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BRIEF COMMUNICATION

Effects of water stress and high temperature on gas exchange and chlorophyll fluorescence in *Triticum aestivum* L.

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Abstract

Wheat plants grown in controlled growth chambers were exposed to drought stress (DS) and high temperature (HT) singly and in combination (DS+HT). The effects of these two stresses on net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), quantum efficiency of photosystem 2 (Φ_{PS2}), variable to maximum chlorophyll (Chl) fluorescence (F_v/F_m), photochemical (q_p) and non-photochemical (NPQ) Chl fluorescence, and yield were investigated. Grain yield was decreased by 21 % due to DS, while it was increased by 26 % due to HT. P_N, g_s, C_i, and Chl fluorescence were dramatically reduced to DS, HT, and their interaction, except NPQ which showed an increase due to HT.

Additional key words: grain yield; intercellular CO_2 concentration; quantum efficiency of photosystem 2; spikelet; stomatal conductance; yield.

Drought stress (DS) and high temperature (HT) are among the most important environmental factors that limit net photosynthetic rate (P_N) (Hassan *et al.* 1998, Yordanov *et al.* 1999, 2000). Water stress leads to a progressive suppression of photosynthetic carbon assimilation in desiccation-tolerant and intolerant wheat plants (Deltoro *et al.* 1998). Reduction in P_N is attributed to both stomatal and non-stomatal control (Ort *et al.* 1994, Shangguan *et al.* 1999).

Increases in temperatures may cause expansion of production into higher elevations. The grain filling period may be reduced as HT may detrimentally affect sensitive developmental stages such as flowering, thereby reducing grain yield and altering crop quality. Increases in temperature by 2–4 °C caused a reduction in yield of many crops depending on species and cultivar used (Yates and Strzpek 1998).

Exposure of plants to water stress can alter response to increased temperature. Havaux (1992) stated that exposure of potato leaves to HT caused an increase in activity of photosystem 2 (PS2) in water-stressed plants, as indicated by a slight increase in variable to maximum chlorophyll (Chl) fluorescence (F_v/F_m). PS2 plays an important role in the response of plants to environmental stresses and it is a very sensitive component of the photosynthetic systems (Berry and Björkman 1980, Chaves 1991, Yordanov *et al.* 1999, 2000). The change in photosynthesis would be reflected ultimately in growth and yield.

The aim of the present investigation was to study the effects of DS and HT singly and in combination on Chl fluorescence, P_N, stomatal conductance (g_s), and yield of wheat plants. Seeds of wheat (*Triticum aestivum* L.) were obtained from the Department of Agronomy, Alexandria University, Egypt. They were sown in 20 cm^2 pots, 5 seeds in each pot with multipurpose compost in a glasshouse [temperature 24–25 °C day/night, air humidity 60–65 %, 16-h photoperiod with additional lighting at 450 $\mu mol\ m^{-2}\ s^{-1}$ (photosynthetic photon flux density, PPFD)], total irradiance was 675 $\mu mol\ m^{-2}\ s^{-1}$. After appearance of expanded top leaf (flag leaf) (12 d after sowing), plants were thinned to one seedling per pot. Pots then were transferred to eight closed climate controlled growth chambers. Two chambers were assigned to DS treatment (withholding irrigation till soil moisture of 13 %). Two other chambers were assigned to HT treatment (40–42 °C), two others were assigned to interaction between DS and HT, while the last two

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chambers were assigned as control plants (soil moisture was kept at 25 % and temperature at 25 ^{o}C). There were 15 pots in each chamber, soil moisture was checked regularly, and lost water was replenished by bringing the pots to their original mass according to Deng *et al.* (2000).

P_N, g_s, and intercellular CO$_2$ concentration (C_i) were measured with a portable infrared gas analyser (*LICOR-6400*). Measurements were taken between 10:00–14:00 h for 55 d on 5-d intervals. Chlorophyll (Chl) fluorescence was measured with a portable Photosynthetic Efficiency Analyser *PEA* (*Hansantech Instrumental,* Hardwick, Norfolk, UK). Leaves were dark adapted for 30 min in leaf-clips before measurements. The ground (F_0), maximum (F_m), and variable (F_v) fluorescence were measured and used for calculations of variable to maximum fluorescence ratio (F_v/F_m). Photochemical (Φ_{PS2} and q_p) and non-photochemical (NPQ) Chl quenching measurements were calculated according to Yordanov *et al.* (1999).

The number of ears, spikelets, grains per ear, spikelets per ear, grains per spikelet, and infertile florets per spikelet on each plant were recorded. The plants were dried in dry oven for one week at 65 °C and dry mass (DM) of grains and straw as well as 1 000 grain mass was recorded.

