Responses of Three Wheat Genotypes to High Soil Temperature during Grain Filling

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Abstract: High temperatures limit wheat (*Triticum aestivum* L.) production in many areas around the world. Soil temperatures near the root zone could be as high as the air temperature during wheat grain filling. The objectives of this study were to investigate the effects of high soil temperature on grain yield and related traits of wheat genotypes and to examine their differential responses. Three genotypes, Imam, Fang and Siete Cerros were grown under three temperature conditions in the daytime during grain-filling period: (i) normal air temperature/normal soil temperature (26/26°C), (ii) normal air temperature/high soil temperature (26/38°C) and (iii) high air temperature/high soil temperature (38/38°C). The night temperature was 18/18°C in all treatments. Temperatures during the daytime were increased at a rate of 4°C hr⁻¹ from 18°C to the designated temperature, which was kept for at least 4 hr around noon. The 26/38°C and 38/38°C treatments significantly decreased the chlorophyll content (SPAD) of flag leaves, grain-filling duration, and increased carbohydrate remobilization or loss from the stem and the root, but with varying degrees among genotypes. Grain yield, biomass, grain weight, grains number spike⁻¹ and harvest index at the 38/38°C treatment were significantly lower than at the other two treatments. In Imam, the grain yield was lower at 26/38°C than at 26/26°C, while in Siete Cerros the grain yield, grain weight, grain number spike⁻¹ and harvest index were lower at the 38/38°C treatment than at the other two treatments. These results indicated that high temperature of soil alone (26/38°C) or high temperature of both air and soil (38/38°C) decreased the chlorophyll content and grain-filling duration, and increased carbohydrate remobilization. Genotypic differences in the responses to high soil temperature (26/38°C) and high air/soil temperature (38/38°C) were also observed.

Key words: Chlorophyll content, Genotypic response, High soil temperature, Water soluble carbohydrates, Wheat.

In many wheat growing regions, high temperatures during grain filling are major factor limiting its productivity. When the air temperature rises, the soil temperature might also rise especially when the crop matures and loses its canopy cover. Soil temperature at a depth of 5 cm under grass sod equals the air temperature, and is only slightly lower at 10 cm during the grain-filling period of wheat (Guedira and Paulsen, 2002). In semiarid areas, soil temperatures of 38°C (or higher) are common (Ishag, 1996; Craufurd et al., 2003). Soil temperature strongly affects the shoot growth in many species including wheat (Kuroyanagi and Paulsen, 1988; Guedira and Paulsen, 2002), maize (Caers et al., 1985), sorghum (Clarck and Reinhard, 1991), groundnut (Awal and Ikada, 2002; Craufurd et al., 2003) and bentgrass (*Agrostis palustris* Huds.) (Xu and Huang, 2000a, b). Even high soil temperatures for a short period can significantly reduce photosynthetic activity and both shoot and root growth (Caers et al., 1985; Udomprasert et al., 1995). Kuroyanagi and Paulsen (1988) concluded that the responses of wheat to high temperatures, either of roots or shoots, accelerate senescence, which might be mediated by the damage of roots during grain development. The effect of high soil temperatures during wheat grain filling on shoot senescence and grain growth (Kuroyanagi and Paulsen, 1988) and grain starch accumulation (Guedira and Paulsen, 2002) resembled that of the high whole-plant temperature.

Despite the importance of soil temperature, little is known about the effect of high soil temperature (Kuroyanagi and Paulsen, 1988; Guedira and Paulsen, 2002) and most of the studies on high-temperature effects on wheat have been done by applying high-temperature stress to the shoot or the whole plant. Significant genotypic differences in the response to high soil temperatures were reported in groundnut (Craufurd et al., 2003), radish (Fukuoka and Enomoto, 2001) and bentgrass (Xu and Huang, 2000a, b). However, studies on the genotypic differences in the response of wheat to high soil temperatures are scarce. Moreover, whether the responses to a high soil temperature of genotypes known to be sensitive or tolerant to high air or whole-plant temperatures...
are the same or not has not been investigated. Such information is important for improving the adaptability of wheat genotypes to such stress. In this study, the effects of high temperature of the soil and high temperature of both soil and air during the grain-filling period on wheat grain yield and related traits and the genotypic difference in the response of wheat to such stresses were examined.

