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EVALUATION OF GROWTH AND GAS EXCHANGE RATES OF TWO LOCAL SAUDI WHEAT CULTIVARS GROWN UNDER HEAT STRESS CONDITIONS

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Abstract

The present study investigated the effects of three temperature regimes, low (20ºC), moderate (25ºC) and high (30ºC), on growth and physiological parameters of two local Saudi wheat (*Triticum durum*) cultivars, Hab-Ahmar and Algaimi. Plants were grown under controlled environment in growth chambers. After four weeks plants were harvested and the following growth parameters were measured; plant height, number of tillers, leaf area, root length, fresh and dry weight. Physiological traits include chlorophyll content, photosynthesis rates, stomatal conductance, dark respiration and chlorophyll fluorescence parameters; *Fo*, *Fm* and *Fv/Fm*. In cultivar Hab-Ahmar, moderate and high temperatures caused significant decrease in most growth and physiological parameters such as plant height, number of tillers, leaf area, fresh and dry weight, chlorophyll content, photosynthesis rates, stomatal conductance, dark respiration and the maximum quantum yield of photosystem II (*Fv/Fm*). In contrast, cv. Algaimi was shown to be more thermotolerant to moderate and high temperatures, with the exception of some growth parameters that were decreased. Unlike cultivar Hab-Ahmar, cultivar Algaimi had an increased rate of dark respiration when temperature was high (30ºC). Stomatal behavior is shown to be positively correlated with the rates of photosynthesis in both cultivars; however, in cultivar Hab-Ahmar such correlation decreased as temperature increased.

Key words: Thermotolerance; Wheat; Growth; Photosynthesis; Fluorescence.

Introduction

Heat stress is caused by elevated temperatures that strongly affect plant growth and yield (Rampino *et al*., 2009). Thermotolerance is defined as the ability of a plant to grow and produce economic yield under high temperatures (Peet & Willits, 1998). Heat stress due to high temperature is considered to be a serious threat to crop production (Hall, 2001) and high temperatures in tropical climates and temperate regions are often the most limiting factors affecting plant growth and crop yield. They can cause considerable damage, including scorching of leaves and twigs, sunburn on leaves, branches and stems, leaf senescence and abscission, fruit discoloration and reduced yield (Guilioni *et al*., 1997; Ismail & Hall, 1999; Vollenweider & Gunthardt-Goerg, 2005). It was also reported that the amount of photosynthetic pigments was reduced by heat shock (Todorov *et al*., 2003). Similar effects of high temperatures to those of water stress have been reported. At the whole plant level, these include reduced cell size, closure of stomata, increased stomatal densities, and greater number of xylem vessels of both roots and shoots (Bañon *et al*., 2004). The effects on leaf structure and stomata obviously have a negative effect on carbon assimilation, and the photosynthetic capacity of C3 plants was found to be more affected than that in C4 plants under hot conditions (Taiz & Zeiger, 2006).

Changes in temperature have considerable effects on cell physiology (Ruelland & Zachowski, 2010), and as a consequence heat can cause damage to both vegetative and reproductive structures (Ruelland *et al*., 2009; Zinn *et al*., 2010). At the sub-cellular level, modifications occur in chloroplasts, leading to significant reduction in rates of photosynthesis by changing the structural organization of thylakoids (Karim *et al*., 1997). In general, high temperature affects anatomical structures at the tissue and cellular levels and also at the sub-cellular level. Injuries caused by heat stress depend on the severity of temperature. For example, very high temperatures may lead to severe cellular injury and even cell death within minutes, which could result in collapse of cellular organization (Schöffl *et al*., 1999). Heat stress results in delayed grain filling and reduction in kernel growth, kernel density and weight of field pea (*Pisum sativum*) by up to 7% according to Guilioni *et al*. (2003). In wheat, both grain weight and grain number appeared to be affected by heat stress, as the number of grains per ear at maturity was reduced with high temperature (Ferris *et al*., 1998). However, considerable genotypic variation exists in crop plants for assimilate partitioning; this was reported in wheat genotypes (Yang *et al*., 2002).

The most important factor affected by changing ambient temperatures is plant water status (Mazorra *et al*., 2002). High temperature stress is usually associated with reduced water availability under field conditions (Simoes-Araujo *et al*., 2003). Under stress conditions, plant species may accumulate sugars, sugar alcohols, proline (Sairam & Tyagi, 2004) and / or glycinebetaine (GB), which are all believed to be involved in enhancing stress tolerance in plants (Sakamoto & Murata, 2002). In order to survive high temperatures, plants use a range of mechanisms including phenological and morphological adaptations. They can avoid damage caused by heat stress through other mechanisms such as changing leaf orientation, transpirational cooling, or alteration of membrane lipid composition. Responses of plants under different types of stress may vary in different developmental stages in different tissues (Queitsch *et al*., 2000).

