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INTEGRATION OF PHYSIO-BIOCHEMICAL PROCESSES AT DIFFERENT PHENOLOGICAL STAGES OF WHEAT (*TRITICUM AESTIVUM* L.) PLANTS IN RESPONSE TO HEAT STRESS

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Abstract

A study was conducted to assess the influence of heat stress imposed at different growth stages of wheat (*Triticum aestivum* L.) plants. Four wheat cultivars namely S-24, Saher-2006, Lasani and AARI-10 were subjected to high temperature (HT) stress at tillering and booting phenological phases. Under stress conditions, root and shoot fresh weights, membrane thermostability (MTS) and non-photochemical quenching (NPQ) were significantly perturbed in all four wheat cultivars at both developmental stages. However, HT stress did not influence all the other attributes significantly including shoot fresh weight, chlorophyll *a* and *b* pigments, photosynthetic rate (*A*), leaf water (Ψ_w), internal CO_2 (C_i), osmotic (Ψ_s) and turgor (Ψ_p) potentials, transpiration rate (*E*), water-use-efficiency (*A*/*E*), stomatal conductance (g_s) as well as F_v/F_m ratio. Among all wheat cultivars, cv. Lasani performed better in shoot and root fresh weight, and chlorophyll *a* contents at the tillering stage, while in MTS at the booting phase, cv. S-24 in shoot fresh weight, *E*, and g_s at the boot stage and highest MTS and WUE at the tillering stage. However, cv. AARI-10 performed well in root fresh weight, Ψ_w, Ψ_s, Ψ_p,,WUE and NPQ when stress was applied at the boot stage, while *E* and F_v/F_m in this cultivar on exposure to stress at the tillering stage. Cultivar Saher-2006 performed better in g_s, leaf Ψ_s and Ψ_p at the tillering stage, while F_v/F_m was recorded better at the boot stage and *A* in the same cultivar at all growth stages. Overall, HT stress applied at different growth stages was only effective in altering root fresh weight, MTS and NPQ in all four wheat cultivars. Of all wheat cultivars, cv. AARI-10 performed better in growth and physiological attributes examined in the present study under HT stress applied at different phenological stages.

Key words: Growth, Stress, Metabolism, Physiology, Wheat.

Introduction

Among the principal abiotic stresses (salinity, drought and temperature) that markedly affect plants, least is understood about heat stress (Rasul *et al*., 2011). Increased incidence, duration and intensity of unfavorable temperature extremes cause significant economic losses annually (Long & Ort, 2010). However, metabolic alterations, changes in fluidity of membrane and protein conformation as well as reassembly of cytoskeleton facilitate plants to detect temperature rise and fall (Ruelland & Zachowski, 2010). High temperature strictly limits growth and productivity of plants and is categorized as one of the most important abiotic threats to many crops (Hassan, 2006).

Plants respond to high temperature by changing phenology and anatomy (Giaveno & Ferrero, 2003; Zhang *et al*., 2008) and physio-biochemical characteristics. Regarding plant physiological phenomena, disturbances in plant water status (Simoes-Araujo *et al*., 2003; Cabanero *et al*., 2004), decreased photosynthesis (Wise *et al.,* 2004), increased concentration of compatible solutes (Sakamoto & Murata, 2002), hormonal disturbances (Maestri *et al*., 2002), production of ROS (Suzuki & Mittler, 2006) and thermostability of cell membrane (Somerville & Browse, 1991) have been reported.

Of the physiological mechanisms in plants, photosynthesis is highly vulnerable to supraoptimal temperatures (Quinn & Williams, 1985; Salvucci & Crafts-Brander, 2004; Camejo *et al*., 2005; Wahid *et al*., 2007). Rate of photosynthesis and respiration continues to rise with increasing temperature up to a certain limit but after this metabolic processes tend to slow down (Larkindale & Knight, 2002). Heat stress-induced reduction in photosynthesis is ascribed to destruction of chloroplast and decreased chlorophyll content (Xu *et al*., 1995). The damage suffered by chloroplast enzymes due to oxidative stress is considered another reason for diminished photosynthesis under elevated temperature (Sairam *et al*., 2000). Supraoptimal temperatures can impose a negative impact on stomatal conductance, photosynthetic rate (*A*) and rate of transpiration (*E*) resulting in an increase in temperature of leaf (Falk *et al*., 1996; Kadir, 2006). Plants use antioxidant enzymes to detoxify reactive oxygen species and mitigate oxidative stress-induced damage under elevated temperature (Shah *et al*., 2001). For example, Sairam *et al*. (2000) showed a protective role of ascorbic acid against oxidative damage in wheat plants occurring during reproductive stage due to supraoptimal temperature. Similarly, heat stress imposed at the reproductive stage prompted a rise in the activities of antioxidants of enzymatic nature in thermotolerant wheat plants (Balla *et al*., 2009).

