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Stability of Different Physiological Characters, Yield and Yield Components under High Temperature Stress in Tolerant and Susceptible Wheat Genotypes

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ABSTRACT

High temperature stress is a major environmental stress that adversely affects wheat growth and productivity worldwide. The effect of high temperature stress on different physiological characters and yield attributes of five wheat genotypes differing in their susceptibility to high temperature stress was studied for two constitutive years. Seeds were planted under normal, late and very late dates in order to expose plants to different levels of temperature stress. Chlorophyll content, membrane stability index, rate of photosynthesis, leaf water spin lattice relaxation time, and transverse relaxation time were determined at the vegetative stage, anthesis and 15 days after anthesis. Water potential was determined at the anthesis stage, 7 and 15 days after anthesis. Pooled data of both years showed a significant reduction in all physiological characters under late and very late planting compared to normal planting date at all growth stages. However, heat-susceptible genotype PBW 343, which performed well when planted normally, showed a maximum reduction in all characters at all growth stages compared to heat-tolerant genotypes HDR-77 and HD 2815, which performed better under late and very late planting conditions. Plant biomass, grain yield/plant, 1000-grain weight, grain number/ear and grain weight/ear were significantly reduced under late and very late planting compared to normal planting. The yield attributes of PBW 343 and PBW 175 were most reduced under very late planting. HD 2815 and HDR-77 performed well and maintained higher yield when planted very late compared to other genotypes and a significant association between all physiological characters and yield components was observed. HD 2815 and HDR-77 showed minimum reduction in yield and yield components under late planting conditions while exhibiting stability and minimum reduction in all physiological characters.

Keywords: leaf spin lattice relaxation time, membrane stability index, photosynthetic rate, transverse relaxation time, water potential
Abbreviations: FYM, farmyard manure; **MSI**, membrane stability index; **NMR**, nuclear magnetic resonance; **Pn**, photosynthetic rate; **T_1 time**, leaf spin lattice relaxation time; **T_2 time**, transverse relaxation time; ψ_w, water potential

INTRODUCTION

High temperature stress limits the productivity of various crops in different regions around the world (Al-Katib and Paulsen 1999). Wheat is often grown in areas where high temperature stress is considered to be a major constraint to growth and productivity (Almeselmani *et al*. 2009). Continual heat stress was a problem in 7 million ha, while terminal heat stress is a problem in 40% of the irrigated wheat-growing areas of the world (Fisher and Byerlee 1991). In North-Western India, popularization of the rice–wheat cropping system has forced wheat to be sown late in about 2.5 million ha. This late sown crop gets exposed to maximum temperatures > 35°C during the grain growth period which reduces yield by 270 Kg/ha/° increase (Rane *et al*. 2000; Nagarajan and Rane 2002). Heat stress affects the metabolism and structure of plants, especially cell membranes and many basic physiological processes such as photosynthesis, respiration and water relations (Wahid *et al*. 2007). Various studies showed the adverse effect of heat stress on physiological processes and yield of wheat (Almeselmani *et al.* 2006, 2009; Efeoglu and Terzioglu 2009). Xu (1991) reported that photosynthetic rate, thylakoid chlorophyll (Chl) and protein content of whole wheat plants remained unaffected at 15/10°C but decreased rapidly at 35/30°C during maturation. Photosynthesis is one of the most sensitive processes to heat stress (Blum 1988). Heat stress decreased photosynthetic rates by 32 and 11% in seedlings and mature wheat plants, respectively (Al-Katib and Paulsen 1990). Shah (1992) also reported a decline in photosynthetic rates due to high temperature in wheat plants. In several plant species, the functional damage incurred during high temperature stress is the consequence of injury to cellular membranes (Nagarajan *et al*. 2005). Deshmukh *et al*. (1991) suggested ion leakage as an index for screening wheat genotypes against heat and drought stress and reported a proportional increase in ion leakage with an increase in temperature. Nagarajan and Rane (1997) also emphasized the use of membrane thermostability as one of the simple parameters for screening wheat genotypes against high temperature stress. Nuclear magnetic resonance (NMR) relaxation times have been widely used to describe the water status as well as heat and freezing injury in plant tissues (Rajashekar and Burke 1986; Abass and Rajashekar 1991; Kaku 1993; Ratcliffe 1994; Millard *et al.* 1996; Yoshida *et al*. 1997; Almeselmani *et al*. 2006).