The objective of the present study was to evaluate the growth and physiology of two wheat cultivars to heat stress under controlled conditions. The results were evaluated by measuring plant growth traits and photosynthetic capacity.

Materials and Methods

Seeds of two local Saudi wheat cultivars (*Triticum durum* Desf. cv. Hab-Ahmar and cv. Algaimi) were used in this study. In a previous study on these two wheat cultivars, it was shown that cv. Algaimi was drought tolerant, while cv. Hab-Ahmar was drought susceptible, and this was estimated by photosynthesis, dark respiration and chlorophyll content (Akhkha *et al*., 2010). Seeds were sown in 12 cm plastic pots containing sand:compost (Plantafor Potting Compost, N:P:K = 200:200:300, Plantaflor® Humus Verkaufs-GmbH, Oldenburger Str.4, D-49377 Vechta, Germany) mix (1:3 v:v). The experiments were conducted in controlled growth rooms at the Department of Biology, Faculty of Sciences, University of Taibah, Al-Madinah Al-Munawarh, KSA. Plants were placed under controlled environment in three different growth chambers (JSR, JS Research Inc., 40-1 Gumsang-Dong, Gongju-City, Korea, 314-240) with 14 hours photoperiod, 60% relative humidity and illuminated with Fluorescent and Hallogen lamps giving 200 µmol quanta m^{-2} s^{-1}; plants were then subjected to one of three temperature levels; 20°C (control), 25°C (medium temperature) and 30°C (high temperature). Plants were watered to field capacity every other day with more water added to plants under higher temperatures. Each treatment consisted of five pots and each pot contained five plants. All measurements were taken in five week old plants after three weeks of heat stress treatments.

Plant weight determination: Three plants of each temperature treatment were harvested, divided into roots, stems and leaves. All plant parts were oven-dried at 85°C for 48 h and then weighed to determine the dry weights.

Leaf area: Total leaf Area was measured with a portable area meter LI-3000C, (LICOR Inc., Lincoln, NE, USA).

Gas exchange measurements: Gas exchange rates were measured on intact leaves using a LICOR Infra Red Gas Analyser IRGA, LI-6400 XT (LICOR Inc., Lincoln, NE, USA), fitted with a leaf chamber mounted with a Red-Blue LED light source. Fully expanded fourth youngest leaves were used for photosynthesis, dark respiration and stomatal conductance measurements. The inside temperature of the leaf cuvette was set at 20°C, 25°C or 30°C according to the growth temperature conditions the plants were subject to. The light response curves were measured at ambient CO_2 concentrations (350-400 µmol). Measurements were made on 5 week old plants after three weeks of heat stress treatments. Leaves were gradually illuminated with a series of photon flux densities ranging gradually from 0 to 2000 µmol photons m^{-2} s^{-1} over 7 steps (0, 100, 150, 500, 1000, 1500 and 2000 µmol m^{-2} s^{-1}).

Chlorophyll fluorescence measurements: Chlorophyll fluorescence parameters were measured fro the fourth youngest leaf of three week-old wheat plants with a Hansatech Chlorophyll Fluorometer (Hansatech Instruments, Narborough Road, Pentney, King's Lynn, Norfolk, PE32 1JL, UK). A leafclip was attached to a leaf and the shutter plate was closed to start the dark adaptation period for 15 minutes then measurements were taken after fitting the sensor head and opening the shutter plate. The chlorophyll fluorescence parameters were recorded for the fourth leaf of each plant.

Chlorophyll content determination: Leaf chlorophyll content was determined using a hand-held chlorophyll content meter (CCM-200, Opti-Sciences, USA). The chlorophyll content determination was measured on the fourth youngest leaves.

Statistical analysis: Analysis of variance (ANOVA) with Tukey's Multiple Comparison was performed on all the data using Minitab version 15.0 (Brandon Court, Unit E1-E2, Progress Way, Coventry CV3 2TE, United Kingdom). The values presented are the means of at least four replicates ± S.E (Standard Errors). The regression coefficients were calculated after fitting a trend line using Microsoft Excel 2007.

Plant height: The plant heights in both wheat cultivars, Hab-Ahmar and Algaimi, were significantly affected by the higher temperatures, as shown in Fig. 1A. Compared with the control plants at 20°C, plant height was significantly decreased in both moderate (25°C) and high temperatures (30°C) for the two cultivars. The reduction was 60% and 75% in Hab-Ahmar and 35% and 65% in Algaimi at 25°C and 30°C, respectively.