**Materials and Methods**

Three wheat genotypes, Fang, Siete Cerros and Imam, were used in this study. Fang and Siete Cerros were characterized by many investigators as heat-tolerant and heat-sensitive genotypes, respectively (Reynolds et al., 1994; Ibrahim and Quick, 2001; Skylas et al., 2002), while Imam is a cultivar released in 2000 for the heat-stress environment of the Sudan. Seeds of the three genotypes were sown on 3 Feb. 2003 in 1/5000a Wagner’s pots. The pots were filled with a mixture of soil: sand: organic matter in a ratio of 2:1:1. A fertilizer containing 1:1:1 of N: P₂O₅: K₂O was incorporated to the soil prior to sowing at a rate of 0.4 g pot⁻¹ per each element. Three seedlings were grown in each pot. The pots were placed in a naturally illuminated vinyl house (February-May 2003, Tottori University, Japan) keeping the maximum temperature below 26°C.

After 3 to 5 days from anthesis (on 12 May), the pots were randomly divided into three groups and assigned for three temperature treatments. These treatments were normal air temperature/normal soil temperature (26/26°C treatment), normal air temperature/high soil temperature (26/38°C treatment) and high air temperature/high soil temperature (38/38°C treatment) during the daytime and 18/18°C at night. A growth chamber (K30-2190, Koito Industries, LTD.) capable of maintaining different air/soil temperature was used. The temperature during the daytime was increased at a rate of 4°C hr⁻¹ from 18°C to the designated temperature, and the designated temperature was held for at least 4 hr and then decreased in the same manner. The soil and air temperatures were monitored every 30 min at a depth of 5 cm and above canopy level, respectively, using Thermo Recorders (Thermo Recorder for Windows, TR-72S, T AND D, Japan) connected to sensors. The
soil temperatures recorded each day throughout the experimental period were almost identical. A sample of soil temperature recorded for 24 hr is given in Fig. 1. The air temperature was ± 1°C of the designated value. Irradiance was 1100-1200 µmol m⁻² s⁻¹ photosynthetically active radiation as measured with a LI-190 quantum sensor (LI-COR, Inc., Lincoln, NE) and applied for 14 hr. The relative humidity was 30/40 % during the day/night time. Plants were watered daily or as needed and kept free from pests and diseases by spraying with appropriate chemicals.

Chlorophyll content of six flag leaves in each pot was measured weekly using a chlorophyll meter (Minolta SPAD-502 meter: Minolta Camera Co., Japan), recorded in SPAD units. Measurements were made on 0, 7, and 14 days after treatment (DAT) initiation.

Date of anthesis was the day when more than two thirds of main stem shed anthers. Fang, Siete Cerros and Imam reached anthesis on 7, 8 and 9 May, respectively. Date of maturity was the day when spike tissues lost their green color. Duration of grain filling was defined as the interval between anthesis and maturity. At 0 DAT, nine plants per genotype were sampled from three pots and separated into main stem and tillers, which were further separated into stems (including leaf sheath), leaves and spikes. At maturity, plants were harvested from the soil level and separated to main stem and tillers. All samples were oven dried at 80°C for 72 hr and weighed to determine the dry weight. Spikes were threshed manually and grains were weighed. The number of grains was counted and grain weight was calculated. In two of the three replications, roots were carefully washed at anthesis and maturity and oven-dried at 65°C for 72 hr.

Main-stem culms and the roots from the samples taken at 0 DAT and maturity were chopped into small pieces and ground in a UDY Cyclone sample mill (UDY Corp., Fort Collins, CO., USA) to pass 0.5 mm sieve. For the measurement of water-soluble carbohydrates (WSC), a sample of 100 mg was extracted three times with hot water (95°C) and combined. Measurement was made by phenol-sulfuric acid method (Dubois et al., 1956) with a sucrose standard. Stem WSC remobilization efficiency was calculated as: [(WSC concentration at 0 DAT - WSC concentration at maturity)/WSC concentration at 0 DAT] × 100.

The experiment was arranged in a randomized complete block design with three replicates. All data were subjected to standard analysis of variance. One-way analysis of variance was done for the samples taken at 0 DAT, while two-way analysis of variance was done for the measurements taken during or at the end of the treatment period.