Although booting and flowering are the phases most susceptible to heat stress (Stone, 2001; Shah *et al*., 2011), high temperature at any stage of plant lifecycle can cause yield loss due to impact on metabolic processes (Maestri *et al*., 2002). Heat stress affects the number of grains as well as grain weight (Ferris *et al*., 1998). Increased phasic development (Stone & Nicolas, 1995; Stone, 2001), diminished photosynthesis, enhanced senescence (Almeselmani, 2010), increased respiratory activity (Berry & Bjorkman, 1980; Peng *et al*., 2004) and reduced starch reserves (Chinnusamy & Khanna-Chopra, 2003; Yan *et al*., 2008) are chief causes of reduced wheat yield under elevated temperature.

Supraoptimal temperature is a real threat to production of many crops including wheat (Alexander *et al*., 2006; Sud & Bhagwat, 2010), because it can influence anthesis and grain filling phases (Stone & Nicolas, 1995). Heat stress during reproductive stages is a major factor of decline in grain yield of wheat crop due to delayed planting in Pakistan (Khan, 2004; Joshi *et al*., 2007; Ubaidullah *et al*., 2007). Therefore, there is a dire need to better understand the plant responses to heat stress, as it will help to develop cultivars that are better capable of withstanding temperature extreme. Increased knowledge of heat stress effects will also enable to foretell the agronomic outcomes of global warming resulting from increased emission of greenhouse gases. Therefore, the aim of the present study were to assess the response of selected wheat cultivars to supra-optimal temperatures in terms of a variety of physio-biochemical parameters which could be used as markers of tolerance to heat stress for selecting heat tolerant cultivars.

Materials and Methods

Four cultivars S-24, Saher-2006, Lasani and AARI-10 of spring wheat (*Triticum aestivum* L.) were tested for thermotolerance. A pot experiment was conducted at UAF, Pakistan during 2011-2012. The experiment was divided in to three sets. One set was used as control, the second set for heat stress imposed at the tillering phase and the third set used to impose high temperature at the booting stage. Temperature stress was applied at two growth phases i.e., boot and tillering stages. High temperature was maintained in transparent plastic enclosures. Maximum and minimum temperatures of the enclosures were noted daily. At the maturity of the experiment two plants were collected carefully and fresh weights of both the roots and shoots were determined separately. In addition, the data were collected for the following parameters.

Cell membrane thermostability (CMT): It was recorded following Sullivan (1972). For it, a fully expanded youngest leaf was collected and leaf discs of equal sizes were prepared. After excision the samples were placed immediately in test tubes each having 2 mL dH_2O. One set of samples was kept at 50°C and the other at 25°C for 1 h. After it, dH_2O (10 mL) was added to each test tube and again treated at 10°C for one day to allow ion diffusion. After this, all samples were kept at 25°C for 30 min and EC of the extract was recorded. Again samples were autoclaved at 0.1 MPa pressure for 10 min to extract all ions from the samples. Relative cell injury (RCI) in percent was calculated using the following formula:

$$\% \text{ Injury} = [1-(1-T1/T2) \div (1-(C1/C2)] \times 100$$

Water relation attributes: A youngest fully expanded leaf was excised and leaf water potential determined using a Scholander type pressure chamber (Arimad-2-Japan). Then, the same leaves were stored at -80°C for seven days. After it, they were thawed and the sap extracted and used for osmotic potential determination using an osmometer (VAPRO, 5520, USA). Turgor potential was estimated as the difference between Ψ_w and Ψ_s following Nobel (1991).

Chlorophyll pigments: The procedure described by Arnon (1949) was adopted for the analysis of major photosynthetic pigments. Fresh leaf (250 mg) was homogenized in 5 mL freshly prepared acetone (80%; v/v) and the extract was filtered. The optical density of the filtrate was recorded at 663 and 645 nm using a UV-visible spectrophotometer (IRMECO, U2020).

Gas exchange characteristics: A portable infra-red gas analyzer (Model LCA-4; ADC, Hoddeson, England) was used for the determination of different gas exchange parameters including rate of photosynthesis and transpiration, concentration of sub-stomatal CO_2 as well as stomatal conductance. For all these measurements, a young leaf from top was used at day time with maximum sunshine.

C**hlorophyll fluorescence:** The quantum yield, non-photochemical quenching and efficiency of PSII were determined on a young fully expanded leaf during daytime following Strasser *et al*. (1995). For the determination of above captioned leaf fluorescence attributes, OS5p Modulated Fluorometer (ADC BioScientific Ltd., Great AmwellHerts, UK) was used.

Statistical analysis: A completely randomized two-factor factorial experiment was designed. Data collected for different attributes were subjected to ANOVA technique to assess the significance level between different treatments using the COSTAT Computer Program, Cohort Berkely, California.

Results

Supraoptimal temperature significantly reduced the shoot fresh biomass of wheat plants. The varietal response to high temperature was also significant (Fig. 1). Cultivar Lasani had slightly higher biomass than the others when exposed to high temperature at tillering stage, while at the boot stage cv. S-24 showed considerably higher biomass production than the other cultivars (Fig. 1). Root fresh weight of all wheat cultivars was reduced significantly by supraoptimal temperature. Cv. Lasani had highest root biomass at the tillering phase, whereas cv. AARI-10 at the boot stage. At the tillering phase, cv. S-24 was inferior to the other cultivars in terms of fresh root biomass while at the boot stage cv. Saher-2006.

