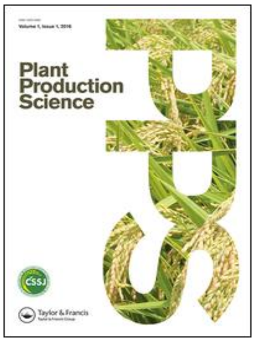

Plant Production Science

ISSN: 1343-943X (Print) 1349-1008 (Online) Journal homepage: https://www.tandfonline.com/loi/tpps20

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To cite this article: Izzat Sidahmed Ali Tahir, Noboru Nakata, Takeshi Yamaguchi, Junichi Nakano & Abdelbagi Mukhtar Ali (2009) Physiological Response of Three Wheat Cultivars to High Shoot and Root Temperatures during Early Growth Stages, Plant Production Science, 12:4, 409-419, DOI: 10.1626/pps.12.409

To link to this article: https://doi.org/10.1626/pps.12.409

Plant Prod. Sci. 12(4) : 409—419 (2009)

Physiological Response of Three Wheat Cultivars to High Shoot and Root Temperatures during Early Growth Stages

Izzat Sidahmed Ali Tahir [1,2,3], Noboru Nakata[1], Takeshi Yamaguchi[1], Junichi Nakano[1] and Abdelbagi Mukhtar Ali[2]

([1] Faculty of Agriculture, Tottori University, Koyama 4-101, Tottori, 680-8553, Japan;
[2] Agricultural Research Corporation, P.O. Box 126, Wad Medani, Sudan;
[3] Arid Land Research Center, Tottori University. 1390 Hamasaka, Tottori 680-0001, Japan)

Abstract : Understanding wheat (*Triticum aestivum* L.) response to high shoot/root temperature during the early growth stages is important for successful production in tropical and subtropical environments. This study examined the physiological response of wheat cultivars to high shoot and/or root temperatures during early growth stages. Three cultivars; Imam, Fang and Siete Cerros were grown in soil and hydroponically at three shoot/root temperatures (23/23, 23/35 and 35/35ºC for the soil experiment; and 22/22, 22/38 and 38/38ºC for the hydroponic experiment). Leaf dry weight and leaf area plant^{-1} were significantly decreased by high shoot/root temperature (HS/HR, 35/35 and 38/38ºC) but was not affected by a normal shoot/high root temperature (NS/HR, 23/35 and 22/38ºC). The NS/HR (22/38ºC) and HS/HR (38/38ºC) treatments in the hydroponic experiment significantly decreased photosystem II quantum yield (Φ_{PSII}), photosynthetic rate (P_n) and specific leaf area (SLA) compared with the normal shoot/normal root (NS/NR, 22/22ºC) temperature treatment. Chlorophyll accumulation was significantly decreased by NS/HR, but increased significantly by HS/HR in most of the measuring dates. The heat-tolerant cultivar, Fang, always had the highest chlorophyll content, Φ_{PSII} and P_n under all temperature treatments, while the heat-sensitive cultivar, Siete Cerros, always had the greatest reduction in these traits especially towards the end of the experiment. Imam and Fang responded to HS/HR in the hydroponic experiment by immediate and greater reductions in leaf dry weight, total leaf area and SLA during the first wk of the treatments compared with Siete Cerros. The response changed with the treatments duration such that Imam showed the least reduction and Siete Cerros was the most affected cultivar towards the end of the experiment. Thus, wheat cultivars differentially responded to high shoot/root temperature by reducing the leaf weight and area and hence accumulating more chlorophyll in the diminished leaves. The failure to undergo such changes led to significantly lower chlorophyll accumulation, Φ_{PSII} and P_n under high root temperature.

Key words : High shoot and root temperature, Net photosynthetic CO_2 assimilation rate, Photosystem II effective quantum yield, Specific leaf area, Wheat.

The development and release of high yielding wheat (*Triticum aestivum* L.) cultivars with better adaptation to various environmental conditions triggered the so-called "Green Revolution" in the 1960s. Thousands of modern cultivars have been released for use in both favorable and marginal environments (Reynolds and Borlaug, 2006). As a result, wheat production extended to marginal areas like those experience high temperatures during various stages of crop growth. Heat stress is considered one of the major factors limiting wheat production in the tropical and subtropical environments. In these areas, high temperatures are known to affect the crop development at all stages and impose morphological and physiological changes that result in considerable grain yield reduction (Al-Khatib and Paulsen, 1990; Tahir et al., 2005a, 2006; Tewolde et al., 2006). High temperatures adversely affect wheat seed germination, seedling establishment and survival (Ali et al., 1994; Ishag et al., 1998).

The upper soil temperature can be as high as air temperature during the early seedling stage before the crop develops good ground cover. As the shoot apex is initially at seed depth, soil temperature considerably influences leaf production during early growth (Hay and Wilson, 1982; Vincent and Gregory, 1989). High root temperature is reported to decrease photosynthetic activity, chlorophyll accumulation and consequently decreases both shoot and root growth (Itai et al., 1973; Kuroyanagi and Paulsen, 1988; Udomprasert et al., 1995; Xu and Huang, 2000). Exposing plants to elevated non-lethal temperature results in the acquirement of thermotolerance, which can transiently raise their injury threshold and protect them from subsequent, otherwise lethal, temperatures (O'Mahony and Burke, 2000; Burke, 2001).

High temperature is known to impair many processes involved in photosynthesis. Chlorophyll accumulation, fluorescence and photosynthesis have been used to assess thermotolerance in wheat and other crops (Moffatt et al., 1990; O'Mahony and

Received 26 May 2008. Accepted 19 February 2009. Corresponding author: T. Yamaguchi (yamaguch@muses.tottori-u.ac.jp, fax +81-857-31-5350).