**Results**

The two-way analysis of variance revealed significant
differences among genotypes across temperature treatments for most of the traits measured including grain yield, main-stem biomass, chlorophyll content, grain-filling duration, grain weight, grain number spike$^{-1}$ and WSC remobilization efficiency (Tables 1, 2 and 3). Significant genotype × temperature interactions (G × T) were also found in stem WSC remobilization efficiency, grain yield and harvest index.

The 26/38°C and 38/38°C treatments significantly accelerated the senescence of leaves compared with the 26/26°C treatment. Chlorophyll content of the flag leaf decreased significantly at 26/38°C and 38/38°C after 7 DAT (Table 1). The 26/38°C and 38/38°C treatments had similar effects on chlorophyll content in Fang and Siete Cerros, but in Imam, 26/38°C treatment was more detrimental than 38/38°C treatment. At 14 DAT, the difference in chlorophyll contents between the 26/26°C treatment and the other two treatments become apparently bigger (Table 1). The chlorophyll contents of the three genotypes were significantly decreased by both 26/38°C and 38/38°C treatments, but the rate of decrease was higher in Imam and Fang than in Siete Cerros. Even at 26/26°C, the chlorophyll content decreased at a higher rate in Imam and Fang than in Siete Cerros.

The accelerated senescence of leaves resulted in a significant decrease in the grain-filling duration at both 26/38°C and 38/38°C (Table 1). The decrease in grain-filling duration at 38/38°C was greater (19.6%) than that at 26/38°C (14.1%). The response of grain-filling duration to high temperature varied with genotype. In Fang and Siete Cerros, the grain-filling duration at 38/38°C was shorter than that at the 26/38°C treatment. However, in Imam, the duration was similar at both 26/38°C and 38/38°C treatments.

The 26/38°C and 38/38°C treatments had the same effect on the stem WSC remobilization efficiency across the three genotypes. The stem WSC remobilization efficiency in both Imam and Fang significantly increased at 26/38°C and 38/38°C treatments despite their remobilization efficiencies were high at 26/26°C (Table 1). On the other hand, no significant differences were found between treatments in the stem WSC remobilization efficiency in Siete Cerros. The root WSC concentration in Siete Cerros at 0 DAT was significantly higher than that in the other two genotypes (Table 1). At maturity, both 26/38°C and 38/38°C treatments caused a significantly higher loss in WSC from the roots of the three genotypes (Table 1). The root WSC concentration at maturity at 26/26°C was lower than at 38/38°C in Imam, while it was higher in Fang and Siete Cerros.

Because the responses to high-temperature treatments of biomass and grain yield differed between

| Genotype/Treatment | Grain Yield (g plant$^{-1}$) | Biomass (g plant$^{-1}$) |
|-------------------|------------------------------|--------------------------|
|                   | Main stem | Tiller | Total | Main stem | Tiller | Total |
| Imam              |           |        |       |           |        |       |
| 26/26 °C          | 2.19      | 8.14   | 10.33 | 4.63      | 18.02  | 22.65 |
| 26/38 °C          | 1.97      | 6.93   | 8.90  | 4.31      | 15.33  | 19.64 |
| 38/38 °C          | 2.06      | 6.82   | 8.88  | 4.42      | 15.33  | 19.75 |
| Fang              |           |        |       |           |        |       |
| 26/26 °C          | 2.47      | 6.73   | 9.20  | 5.46      | 15.15  | 20.61 |
| 26/38 °C          | 2.59      | 7.17   | 9.76  | 5.34      | 15.13  | 20.47 |
| 38/38 °C          | 2.21      | 6.29   | 8.50  | 4.94      | 14.89  | 19.83 |
| Siete Cerros      |           |        |       |           |        |       |
| 26/26 °C          | 2.72      | 6.77   | 9.49  | 5.83      | 15.14  | 20.97 |
| 26/38 °C          | 2.63      | 7.10   | 9.73  | 5.57      | 15.41  | 20.98 |
| 38/38 °C          | 2.09      | 5.45   | 7.54  | 5.27      | 13.77  | 19.04 |

ANOVA

| Genotype (G) | *** | * | NS | *** | NS | NS |
| Treatment (T) | *** | ** | *** | ** | NS | * |
| G x T | ** | NS | * | NS | NS | NS |
| CV, % | 6.1 | 8.5 | 6.9 | 5.0 | 8.5 | 7.1 |
main stem and tillers, both the data for the main stem and tillers are shown in Table 2. Main-stem grain yield across the three genotypes decreased by 2.4 and 13.8% at 26/38°C and 38/38°C treatments, respectively, compared with the 26/26°C treatment. The main-stem grain yield of Imam decreased by 10% at 26/38°C and by 5.9% at 38/38°C (Table 2). The 26/38°C treatment had no significant effect on the main-stem grain yield of both Fang and Siete Cerros. However, the 38/38°C treatment significantly decreased the grain yield of Fang (10.5%) and Siete Cerros (23.2%).