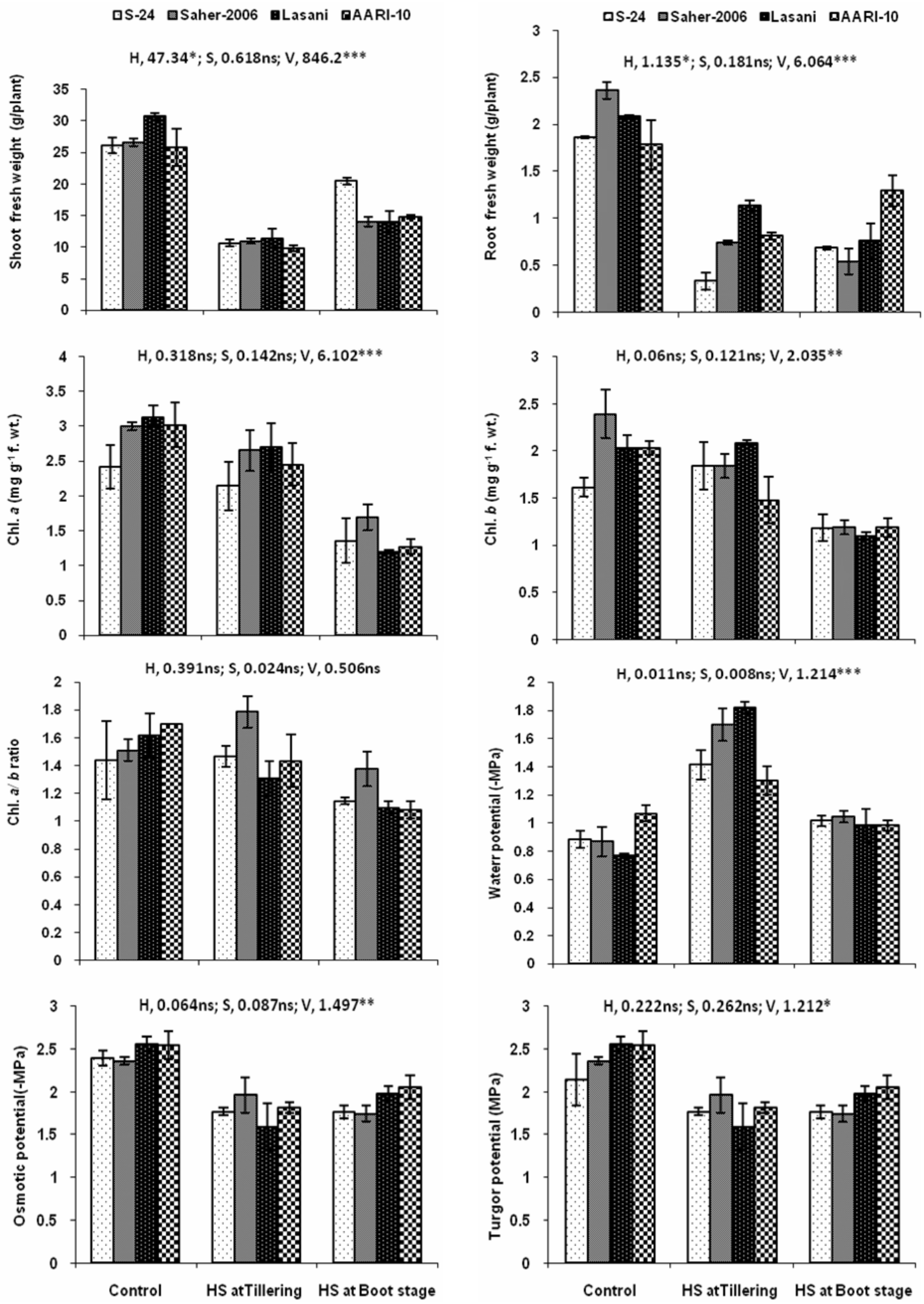

Fig. 1. Shoot and root fresh weights, chlorophyll pigment and water relation attributes of four wheat cultivars exposed to supraoptimal temperature at two growth stages.