Burke, 2000; Burke, 2001; Dash and Mohanty, 2001). Accumulating high chlorophyll and maintaining effective photosystem II (PSII) quantum yield under high temperature are genetically controlled and demonstrate the ability of wheat genotypes to acquire thermotolerance (Al-Khatib and Paulsen, 1990; Moffatt et al., 1990; O'Mahony and Burke, 2000; Dash and Mohanty, 2001). Variations were reported in response of wheat genotypes to increasing temperatures during germination, vegetative and reproductive stages (Al-Khatib and Paulsen, 1990; Ali et al., 1994; Tahir and Nakata, 2005; Tahir et al., 2006; Tewolde et al., 2006). Wheat genotypes also differentially responded to high shoot and/or root temperature during grain filling stage (Tahir et al., 2005b). However, little is known about the response of different wheat genotypes to high shoot/root temperature during early growth stages. Moreover, the majority of studies thus far carried out to investigate the effect of high root temperature during early growth stages used constant temperatures throughout the experiment. This might exert drastic effects on the physiological processes and could not allow PSII to recover from the effects of high temperature during the night. Better adaptation of wheat genotypes to high temperatures was found when gradual increments in high temperature treatments were applied coupled with relatively cool night temperature (Havaux, 1993; Law and Crafts-Brandner, 1999; Tahir and Nakata, 2005; Tahir et al., 2005b). Here, we studied the effects of high shoot/root temperatures on chlorophyll content, fluorescence, photosynthesis and leaf growth in wheat during early growth stages using three cultivars and three shoot and/or root temperature combinations.

Materials and Methods

1. Plant materials and growing conditions

Three bread wheat cultivars varying in heat sensitivity and tolerance were used: Fang, heat tolerant, Siete Cerros, heat sensitive and Imam, a recently released cultivar for the hot dry environment of Sudan (Tahir et al., 2005b). Imam demonstrated high yielding potential under the heat-stressed condition of Sudan. It has the characteristics of maintaining relatively long duration to heading despite high temperatures during the vegetative stage (Tahir, I.S.A., unpublished data). Two experiments were conducted at the Faculty of Agriculture, Tottori University, Japan. The first experiment (Feb-Mar, 2003) was conducted using soil (hereafter referred to as soil Expt). The second experiment (Jan-Feb, 2004) was carried out using a nutrient solution (hereafter referred to as hydroponic Expt).

In soil Expt, seeds of the three cultivars were sown in 1/5000a Wagner's pots filled with a mixture of soil: sand: organic matter at a ratio of 2:1:1. A fertilizer containing 1:1:1 of N: P_2O_5: K_2O was incorporated to the soil at a rate of 0.4 g pot^{-1} for each element. Three seedlings were grown in each pot and kept in a vinyl house under natural light and maximum temperature around 20ºC until the temperature treatments were initiated.

For the hydroponic Expt, seeds of the three cultivars were germinated in moist Metro-Mix® 350 growing medium containing horticultural vermiculate, Canadian sphagnum peat moss and processed bark ash. Seven-day-old seedlings were transplanted to opaque plastic plates. Five seedlings were grown through holes in each plate, which were placed over 1/5000a Wagner's pots. Pots were filled with half-strength nutrient solution (Hoagland and Arnon, 1950), which was continuously aerated, adjusted to pH 5.0 semiweekly and replaced weekly. Plants were placed for one week in a naturally illuminated phytotron set to a day/night temperature of 22/18ºC.

At the three-leaf stage in both experiments, plants were subjected to three shoot/root temperatures during the daytime. These temperatures were (i) normal shoot/normal root temperature (NS/NR, 23/23ºC and 22/22ºC, in soil and hydroponic Expts, respectively), (ii) normal shoot/high root temperature (NS/HR, 23/35ºC and 22/38ºC in soil and hydroponic Expts, respectively) and (iii) high shoot/high root temperature (HS/HR, 35/35ºC and 38/38ºC in soil and hydroponic Expts, respectively.)

The temperatures were chosen considering the prevailing temperatures under field conditions in the tropics and subtropics where wheat experiences high temperature during the day and a reduced temperature at night especially during the early growth stages.

A growth chamber (K30-2190, Koito Industries, Ltd. Yokohama, Japan) consisting of three-connected cabinets with identical settings and capable of maintaining different shoot/root temperature was used for both experiments. In the soil Expt, a night temperature of 19ºC was maintained for 11 hr, but in the hydroponic Expt the night temperature was 18ºC and maintained for 9 hr. The maximum temperatures of 35 and 38ºC were kept for 5 hr in both experiments. Heating and cooling of the temperature was done gradually at a rate of 4ºC/hr. The air, soil and solution temperatures were monitored by Thermo Recorders (Thermo Recorder for Windows, TR-72S, T & D, Nagano, Japan) connected to sensors and records were taken every hour. Irradiance was 900-1000 μmol m^{-2} s^{-1} photosynthetically active radiation at the canopy level as measured by LI-190 quantum sensor (LI-COR Inc., Lincoln, NE, USA) and day-length was 14 hr. The relative humidity was set at 30/40% during the day/night time. The pots in the soil Expt were irrigated daily or as needed to avoid any water-deficit effect under high temperature treatments. Plants were kept free from pests and diseases by frequent spraying with appropriate chemicals and the temperature treatments

Table 1. Leaf dry weight, total and specific leaf areas of three wheat cultivars (C) grown in soil under three shoot/root temperature treatments (T). Measurements were taken at 20 days after treatments (DAT) initiation.

	Temperature treatment, shoot/root (°C)											
	23/23	23/35	35/35	Mean	23/23	23/35	35/35	Mean	23/23	23/35	35/35	Mean
Cultivar	Leaf dry weight (g/plant)				Total leaf area (cm^2/plant)				Specific leaf area (cm^2/g)			
Fang	1.023	1.085	0.922	1.010	185.5	177.8	150.4	171.3	200.7	163.7	162.8	175.7
Imam	1.075	1.158	0.977	1.070	210.0	201.5	155.6	189.0	195.0	174.0	159.5	176.2
Siete Cerros	0.951	1.008	0.919	0.959	189.3	167.6	152.0	169.6	199.3	166.0	165.4	176.9
Mean	1.016	1.083	0.939		194.9	182.3	152.7		198.3	167.9	162.6	
ANOVA mean square for:												
Cultivar	0.0291*				904.0^{ns}				3.1^{ns}			
Temperature	0.0480**				4484.8***				3343.2***			
C × T	0.0032^{ns}				288.3^{ns}				69.0^{ns}			
SE (DF=16) for:												
C and T	0.0251				7.70				4.20			
C × T	0.0435				13.34				7.28			
CV %	7.7				11.4				7.2			

SE, Standard error of the mean; DF, Degree of freedom for the error mean square; C × T , Cultivar × temperature treatment interaction. *, ** and ***, Significant at 5, 1 and 0.1% levels, respectively. ns, Not significant.

were continued for 20 days in the soil Expt and 30 days in the hydroponic Expt.