Number of tillers: Although the number of tillers at this stage was very low, in the range of 1-3, it was affected by the temperature and in particular by the high temperature for both wheat cultivars (Fig. 1B). The reduction in number of tillers was 40% and 53 % in Hab-Ahmar and 20% and 60% in Algaimi at 25°C and 30°C, respectively.

Leaf area: Leaf area was significantly reduced in plants of cv. Hab-Ahmar grown under 25°C and 30°C, although no significant differences (p<0.05) were found between the effects at 25°C and 30°C (Fig. 1C). The reduction in leaf area due to the moderate and high temperature was 55% and 67% in Hab-Ahmar, respectively. In cv. Algaimi, a very slight increase, 25%, was observed in plants grown under 25°C and a decrease of 50% in plants grown under the high temperature conditions.

Root length: A slight (although not significant (p<0.05)) reduction in root length was observed in plants of cv. Hab-Ahmar grown under 25°C and 30°C conditions (Fig. 1D). In contrast, for cv. Algaimi, no changes at either 25°C or 30°C were observed.

Fresh and dry weights: Temperature significantly reduced (p<0.05) the fresh weight of both roots and shoots and the total fresh weight in Hab-Ahmar under both 25°C and 30°C temperatures, as shown in Fig. 2A, 2B and 2C, respectively. In contrast, increasing temperature caused significant change (p<0.05) in root fresh weight of Algaimi. However, under high temperature there was a significant decrease in shoot fresh weight and total plant fresh weight. The results showed that higher temperatures significantly (p<0.01) decreased dry weights of roots (Fig. 2D), shoots (Fig. 2E) and total plants of the Hab-Ahmar cultivar (Fig. 2F). In contrast, Algaimi was less affected by higher temperatures, showing no significant change (p<0.05) in response to an increase of temperature from 20 to 25ºC. The high temperature significantly decreased roots, shoots and whole plant dry weights.

Results

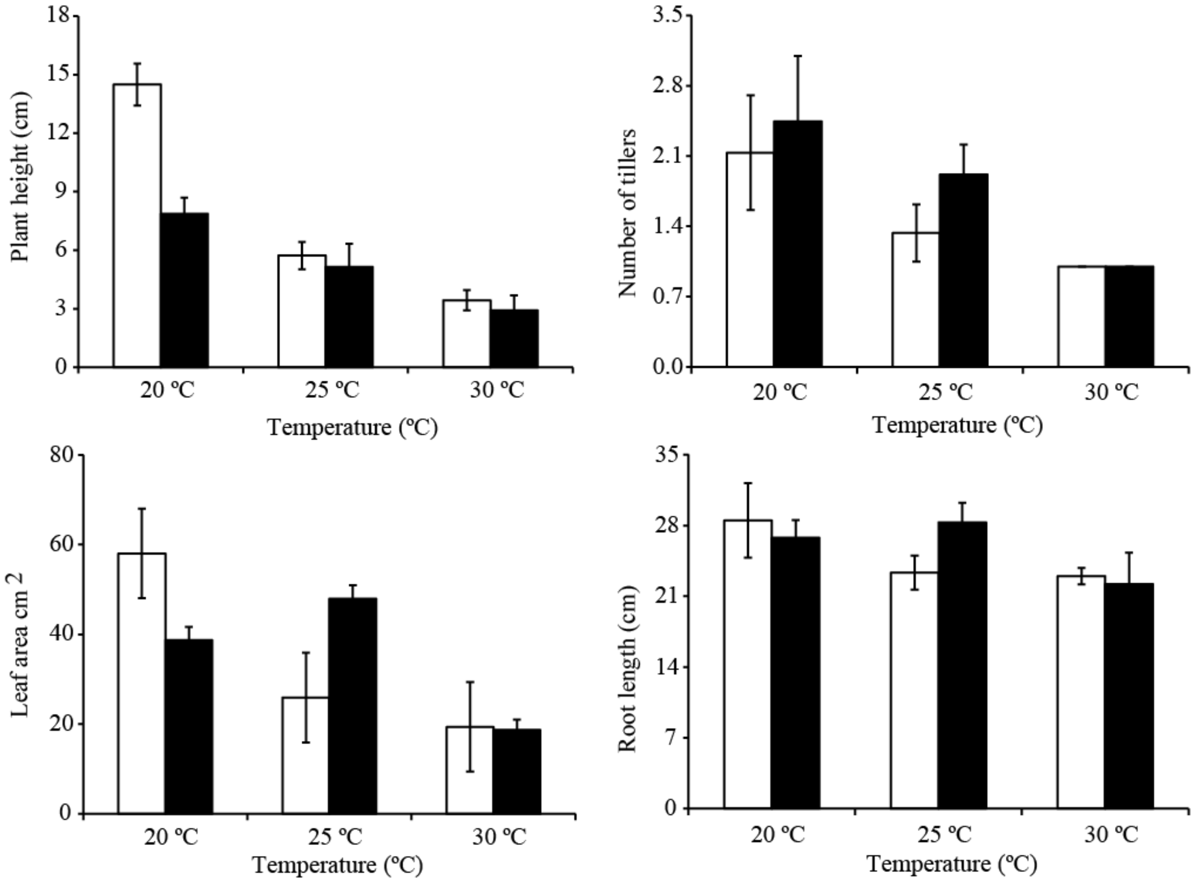

Fig. 1. Effects of temperature on (A) plant Height (B) number of tillers (C) leaf area (D) root length of two Saudi wheat cultivars after 35 days. ($n = 4$, vertical bars represent ± SE of the means).