Two-way ANOVA was applied to log-transformed data. There was no covariate used except for P_N and g_s, where PPFD was used as a covariate. Significant difference between means was tested by LSD (*Stattgraphics* Statistical Package).

P_N was reduced by 60, 65, and 66 % due to DS, HT, and their interaction (DS+HT), respectively (Fig. 1*A*). Moreover, g_s was decreased by 33, 34, and 37 % (Fig. 1*B*), and C_i was also decreased by 23, 32, and 26 %, respectively (Fig. 1*C*).

DS caused a reduction by 6, 19 and 17 % in F_v/F_m, Φ_{PS2}, and q_p, respectively, while exposure to HT caused a decrease in Φ_{PS2} and q_p by 12 and 18 %, respectively (Table 1). On the other hand, non-photochemical quenching (NPQ) increased due to single DS or HT, and DS+HT less than additive, *i.e.* antagonistically (Table 1).

DS caused a significant ($p<0.05$) reduction (14 %) in the number of grains per ear as a consequence of a DS-induced reduction in the number of grains per spikelet (16 %) and an increase in the number of infertile florets per spikelet (24 %). Moreover, the 1 000-grain mass and grain yield were reduced by 11 and 21 %, respectively (Table 1). On the other hand, HT caused increases in the number of grains per ear and number of grains per spikelet by 12 % each, which was reflected in an increase in the 1 000 grain DM and grain yield by 12 and 26 %, respectively. However, number of infertile florets was reduced by 12 % (Table 1). DS+HT caused significant ($p<0.05$) reductions in all yield parameters except number of infertile florets as it increased by 49 % (*i.e.* the interactive effect was more than additive on this component).

Under natural conditions, environmental factors contributing to photosynthetic response function in complex and vary simultaneously and these anticipate intricacy (Jones 1992, Kobayashi *et al.* 1999, Deng *et al.* 2000, Hassan 2004). Kassim and Paulsen (1999) indicated that wheat plants had higher P_N at 22 ^{o}C than when exposed to 45 ^{o}C, whereas leaf P_N of rice increased at 22 ^{o}C and decreased at 42 ^{o}C.

Chl fluorescence is a good indicator of dehydration (Pol *et al.* 1999). I found that F_v/F_m decreased due to DS but not due to HT and this may be a regulation that allows stressed plants to reduce the risk of over-excitation and photooxidative damage (Munné-Bosch and Alegre 1999). The quantum efficiency of PS2 photochemistry (Φ_{PS2}) reflects the fraction of radiation absorbed by PS2 that is utilized in photochemistry (Demmig-Adams and Adams 1992, Calatayud and Barreno 2000) and it is also a good indicator of environmental stress (Yordanov *et al.* 2000).

In the present investigation, DS and HT caused a marked decrease in PS2 and P_N, and this is in agreement with the results of Flagella *et al.* (1998) who reported a reduction in Φ_{PS2} of durum wheat due to DS. They related such reduction to Calvin cycle metabolism. Declines in photon yield of photosynthesis during desiccation or heat stress can be due either to damage of the photosynthetic apparatus or to PS2 down-regulation

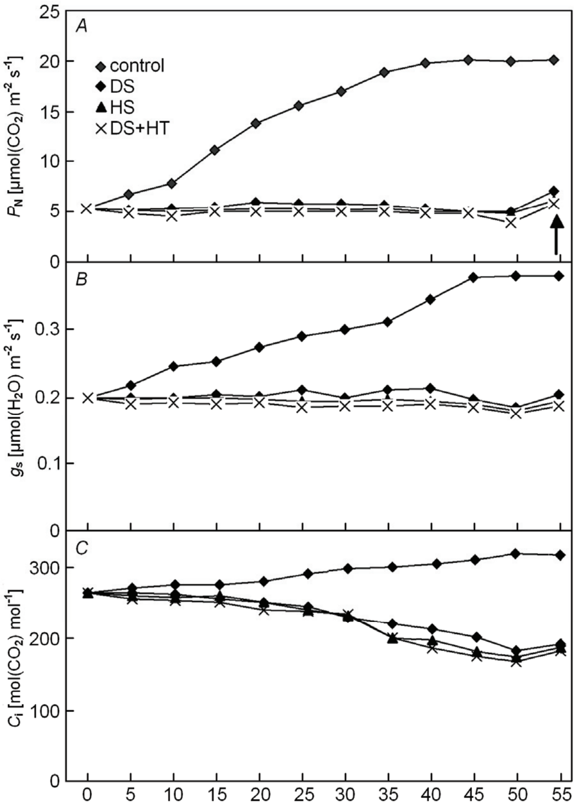

Fig. 1. Changes in net photosynthetic rate, P_N (*A*), stomatal conductance, g_s (*B*), and intercellular CO$_2$ concentration, C_i (*C*). *Arrows* indicate the time in which flag leaf was replaced by 2nd nearest leaf in DS and HT plants.

