Agric. Sci. Digest., 37(3) 2017: 221-225
Print ISSN:0253-150X / Online ISSN:0976-0547

AGRICULTURAL RESEARCH COMMUNICATION CENTRE
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Variability in gas exchange attributes of wheat RILs subjected to high temperature stress

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Received: 22-02-2017 Accepted: 11-07-2017 DOI:10.18805/asd.v37i03.8990

ABSTRACT

High temperature above the optimum has a drastic effect on the stomatal activity and gaseous exchange which ultimately affect the yield and yield attributing traits. In this study, the Net photosynthetic rate (A_n), stomatal conductance (gs), transpiration rate (E), and intrinsic water use efficiency (iW_T) on flag leaves of 100 recombinant inbred lines of bread wheat derived from the cross of WH1021 (heat-tolerant) and WH711 (heat-sensitive) were evaluated. Recombinant inbred lines and both parents were assessed for various gas attributes under two sowing dates i.e., normal (17.11.2015) and late sowing (27.12.2015). The temperature persisted normal from December, 2015 to February, 2016 and there was a consistent rise in temperature in the last week of March. Measurements were made at anthesis and 10 days after anthesis. Average A_n, E, gs and iW_T decreased as the temperature increase. A contrasting difference was observed in timely sown and late sown at 10 days after anthesis for photosynthetic rate and transpiration rate. Decrease in stomatal conductance and water use efficiency was found with delayed sowing and high temperature. There results may prove useful in the selection of physiologically efficient heat-tolerant genotypes with higher rate of photosynthesis.

Key words: High temperature stress, Photosynthesis, Recombinant Inbreed Lines, Stomatal conductance.

INTRODUCTION

High temperature is predicted to have a general negative effect on plant growth due to its damaging effect on plant development (Talukder *et al*., 2014). Wheat is a major food crop critical to global food security. The current increase in wheat production of around 1% per year is not keeping pace with the rate of yield growth required to achieve the target of doubling crop production by 2050 (Ray *et al*., 2013). The optimum temperature entailed for growth and development of wheat is 18–24°C range even short periods of high temperature may result up to 20% decrease in yield (Mullarkey and Jones, 2000). Temperatures above this optimum for wheat growth causing injury or irreversible damage, which is known as heat stress, is a function of magnitude and rate of temperature increase as well as duration of exposure to increased temperature (Wahid *et al*., 2007). Increase in temperature from 22 to 32°C caused decrease in photosynthesis rate and transpiration (Zhang *et al*., 2010). Photosynthesis is the most sensitive physiological process to increasing temperature (Wahid *et al*., 2007) and any reduction in photosynthesis diminish growth and grain yield of wheat (Al-Khatib and Paulsen, 1990).

High temperature directly cause injury to the photosynthetic apparatus and diminish the rate and duration of assimilation (Paulsen, 1994). Heat stress also causes considerable reduction in physiological parameters like chlorophyll content, efficiency of PSII, net assimilation rate, transpiration, stomatal conductance, intercellular CO_2 concentration and intrinsic water use efficiency (Harding *et al*., 1990). Solubility of CO_2 in water decreases with increases in ambient temperature, which not only reduces carboxylation directly but also diverts more electrons to form ROS and promotes photorespiration. The rate of gas exchange (i.e., carbon dioxide uptake) and transpiration (i.e., water loss) through the leaf stomata is estimated by stomatal conductance, determined by the degree of stomatal aperture (and therefore the physical resistances to the movement of gases between the air and the interior of the leaf). Greater conductance, and consequently photosynthesis and transpiration rates are potentially higher with more open stomata as it is a function of the density, size and degree of opening of the stomata. Breeding plants with both high carbon gain and water-use efficiency (WUE) is a key objective for sustainable agriculture. At the level of leaf physiology, this implies increasing net photosynthesis (A_n) relative to stomatal conductance (g_s). Here, we review evidence for CO_2 diffusional constraints on photosynthesis and ultimately on yield.