2. Measurements

(1) Leaf weight and area

Plants were sampled at 20 days after the start of treatments (DAT) in the soil Expt and at 0, 7, 15 and 30 DAT in hydroponic Expt and separated into different parts. Three plants per pot were sampled at 0 and 20 DAT in the soil Expt and at 30 DAT of the hydroponic Expt while one plant per pot was sampled at 7 and 15 DAT in the hydroponic Expt. Leaf area was measured from a sub-sample of leaves using a leaf area meter (AAC-410, Hayashi Denko Co. Ltd. Japan). Leaves were oven-dried at 80°C for at least 48 hr, weighed and leaf area per plant and specific leaf area (SLA) were calculated.

(2) Chlorophyll content, fluorescence and photosynthetic rate

Chlorophyll content, fluorescence and photosynthetic rate were measured only in the hydroponic Expt. Chlorophyll content was indirectly measured using a chlorophyll meter (Minolta SPAD-502 meter: Minolta Camera Co., Japan), recording in SPAD value. The SPAD meter measures leaf chlorophyll content by measuring the reflection from leaves in light using wavelengths of 650nm and 940nm (Pinter et al., 1994). Measurements were made weekly after treatments were initiated. Six measurements were taken from the most recently fully expanded leaves in each pot and then averaged.

The chlorophyll fluorescence was measured in terms of photosystem II (PSII) effective quantum yield or actual PSII efficiency (Φ_{PSII}) using a leaf chamber fluorometer (LI-6400-40 LCF, LI-COR Inc., Lincoln, NE, USA) at 15, 21 and 28 DAT. The Φ_{PSII} was measured on the most recently fully expanded light-adapted leaves and expressed as $(F_m'-F_s)/F_m'$; where F_m'=maximum fluorescence yield; F_s= steady state fluorescence yield. At least six measurements were taken from each cultivar in each temperature treatment. All measurements were taken between 1000 and 1500 hr when the temperature was constant and at its maximum values. Simultaneously, the net photosynthetic CO_2 assimilation rate (P_n, μmol CO_2 m^{-2} s^{-1}) was recorded for the same leaf sample used for fluorescence measurement.

3. Statistical analysis

In both experiments, a randomized complete block design with three replications was used and the pots were rearranged regularly within the cabinets to avoid any positional effects. Two-way analysis of variance was carried out for the data taken during and at the end of temperature treatments while the data taken at 0 DAT were analyzed using one-way analysis of variance. Standard errors (SE) of means for temperature treatments, cultivars and their interaction are presented in the tables. Where appropriate, means were compared using least significant difference test (LSD) at 0.05 probability level in the figures.

Results

1. Analysis of variance

Tables 1 and 2 show the effects of cultivars (C),

Table 2. Mean square for wheat cultivars (C), temperature treatments (T), and their interaction (C×T) derived from the analysis of variance for traits measured at different days after the start of treatment (DAT) initiation in the hydroponic experiment.

Trait	Mean square for: Cultivar	Temperature	C×T	CV %
1- Leaf dry weight at:				
7 DAT	0.0065***	0.0265***	0.0010 ns	9.8
15 DAT	0.0659*	0.418***	0.0073 ns	14.2
30 DAT	1.234**	12.472***	0.570*	10.5
2- Total leaf area at:				
7 DAT	134.0*	278.9**	14.2 ns	15.2
15 DAT	1745.3*	21073.1***	260.7 ns	16.8
30 DAT	34117.0*	503068.0***	22779.0*	14.8
3- Specific leaf area at:				
7 DAT	149.9 ns	1063.7**	139.5 ns	7.6
15 DAT	834.4*	5235.1***	173.2 ns	9.1
30 DAT	1308.5***	3536.8***	174.4 ns	7.5
4- Chlorophyll content at:				
7 DAT	2.8 ns	183.9***	11.9 ns	5.1
14 DAT	14.2 ns	86.8***	17.8*	4.9
21 DAT	24.1*	21.3*	11.8 ns	5.0
28 DAT	26.5***	10.1**	7.5**	2.2
5- Chlorophyll fluorescence at:				
15 DAT	0.00305***	0.00172***	0.00045*	2.9
21 DAT	0.00361***	0.00204**	0.00036 ns	4.3
28 DAT	0.00167*	0.00320**	0.00040 ns	4.9
6- Photosynthetic rate at:				
15 DAT	39.3***	73.1***	4.75 ns	6.4
21 DAT	83.6***	51.0***	11.63**	7.0
28 DAT	30.2***	22.8***	0.95 ns	5.5

*, ** and ***, Significant at 5, 1 and 0.1% levels, respectively. ns, Not significant.

temperature treatments (T) and their interaction (C×T) on different traits measured in both soil and hydroponic experiments. In the soil Expt, significant differences among temperature treatments were found in all traits measured while cultivar difference was significant only in leaf dry weight and no significant C×T interactions were found (Table 1). In the hydroponic Expt, significant differences between temperature treatments were observed in all traits at all measuring dates (Table 2). Significant differences among cultivars were also found in all traits except specific leaf area at 7 DAT, and chlorophyll content at 7 and 14 DAT. The C×T interaction was significant in leaf dry weight at 30 DAT, total leaf area at 30 DAT, chlorophyll content at 14 and 28 DAT, chlorophyll fluorescence at 15 DAT, and photosynthetic rate at 21 DAT (Table 2).

2. Leaf weight and area

High shoot/root temperatures (35/35 and 38/38ºC) in both experiments significantly reduced leaf dry weight plant^{-1} compared with the control (Tables 1, 2 and 3). During the first wk of 38/38ºC treatment in the hydroponic Expt, Fang showed the highest decline in the leaf weight (41%) followed by Imam (33%) while that of Siete Cerros was the least affected (24%) compared with the control. At 30 DAT, Fang and Siete Cerros showed more than 50% reduction in their leaf weight while Imam showed 33% reduction. NS/HR (23/35 or 22/38ºC) in both experiments showed no effect on the leaf dry weight in the three cultivars throughout the experimental period apart from the reduction in leaf dry weight in Siete Cerros at 30 DAT in the hydroponic Expt.