Table 1. Effects of temperature on chlorophyll fluorescence parameters: *Fo, Fm* and *Fv/Fm,* of two wheat cultivars after 35 days. (n = 4, Mean ± S.E.).

Cultivar	Temperature	*Fo*	*Fm*	*Fv/Fm*
	20ºC	310 ± 14	1541 ± 93	0.798 ± 0.009
Hab-Ahmar	25ºC	306 ± 36	1503 ± 121	0.798 ± 0.009
	30ºC	287 ± 52	1794 ± 20	0.767 ± 0.019
	20ºC	324 ± 24	1576 ± 8	0.794 ± 0.007
Algaimi	25ºC	348 ± 8	1694 ± 63	0.794 ± 0.005
	30ºC	350 ± 12	1749 ± 57	0.800 ± 0.002

Chlorophyll Content: Chlorophyll content (Fig. 3) was significantly reduced by both 25°C and 30°C, reaching 50% reduction in leaves of Hab-Ahmar. In contrast, leaves of Algaimi were not affected by either of the two temperatures.

Chlorophyll fluorescence: Chlorophyll fluorescence parameters were measured to see the effect of different temperatures on the flow of electrons in photosystem II, which is an indicative of the overall rate of photosynthesis. The results in table 1, showed that there was a slight decrease in both *Fo* and *Fv/Fm* when temperature reached 30ºC, while *Fm* increased very significantly as temperature reached 30ºC for cv. Hab-Ahmar. In contrast, Algaimi cv. showed an increase in both *Fo* and *Fm* with insignificant increase in *Fv/Fm*.

Photosynthesis activity

Photosynthetic Rate: The rate of photosynthesis was also determined in both Hab-Ahmar (Fig. 4A) and Algaimi (Fig. 4B) cvs. The results showed that the rate of photosynthesis was significantly ($p<0.05$) reduced with higher temperature in the cv. Hab-Ahmar. In contrast, higher temperature had no significant ($p<0.05$) effect on the rate of photosynthesis of cv. Algaimi; this suggests that the photosynthetic machinery of the latter was more tolerant of high temperatures than in Hab-Ahmar. However, the level of photosynthesis was higher in Hab-Ahmar than in Algaimi under the low temperature of 20ºC.