Heat stress is considered as a major determinant of wheat growth and development, decreasing yield by 3-5% for every 1°C increase in temperature above 15°C. It is a common constraint during anthesis and grain-filling stages in many temperate environments (Reynolds *et al*. 1994). Munjal and Dhanda (2004) reported that 1000-grain weight was significantly reduced due to late sowing and different wheat genotypes showed a reduction in grain weight due to

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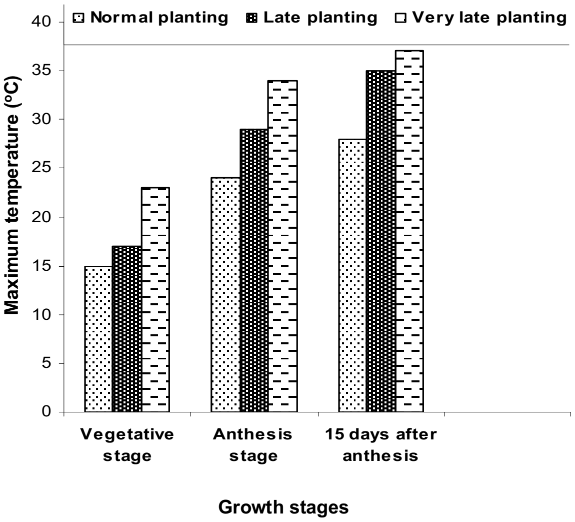

Fig. 1 Maximum temperature (°C) at the vegetative stage, anthesis and 15 days after anthesis, during normal, late and very late planting in the first year of the experiment.

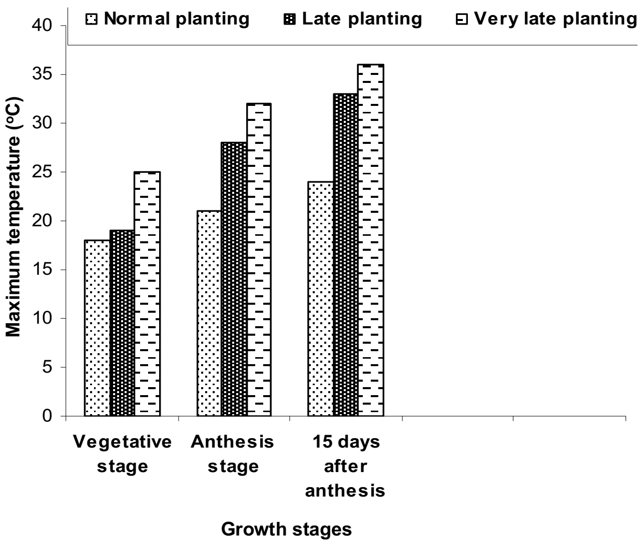

Fig. 2 Maximum temperature (°C) at the vegetative stage, anthesis and 15 days after anthesis, during normal, late and very late planting in the second year of the experiment.

high air temperature during late sowing time (Haque 2002). A temperature above 34°C affects grain weight by reducing the duration of grain filling due to suppression of current photosynthesis and by directly inhibiting starch biosynthesis in the endosperm (Jenner 1994). The present study aimed to assess the effect of temperature stress on some physiological parameters, yield and yield components of wheat genotypes differing in their susceptibility to high temperature stress, in order to find simple and easy-to-measure physiological traits associated with yield stability under heat stress conditions.