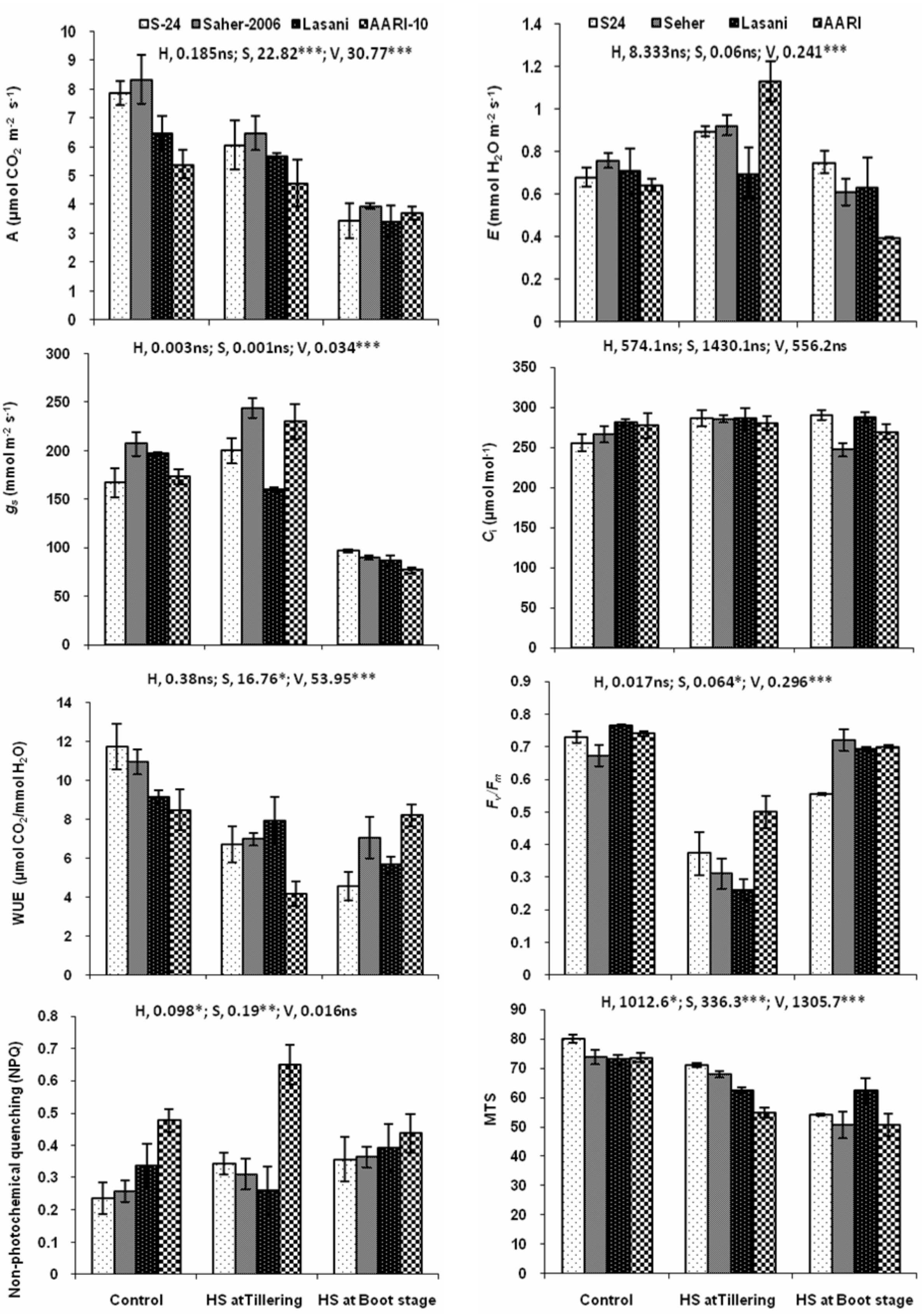

Fig. 2. Gas exchange and fluorescence attributes of four wheat cultivars exposed to supraoptimal temperature at two growth stages.

A non-significant decrease in chlorophyll *a* and *b* contents in the four wheat cultivars was recorded at both stages, but the response of the varieties to the stress was highly significant ($p \leq 0.001$). Cv. Lasani had the highest chlorophyll *a* contents under control and stress at the tillering phase. The cultivars which showed minimum value of this parameter were S-24 at the tillering phase and Lasani at the boot phase. Chlorophyll *a*/*b* ratio was not influenced by supraoptimal temperature significantly imposed at any stage and all interactions among different factors were non-significant (Fig. 1).

Heat stress did not cause a significant decrease in leaf water potential (Ψ_w) of four wheat cultivars at both stages. However, the varietal response to stress was highly significant ($p \leq 0.001$). Cv. AARI-10 maintained highest Ψ_w when the stress was applied at the tillering phase. Under control conditions, highest Ψ_w was recorded for cv. Lasani. The lowest Ψ_w was recorded for cv. Lasani at the boot phase and for cv. Saher-2006 at the tillering phase (Fig. 1). Leaf osmotic potential (Ψ_s) of the wheat plants was not influenced by supraoptimal temperature at both stages. However, the varieties responded to the stress significantly ($p \leq 0.01$). Cv. Lasani showed the lowest Ψ_s at the tillering phase and cv. Saher-2006 at the boot phase. All interactions among different factors were non-significant (Fig. 1). Leaf turgor potential (Ψ_p) was not influenced significantly by supraoptimal temperature. Again, the varietal response to heat stress was significant ($p \leq 0.05$) with cv. Saher-2006 being the best at the tillering phase and cv. AARI-10 at the boot phase (Fig. 1).

Supraoptimal temperature caused a non-significant decrease in photosynthetic rate (A) of wheat plants. However, the response of varieties and stages to high temperature was highly significant ($p \leq 0.001$). More drastic decrease in A was observed at the boot stage. The highest A was maintained by cv. Saher-2006 under control and stress conditions at both stages. Cv. AARI-10 showed a minimal photosynthetic activity at the tillering stage, while cv. Lasani at the boot stage (Fig. 2). Influence of high temperature on transpiration rate (E) in all wheat cultivars was non-significant but the varieties differed significantly in this attribute ($p \leq 0.001$). Maximum E was observed in cv. AARI-10 at the tillering stage and in S-24 at the boot stage. Minimum transpiration rate was shown by cv. Lasani at the tillering stage and by cv. AARI-10 at the boot stage (Fig. 2).