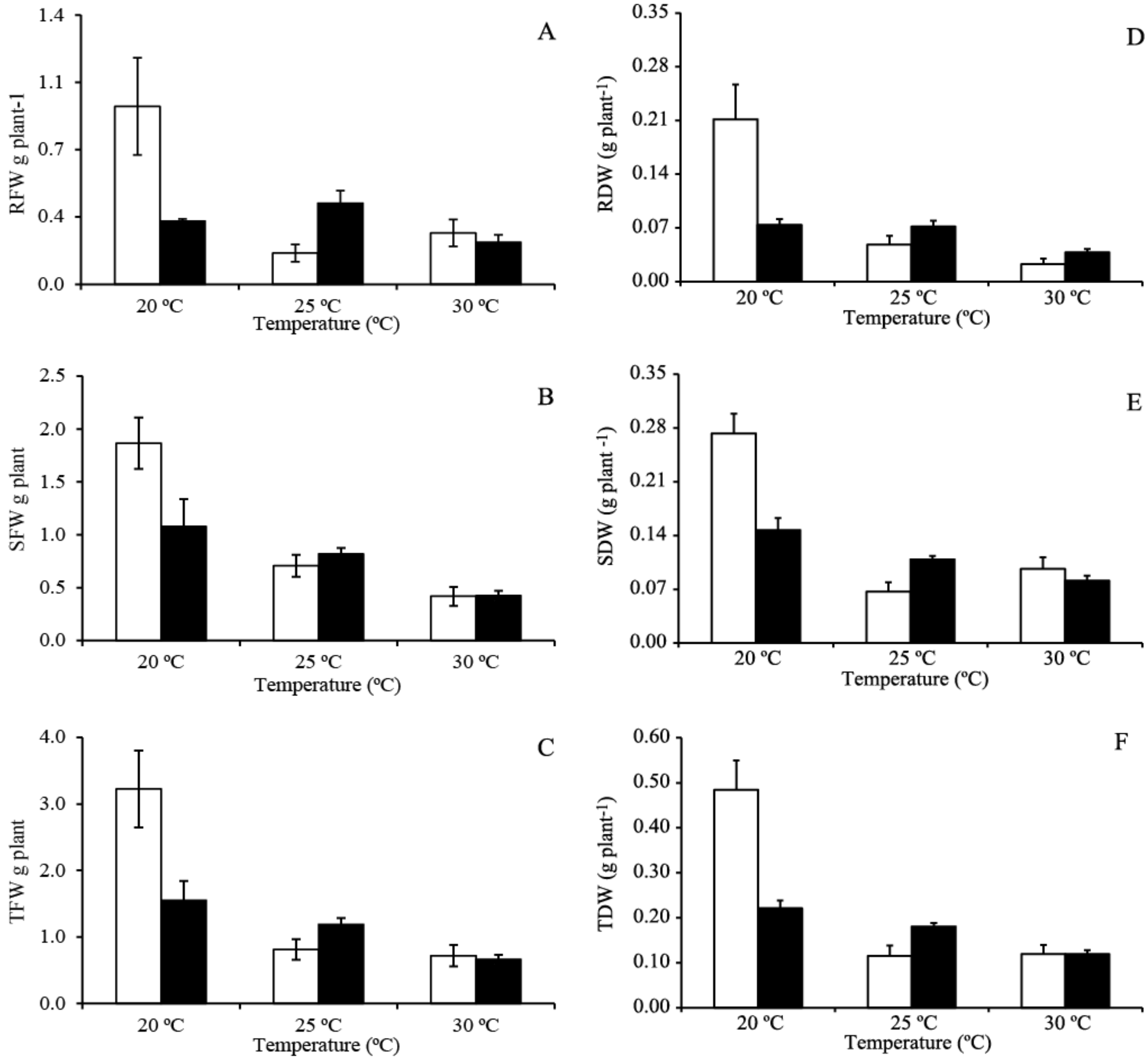

Fig. 2. Effects of temperature on fresh weights of roots (A), shoots (B) and whole plant (C) and on dry weights of roots (D), shoots (E) and whole plant (F) of two wheat cultivars after 35 days. (*n* = 4, vertical bars represent ± SE of the means).

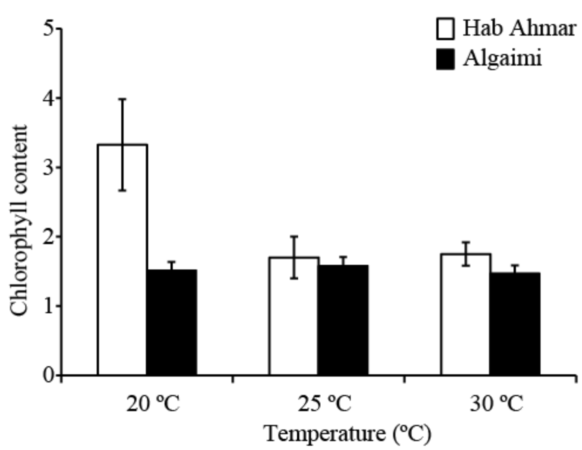

Fig. 3. Effects of temperature on chlorophyll content in leaves of two wheat cultivars after 35 days. (*n* = 4, vertical bars represent ± SE of the means).

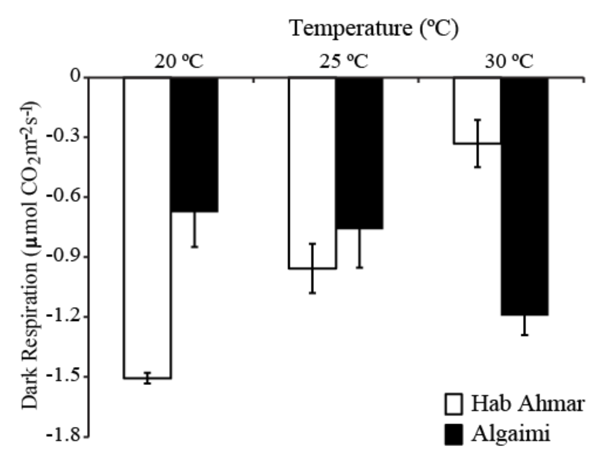

Fig. 5. Effects of temperature on dark respiration in leaves of cvs. Hab-Ahmar, and Algaimi after 35 days. (*n* = 4, vertical bars represent ± SE of the means).