MATERIALS AND METHODS

Plant material and growth conditions

Experiments were conducted in pot culture with five wheat genotypes: PBW 343 (susceptible), PBW 175 and HD 2865 (moderately susceptible), HDR-77 and HD 2815 (tolerant) (Almeselmani *et al.* 2006). Seeds were obtained from the Division of Genetics and Plant Breeding, Indian Agricultural Research Institute (IARI) and five seeds were sown in each pot, which was prepared before sowing by mixing IARI loam soil with farmyard manure (FYM) at a rate of 3:1. The experiments were conducted for two consecutive years. During both seasons sowing was performed during November, December and January, considered as normal, late and very late sowing, respectively, with the aim of exposing the wheat plants to normal, high and very high temperature during the grain development period. Temperatures in both years was recorded with a field meteorological laboratory fitted with a microprocessor controlled data logger, which recorded daily maximum/minimum, temperature, sunlight duration, relative humidity, rainfall, wind velocity and other metereological parameters. The maximum temperature in both crop seasons at the time of sampling is summarized in **Figs. 1** and **2**, showing clearly that plants were exposed to high temperature stress under late and very late planting during anthesis and post anthesis stages. The parameters recorded were Chl content, membrane stability index (MSI), photosynthesis rate (Pn), transverse relaxation time (T_2) and leaf water spin lattice relaxation time (T_1) at three stages of plant growth: vegetative, anthesis, and post anthesis (15 days after anthesis). Water potential was estimated at the anthesis stage, 7 days and 15 days after anthesis and for all estimations, the first fully expanded leaf (3rd from the top) at the vegetative stage and flag leaf at anthesis and post anthesis stages were used.

Chl content estimation

Chl estimation was done by incubating 50 mg of leaf material in 10 ml of dimethyl sulphoxide (Hiscox and Israelstom 1979) samples kept in an oven for 4 h at 65°C and the absorbance of the clear solvent after cooling was recorded at 663 and 645 nm (Arnon 1949).

Membrane stability index

MSI was determined by recording the electrical conductivity of leaf leachates in double distilled water (DDW) at 40 and 100°C (Deshmukh *et al.* 1991). Leaf samples (0.1 g) were cut into discs of uniform size and placed in test tubes containing 10 ml of DDW in two sets. One set was kept at 40°C for 30 min and another set at 100°C in boiling water bath for 15 min and their respective electric conductivities, C_1 and C_2, were measured by a conductivity meter (Century Instruments, Chandigarh, India).

$$MSI = 100 - \{[(C_1/C_2)] \times 100\}$$

Estimation of photosynthesis rate

The rate of leaf photosynthesis was measured by using an Infrared gas analyzer (LiCOR 6200, LI-COR Inc., Lincoln, NE).

Transverse and spin lattice relaxation time estimation

For estimation of T_2, 3-4 fully expanded leaves were rolled into a cylinder (2 cm height) to fit tightly into a 10-cm diameter NMR sample tube. T_2 water, a proton, was measured by the Carr-Purcell-Meiboom-Gill (CPMG) method at 20 MHz with a Bruker NMS 120-pulsed NMR spectrophotometer. Each measurement had the following settings: 250 data points, pulse separation - 0.5 ms, dummy echo 3, and 10 scans. Gain was adjusted to maximize the signal to noise ratio. The data points were fitted mono-exponentially by the built-in Expspel program and average value of T_2 was obtained (Nagarajan *et al.* 2005). Leaf water spin lattice relaxation time (T_1) was measured at 20 MHz and at an ambient temperature of 25°C by a pulsed NMR instrument (Bruker Minispec PC-20) using a $90°_{-T-}90°$ pulse sequence (Farrar and Becker 1971).

Water potential estimation

Leaf water potential was measured on leaf samples using pressure chamber (S-pms Instruments, New Delhi, India) following the method of Scholander *et al.* (1964).

Yield and yield components

Three pots/ treatment were selected for recording yield parameters. Total plant biomass (g), grain yield (g), 1000-grain weight (g), grain number and grain weight/ear (g) were recorded from 9 plants kept untouched during the experiments.

Experimental design and statistical analyses

Since there were no significant differences between observations for both years, data were pooled together and presented as the mean of data recorded during both years. The experiment was laid out in a factorial randomized block design with three replications, the treatment (sowing data) was the main plot and genotypes constituted the subplots. Data was analyzed by analysis of variance and least significant differences (LSD) were calculated. Each data point represents the mean of 3 replicates analyzed three times, and each value is therefore the mean of 9 estimations.