Water-use-efficiency ($WUE = A/E$) showed a non-significant decline under stress at both stages. Different stages and varieties were differentially affected by supraoptimal temperature. At the tillering phase, highest WUE was recorded in cv. Lasani and the lowest in cv. AARI-10 at the same stage but maximum at the boot stage (Fig. 2). The cultivar which had lowest WUE at the boot stage was S-24. The influence of heat stress on internal CO_2 concentration (C_i) was non-significant for all varieties at both stages. All interactions among different factors were non-significant. Effect of supraoptimal temperature on stomatal conductance (g_s) was not significant but the varietal response was highly significant ($p \leq 0.001$). The highest value of g_s was recorded in cv. Saher-2006 at the tillering phase and in cv. S-24 at the boot stage (Fig. 2).

F_v/F_m ratio was not affected significantly by supraoptimal temperature. The varieties and the two stages responded significantly to high temperature. Maximum value of F_v/F_m was recorded in cv. Saher-2006 at the boot stage and in cv. AARI-10 at the tillering phase, while cvs. Lasani and S-24 had minimum values of this parameter at the tillering and the boot stage, respectively (Fig. 2). High temperature had a significant influence on non-photochemical quenching (NPQ) at both stages of growth. Cv. AARI-10 had the highest values of NPQ at both stages. At the tillering phase, the lowest value of this parameter was recorded in cv. Lasani and at the boot stage in cv. S-24 (Fig. 2).

Supraoptimal temperature significantly influenced membrane thermostability (MTS) of all wheat cultivars at both growth stages. All cultivars showed a decrease in MTS under stress. Cultivar Lasani showed relatively higher MTS at the boot phase and cv. S-24 at the tillering phase (Fig. 2).

Discussion

Twenty first century has witnessed an ever-increasing rise in temperature due to change in climate (Gornall *et al*., 2010). This rise in temperature has put most of the crops to an increased incidence of heat stress (Watanabe & Kume, 2009). Plant physiological processes like photosynthesis, respiration and membrane integrity can be affected by supraoptimal temperature. Extremely high temperature might lead to cellular damage and even cell death within a very short time span (Wahid *et al*., 2007), but if the temperature is not high enough, the exposure period should be long to cause damage or death (Howarth, 2005). Although all stages of plants can be affected by high temperature, the particular stage of the plant has a role in the susceptibility of the plant to high temperature (Young *et al*., 2004).

In the present experiment, heat stress caused a significant reducing effect on growth parameters including shoot and root fresh biomass. The observed effect of supraoptimal temperature on shoot fresh biomass is analogous to Gilani *et al*. (2008) and Cheng *et al*. (2009), they noted a significant decline in shoot fresh weight as a result of high temperature in sugarcane and wheat plants, respectively. However, non-significant effect on root mass of grapes was recorded by Kadir & Weihe (2007) which is in contrast to the results of the present study.

Cell membrane thermostability is a rapid technique, measured as outflow of solutes from leaf pieces. It gives an indirect measure of plant heat tolerance (Saelim & Zwiazek, 2000; Stoddard *et al*., 2006; Wahid *et al*., 2007; Acosta *et al*., 2010). In the present study, heat stress significantly decreased the cell membrane thermostability (CMT). Cv. S-24 had the highest MTS at the tillering stage while cv. Lasani at the boot phase. This decrease in CMT is in conformity with Yildrim *et al*., (2009) who reported a decrease in membrane thermostability of wheat genotypes as a result of heat stress.

The speed with which water and gases pass through stomata is called stomatal conductance (g_s). So the stomatal orifice has a very vital role as the photosynthetic efficiency depends upon influx of water and gases through stomata (Ashraf & Harris, 2013). No significant effect of supraoptimal temperature on stomatal conductance was observed. Similar results were recorded by Bahar *et al*., (2011), for wheat genotypes exposed to supraoptimal temperature. But Anjum *et al*., (2008) observed an increase in stomatal conductance of wheat genotypes under heat stress. Transpiration rate is highly changeable under always changing climatic situations and is a vital indicator of physiological characteristics (Ahmed *et al*., 2012). Like stomatal conductance, no significant effect of supraoptimal temperature was observed on transpiration rate (E), internal CO_2 concentration (C_i) and photosynthetic rate (A). The results of Amirjani (2012) were opposite to what have been recorded here in the way they reported a decrease in transpiration rate and A but arise in C_i in wheat genotypes under heat stress.

Concentrations of photosynthetic pigments (chl. *a*, *b*, carotenoids and chl. *a*/*b* ratio) may reflect the degree of stress tolerance in different plants (Zhang *et al*., 2008). This study reports no significant effect of supraoptimal temperature on chlorophyll contents. This is what Amirjani (2012) reported after exposing wheat plants to a temperature of 30/25^{o}C (day/night) but a reduction in chlorophyll contents was observed at 35/30^{o}C (day/night). He also reported no significant effect of heat stress on chl. *a*/*b* ratio.