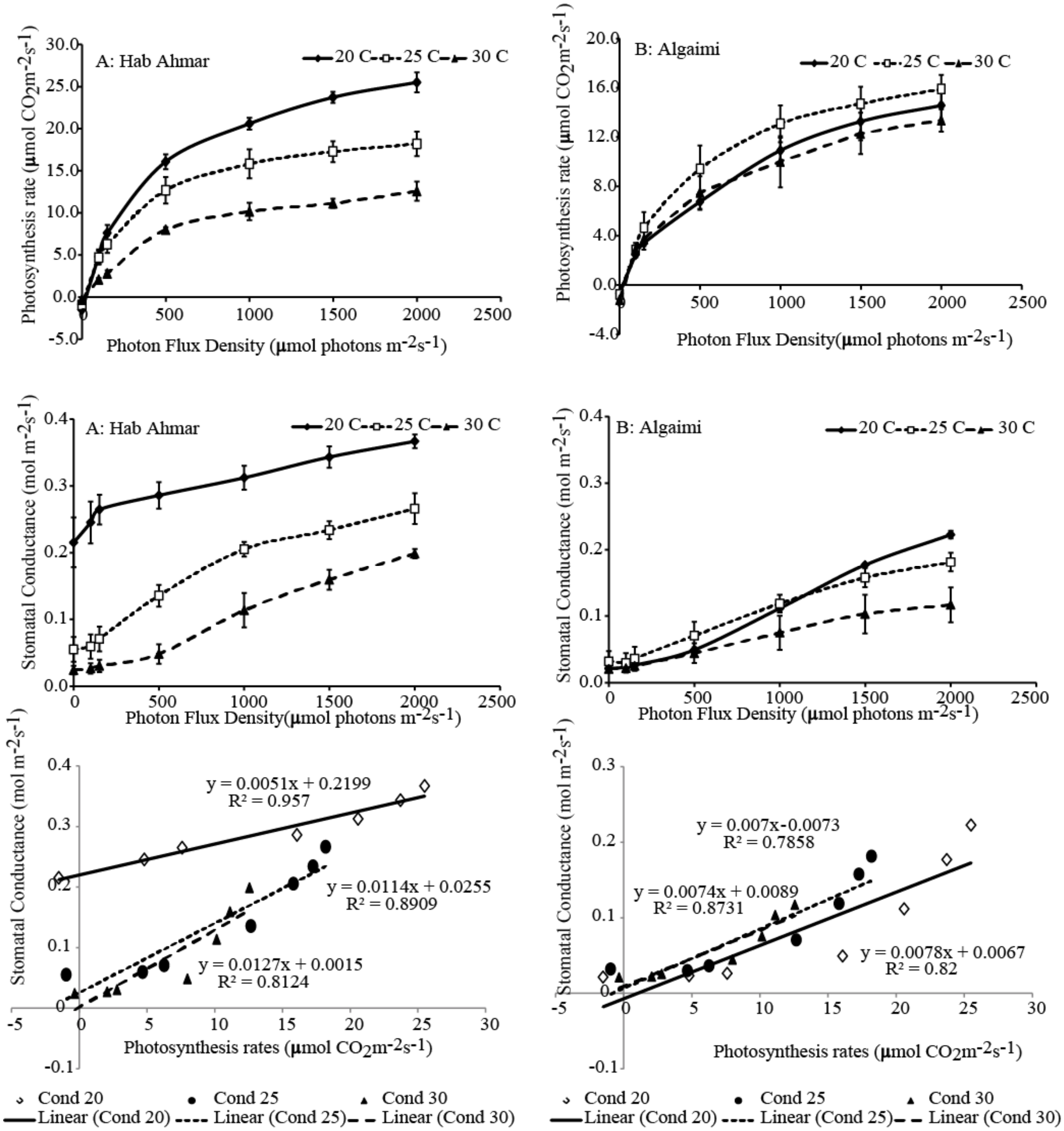

Fig. 4. Effects of temperature on (A) and (B) photosynthesis rates in leaves of cv. Hab-Ahmar and cv. Algaimi, (C) and (D) light-dependent stomatal conductance of cv. Hab-Ahmar and Algaimi, and (E) and (F) relationship between photosynthesis rates and stomatal conductance in cvs. Hab-Ahmar and Algaimi, respectively, (n = 4, vertical bars represent ± SE of the means).