RESULTS AND DISCUSSION

Effect of heat stress on different physiological characters

An increase in temperature due to late planting affected plant growth and all measured physiological characters. The effect of high temperature stress was more severe for plants planted very late compared to normal and late planting. The reduction in Chl content was more than the reduction that occurred to the rate of photosynthesis under late and very late planting. A decrease in Chl content due to high temperature stress has been reported in crops such as rye (Feirabend 1977), and wheat (Liu and Su 1985; Almeselmani *et al.* 2006). Reynolds *et al.* (1994) showed the premature loss of Chl in wheat due to heat sensitivity. Among the five wheat genotypes, PBW 343 exhibited maximum reduction in Chl content under very late planting at all three sampling stages. Changes in Chl content of PBW 175, HD 2865, HDR-77 and HD 2815 were almost similar at the vegetative and anthesis stage but at 15 days after anthesis PBW 175 showed a higher reduction under very late planting compared to the other genotypes (**Fig. 3**). Changes in Chl content may influence the photosynthetic rate of crop plants. Buttery *et al.* (1981) reported that the variability in photosynthetic rate, nearly 44%, was due to variability in Chl content. In this study, a reduction in the rate of photosynthesis along with a decrease in Chl content was observed in all genotypes under late planting conditions. The rate of photosynthesis decreased due to temperature stress in late and very late planting and the percentage reduction was higher at anthesis and post anthesis. Among the five genotypes, PBW 343 showed high reduction in the rate of photosynthesis under very late planting compared to normal, 46.6 and 51% at anthesis and post anthesis, respectively. The reduction in the photosynthetic rate under late planting was marginal compared to normal planting in all genotypes except for PBW 343 and HD 2865, which showed a high reduction i.e. 20 and 21% at the anthesis stage. Under late and very late planting, when compared to normal, HD 2815 and HDR-77 performed well and maintained a comparatively high photosynthetic rate at different growth stages (**Fig. 4**). Efeoglu and Terzioglu (2009) reported that photosynthesis is known to be one of the most heat-sensitive processes and it can be completely inhibited by high temperature. Even in the absence of heat stress injury, photosynthesis would be expected to decline as temperature increases because photorespiration increases with temperature faster than does photosynthesis. It is now well established that moderately high temperature (e.g. 35-40°C) reduces the rate of photosynthesis more than can be explained by stimulated photorespiration (Sharkey 2005).

The significant reduction in Chl content due to heat stress may be due to premature leaf senescence which led to a significant reduction in photosynthetic rate. Al-Katib and Paulsen (1984) and Harding *et al.* (1990) reported that differences in photosynthesis among wheat genotypes under high temperature conditions were associated with a loss of Chl and a change in the Chl *a*:*b* ratio due to premature leaf senescence (Almeselmani *et al.* 2006, 2009). Pastenes and Horton (1995) reported that an increase in temperature from 20 to 25°C increased photosynthesis with a Q_{10} value of 1.90. As the temperature increased from 25 to 30°C, Q_{10} decreased possibly following a restriction in the regeneration of the acceptor for CO_2, and as temperature increased from 30 to 35°C, Q_{10} decreased further as a result of the inability of thylakoid membranes to maintain an adequate supply of NADPH. Sharkova and Bubolo (1996) observed that high temperature reduced the rates of photosynthesis. Physiological studies have shown that the rate of photosynthesis depends greatly on the temperature under which the plants are grown.

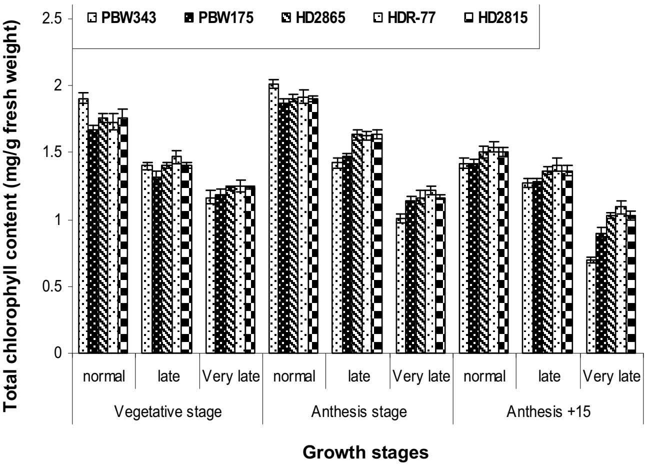

Fig. 3 Total chlorophyll content (mg.g^{-1} fresh weight) at the vegetative stage, anthesis and 15 days after anthesis, during normal, late and very late planting represented as pooled data of both years. CD value at $P \leq 0.05$ planting date × genotype, at vegetative stage = 0.57, anthesis = 0.62, at 15 days after anthesis = 0.34.

