Yield losses at these two stages of reproductive development resulted mainly from decreases in seed number caused by a decrease in the percentage of seed set (Fig. 4). The lower seed set at HT was due to decreased number of filled sites rather than total number of reproductive sites per panicle, suggesting that the processes leading to fertilization (pollen viability, ovule viability, pollen tube growth, and/or fertilization) were sensitive to HT stress. This concurs with previous studies on the same grain sorghum hybrid, which suggests that pollen viability, as measured by pollen germination, was decreased at temperatures ≥36/26°C (Prasad et al., 2006a). Similarly, Downes (1972) revealed that HT (33/28°C compared with 27/22°C) at panicle initiation and the early phase of panicle development did not reduce floret numbers (flower production), but HT in the later stages of panicle development and at flowering induced floret abortion and early embryo abortion resulting in lower grain yields. In most cereals (sorghum, Prasad et al., 2006a; rice, Prasad et al., 2006b; wheat [Triticum aestivum L.], Saini et al., 1983) and legumes (peanut, Prasad et al., 2000, 2001; soybean [Glycine max (L.) Merr.], Koti et al., 2005; Salem et al., 2007; cowpea [Vigna unguiculata, Fabaceae], Ahmed et al., 1992; and common bean [Phaseolus vulgaris L.], Gross and Kigel, 1994; Prasad et al., 2002), reproductive processes that occur during flowering, such as pollen production, pollen germination, pollen tube growth, fertilization, and seed set, were found to be highly sensitive to HT stress.

In the present study, the preflowering stage (10 d before flowering) was also highly sensitive to HT stress (Fig. 4). This period in grain sorghum is likely to be associated with timing of later stages of microsporogenesis (pollen development) or megasporogenesis (ovule development). Although both microsporogenesis and megasporogenesis are injured under HT stress, which results in lower seed set (Cross et al., 2003; Young et al., 2004), pollen is known to be relatively more sensitive to HT stress than ovules. Recent biochemical studies on developing anthers...
suggest that HT stress (36/26°C compared with 30/20°C) during prefl owering stages of grain sorghum (early stages of microsporogenesis) results in loss of pollen viability (Jain et al., 2007), which is associated with altered carbohydrate metabolism and starch deficiency in developing pollen grains (Jain et al., 2007). Loss of pollen viability due to HT stress during microsporogenesis also could be related to degeneration of the tapetum tissue (Suzuki et al., 2001; Porch and Jahn, 2001) or decreased carbohydrate metabolism (Pressman et al., 2002; Karni and Aloni, 2002), which can influence nourishment of pollen mother cells and lead to infertile pollen. Previous studies on pea nut (Prasad et al., 1999) and common bean (Gross and Kigel, 1994) also suggested that HT stress during prefl owering stages, particularly during microsporogenesis, causes loss in pollen viability that results in lower seed set, seed numbers, and seed yield.

Yield losses at postfl owering stages were mainly due to decreases in seed size (Fig. 4). Furthermore, earlier postfl owering stages (10 and 20 DAF) were more sensitive and had greater decreases in seed yield and seed size compared with later postfl owering stages (30 and 40 DAF) (Fig. 4 and 5). Lower seed yields were not a result of decreased leaf photosynthetic rates, as they did not decrease even under continuous exposure to HT stress (Fig. 2). However, mobilization of stored carbohydrates from leaves and stems is important for seed development (Hammer and Broad, 2003). High-temperature stress can directly affect seed yield by influencing seed-filling duration and rate, both of which are highly sensitive to HT stress (Prasad et al., 2006a).

Chowdhury and Wardlaw (1978) reported that increasing temperatures increased seed-filling rate but decreased seed-filling duration; therefore, there was no effect on seed size at temperatures between 24/19°C and 30/25°C. Above 30/25°C, however, seed-filling rate was not affected, but seed-filling duration decreased, resulting in a 50% reduction in seed size. These results suggest that HT stress reduces seed size by decreasing seed-filling duration when the decrease in seed-filling duration is not accompanied by a compensatory increase in seed-filling rate (Peacock and Heinrich, 1984). There was a significant delay in panicle emergence when continuous HT stress was imposed at panicle initiation (Table 1). This is consistent with our previous study, in which exposure to 40/30°C from sowing delayed panicle emergence by about 20 d (Prasad et al., 2006a). Optimum temperatures for panicle initiation range from 26 to 27°C, and further temperature increase delays panicle initiation (Craufurd et al., 1998).

In summary, the two stages of grain sorghum reproductive development most sensitive to HT stress are flowering and 10 d before flowering. High-temperature stress in these stages caused maximum reduction in seed set, seed numbers, and seed yields. Early seed-filling periods were relatively more sensitive to HT stress compared with later periods. Seed yield losses during postfl owering stages were mainly due to decreases in seed size. This research highlights the importance of understanding consequences of short periods of HT stress and its occurrence relative to crop growth stages. In addition, results also suggest a need to develop sorghum hybrids that can better tolerate HT stress during sensitive stages of reproductive development.
to minimize losses and improve grain sorghum yield in the semiarid regions.

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