Stomatal Conductance: Results in Fig. 4C, show that in cv. Hab-Ahmar light-dependent stomatal conductance was significantly ($p<0.05$) decreased by both moderate and high temperatures to about 28% and 46% respectively, compared with that of leaves under the lower temperature of 20ºC. In contrast, no significant effect of temperature was observed in stomatal conductance of cv. Algaimi leaves (Fig. 4D). In relation to the photon flux density (PFD), stomatal conductance increased with increasing PFD in both cultivars. Stomatal behavior showed a high positive correlation with the rates of photosynthesis in all cultivars; however, in cv. Hab-Ahmar such correlation decreased slightly as temperature increased (Fig. 4E and 4F). The results of correlation between photosynthesis and stomatal conductance were presented in figure 4E and 4F. The results showed that in Hab-Ahmar, there was a high positive correlation between the stomatal conductance and photosynthesis rate under the three temperature regimes, with percent variation (R^2) of 0.96, 0.89 and 0.81 at 20, 25 and 30^{o}C respectively. Algaimi was not different from Hab-Ahmar except at 20^{o}C where the percent variation (R^2) was lower (0.79) than that of Hab-Ahmar. This suggests that any effect on photosynthesis could be at least partly due to effects on stomatal conductance.

Dark respiration: Dark respiration was shown to decrease with increased temperature regimes in cv. Hab-Ahmar (Fig. 5); on the contrary, moderate temperature (25ºC) had no significant effect on dark respiration in cv. Algaimi, while high temperature (30ºC) caused an increase.

Discussion

The current study investigated the effects of three temperature regimes, low, moderate and high, on growth and physiology of two local Saudi wheat cultivars, Hab-Ahmar and Algaimi. The results showed that high temperature negatively affected most growth parameters. The plant height was the parameter most reduced by moderate and high temperature levels in both wheat cultivars (Fig. 1A). High temperature can result in a number of morphological effects, including sunburn of leaves, stems and branches, leaf senescence, root and shoot growth inhibition (Wahid *et al*., 2007), thus leading to reduced yield (Vollenweider & Gunthardt-Goerg, 2005). It was also observed in our studies that high temperatures significantly reduced the number of tillers for the two cultivars (Fig. 1B). The leaf area was reduced in both cultivars, 67% in Hab-Ahmar and 50% in Algaimi (Fig. 1C), as a result the photosynthesis rates were reduced in Hab-Ahmar (Fig. 4A), but was not affected in Algaimi (Fig. 4B). This might be due to the increase of leaf thickness under heat stress that can increase the photosynthesis, and can prevent leaf from high temperature damage (Leigh *et al*., 2012). These finding are in full accordance with Qaderi *et al*. (2011), who reported that the negative effects of high temperature were significant only for stem height and leaf area in canola (*Brassica napus*) seedlings. It was reported also that heat stress caused poor seedling establishment as reflected by inhibition of leaf growth in all investigated wheat cultivars (Dash & Mohanty, 2001). In warm areas, temperature particularly affects leaf growth and consequently photosynthesis (Pritchard & Amthor, 2005). No effects of temperature stress on root length were found for either cultivar in the two temperature regimes. Fresh and dry weight of leaves, stems and root were clearly and significantly affected by the two temperature regimes, moderate and high. This is in accordance with a number of studies in several crops. For example, high temperature caused significant decreases in shoot dry weight in a number of crops, such as maize, pearl millet and sugarcane (Ashraf & Hafeez, 2004; Wahid *et al*., 2007). It has been also reported that wheat cultivars grown under high temperature (40^{o}C) for a short period of time (60 hours) resulted in reduction in leaf fresh and dry weights (Dash & Mohanty, 2001). The sensitivity of above ground growth to heat stress was reported in a number of crops (Howarth, 1991; Howarth *et al*., 1997; Karim *et al*., 1999).

In the present study we found that chlorophyll content in Algaimi was not affected by any of the two temperature levels. In contrast to Algaimi, a significant and sharp decline in chlorophyll was observed in Hab-Ahmar, equally, at moderate and high temperatures. Several studies reported that chlorophyll decreased under heat-stress conditions. The sensitivity of leaf pigmentation to the heat was reported by Dash & Mohanty (2001) who reported that the reduction was between 50 and 57% in two wheat cultivars. It has been revealed that the effect of high temperature resulted in the loss of grana stacking (Zhang *et al*., 2005), and the reduction of photosynthesis could be due to the changing of thylakoid structure (Karim *et al*., 1997).

No clear effects of high temperature on chlorophyll fluorescence parameters were detected in wheat plants grown under heat stress conditions in the present study (Table 1). These findings can be supported by early studies of Dash and Mohanty (2001), who reported that fluorescence characteristics of dark-adapted wheat leaves (*Fv*/*Fm* and *Fo*) only changed marginally in response to heat stress. It has been also reported that reduction in *Fv/Fm* ratio in wheat cultivars was mainly due to the reduced *Fv* magnitude, while *Fo* level was slightly affected under heat stress at 40^{o}C and 42^{o}C for a 20 min period of time (Kreslavki *et al*., 2008). It was reported that wheat leaves may be able to withstand high temperatures up to 40ºC as an adaptive mechanism by changing the heterogeneity of Photosystem II (Mathur *et al*., 2011). This could explain the insensitivity of PS II of both Hab-Ahmar and Algaimi cultivars as no changes were shown by chlorophyll fluorescence measurements.