The principal objectives of the present study were to: (i) determine genetic differences in flag leaf A_n in 100 RILs developed from WH1021×WH711 grown under timely sown and late sown field conditions (ii) observe whether A_n

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of different RILs and both parents interacted with phenological stage, and growing environment (i.e. sowing date) (iii) compare A_n and other gaseous parameters with agronomic performance.

MATERIALS AND METHODS

Experiment: The experiment was laid out in augmented design and conducted at Wheat Research Area, Department of Genetics and Plant Breeding, CCSHAU, Hisar (Haryana), India. Each plot was consisted of single row of 2 m length with a 23×10 cm spacing within rows and between plants. To create heat stress at anthesis and reproductive stage the sowing of heat stress experiment was delayed by 4 weeks from normal period of sowing. The experiment under timely sown environment was sown in the second week of November and the experiment under late sown was sown in last week of December. Data regarding temperature were recorded from Meteorological Laboratory, CCS Haryana Agriculture University, Hisar, India.

Plant material: A mapping population consisting of 100 Recombinant Inbred Lines (RILs) of advanced generation developed from a cross between WH1021×WH711. Parents differing in their performance under heat stress environment. WH1021 is the variety for cultivation in the areas subjected to heat stress while WH711 is a dwarf high yielding variety, which is comparatively heat sensitive, recommended for cultivation under normal sown condition in India. Both timely sown and late sown experiments were conducted under irrigated conditions and provided recommended dose of fertilizers during plant growth by keeping the difference of heat stress variable for the evaluation of RILs of bread wheat. Data for grain yield per plant, photosynthetic rate, transpiration rate, stomatal conductance and intrinsic water use efficiency were recorded as average of three competitive plants selected randomly from each row.

Gas exchange attributes: Flag leaves of all the RILs and both parents were used to collect data regarding net photosynthesis (An), stomatal conductance (gs), transpiration rate (E), by infrared gas analyzer (IRGA, LC*i*-SD, ADC biosciences) with 6.25 cm^2 leaf area and 1300 ìmol$m^{-2}s^{-1}$ PAR. The data was recorded at anthesis and 10 days after anthesis in both timely sown and late sown experiments. For the measurements of the above physiological parameters clean, dry, green flag leaves with no sign of disease or damage were selected from the three plants in each row. Leaf was handled in leaf chamber of IRGA facing it towards the sunlight and waited till the values stabilized after that values were recorded. Intrinsic water use efficiency was calculated from the ratio of net photosynthesis (A_n)to transpiration rate (E).

$$\text{Intrinsic water use efficiency} = \frac{\text{Net photosynthesis(An)}}{\text{Transpiration rate (E)}}$$

Statistical analysis: **A**nalysis of data is done by OPSTAT software available at CCS HAU website hau.ernet.in.

RESULTS AND DISCUSSION

Net CO_2 assimilation rate (An) (µ mole/m^2/second): Analysis of variance showed a significant variation for A_n in environments and genotypes (Table 1). The results described by fig1 revealed that grain yield increases with photosynthetic rate. Higher photosynthetic rate during timely sown conditions resulted in higher grain yield as compared to late sown experiment. Genotypes showed significant differences for photosynthetic rate. The parent WH1021 (16.87 and 10.69 µ mole/m^2/second at anthesis and 10 days after anthesis respectively during timely sown and 10.15 and 8.14 µ mole/m^2/second at anthesis and 10 days after anthesis respectively during late sown) showed higher net photosynthesis than WH 711 (12.05 and 10.21 µ mole/m^2/second at anthesis and 10 days after anthesis respectively during timely sown and 9.96 and 6.08 µ mole/m^2/second at anthesis and 10 days after anthesis respectively during late sown) (Table2 & 3). RILs showed range of net photosynthetic rate from 8.7-19.45 and 7.43-15.75 µ mole/m2/second at anthesis and 10 days after anthesis respectively during timely sown and 3.89-14.87 and 2.03-11.43 µ mole/m2/second at anthesis and 10 days after anthesis respectively during late sown.