The total leaf area plant^{-1} was not affected significantly by NS/HR treatment in the soil Expt (Table 1), and in the hydroponic Expt until 15 DAT in all

Table 3. Leaf dry weight, total and specific leaf areas of three wheat cultivars (C) grown hydroponically at three shoot/root temperature treatments (T). Measurements were taken at 7, 15 and 30 DAT.

	Temperature treatment, shoot/root (°C)											
	22/22	22/38	38/38	Mean	22/22	22/38	38/38	Mean	22/22	22/38	38/38	Mean
DAT/cultivar	Leaf dry weight (g/plant)				Total leaf area (cm^2/plant)				Specific leaf area (cm^2/g)			
7 DAT												
Fang	0.277	0.291	0.163	0.244	42.78	40.15	29.56	37.50	156.8	140.2	131.8	142.9
Imam	0.255	0.281	0.170	0.236	41.22	36.47	23.36	33.68	157.2	115.9	127.2	133.4
Siete Cerros	0.204	0.222	0.155	0.194	30.32	30.91	23.07	28.10	149.2	136.0	137.2	140.8
Mean	0.245	0.265	0.163		38.11	35.84	25.33		154.4	130.7	132.1	
SE (DF=16)	C and T=0.0074, C×T=0.0127				C and T=2.05, C×T=3.55				C and T=4.33, C×T=7.50			
15 DAT												
Fang	0.924	0.927	0.534	0.795	171.0	160.7	75.9	135.9	185.6	173.2	143.4	143.4
Imam	1.010	1.006	0.561	0.859	168.0	153.2	68.7	130.0	169.0	153.9	122.8	122.8
Siete Cerros	0.772	0.795	0.502	0.670	144.0	118.4	65.6	109.3	186.4	146.5	130.2	130.2
Mean	0.902	0.909	0.533		161.0	144.1	70.1		180.3	157.9	132.1	
SE (DF=16)	C and T=0.0369, C×T=0.0638				C and T=6.99, C×T=12.11				C and T=4.77, C×T=8.27			
30 DAT												
Fang	4.93	4.66	2.25	3.95	918.5	668.9	343.9	643.8	185.5	148.1	151.5	161.7
Imam	4.45	4.79	3.00	4.08	679.1	649.8	374.7	567.9	152.6	136.1	124.2	137.6
Siete Cerros	4.53	3.50	2.12	3.38	802.9	492.9	269.8	521.9	177.0	141.2	127.1	148.4
Mean	4.64	4.32	2.46		800.2	603.9	329.5		171.7	141.8	134.3	
SE (DF=16)	C and T=0.133, C×T=0.231				C and T=28.44, C×T=49.27				C and T=3.72, C×T=6.44			

SE, Standard error of the mean; DF, Degree of freedom for the error mean square; C×T , Cultivar×temperature treatment interaction.

three cultivars (Tables 2, 3), despite the trend of reduction observed. However, after 30 days in 22/38°C treatment in the hydroponic Expt, the leaf area plant^{-1} significantly ($P<0.05$) decreased compared with the control especially in Fang and Siete Cerros, although it remained unaffected in Imam. The total leaf area plant^{-1} was significantly affected by 35/35°C treatment in the soil Expt (Table 1) and by 38/38°C treatment in the hydroponic Expt from as early as 7 DAT (Tables 2, 3). After 7 days under HS/HR treatment in the hydroponic Expt, the percent reduction in leaf area plant^{-1} of the three cultivars ranged between 24 and 43%. The three cultivars showed more than 50% reduction in their leaf area at 15 DAT (Table 3). At 30 DAT, both Fang and Siete Cerros showed above 60% reduction in their leaf area while Imam showed 45% reduction under 38/38°C treatment in the hydroponic Expt.

In the soil Expt, SLA significantly decreased at both 23/35 and 35/35°C compared with 22/22°C, and the three cultivars reacted similarly (Table 1). In the hydroponic Expt, significant differences ($P<0.01$) in SLA were observed among temperature treatments at all sampling dates; however, the difference among cultivars started to be significant at 15 DAT and became more apparent towards the end of the experiment (Tables 2, 3). Across cultivars, the mean reductions were 15.3 and 14.4% in SLA under 22/38 and 38/38°C treatments at 7 DAT, respectively. The mean reductions in SLA became 12.4 and 26.7% at 15 DAT, 18.3 and 21.8% at 30 DAT under 22/38 and 38/38°C treatments, respectively (Table 3).

At 7 DAT, Imam was the most affected cultivar under both high temperature treatments, while Siete Cerros was the least affected in terms of SLA. The situation was reversed after 15 DAT especially under 22/38°C treatment when Siete Cerros showed a reduction of 21.4% in its SLA compared to 8.9% for Imam and 6.7% for Fang. At 30 DAT, the percent reduction in SLA of Fang and Siete Cerros was almost twice that in Imam under 22/38°C treatment. Under 38/38°C treatment, Siete Cerros showed the highest reduction (28.2%) in SLA while Fang and Imam showed reduction of about 18%.