The effect of 26/38°C and 38/38°C treatments on tiller grain yield across the genotypes was similar to that on the main-stem grain yield and decreases of 2% at 26/38°C and 14.1% at 38/38°C were observed, compared with the 26/26°C treatment. The tiller grain yield in Imam was decreased by 14.9 and 16.2% at 26/38°C and 38/38°C treatments, respectively (Table 2). While the tiller grain yield of Siete Cerros was not affected by 26/38°C treatment, it was significantly decreased by 38/38°C treatment (19.5%). No significant differences were found in the tiller grain yield in Fang among the three temperature treatments.

Across the three genotypes, biomass production of the main stem was significantly decreased by the 38/38°C treatment, but only slightly ($P = 0.078$) by 26/38°C treatment, compared with the 26/26°C treatment (Table 2). However, no significant difference was found between the biomass of the main stem at 26/38°C and 38/38°C. The main-stem biomass of Imam was not significantly influenced by either 26/38°C or 38/38°C treatment, while the biomass of both Fang and Siete Cerros was decreased by the 38/38°C treatment (Table 2). Tiller biomass of Imam was also significantly decreased by the 26/38°C and 38/38°C treatments, but that of Fang and Siete Cerros was not significantly decreased by either the 26/38°C or 38/38°C treatment (Table 2).

High soil temperature (26/38°C) had no significant effect on the grain number spike$^{-1}$ of the three genotypes (Table 3). The main-stem grain number spike$^{-1}$ of Imam and Fang was also not affected by the 38/38°C treatment, but that of Siete Cerros was significantly decreased by the 38/38°C treatment.

The main-stem harvest index of Imam and Fang was not significantly decreased by either 26/38°C or 38/38°C treatment, but that of Siete Cerros was significantly decreased by 38/38°C treatment though not by 26/38°C treatment (Table 3). The 38/38°C treatment also significantly decreased the tillers harvest index of Fang (5.5%) and Siete Cerros (11.6%) compared with the 26/26°C treatment. Grain weight was significantly decreased by the 38/38°C treatment only in Siete Cerros (Table 3).

Discussion

Considerable differences were found among the wheat genotypes used in this study in the response of grain yield and other traits to high soil and air/soil temperatures. In the heat-sensitive Siete Cerros and

| Genotype/Treatment | Grain number spike$^{-1}$ | Harvest index (%) | Grain weight (mg) |
|--------------------|---------------------------|-----------------|-----------------|
| Imam               |                           |                 |                 |
| 26/26°C            | 62                        | 47.33           | 34.24           |
| 26/38°C            | 57                        | 45.76           | 33.99           |
| 38/38°C            | 59                        | 46.55           | 33.71           |
| Fang               |                           |                 |                 |
| 26/26°C            | 63                        | 45.21           | 38.34           |
| 26/38°C            | 64                        | 48.48           | 38.94           |
| 38/38°C            | 60                        | 44.48           | 36.35           |
| Siete Cerros       |                           |                 |                 |
| 26/26°C            | 76                        | 46.76           | 34.49           |
| 26/38°C            | 76                        | 47.20           | 34.17           |
| 38/38°C            | 67                        | 39.59           | 30.79           |

ANOVA

| Factor          | df | Mean Square | F    | P   |
|-----------------|----|-------------|------|-----|
| Genotype (G)    | 2  | 6.69        | 6.32 | 0.05|
| Treatment (T)   | 1  | 0.12        | 0.4  | 0.55|
| G x T           | 2  | 0.00        | 0.0  | 1.00|

NS: not significant

Table 3. Main-stem grain number spike$^{-1}$, harvest index and grain weight of three wheat genotypes grown under three air/soil temperature treatments during grain filling.
the heat-tolerant Fang, some of the traits measured including biomass, grain yield, grain number spike, harvest index and grain weight were unaffected by the high soil temperature of 26/38°C. On the other hand, in Imam, the 26/38°C treatment significantly decreased the biomass and grain yield especially those of the tillers. The responses of grain yield, biomass, grain number spike, harvest index and grain weight of the three genotypes to 38/38°C treatment also showed variations. For example, the total grain yield at 38/38°C decreased 14% in Imam, 7.6% in Fang and 20.5% in Siete Cerros compared with that at 26/26°C. In both Imam and Fang, the 38/38°C treatment similarly decreased grain number spike and harvest index by 4.8 and 1.6%, respectively, while in Siete Cerros it decreased grain number spike and harvest index by 11.8 and 15.3%, respectively.