Stomatal conductance (gs) (mole/m^2/second): Analysis of variance also showed significant differences for RILs and both parents under two environments for gs (Table 1). The high gs was observed during timely sown as compare to late sown. The parent WH1021 (0.24 and 0.18 mole/m^2/second at anthesis and 10 days after anthesis respectively during timely sown and 0.16 and 0.1 mole/m^2/second at anthesis and 10 days after anthesis respectively during late sown) showed higher gs than WH711 (0.21 and 0.17 mole/m^2/second at anthesis and 10 days after anthesis respectively during timely sown and 0.14 and 0.07 µ mole/m^2/second at anthesis and 10 days after anthesis respectively during late

Table 1: Analysis of variance for Net CO_2 assimilation rate (A_n), transpiration rate (E), stomatal conductance (gs), intrinsic water use efficiency (iWUE), grain weight/plant (GWP) and 100 grain weight (100GW).

Traits		A_n		E		gs		iWUE		GWP		100GW	
Source	DF	TS	LS	TS	LS	TS	LS	TS	LS	TS	LS	TS	LS
Genotype	101	6.405	5.181	2.581	0.940	0.087	0.001	1.230	0.548	3.882	2.102	1.400	0.464
Replication	2	710.846	638.442	29.698	15.148	0.001	0.242	7.115	14.173	0.002	0.012	0.037	0.003
Error	101	2.125	2.314	0.260	0.833	0.000	0.000	0.123	0.556	0.051	0.023	0.013	0.011
CV%	10.74	17.231	9.102	12.838	8.460	16.379	13.727	11.298	2.889	2.466	2.375	2.811	