3. Chlorophyll accumulation

Averaged across cultivars, chlorophyll content increased during the first wk of the hydroponic Expt by 26, 21 and 46% under 22/22, 22/38 and 22/38°C treatments, respectively (Fig. 1). Differences among temperature treatments were highly significant ($P<0.01$) at 7 DAT and continued to exist during the experiment (Table 2). Chlorophyll content under

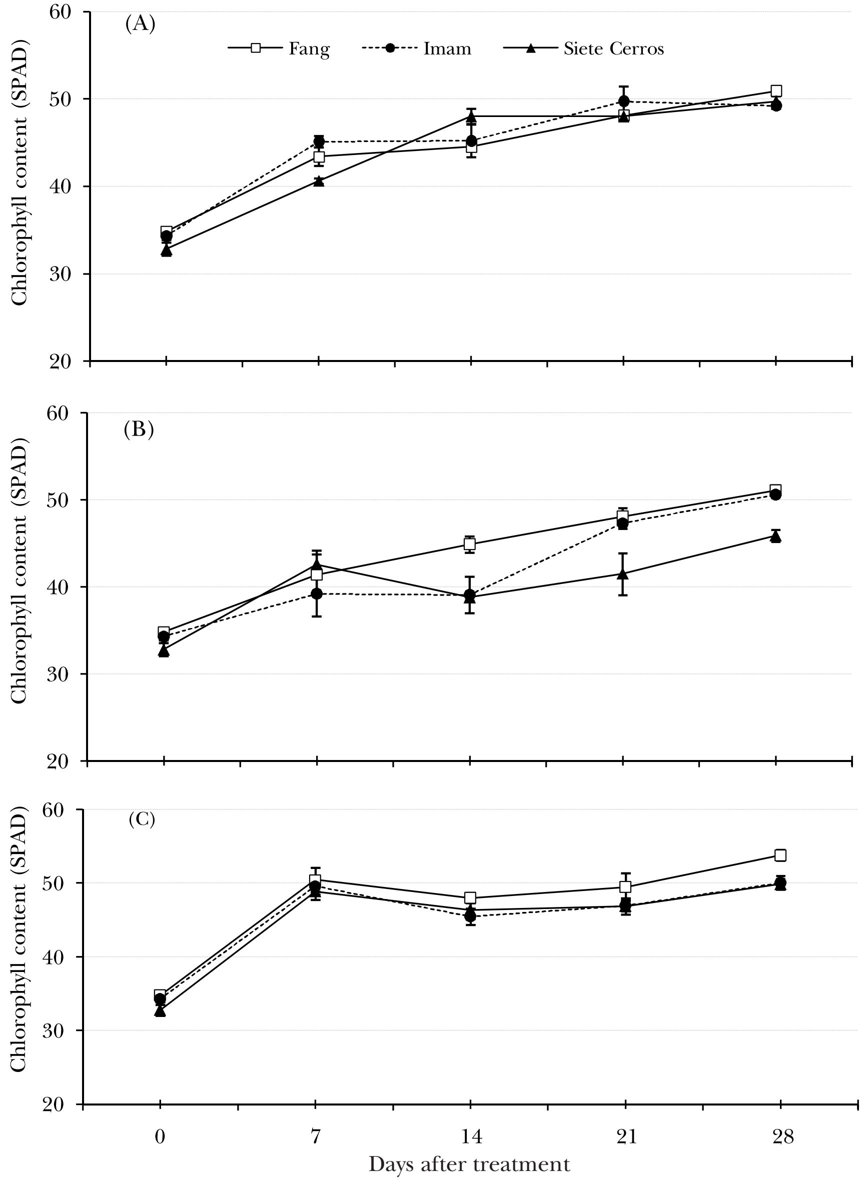

Fig. 1. Accumulation of chlorophyll in leaves of three wheat cultivars grown hydroponically at shoot/root temperatures of (A) 22/22ºC (B) 22/38ºC and (C) 38/38ºC during early stages of growth. Vertical bars are standard errors (SE). Where there is no vertical bar, SE is smaller than the data point.

22/38ºC treatment was significantly lower than that under the other two treatments throughout the experiment.

The difference in the chlorophyll content of the three cultivars was not significant at 0 DAT. Similarly, no significant differences were observed between cultivars at 7 DAT within each treatment except that Imam accumulated more chlorophyll than Siete Cerros under 22/22ºC treatment. At 14 DAT, the response of cultivars to high temperature treatments started to vary especially under 22/38ºC treatment (Fig. 1). Fang showed about 13% higher chlorophyll content over both Imam and Siete Cerros at 14 DAT under 22/38ºC treatment. Moreover, the prolonged exposure to 22/38ºC and 38/38ºC resulted in significant differences among cultivars at 21 and 28 DAT (Table 2) especially between Siete Cerros and the other two cultivars (Fig. 1). For instant, under 22/38ºC treatment, Siete Cerros showed 16 and 11% less chlorophyll content than Fang at 21 and 28 DAT, respectively. The chlorophyll content of Fang at 21 DAT increased by about 7% under 22/22ºC and 22/38ºC treatment, but no big changes were occurred under 38/38ºC treatment.

The chlorophyll content of Imam at 14 DAT showed a reduction of 8% under 38/38ºC treatment but remained unchanged under the other two treatments before it started to show gradual increase thereafter. On the other hand, Siete Cerros at 14 DAT accumulated 15% more chlorophyll under 22/22ºC