Table 1. Effects of drought stress (DS) and high temperature (HT) singly and in combination on yield components on the ratio of variable to maximum chlorophyll fluorescence (F_v/F_m), the quantum efficiency of PS2 (Φ_{PS2}), photochemical (q_p) and non-photochemical Chl fluorescence (NPQ) [LSD at $p \leq 0.05$ was 0.02, or 0.04 for Φ_{PS2}], and yield components.

Yield component	Treatment Control	DS	HT	DS+HT
F_v/F_m	0.77 cd	0.72 a	0.76 cb	0.74 ab
Φ_{PS2}	0.731 c	0.349 b	0.381 b	0.302 a
q_P	0.861 d	0.713 c	0.701 b	0.615 a
NPQ	0.569 a	0.734 b	0.832 c	0.859 d
Ears per plant	3.31 ± 0.06	3.11 ± 0.09	3.50 ± 0.05	2.91^a ± 0.05
Spikelets per ear	20.25 ± 1.10	19.11 ± 2.01	20.31 ± 2.10	16.13 ± 1.08
Grains per spikelet	4.18 ± 0.07	3.49 ± 0.08	4.59 ± 0.06	2.39 ± 0.04
Grains per ear	71.03 ± 3.6	61.32 ± 1.50	79.61 ± 5.31	58.12 ± 3.15
1 000 grain dry mass [g]	45.91 ± 3.7	40.62 ± 2.40	51.36 ± 4.12	34.61 ± 3.71
Grain yield [kg m^{-2}]	1.16 ± 0.11	0.91 ± 0.10	1.47 ± 0.13	0.73 ± 0.11
Straw yield [kg m^{-2}]	3.62 ± 0.42	2.69 ± 0.21	4.26 ± 0.39	2.24 ± 0.18
Infertile florets per spikelet	1.30 ± 0.03	1.62 ± 0.02	1.03 ± 0.03	1.94 ± 0.05

(Calatayud *et al.* 1997). The reduction in PS2 activity leads to inhibition of P_N. This is in agreement with the results of Yordanov *et al.* (1997, 1998) on bean leaves. The reduction in P_N due to DS, HT, or their interaction could be attributed to stomatal and non-stomatal limitations. Stomatal closure usually occurs before inhibition of photosynthesis and restricts CO_2 availability at the assimilation sites in chloroplast. This was not the case in the present study, as the inhibition in P_N occurred before any change in g_s or C_i which suggests that non-stomatal limitation was in operation. Non-stomatal limitation of photosynthesis has been attributed to reduced carboxylation efficiency (Wise *et al.* 1992), reduced ribulose-1,5-bisphosphate (RuBP) regeneration (Tezara and Lawlor 1995), or to inhibition in chloroplast activity (Shanggunan *et al.* 1999).

DS shifts the temperature threshold towards higher value, *i.e.* causes an increase in heat resistance for a few degrees (Havaux 1992). This is extremely important for plant's survival because heat inactivates photosynthesis (Yordanov *et al.* 2000). When Yordanov *et al.* (1997) exposed maize plants to temperatures above 40 °C, there was less damage in water-stressed plants, indicating that DS counteracts the negative effects of HT. In wheat plants I did not observe such changes as DS exacerbated the magnitude of HT. Yordanov *et al.* (1998) found similar results with sunflower plants. Recently El-Shintinawy *et al.* (2004) reported a change in PS2 in heat-shocked barley seedlings.

Cornic and Ghashghaie (1991) showed that drought-induced changes in thermal optimum of *P. vulgaris* leaf photosynthesis at normal CO_2 and limiting irradiance can be substantial. These changes in leaf photosynthesis in response to temperature are correlated to similar changes in g_s (Yordanov *et al.* 2000) and this is the case in wheat plants in the present study.

The reduction in yield induced by DS and/or HT was the result of (*1*) a decrease in the number of grains per spikelet, and (*2*) increases in the number of infertile florets per spikelet. Such reductions in grain yield have been attributed to decreased P_N (Amundson *et al.* 1987, Lehnherr *et al.* 1987) and accelerated flag leaves' senescence or alteration in Chl fluorescence (Soja and Soja 1995). Deng *et al.* (2000) related the decline in growth and yield of spring wheat grown under semiarid environmental conditions to the decline in P_N.

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