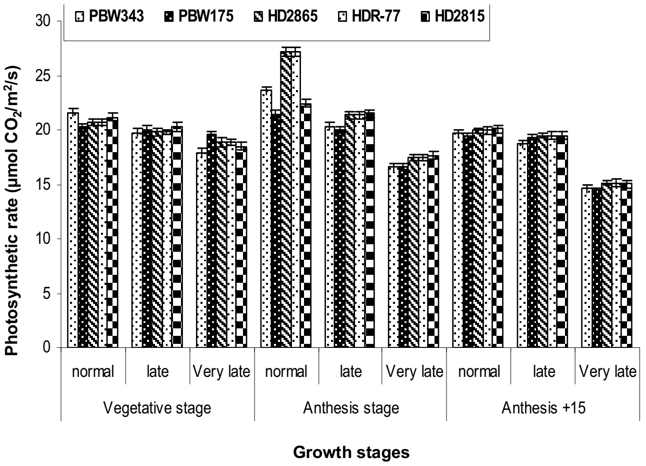

Fig. 4 Photosynthetic rate (µmol CO_2 m^{-2}. s^{-1}) at the vegetative stage, anthesis and 15 days after anthesis, during normal, late and very late planting represented as pooled data of both years. CD value at $P \leq 0.05$ planting date × genotype, at vegetative stage = 0.87, anthesis = 1.23, at 15 days after anthesis = 1.04.

MSI is an important parameter which has been used extensively for screening crop plants for heat stress tolerance (e.g., Almeselmani *et al.* 2006, 2009). A significant reduction in MSI was recorded under late and very late planting compared to normal planting, and maximum reduction was recorded at the reproductive stage compared to the vegetative stage. Blum (1988) suggested that the membrane is one of the sites of primary physiological injury by heat. The reduction in MSI under heat stress could be the reason for the reduction in Pn rate under heat stress conditions. Christiansen (1978) reported that membrane disruption under high temperature stress may alter water, ion and organic solute movement, as well as photosynthesis and respiration. MSI decreased even under normal growth conditions as the

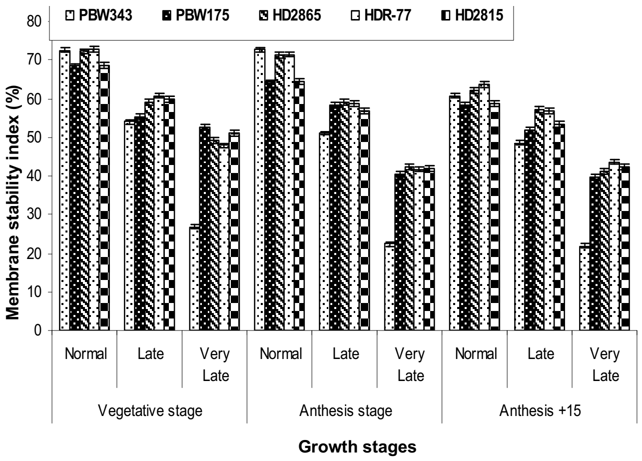

Fig. 5 Membrane stability index (%) at the vegetative stage, anthesis and 15 days after anthesis, during normal, late and very late planting represented as pooled data of both years. CD value at $P \leq 0.05$ planting date × genotype, at vegetative stage = 15.3, anthesis = 18.7, at 15 days after anthesis = 17.1.

plant's age advanced. The reduction in MSI under very late planting was almost two-fold that which was observed under late planting in all genotypes. The magnitude of reduction in MSI was highest in PBW 343, up to 69% at the anthesis stage under very late planting, while HDR-77 and HD 2815 compared to other genotypes exhibited highest MSI under late planting conditions (**Fig. 5**).