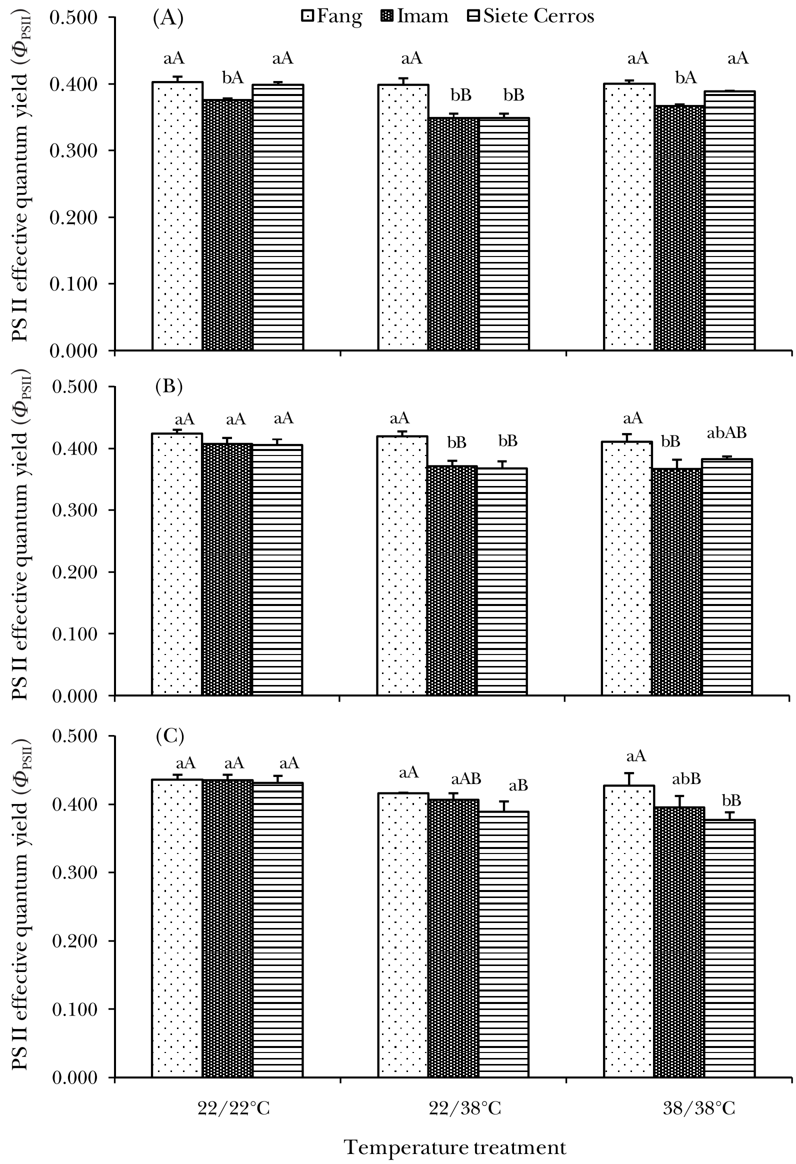

Fig. 2. Effective quantum yield of photosystem II (Φ_{PSII}) in three wheat cultivars grown hydroponically at three shoot/root temperatures measured at (A) 15 DAT, (B) 21 DAT and (C) 28 DAT. Vertical bars are standard errors. Columns marked with the same letters are not significantly different according to LSD (P=0.05). The lowercase letters indicate cultivar comparisons within a given shoot/root temperature. The uppercase letters indicate shoot/root temperature comparisons for a given cultivar.

treatment compared to that at 7 DAT but 9 and 5% less under 22/38°C and 38/38°C treatments, respectively. It was only during the last wk of temperature treatment when the chlorophyll content of Siete Cerros started to increase under the 22/38°C and 38/38°C treatments.

The cultivar (C) by temperature treatment (T) interactions were significant at 14 DAT ($P<0.05$) and 28 DAT ($P<0.01$), but not at 7 and 21 DAT (Table 2). The significant C×T interactions at 14 and 28 DAT were due to that the chlorophyll content of Siete Cerros was higher under 22/22°C, but lower under 22/38°C treatment compared to that of Imam.

4. Chlorophyll fluorescence

Significant differences in leaf chlorophyll fluorescence in terms of effective quantum yield of PSII (Φ_{PSII}) were found among temperature treatments (T) and cultivars (C) on all measurement occasions in the hydroponic Expt (Table 2, Fig. 2).

Across cultivars, the Φ_{PSII} of the light-adapted leaves decreased significantly under both high temperature treatments. The effect of 22/38°C treatments on Φ_{PSII} was greater than that of 38/38°C treatment at 14 DAT. The mean declines in Φ_{PSII} in the three cultivars were 6.9 and 2% under 22/38°C and 38/38°C treatments, respectively. The mean decline at 21 DAT became 6.3% under both 22/38°C and 38/38°C treatments. At 28 DAT, the reductions were 6.9 and 7.8% under 22/38°C and 38/38°C treatments, respectively (Fig. 2).

During the experimental period, Fang showed the least and non-significant decline in Φ_{PSII} under both high temperature treatments (Fig. 2). Siete Cerros, on the other hand, was the most affected cultivar under 22/38°C treatment and towards the end of the experiment under 38/38°C treatment. Imam was intermediate in its reaction to 22/38°C treatment, but did not show a definite trend under 38/38°C treatment.

5. Photosynthetic rate

Highly significant differences were found between temperature treatments and cultivars at all measuring dates (Table 2). The C×T interaction was significant only at 21 DAT because the photosynthetic rate (P_n) of Siete Cerros was higher than that of Imam under 22/22°C and 38/38°C treatments, but not under 22/38°C treatment. Similar to Φ_{PSII}, Fang showed the highest P_n under all temperature treatments while Imam showed the lowest rate in most of the occasions (Fig. 3).

Averaged across the three cultivars, P_n at 15 DAT reduced more under the 22/38°C treatment even when compared with the 38/38°C treatment. Under 22/38°C treatment, reductions of 15.8, 25.9 and 28% were found in the P_n of Fang, Imam and Siete Cerros, respectively, when compared with the control. The corresponding reductions under 38/38°C treatment were 5.1, 25.2 and 16.9% in Fang, Imam and Siete Cerros, respectively. Both Fang and Imam started to adapt to the 22/38°C treatment after 21 days of treatment and showed reductions of 4.6 and 16.2% in P_n, respectively, compared with the control. On the other hand, the P_n of Siete Cerros declined by 31.8% under 22/38°C treatment compared with the control. It is also Siete Cerros that showed more reduction in the P_n under both 22/38°C (15.8%) and 38/38°C (14.4%) treatments at 28 DAT compared with the other two cultivars, which showed less than 10% reduction under both temperature treatments (Fig. 3).

Discussion

The physiological response of three wheat cultivars to normal shoot/high root (NS/HR) and high shoot/high root (HS/HR) temperatures during early growth stages were studied in terms of chlorophyll accumulation, PSII quantum yield (Φ_{PSII}), photosynthetic rate (P_n), leaf dry weight, leaf area and specific leaf area (SLA).

Averaged across cultivars, chlorophyll accumulation significantly declined under NS/HR treatment and increased under HS/HR treatment. High shoot and root temperatures are reported to suppress photosynthesis mainly by decreasing the proportion of soluble protein to total leaf nutrient status especially nitrogen, hence adversely affecting Rubisco protein and activity (He et al., 2001; Xu and Zhou, 2006). In addition, the available amount of cytokinin and other growth regulators, necessary for various activities including chlorophyll accumulation, and the uptake of water and nutrients by roots and their supply to shoot are expected to greatly decreased and altered (Itai et al., 1973; Kuroyanagi and Paulsen, 1988; Udomprasert et al., 1995).