Water status of plants is thought to be highly variable in response to fluctuating temperatures (Mazzora *et al*., 2002). In contrast to our study in which no significant effect of heat stress on water relation attributes (water, osmotic and turgor potentials) was recorded, Gilani *et al*., (2008) reported a significant reduction in water status of sugarcane plants in response to high temperature.

Chlorophyll fluorescence is thought to be a reliable technique for *in situ* measurement of supraoptimal temperature-induced damage to photosynthetic machinery (Xu & Huang, 2001). The only chlorophyll fluorescence parameter to be significantly affected by supraoptimal temperature was non-photochemical quenching (NPQ) in which a significant rise was observed under stress. In other fluorescence parameters (F_v/F_m ratio and quantum yield) no significant change was recorded due to heat stress. In contrast to this, Anjum *et al*., (2008) observed a significant decrease in F_v/F_m ratio in wheat plants at high temperature, but no significant effect on NPQ.

In conclusion, high temperature adversely affected only root and shoot fresh weights, MTS and NPQ in all four wheat cultivars at both developmental stages. However, HT stress did not influence all the other studied attributes significantly. Among all wheat cultivars, cv. Lasani performed better in shoot and root fresh weight, and chlorophyll *a* contents at the tillering stage, while in MTS at the booting phase, cv. S-24 in shoot fresh weight, E, and g_s at the boot stage and highest MTS and WUE at the tillering stage. However, cv. AARI-10 performed well in root fresh weight, Ψ_w, Ψ_s, Ψ_p, WUE and NPQ when stress was applied at the boot stage, while E and F_v/F_m in this cultivar on exposure to stress at the tillering stage. Cultivar Saher-2006 performed better in g_s, and leaf Ψ_s and Ψ_p at the tillering stage, while F_v/F_m was recorded better at the boot stage and A in the same cultivar at all growth stages. Overall, HT stress applied at different growth stages was only effective in altering root fresh weight, MTS and NPQ in all four wheat cultivars. Of all wheat cultivars, cv. AARI-10 performed better in growth and potential physiological attributes under stress conditions applied at different phenological stages.

References

Acosta, M.L., M.C.M. Ballesta, J.A. Teruel and M. Carvajal. 2010. The response of broccoli plants to high temperature and possible role of root aquaporins. *Environ. Exp. Bot.*, 68: 83-90.

Ahmed, M., Fayyaz-ul-Hassan, M. Aslam and M.A. Aslam. 2012. Physiological attributes based resilience of wheat to climate change. *Int. J. Agric. Biol.,* 14: 407-412.

Alexander, L.V., X. Zhang, T.C. Peterson, J. Caesar, B. Gleason and A. Tank. 2006. Global observed changes in daily climate extremes of temperature and precipitation*. J. Geophys. Res. Atmosphere,* 111: 1-22.

Almeselmani. 2010. Effect of high temperature on physiological characters and yield attributes of wheat genotypes. In: International Conference on Agricultural Productivity Increase: Challenges and Means of Development, 28-30 November, Al-Farat University Campus and Directorate of Agriculture and Agrarian Reform Der-Azzor, pp. 50.

Amirjani, M. 2012. Estimation of wheat responses to high heat stress. *Am-Eur. J. Sustain. Agric.,* 6: 222-233.

Anjum, A., A. Wahid, F. Javed and M. Arshad. 2008. Influence of foliar applied thiourea on flag leaf gas exchange and yield parameters of bread wheat (*Triticum aestivum* L.) cultivars under salinity and heat stress. *Int. J. Agric. Biol.,* 10: 619-626.

Arnon, D.T. 1949. Copper enzyme in isolated chloroplasts polyphenoloxidase in *Beta vulgaris*. *Plant Physiol*., 24: 1-15.

Ashraf, M. and P.J.C. Harris. 2013. Photosynthesis under stressful environments: An overview. *Photosynthetica*, 51(2): 163-190.

Bahar, B., M. Yildirim and C. Yucel. 2011. Heat and drought resistance criteria in spring bread wheat: morpho-physiological parameters for heat tolerance. *Sci. Res. Essays*, 6: 22120-2220.

Balla, K., S. Bencze, T. Janda and O. Veisz. 2009. Analysis of heat stress tolerance in winter wheat. *Acta Agron. Hung.,*57: 437–444.

Berry, J.A. and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.*, 31: 491-543.

Cabanero, F.J., V. Martínez and M. Carvajal. 2004. Does calcium determine water uptake under saline conditions in pepper plants, or is it water flux which determines calcium uptake?. *Plant Sci.,* 166: 443-450.

Camejo, D., P. Rodriguez, M.A. Morales, J.M.D. Amico, A. Torrecillas and J.J. Alarcon. 2005. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *J. Plant Physiol*., 162: 281-289.

Cheng, W., H. Sakai, K. Yagi and T. Hasegawa. 2009. Interaction of elevated CO_2 and night temperature on rice growth and yield. *Agric. Forest Metreol.,* 149: 51-58.

Chinnusamy, V. and R. Khanna-Chopra. 2003. Effect of heat stress on grain starch content in diploid, tetraploid and hexaploid wheat species. *J. Agron. Crop Sci.,* 189: 242-249.