Transverse relaxation time (T_2) and spin lattice relaxation time (T_1) of leaf water are closely related to classical water status parameters such as leaf water content, relative water content, water potential and absolute potential (Nagarajan *et al.* 1993). **Table 1** shows the changes in T_2 of the wheat genotypes planted under normal, late and very late planting conditions. Among the five genotypes, PBW 343 showed highest T_2 value under normal planting, which decreased significantly under late planting conditions as well as with the advancement of the crop's age. A reduction in T_2 values was observed under late and very late planting in all genotypes, and PBW 343 showed the highest reduction among all genotypes while HDR-77 and HD 2815 exhibited only marginal reduction in T_2 values under late planting.

Leaf T_1 values also showed a significant reduction under late and very late planting similar to T_2 values in all five wheat genotypes. Maximum reduction in T_1 values was observed in PBW 343 under late and very late planting at all stages and was almost of similar magnitude under both delayed planting when compared to the control (**Table 2**). HDR-77 and HD 2815 maintained highest T_1 values compared to three other genotypes under late planting conditions, particularly at the post-anthesis stage. T_1 and T_2 of barley leaves were closely related to relative water content and a linear relationship were observed between relative water content and leaf water T_1 in wheat under water stress. These relaxation times were extensively used to study water status and its compartmentation and variation under stress conditions (Coliar *et al.* 1988). The significant reduction in T_2 and T_1 values under heat stress may be due to structural damage that occurred to membranes during stress, since membranes are primarily composed of proteins and lipids and any damage to these two components are likely to affect their structures while high temperature denatures membrane proteins and causes lipid phase transitions. Nagarajan *et al.* (2005) reported that structural changes in the membranes are likely to affect the transverse relaxation time T_2 of cells and highest T_2 values were recorded in heat-tolerant genotypes compared by heat-susceptible ones when grown under heat stress. Heat-tolerant wheat varieties, which suffered less membrane injury, had a higher T_2 than susceptible varieties under heat stress, and susceptible varieties showed a sharp decline in T_2 which corresponded to a loss of membrane integrity (Maheswari *et al.* 1999), as was observed in our experiments.

Leaf water potential (ψ_w) was also affected in all genotypes under late plantings. The reduction in PBW 343 was higher at all three growth stages and maximum reduction (48.8%) occurred at the anthesis stage, i.e. under very late planting. Minimum reduction in ψ_w was recorded in HD 2815 at all stages. The magnitude of reduction in ψ_w in

Table 1 Transverse relaxation time T_2 (ms) during normal, late and very late planting at vegetative stage, anthesis and 15 days after anthesis.

Genotypes	Vegetative stage			Anthesis stage			15 days after anthesis		
	Normal	Late	Very late	Normal	Late	Very late	Normal	Late	Very late
PBW 343	400	316	289	337	212	196	229	175	147
PBW 175	390	364	328	323	278	239	236	212	200
HD 2865	384	353	327	331	272	254	239	211	188
HDR-77	365	361	349	307	265	255	229	204	199
HD 2815	367	341	323	327	305	263	230	218	204
CD	8	10	18	7	8	15	6	7	13

CD value at $P \leq 0.05$; planting date × genotype

Table 2 leaf spin lattice relaxation time T_1(ms) during normal, late and very late planting at vegetative stage, anthesis and 15 days after anthesis.

Genotypes	Vegetative stage			Anthesis stage			15 days after anthesis		
	Normal	Late	Very late	Normal	Late	Very late	Normal	Late	Very late
PBW 343	527	366	349	401	246	209	250	196	168
PBW 175	513	456	357	408	271	223	258	230	202
HD 2865	485	387	354	363	324	302	276	224	216
HDR-77	515	469	395	379	350	326	298	276	256
HD 2815	490	452	392	400	376	327	285	266	219
CD	6	7	13	4	5	9	6	7	12

CD value at $P \leq 0.05$; planting date × genotype

Table 3 Water potential (MPa) during normal, late and very late planting at vegetative stage, anthesis and 15 days after anthesis.