Since high root temperature in both NS/HR and HS/HR treatments is expected to impose the above-mentioned effects, the exact reason for reduction in chlorophyll accumulation under NS/HR treatment, and not under HS/HR treatment, is not clear. However, the shoot/root ratio could have been a critical factor especially during the first two wks of treatment (Tahir et al., 2008) beside the induction of some antioxidant enzymes (Badawi et al., 2007). Under NS/HR treatment, the root system diminished while the NS treatment was favorable for the growth of the aboveground parts (Tahir et al., 2008). Under such condition, the shoot demand for more nutrients might be beyond the capacity of the reduced root system. This was evidence when chlorophyll content of a specific cultivar was compared with its shoot/root ratio in a specific sampling date. For example, the low chlorophyll content of Imam under NS/HR treatment coincided with the high shoot/root ratio at 7 DAT (Tahir et al., 2008). Similarly, Siete Cerros showed a low chlorophyll content when its shoot/root ratio decreased sharply at 15 DAT. Moreover, our previous results showed that the xylem sap flow rate was significantly reduced under NS/HR treatment (23/35°C) in the soil experiment, especially that of Seite Cerros (Tahir et al., 2008). On the other hand, reduced shoot as well as root growth by HS/HR treatment might decrease the competition for nutrients and assimilates. This could lead to the accumulation of more chlorophyll in the small confined leaves. This is supported by the data of leaf dry weight and leaf area/plant, which were greatly declined under HS/HR treatment while remained unchanged or slightly increased under NS/HR treatment.

Significant and similar decreases in Φ_{PSII} and P_n under both NS/HR and HS/HR treatments were found. The similar effects of these high temperature treatments on the Φ_{PSII} and P_n in most cases agreed with earlier reports that the shoot activities and growth are mediated by root (Kuroyanagi and Paulsen, 1988; Udomprasert et al., 1995; Xu and Huang, 2000). Maintaining normal root temperature while applying high shoot temperature restored the gas exchange rate to nearly the control level (Udomprasert et al., 1995).

Averaged across all measuring dates and temperature treatments, Φ_{PSII} significantly correlated with the simultaneously measured P_n ($r=0.82$, $P<0.001$, $n=27$). The reduction in Φ_{PSII} significantly correlated with the reduction in P_n under NS/HR (0.89, $P<0.001$,

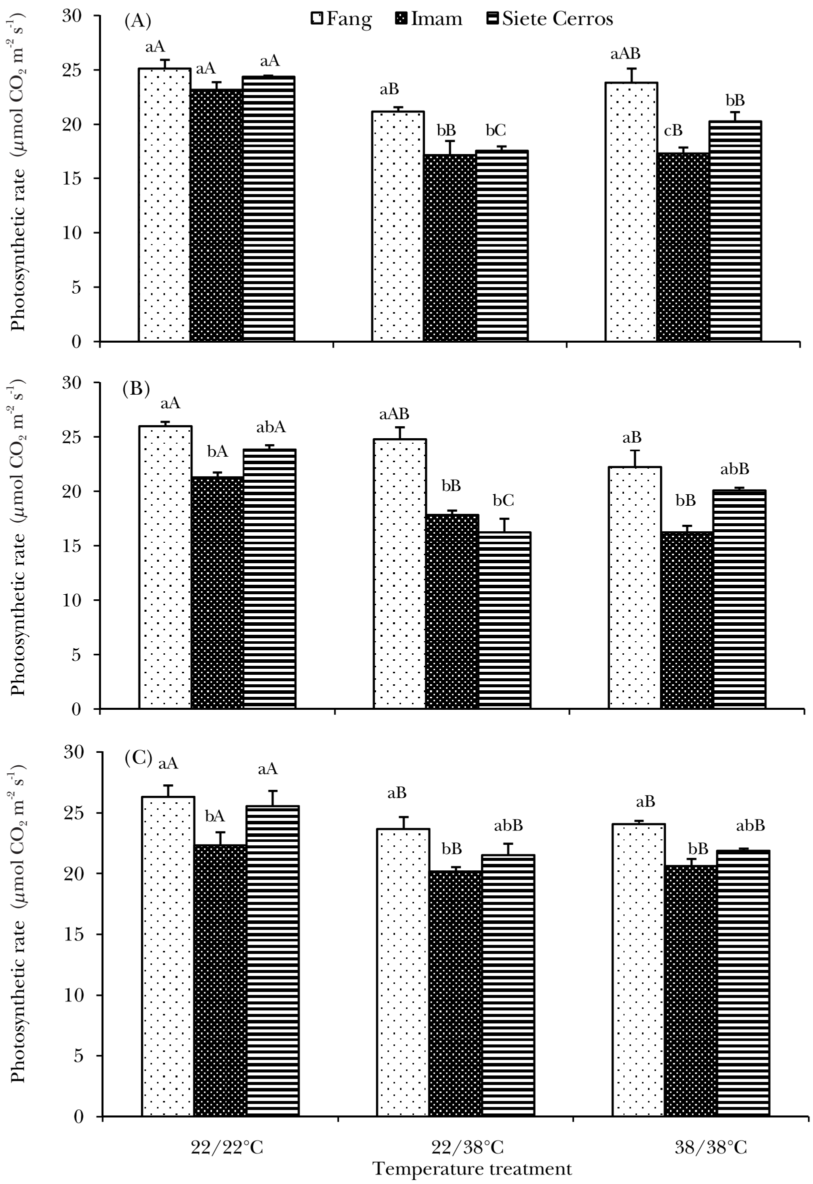

Fig. 3. Photosynthetic rate (μmol CO_2 m^{-2} s^{-1}) of three wheat cultivars grown hydroponically at three shoot/root temperatures measured at (A) 15 DAT, (B) 21 DAT and (C) 28 DAT. Vertical bars are standard errors. Columns marked with the same letters are not significantly different according to LSD (P=0.05). The lowercase letters indicate cultivar comparisons within a given shoot/root temperature. The uppercase letters indicate shoot/root temperature comparisons for a given cultivar.

n=9) and HS/HR (0.83, P<0.01, n=9) treatments. This close association between Φ_{PSII} and P_n agrees with other reports and supports the use of chlorophyll fluorescence as, an easy to measure, selection criterion under heat stress conditions (Al-Khatib and Paulsen, 1990; Moffatt et al., 1990; Dash and Mohanty, 2001).