DF-degree of freedom, TS-timely sown, LS-late sown, Coefficient of variation

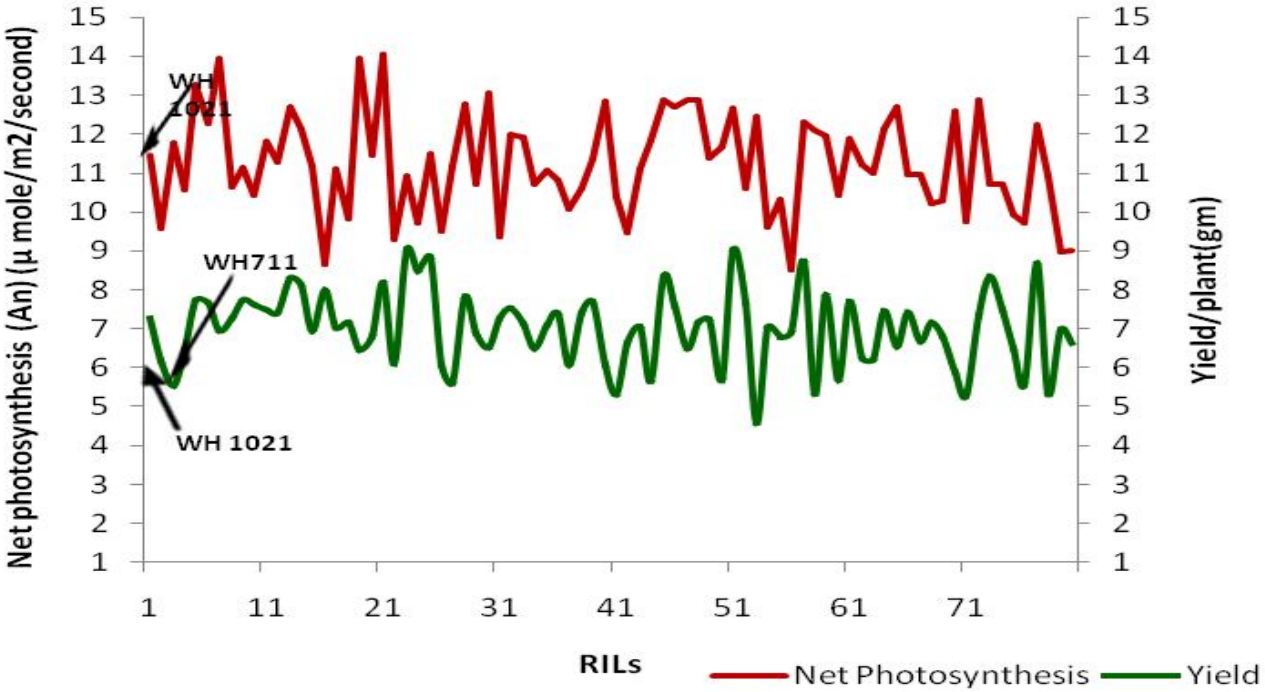


Fig. 1: Correlation between photosynthesis and wheat RILs

sown) in both timely sown and late sown. RILs showed range of stomatal conductance from 0.16-0.28 and 0.12-0.26 mole/ m^2/second at anthesis and 10 days after anthesis respectively during timely sown and 0.11-0.23 and 0.04-0.15 mole/m/ ^{2}second at anthesis and 10 days after anthesis respectively during late sown(Table2 & 3).

Transpiration rate (Em mole/m2/second): Results showed that temperature and moisture directly affected E, while E was inversely related to yield. Increasing transpiration rate led to increase in yield under high temperature if moisture is sufficient. The higher transpiration was recorded in WH1021 in timely sown and least in WH711 in late sown conditions. RILs mean transpiration was recorded in range between both parents. Due to this high transpiration rate plant adapt in high temperature conditions.

Intrinsic water use efficiency: Significant variation was showed in RILs and both parents by analysis of variance in timely sown and late sown conditions (Table 1). RILs having

Table 2: Mean and range of RILs & parents for gaseous attributes under timely sown & late sown at anthesis during 2015-16

Traits	WH1021		WH711		RILS			
	TS	LS	TS	LS	TS		LS	
					MEAN	RANGE	MEAN	RANGE
A_n	16.87±2.47	10.15±1.31	12.05±1.88	9.96±1.06	15.68±2.38	8.7-19.45	10.82±1.86	3.89-14.87
E	7.17±0.45	5.07±0.97	6.07±0.80	4.76±0.82	6.01±1.28	2.67-8.05	4.68±0.99	2.62-7.01
gs	0.24±0.02	0.16±0.01	0.21±0.02	0.14±0.01	0.23±0.03	0.16-0.28	0.16±0.02	0.11-0.23
iWUE	2.36±0.38	2.06±0.43	2.04±0.57	2.15±0.40	2.77±0.92	1.22-5.79	2.41±0.63	2.60-4.22

A_n = net CO_2 assimilation rate, E = transpiration rate, gs = stomatal conductance, iWUE = intrinsic water use efficiency.

Table 3: Mean and range of RILs & parents for gaseous attributes under timely sown & late sown at 10 days after anthesis during 2015-16

Traits	WH1021		WH711		RILS			
	TS	LS	TS	LS	TS		LS	
					MEAN	RANGE	MEAN	RANGE
A_n	10.69±0.86	8.14±1.58	10.21±1.37	6.08±1.12	11.51±1.70	7.43-15.75	6.85±2.04	2.03-11.43
E	6.32±0.80	4.5±0.87	5.29±o.74	3.96±0.44	5.16±1.11	2.46-7.28	4.07±0.92	2.07-6.00
gs	0.18±0.01	0.1±0.02	0.17±0.02	0.07±0.02	0.19±0.02	0.12-0.26	0.09±0.03	0.04-0.15
iWUE	1.72±0.29	1.88±0.53	1.94±0.34	1.55±0.27	2.36±0.72	1.21-5.02	1.82±0.85	0.45-5.04

A_n = net CO_2 assimilation rate, E = transpiration rate, gs = stomatal conductance, iWUE = intrinsic water use efficiency.

high transpiration rate showed low intrinsic water use efficiency while the RILs with low transpiration rate showed high intrinsic water use efficiency. Intrinsic water use efficiency was observed higher in WH1021 than WH711. RILs also showed range around both the parents.