Photosynthesis is one of the most important physiological processes in plants and its study provides information about the sensitivity or tolerance of plants to environmental stresses such as high temperatures, which consequently affect plant growth and survival. Many workers reported that photosynthesis is one of the most sensitive processes that can be inhibited by heat (Wahid *et al*., 2007; Yamori *et al*., 2010; Zhang & Sharkey, 2009). In the present study, the two cultivars responded differently to high temperature as measured by photosynthesis capacity. Photosynthesis rates of cv. Hab-Ahmar were significantly inhibited under relatively high temperatures. In contrast to Hab-Ahmar, rates of photosynthesis were not altered in cv. Algaimi leaves. The fact that photosynthesis was not affected in Algaimi plants under both moderate and high temperatures, compared to the control plants, could be an indication that the photosynthetic machinery was not affected by exposing plants to heat stress, which suggests that cv. Algaimi is more tolerant to high temperatures than cv. Hab-Ahmar. Similarly Iglesias-Acosta *et al*. (2010) reported that photosynthesis rates of broccoli leaves were not affected by high temperature treatment (35 ^{o}C) compared to the control plants.

The inhibition in photosynthesis rates observed in cv. Hab-Ahmar might be due to the inhibition of Rubisco activation (Kumar *et al*., 2009; Salvucci *et al*., 2006), due to its sensitivity to thermal denaturation, even at moderate temperature (Salvucci, 2008). It has been also suggested that the decline in photosynthesis rates under heat stress conditions could be due to the inhibition of PSII (Berry & Björkman, 1980; Ciaffi *et al*., 1996) that leads to disruption in electron transport in both PSII and PSI (Pshybytko *et al*., 2008; Zhang & Sharkey, 2009). This was supported by the chlorophyll fluorescence which demonstrated that high temperatures decreased the maximum quantum yield of photosystem II (*Fv/Fm*) which is an indicator of damaged electron transport system in the thylakoids. However, the unchanged photosynthesis rate in Algaimi cv. agreed with the no changes in *Fv/Fm*. It was also clear that the chlorophyll content results matched those of *Fv/Fm*, as it was reduced in Hab-Ahmar cv. but not altered in Algaimi cv.; hence, this indicates clearly the involvement of the chlorophyll content in the behaviour of chlorophyll fluorescence, when under heat stress, which represents the functional state of the PSII. Heat stress could also affect photosynthesis through stomatal and non-stomatal limitations (Caemmerer & Farquhar, 1981). For example, Monneveux *et al*. (2003) reported that inhibition of stomatal conductance (*gs*) in wheat resulted in photosynthesis inhibition under high temperature conditions. This could be strongly the case in the cv. Hab-Ahmar, which showed a gradual decrease of stomatal conductance as temperature increased. Furthermore, the absence of change in photosynthetic rates in cv. Algaimi was correlated with no change in stomatal conductance. The results of correlation between photosynthesis and stomatal conductance might indicate that stomata behave optimally at the high temperature in cv. Algaimi. This can be seen from the higher rates of photosynthesis that were correlated with larger ratios of stomatal conductance. The response of stomatal conductance to environmental conditions can be influenced by the environment during leaf development (Bunce, 1998).

Dark respiration is a parameter that was not extensively looked at in plants under heat stress; the present work concluded that dark respiration in the two cultivars behaved differently to heat stress in that the most sensitive cultivar (Hab-Ahmar) showed a dramatic decrease as temperature increased, and in the more tolerant cv. Algaimi dark respiration was only affected by the high temperature (30ºC), showing an increase. Different results were reported by Delatorre *et al*. (2008), who showed an increase in dark respiration at 35-40 ºC in *Prosopis tamarugo* (tamarugo) a sensitive species to heat stress; dark respiration remained unchanged in the very tolerant species, *P. chilensis* (Chilean algarrobo). However, when high temperatures were combined with water deficit, the effects were reversed. Law and Crafts-Brandner (1999) also reported an increase in dark respiration in response to temperatures up to 37.5ºC in wheat and 40ºC for cotton; however, as temperature increased a decline in dark respiration was reported. Furthermore, six black locust families were also observed to have an increased rate of dark respiration as temperature increased (Mebrahtu *et al*., 1991). The increase in dark respiration in cv. Algaimi could be due to a more active metabolism which is stimulated by increasing temperature (Farrar, 1988).

Conclusion

It can be concluded from the present study that the wheat cultivar Algaimi is more thermotolerant than the cultivar Hab-Ahmar. This may give an advantage to cv. Algaimi in areas where temperature is relatively high.

Acknowledgments

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