Genotypes	Vegetative stage			Anthesis stage			15 days after anthesis		
	Normal	Late	Very late	Normal	Late	Very late	Normal	Late	Very late
PBW 343	-1.92	-2.28	-2.60	-1.65	-2.07	-2.46	-2.18	-2.56	-2.81
PBW 175	-1.93	-2.28	-2.43	-1.73	-1.92	-2.20	-2.08	-2.26	-2.56
HD 2865	-1.80	-1.99	-2.21	-1.86	-1.93	-2.17	-1.92	-2.09	-2.19
HDR-77	-1.93	-2.25	-2.36	-1.77	-1.96	-2.14	-2.09	-2.21	-2.29
HD 2815	-1.82	-2.01	-2.12	-1.87	-2.01	-2.26	-2.03	-2.16	-2.27
CD	0.06	0.08	0.14	0.05	0.07	0.12	0.05	0.07	0.12

CD value at $P \leq 0.05$; planting date × genotype

PBW 175, HD 2865 and HDR-77 was almost similar due to temperature stress under late and very late planting at all stages (**Table 3**). The significant reduction in water potential under late planting compared to normal planting was observed and the genotypes which showed minimum reduction in Chl content, MSI, Pn rate, T_2 and T_1 values under late planting condition possessed highest ψ_w since water is required for all the physiological and biochemical processes in plant and any stress condition (heat stress in our experiment) which caused less water content in plant tissues could be reflected through a reduction in various physiological processes operating in the plant, indicating the close association between all these physiological traits and water status in plant tissues.

Effect of heat stress on yield and yield components

As stress increased, a progressive and significant decrease was observed in yield and yield-related traits in wheat (Singh *et al.* 2007). A significant reduction in yields and yield components was observed in this study and the reduction in yield as a result of heat stress may be due to the negative effect of high temperature on Pn rate which could reduce the assimilate supply for sink development. Bahar *et al.* (2011) reported that if heat stress occurs during the post-anthesis (grain filling period), it has a negative influence on the movement of photosynyhetic products to the developing kernels and inhibits the starch synthesis; thus, it causes lower grain weight also lower yield and alters grain quality. Moot *et al.* (1996) reported that wheat plants which experienced a 3°C increase in day and night temperatures showed an 18% reduction in yield compared to the control. Many reports indicate that unfavorable temperature exposure due to early or late sowing – by deviating from the recommended time – reduce total plant biomass in wheat (Singh and Rajat 1978; Randhawa *et al.* 1981; Chaturvedi *et al.* 1985; Bhanu-Parkash 1997). Yield reduction in wheat under stress can be caused by accelerated phasic development (Warrington *et al.* 1977; Rawson and Bagga 1979; Frank and Bauer 1997), accelerated senescence (Kuroyanagi and Paulsen 1985), an increase in respiration (Berry and Bjorkman 1980), a reduction in photosynthesis (Blum 1986; Conroy *et al.* 1994) and inhibition of starch synthesis in developing kernels (Jenner 1994). Singh *et al.* (1982) reported that Pn rate and stomatal conductance were significantly correlated with yield at all stages of crop development, but the relationship was stronger during grain filling, which might be due to premature loss of Chl associated with leaf sensitivity.

Under normal planting, highest biomass/plant was recorded in PBW 343, while under late and very late planting highest biomass was recorded in PBW 175 and HD 2815, respectively (**Table 4**). Under very late planting maximum reduction in biomass was recorded in PBW 175 followed by PBW 343 i.e., 66 and 58%, respectively. Highest grain yield/plant under normal and late planting was recorded in PBW 175, while under very late planting HD 2815, HDR-77 and HD 2865 produced highest grain yield and minimum grain yield in PBW 343 followed by PBW 175 (**Table 4**). However, there was a significant reduction in grain yield under late and very late planting compared to normal planting; maximum reduction under late and very late planting compared to normal was recorded in PBW 175 and PBW 343 i.e. 24 and 20%, respectively under late planting and 54 and 53%, respectively under very late planting. Wardlaw *et al.* (1989) reported that reduction in grain yield associated with high temperature stress during post anthesis occurred due to variation in kernel size and not due to changes in kernel number. Stone and Nicolas (1994) observed that a short period of very high temperature (>35°C) during the post anthesis period can significantly reduce grain yield in wheat.