Yield attributes: Analysis of variance showed significant difference in grain weight/plant and 100 grain weight among RILs and parents in both timely and late sown experiments (Table 1). WH1021 showed higher grain weight and 100 grain weight (GW/plant 8.330 and 6.248 gms for timely sown and late sown respectively) as compare to WH711 ((GW/plant 7.317 and 5.004 gms for timely sown and late sown respectively). The range for grain weight/plant in RILs was 5.177-10.956 and 2.575-8.105 gms for timely sown and late sown respectively and range for 100 grain weight was 3.58-6.617 and 2.244-4.605 (Table 4) gms for timely sown and late sown respectively.

Supra-optimal temperatures occurring at any plant growth stage result in 10% yield loss which is due accelerated plant development resulting in reduced photosynthetic rate, plant biomass, and seed set (Reynolds *et al*., 2016). The photosynthetic efficiency effect the yield of crop. Grain filling is endured by photosynthesis at anthesis in C3 cereals, such as wheat (Tambussi *et al*., 2007) hence, photosynthesis and grain yield showed a direct relationship in this study. High temperature negatively affect the balance between photosynthesis and respiration rates, reducing the overall carbohydrate pool and biomass leading to decreased yield and lower harvest index (HI) (Bahuguna *et al*., 2016). In the present study, WH1021 and some RILs have shown adaptability characteristics to resist stress conditions. Adequate moisture and relatively low temperature during timely sown conditions encouraged growth and development, whereas, late sown was a stressed conditions with relatively higher temperature, affecting physiological processes of the crop. The contribution of assimilates to grain was limited due to rapid decline in photosynthesis under high temperature. The decline in A_n under stress is due to stomatal closure with reduced CO_2 diffusion. So stomatal closure is responsible for high temperature induced reduction in A_n during late sown. Stomatal conductance is the speed of removal of water from plant parts and is indicative of roots extracting soil water under variable soil and climatic conditions. The higher values of gs, recorded during the timely sown, can be attributed to favorable environmental conditions like availability of adequate moisture and optimum temperature which promoted growth. Increase in temperature resulted in reduction in available moisture led to low stomatal efficiency and, ultimately, reduced yield (Ahmed *et al*., 2010). During late sown, relatively higher temperature at anthesis caused a reduction in stomatal conductance and photosynthetic efficiency, consequently, resulting in less grain yield, as high temperature created water deficit. Transpiration is an important process to maintain leaf temperature by providing a cooling effect. Since transpiration is significantly affected by abiotic stresses, genotypes having higher transpiration efficiency (the ratio of dry matter to transpiration) can be considered best for stress conditions. In this study, adequate temperature resulted in an optimum transpirational rate during timely sown while increase in temperature and reduction in humidity enhances the transpiration rate that led to less water availability for photosynthesis in plant tissues, causing yield reduction during late sown. Reduction in intrinsic water use efficiency during late sown also affect the yield of crop because both photosynthesis and transpiration were reduced. So the effect of high temperature stress can sustain by alteration in sowing dates.

CONCLUSION

Data analyzed showed clear differences in A_n among cultivars, the differences were consistent across phenological stage and environment, and revealed a significant association with yield performance differences in A_n and gs at all growth stages and were associated with cultivar differences in performance in warm conditions, stomatal conductance (gs) possibly having a role in heat escape. For improving wheat productivity increase in total plant biomass through efficient carbon capture by photosynthesis is now more crucial.

ACKNOWLEDGEMENT

The authors wish to express special thanks to Council of Scientific & Industrial Research (CSIR), India, for the financial support to complete this research work.

Table 4: Mean and range of RILs & parents for yield attributes under timely sown & late sown during 2015-16.

Trait	WH1021		WH711		RILs			
	TS	LS	TS	LS	TS		LS	
	Mean	Mean	Mean	Mean	Mean	Range	Mean	Range
GW/plant	8.330±0.78	6.248±0.46	7.317±0.35	5.004±0.40	7.802±1.40	5.177-10.956	6.215±1.04	2.575-8.105
100 GW	5.031±0.61	4.388±0.12	5.6±0.46	4.116±0.41	4.693±0.62	3.58-6.617	3.784±0.47	2.244-4.605

TS = timely sown, LS = late sown, RILs = recombinant inbred lines, GW = grain weight

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