The leaf dry weight and leaf area plant^{-1} significantly reduced under HS/HR treatment in both experiments. The reductions in the leaf weight and area under HS/HR treatment during the first wk were most probably due to reduction in the tillers number/plant (Tahir et al., 2008). The production of less (but productive) tillers seems to be one of the mechanisms for efficient assimilates allocation and hence better adaptation to such stress (Midmore et al., 1984). The NS/HR treatment did not affect the leaf dry weight and leaf area of the three cultivars during the first two wk. Only after prolonged exposure to NS/HR treatment, the leaf weight and area of Fang and Siete Cerros were decreased.

An immediate reduction in the SLA was observed from as early as 7 DAT under both NS/HR and HS/HR treatments in the hydroponic Expt. Biotic and abiotic stresses force plants to undergo anatomical and chemical composition changes in SLA as a protection defense. High temperature is one of the abiotic stresses that cause reduction in SLA of wheat and other crops (McDonald and Paulsen, 1997; Hotsonyame and Hunt, 1998). However, greater leaf area under high temperature conditions could be an important trait for better light interception by wheat seedling and shading the soil surface to reduce the soil temperature and water evaporation.

Our results showed considerable variability among the three cultivars in their response to high temperature in terms of different traits measured in this study. The responses of the three cultivars were also reported to vary under high temperature treatments during early growth stages in terms of shoot and root growths (Tahir et al., 2008) and antioxidant enzyme activities (Badawi et al., 2007). Moreover, differential response of the three cultivars was reported when exposed to HS/HR during grain filling (Tahir et al., 2005b).

The responses to high temperatures with respect to chlorophyll accumulation varied with the cultivar considerably especially under NS/HR treatment. The heat-tolerant cultivar, Fang, always maintained an increasing trend in its leaf chlorophyll content throughout the experiment under NS/HR treatment. Imam under NS/HR treatment showed a significantly lower chlorophyll content than Fang during the first two wk but not during the last two wk. On the other hand, the heat-sensitive cultivar, Siete Cerros, was the most affected cultivar especially from 14 DAT onward and failed to increase the chlorophyll content similar to that in Fang.

The response of the three cultivars to NS/HR and HS/HR treatments during early growth stages was differential as judged from the analysis of Φ_{PSII} and P_n at all sampling dates. For example, at 28 DAT, compared with 4.6 and 2.1% decrease in Φ_{PSII} under NS/HR and HS/HR treatments, respectively, in Fang, the decline was 6.7 and 9.2% in Imam, and 9.7 and 12.5% in Siete Cerros, respectively. Variations among wheat genotypes in their leaf chlorophyll fluorescence and P_n at high temperatures support the reports by other investigators (Moffatt et al., 1990; Dash and Mohanty, 2001).

The capability of accumulating high chlorophyll and maintaining high Φ_{PSII} and P_n per unit leaf area during the first wk of the treatments was associated with high reduction in the leaf dry weight and leaf area plant^{-1} under HS/HR treatment. The two cultivars (Fang and Imam), which accumulated high chlorophyll under HS/HR treatment compared to the control (NS/NR), showed higher reduction in the leaf weight and leaf area. These results suggested that reduction in leaf area and SLA was an immediate mechanism for the response to the high temperature especially under the HS/HR treatment. Fang showed, in most cases, the highest chlorophyll content, PSII quantum yield, P_n and the largest SLA under all conditions. Similarly, Fang always showed higher antioxidant enzymes activities such as superoxide dismutase (SOD), ascorbate peroxidase (APX) compared to Imam and Siete Cerros under the same experimental condition of this study (Badawi et al., 2007). However, the leaf dry weight and leaf area plant^{-1} of Fang were affected more than that of Imam at the end of the experiment. In addition, Fang showed reduced number of tillers plant^{-1} and accelerated vegetative development as indicated by the stem elongation under both high temperature treatments (Tahir et al., 2008). On the other hand, the leaf dry weight and area of Imam were less affected than that in Fang at the end of the experiment despite the relatively low P_n and SLA under high temperature treatments. Moreover, Imam showed the highest number of tillers plant^{-1} and no signs of vegetative growth acceleration under high temperature treatments (Tahir et al., 2008). Similarly, under heat-stressed field conditions, Imam always shows little signs of accelerated vegetative development (Tahir I.S.A, unpublished data). Therefore, combining high Φ_{PSII}, $P_{n,}$ and SLA with high leaf weight and area in addition to the adaptability of other physiological processes and morphological features to high temperature stress condition could be crucial.

Significant reduction in grain yield of wheat subjected to high temperatures during early vegetative growth has been reported in Sudan and found to be associated with significant reductions in biomass, number of tillers and grains per unit area, and vegetative growth duration and rate (Tahir et al., 2005a). Therefore, high biomass production, high number of grains and spikes per unit area and high vegetative growth rate were suggested as selection criteria under hot, dry environment of Sudan (Tahir et al., 2005a). Moreover, Ishag et al. (1998) speculated that suitable wheat cultivar for warm tropical environment would be late maturing cultivar with relatively long vegetative growth duration.

In this study, very high temperatures were applied to both roots and shoots for a prolonged time. Nevertheless, the effects of high temperatures were relatively small especially in terms of Φ_{PSII} and P_n. Moreover, two of the three cultivars accumulated more chlorophyll under HS/HR treatment than under the control. This could be largely due to the gradual increment in the temperature practiced in this study. Better photosynthetic acclimation to a gradual increment in temperature was found in different plant species (Havaux, 1993; Law and Crafts-Brandner, 1999). Plants might have also benefited from the moderately cool night temperature in this study. Nocturnal warming significantly decreased leaf weight, whole plant biomass and photosynthetic rate in some plant species (McDonald and Paulsen, 1997; Xu and

Zhou, 2005).

Acknowledgements

We would like to thank the Japanese Ministry of Education, Culture, Sports, Science and Technology for the financial support. We are also grateful to the Arid Land Research Center, Tottori University for allowing us to use their facilities.

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