Coskun, Y., A. Coskun, U. Demirel and M. Ozden. 2011. Physiological response of maize (*Zea mays* L.) to high temperature stress. *Aust. J. Crop Sci.,* 5: 966-972.

Falk, S., D.P. Maxwell, D.E. Laudenmach and N.P.A. Huner. 1996. Photosynthetic adjustment to temperature. In: Advances in Photosynthesis: Photosynthesis and Environment. (Ed.): Baker, N. R. Vol. 5, Kluwer Academic Publishers, Dordrecht, The Netherlands.

Ferris, R., R.H. Ellis and W. Hadley. 1998. Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. *Ann. Bot.,* 82: 631-639.

Finka, A, R.U. Mattoo and P. Goloubinoff. 2010. Meta-analysis of heat- and chemically upregulated chaperone genes in plant and human cells. *Cell Stress Chaperones*, 16: 15-31.

Giavenno, C. and J. Ferrero. 2003. Introduction of tropical maize genotypes to increase sillage production in the central area of Santa Fe Argentina. *Crop Breed. Appl. Biotechnol*., 3: 89-94.

Gilani, S., A. Wahid, M. Ashraf, M. Arshad and Islam-ud-Din. 2008. Changes in growth and leaf water status of sugarcane (*Sacharum officinarum* L.) during heat stress and recovery. *Int. J. Agric. Biol.,* 10: 191-195.

Gornall, J., R. Betts, E. Burke, R. Clark, J. Camp, K. Willett and A. Wiltshire. 2010. Implications of climate change for agricultural productivity in the early twenty-first century. *Philos. Transaction Royal Soc. B.,* 365: 2973-2989.

Hassan, I.A. 2006. Effect of water stress and high temperature on gas exchange and chlorophyll fluorescence in *Triticum aestivum* L. *Photosynthetica,* 44: 312-315.

Howarth, C.J. 2005. Genetic improvements of tolerance to high temperature. In: Abiotic Stresses: Plant Resistance through Breeding and Molecular Approaches. (Eds.): M. Ashraf and P.J.C. Harris . Howarth Press Inc., New York.

Joshi, A.K., B. Mishra, R. Chatrath, G.O. Ferrara and R.P. Singh. 2007. Wheat improvement in India: present status, emerging challenges and future prospects. *Euphytica*, 157: 431-446.

Kadir, S. 2006. Thermostability of photosynthesis of *Vitis aestivalis* and *Vitis vinifera. J. Am. Soc. Hort. Sci.,* 131: 476-483.

Kadir, S. and M.V. Weigh. 2007. Photochemical efficiency and recovery of PSII in grapes after exposure to sudden and gradual heat stress. *J. Am. Soc. Hort. Sci.,* 132: 764-769.

Khan, M.A. 2004. Wheat crop management for yield maximization-II. Wheat Research Institute, AARI, pp. 23-28.

Larkindale, J. and M.R. Knight. 2002. Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene and salicylic acid. *Plant Physiol.,* 128: 682-695.

Long, S.P. and D.R. Ort. 2010. More than taking the heat: crops and global change. *Curr. Opin. Plant Biol.*, 13: 240-247.

Maestri, E., N. Klueva, C. Perrotta, M. Gulli, H.T. Nguyen and N. Marmiroli. 2002. Molecular genetics of heat tolerance and heat shock proteins in cereals. *Plant Mol. Biol.,*48: 667-681.

Mazorra, L.M., M. Nunez, E. Echerarria, F. Coll and M.J. Sánchez-blanco. 2002. Influence of brassinosteriods and antioxidant enzymes activity in tomato under different temperatures. *Plant Biol*., 45: 593-596.

Nobel, P.S. 1991. Physiological and Environmental Plant Physiology. Academic Press, New York.

Peng, S., J. Huang, J.E. Sheehy, R.C. Laza, R.M. Visperas, X. Zhong, G.S. Centeno, G.S. Khush and K.G. Kassman. 2004. Rice yields decline with higher night temperature from global warming. *Proc. Natl. Acad. Sci. USA*, 101: 9971-9975.

Quinn, P.J. and W.P. Williams. 1985. Environmentally induced changes in chloroplast membranes and their effects on photosynthesis. In: *Photosynthetic Mechanism and the Environment*. (Eds.): Barber, J. and N. R. Baker. Elsevier, Amsterdam, The Netherlands, pp. 1-47.

Rasul, G., Q.Z. Chaudhry, A. Mahmood and K.W. Hyder. 2011. Effect of temperature rise on crop growth and productivity. *Pak. J. Metreol*., 8: 53-62.

Ruelland, E. and A. Zachowski. 2010. How plants sense temperature. *Environ. Exp. Bot*., 69: 225-232.

Saelim, S. and J.J. Zwiazek. 2000. Preservation of thermal stability of cell membranes and gas exchange in high temperature acclimated *Xylia xylocarpa* seedlings. *J. Plant Physiol.,* 156: 380-385.

Sairam, R.K., G.C. Srivastava and D.C. Saxena. 2000. Increased antioxidant activity under elevated temperature: a mechanism of heat stress tolerance in wheat genotypes. *Biol. Plant.,* 43: 245-251.

Sakamoto, A. and N. Murata. 2002. The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. *Plant Cell Environ*., 25: 163-171.