Table 4 Biomass per plant (g) and grain yield per plant (g) during normal, late and very late planting.

Genotypes	Total biomass/plant (g)			Grain yield/plant (g)		
	Normal	Late	Very late	Normal	Late	Very late
PBW 343	53.5	35.1	22.7	14.8	11.8	7
PBW 175	51	37.8	17.5	16.3	12.3	7.5
HD 2865	46.8	29.5	20.3	15.1	12	7.7
HDR-77	49.5	36.6	24.3	13.6	11.2	7.7
HD 2815	50.5	37.8	25.6	14.7	12	7.7
CD	2.1	2.8	4.8	0.6	0.7	1.3

CD value at $P \leq 0.05$; planting date × genotype

Highest 1000-grain weight was recorded in PBW 175 under normal planting and a significant reduction in 1000-grain weight under late and very late planting compared to normal was observed (**Table 5**). Maximum reduction under late and very late planting compared to normal was recorded in PBW 343, 11 and 27%, respectively. Shah *et al.* (1994) and Abdelghani *et al.* (1994) reported that delayed sowing decreased 1000-grain weight. Highest grain number/ear under all plantings was recorded in HDR-77, and grain weight/ear showed highest values under all planting conditions in HD 2815 (**Table 5**). A maximum reduction in grain number/ear under late and very late planting compared to normal (14 and 26%, respectively) and grain weight/ ear (31 and 38%, respectively) were recorded in PBW 343. Grain number in wheat was reduced by warmer weather prevailing between floral initiation and anthesis (Owen 1971). Saini and Aspinall (1982) reported a reduction in grain number/ear associated with high temperature during the booting stage. Under hot conditions heat-tolerant cultivars sustain relatively more kernels/spike than heat-susceptible cultivars (Shpiler and Blum 1991). Ferris *et al.* (1998) also reported that grain fertilization and grain set were most sensitive to high temperatures.

CONCLUSION

High temperature may shorten a plant's life span and reduce the duration of all the phenophases, which could be a reason for the significant reduction in yield under heat stress and could also explain why the heat stress-tolerant genotypes HDR-77 and HD 2815, which possessed a partially stable physiological system, were able to maintain high yield under high temperature stress. Since maintenance of favorable water status is essential for plant tolerance to heat stress (Jiang and Huang 2000), our observation showed clearly that heat stress-tolerant genotypes which maintained high water potential and high water status in leaf tissues (T_1 and T_2) also maintained high and stable yield and corresponds physiologically better than susceptible genotypes under high temperature.

The findings of this study showed a clear relationship

Table 5 1000-grain weight (g), grain number and grain weight/ear (g) during normal, late and very late planting.

Genotypes	1000-grain weight (g)			Grain number/ear			Grain weight/ear (g)		
	Normal	Late	Very late	Normal	Late	Very late	Normal	Late	Very late
PBW 343	44.8	39.7	32.5	49.7	41.7	37.0	2.49	1.71	1.54
PBW 175	45.3	41.6	39.4	49.5	43.3	38.7	2.37	1.88	1.57
HD 2865	40.5	37.9	35.0	48.0	44.3	36.8	2.19	1.74	1.51
HDR-77	45.2	41.3	38.2	50.8	45.3	40.8	2.37	1.90	1.71
HD 2815	45.2	42.9	40.2	50.5	46.7	40.5	2.31	2.07	1.64
CD	0.5	0.7	1.2	0.78	1.01	1.75	0.75	0.97	1.68

CD value at $P \leq 0.05$; planting date × genotype between physiological parameters and yield attributes of wheat genotypes under heat stress. In heat-sensitive genotypes, a reduction in Chl content and low Pn due to high temperature during late planting might have resulted in less supply of assimilate for development and reproduction and may have caused a reduction in yield parameters; moreover, the reduction in leaf water potential and relaxation time under temperature stress in heat-sensitive genotypes could cause structural damage to cell membranes which resulted in lower membrane stability. In heat-tolerant genotypes like HD 2815 and HDR-77, relatively high MSI was associated with comparatively higher water status in plant tissue and temperature tolerance and yield stability.

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