Thus, even in the same genotype, the responses to high soil temperature or high air/soil temperature were not always the same. Differential responses of yield and quality components to post-anthesis heat stress in the same wheat genotype has been reported (Stone and Nicolas, 1994).

The genotypic difference in the responses to different types of heat stress also suggests that the mechanisms involved in the heat-stress tolerance in various plant parts and various genotypes might be different. The relatively light dry root weight at anthesis and the low water soluble carbohydrate content of roots at maturity in Imam (data not shown) might be among the causes of its sensitivity to high soil temperature (26/38°C). High soil and high air/soil temperatures result in imbalance between photosynthesis and respiration and decrease carbohydrate availability, which could contribute to the decrease in shoot and root growth (Xu and Huang, 2000b). On the other hand, the failure in utilizing more soluble carbohydrates by Siete Cerros at 38/38°C might be one of the reasons for the sensitivity to whole-plant high-temperature treatment (Blum et al., 1994). The rapid loss of chlorophyll content and the great decrease in grain-filling duration promoted the remobilization efficiency of WSC from the stem in both Imam and Fang (Blum et al., 1994; Fokar et al., 1998). On the other hand, only the high soil (26/38°C) temperature treatment slightly increased the WSC remobilization efficiency in Siete Cerros.

Although temperatures as high as 38°C were used in this study, the decrease in grain yield and other related traits caused by the high-temperature treatments was less than those reported earlier (Kuroyanagi and Paulsen, 1988; Xu and Huang, 2000a; Guedira and Paulsen, 2002). For example, in the report of Guedira and Paulsen (2002), the high root and shoot/root temperatures decreased grain-filling duration of wheat by 53 and 62%, respectively, and the grain weight by 57 and 61%, respectively. In this study, however, high soil (26/38°C) and high air/soil (38/38°C) temperatures decreased grain-filling duration by 14 and 20%, respectively. The grain weight was not decreased by the 26/38°C treatment and decreased only 6% by the 38/38°C treatment. This might be, in part, due to the gradual increase in the temperature in this study, which might have mitigated the effect of the high temperature and hence led to better adaptation to the high temperature (Stone and Nicolas, 1995; Law and Crafts-Brandner, 1999). Moreover, the use of constant day/night temperature does not represent the fluctuating temperature rhythm in the field, and might overestimate the effect of the high temperature. Therefore, it is important to subject plants to high temperature gradually and apply different day/night temperature to reveal the actual genetic variability.

The high soil temperature simulated by the 26/38°C treatment might not occur under field conditions. Nevertheless, this treatment is useful to study the response of shoot and root to high soil temperature without the effect of air temperature. Previous reports showed that the high soil temperature was more critical in its effect on the shoot growth than the high air temperature (Kuroyanagi and Paulsen, 1988; Xu and Huang, 2000a; Guedira and Paulsen, 2002).

In conclusion, the most prominent effects of high soil temperature were the reductions of leaf chlorophyll content and the grain-filling duration...
and the promotion of WSC remobilization from the stem. Under such conditions, the efficient grain filling and remobilization of assimilates stored prior to anthesis could be critically important. The results also demonstrated clear genotypic variability in responding to high soil and high air/soil temperatures in terms of various traits including grain yield. This is the first report, to our knowledge, on the genotypic difference in the responses to high soil and high air/soil temperatures in wheat.

The relatively small decrease of grain yield and other related traits by the high-temperature treatments in this study compared with other reports suggested that the effect of high temperature could be alleviated by the adoption of gradual increment and decrement of temperature treatment under controlled environment and probably by proper managements under field condition.

Acknowledgments

Financial support of the Japanese Ministry of Education, Culture, Sports, Science and Technology is gratefully acknowledged. We are also grateful to the Arid Land Research Center, Tottori University for the permission to use the growth chamber facility.

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