Salvucci, M.E. and S.J. Crafts-Brandner. 2004. Inhibition of photosynthesis by heat stress: the activation state of rubisco as a limiting factor in photosynthesis. *Physiol. Plant*., 120: 179-186.

Shah, K., R.G. Kumar, S. Verma and R.S. Dubey. 2001. Effect of cadmium on lipid peroxidation, superoxide anion generation and activities of antioxidant enzymes in growing rice seedlings. *Plant Sci.,* 161: 1135-1144.

Simoes-Araujo, J.L., N.G. Rumjanek and M. Margis-Pinheiro. 2003. Small heat shock protein genes are differentially expressed in distinct varieties of common bean. *Braz. J. Plant Physiol.,* 15: 33-41.

Somerville, C. and J. Browse. 1991. Plant lipids, metabolism and membranes. *Science,* 252: 80-87.

Srivastava, K., S. Kumar, S. Kumar, P. Prakash and A. Vaishampyan. 2012. Screening of tomato genotypes for reproductive characters under high temperature stress conditions. *Sabrao J. Breed. Genetics,* 44: 263-276.

Stoddard, F.L., C. Balko, W. Erskine, H.R. Khan, W. Link and A. Sarker. 2006. Screening techniques and source of resistance to abiotic stresses in cool season food legumes. *Euphytica*, 147: 167-186.

Stone, P. 2001. The effects of heat stress on cereal yield and quality. In: *Crop Responses and Adaptations to Temperature Stress*. (Ed.): Basra, A.S. Food Products Press, Binghamton, New York, USA, pp. 243-291.

Stone, P.J. and M.E. Nicolas. 1995. Effect of heat stress during grain filling on two wheat varieties differing in heat tolerance grain growth. *Aust. J. Plant Physiol.,* 22: 927-934.

Strasser, R.J., A. Srivastava and Govindgee. 1995. Polyphasic chlorophyll *a* fluorescence transients in plants and cyanobacteria. *Photochem. Photobiol.,* 61: 32-42.

Sud, S. and S.G. Bhagwat. 2010. Assessment of acquired thermotolerance in Indian bread wheat and association with yield and component traits under heat stress environment. *J. Food Agric. Environ.,* 8: 622-627.

Sullivan, C.Y. 1972. Mechanism of heat and drought resistance in grain sorghum and methods of measurement. In: *Sorghum in the Seventies*. (Eds.): Rao, N.G.P. and L.R. House.. Oxford and IBH Publishing Co., New Delhi, pp. 247-264.

Suzuki, N. and R. Mittler. 2006. Reactive oxygen species and temperature stresses: A delicate balance between signaling and destruction. *Physiol. Plant.,* 126: 45-51.

Ubaidullah, R., T. Mohammad, H. Ullah and S. Ali. 2007. Characterization of wheat genotypes for yield and yield associated traits against terminal heat stress. *Sarhad J. Agric.,* 23: 947-954.

Wahid, A. and T.J. Close. 2007. Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. *Biol. Plant.,* 51: 104-109.

Wahid, A., S. Gelani, M. Ashraf and M.R. Foolad. 2007. Heat tolerance in plants: an overview. *Environ. Exp. Bot.,* 61: 199-223.

Watanabe, T. and T. Kume. 2009. A general adaptation strategy for climate change impacts on paddy cultivation: special reference to the Japanese context. *Paddy Water Environ.,* 7: 313-320.

Wise, R.R., A.J. Olson, S.M. Schrader and T.D. Sharkey. 2004. Electron transport in the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. *Plant Cell Environ.,* 27: 727-724.

Xu, Q., A. Paulsen, J.A. Guikema and G.M. Paulsen.1995. Functional and ultrastructural injury to photosynthesis in wheat by high temperature during maturation. *Environ. Exp. Bot.,* 35: 43-54.

Xu, Q.Z. and B.R. Huang. 2001. Morphological and physiological characteristics associated with heat tolerance in creeping bentgrass. *Crop Sci.,* 41: 127-133.

Yan, S.H., Y.P. Yin, W.Y. Li, Y. Li, T.B. Liang, Y.H. Wu, Q.H. Geng and Z.L. Wang. 2008. Effect of high temperature stress after anthesis on starch formation of two wheat cultivars differing in heat tolerance. *Acta Ecol. Sinica*, 28: 6138-6147.

Yildrim, M., B. Bahar, M. Koc and C. Barutcular. 2009. Membrane thermal stability at different developmental stages of spring wheat genotypes and their diallel cross populations. *Trim Bilimeri Dergesi,* 15: 293-300.

Young, L.W., R.W. Wilen and P.C. Bonham-Smith. 2004. High temperature stress of *Brassica napus* during flowering reduces micro- and megagametophyte fertility, induces fruit abortion and disrupts seed production. *J. Exp. Bot.,* 55: 485-495.

Zhang, X., B. Wollenweber, D. Jiang, F. Liu and J. Zhao. 2008. Water deficits and heat shock effects on photosynthesis of a transgenic *Arabidopsis thaliana* constitutively expressing ABP9, a bZIP transcription factor. *J. Exp. Bot*., 59: 839-548.

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