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Drought stress effects on photosynthetic rate and leaf gas exchange of wheat

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Abstract. Drought stress effects on photosynthetic rate and leaf gas exchange characteristics of four wheat cultivars were evaluated under semi-controlled conditions. Four cultivars—Kanchan, Sonalika, Kalyansona, and C306, grown in pots—were subjected to four levels of water stress. Among the cultivars, Kalyansona showed the highest photosynthesis rates both at vegetative and at anthesis. Exposure of plants to drought stress led to noticeable decrease in photosynthesis rate, stomatal conductance and mesophyll conductance and a concomitant increase in intercellular CO_2 concentration. Plants subjected to drought at the early vegetative stage displayed similar physiological characters subsequently under well-watered conditions as compared with control. Photosynthesis rates decreased with decrease in stomatal conductance, but a weak relationship between them implied that non-stomatal limitations to photosynthesis might have been in operation.

Keywords: Drought stress; Leaf gas exchange; Photosynthesis; *Triticum aestivum* L.

Abbreviations: $\mathbf{C_i}$, intercellular CO_2 concentration; $\mathbf{g_m}$, mesophyll conductance; $\mathbf{g_s}$, stomatal conductance; $\mathbf{P_n}$, photosynthetic rate; $\mathbf{T_a}$, air temperature; $\mathbf{T_l}$, leaf temperature.

Introduction

Wheat (*Triticum aestivum* L.) is an important cereal crop that ranks first globally and second in Bangladesh. In Bangladesh wheat is grown generally after the harvest of aman rice on residual soil moisture. Even with substantial improvement of irrigation facilities, 60–65% of the total wheat area remains unirrigated (Ahmed et al., 1986). The growing season is characterized by low rainfall and relatively high evaporative demand. Crop grown without irrigation during the dry season thus encounters drought stress of varying degrees at different growth stages. Drought is probably the most important factor controlling crop yield worldwide. But the yield reduction is mediated through reduced leaf growth (Ephrath and Hesketh, 1991) and consequential lower photosynthetic productivity (Chen et al., 1993). The effect of drought stress on the plant growth process has been extensively reported (Hsiao, 1973; Schulze, 1986).

Drought affects nearly all the plant growth processes; however, the stress response depends upon the intensity, rate, and duration of exposure and the stage of crop growth (Brar et al., 1990). Reduction in photosynthesis in water stressed leaves may be due to stomatal closure (Hsiao, 1973). Farquhar and Sharkey (1982) gave a detailed account of the stomatal functioning in relation to stress conditions. Recent studies indicate that a decrease in photosynthesis under deficient soil moisture may not necessarily be related to stomatal opening, rather non-stomatal control of photosynthesis might have greater influence (Farquhar et al., 1989).

This study was undertaken to investigate the photosynthetic rate and leaf gas exchange characteristics of wheat under different levels of drought stress.

Materials and Methods

An experiment was conducted under semi-controlled conditions at the Institute of Postgraduate Studies in Agriculture (IPSA), Bangladesh, between November 1994 and March 1995. Four cultivars—namely Kanchan (V_1), Sonalika (V_2), Kalyansona (V_3), and C306 (V_4)—were grown in Waggner pots (24 cm diameter) containing 12 kg sandy clay loam soil. A fertilizer dose of 600 mg N, 360 mg P, 240 mg K, and 120 mg S as urea, TSP, MP, and gypsum was applied to each pot. Ten seeds were planted per pot, and one week after emergence the seedlings were thinned to three seedlings per pot.

There were 160 pots, with 40 pots assigned to each cultivar. The plants were subjected to four levels of water regimes. These were:

1) Control. No drought stress was imposed, and pots were never allowed to dry out, (S_1).

2) Vegetative. Drought stress was imposed at an early vegetative stage by withholding irrigation, (S_2).

3) Anthesis. Drought stress was imposed at anthesis by withholding irrigation, (S_3).

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4) Both. Drought stress was imposed both at early vegetative stage and anthesis by restricting irrigation, (S_4).

The experiment thus consisted of 16 treatments. The pots were arranged in a 4×4 factorial randomized complete block design. Each treatment was replicated 10 times.

All plants received irrigation and intercultural operations uniformly until the imposition of treatments. Drought treatments imposed by restricting irrigation were re-irrigated when the plants showed signs of wilting or leaf rolling, particularly during the morning. Control pots were irrigated as frequently as needed.

Gas exchange characteristics were measured on young fully-expanded leaves of seedlings and subsequently on flag leaves of full grown plants of both stressed and non-stressed treatments using a portable photosynthesis system (Li-COR LI-6200) assembled with an infra-red gas analyzer (Li-COR LI-6250) and data logger following the procedure described by Al-Khatib and Paulsen (1990). Measurements were initiated when CO_2 concentration in the 0.25 L leaf chamber approached ambient concentration. Temperature and irradiance during measurements duplicated daytime conditions for growing plants. Photosynthetic active radiation (PAR), leaf temperature (T_l), and air temperature (T_a) were recorded simultaneously, and net photosynthetic rate (P_n), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were also calculated. The mesophyll conductance (g_m) was determined as the ratio of photosynthesis rate (P_n) and intercellular CO_2 concentration (C_i) following Kubota and Hamid (1992).

Results and Discussion

Photosynthesis (P_n)

Significant varietal difference in net photosynthesis (P_n) was found both at vegetative and anthesis stage. At the vegetative stage cultivars Kanchan, Sonalika, and Kalyansona showed the higher P_n rate compared with C306 (Table 1). During anthesis Kalyansona showed the highest P_n rate relative to other cultivars. A reduction in P_n was found at anthesis, as compared to the vegetative stage, in all the cultivars except Kalyansona.

Both vegetative and anthesis water deficit significantly decreased P_n. Stress induced reductions in P_n were 65% and 80% for vegetative and anthesis drought, respectively, as compared with the control treatment. The results are in general agreement with Brar et al. (1990). Single stress at anthesis or repeated stress at vegetative as well as at anthesis caused no significant difference in P_n. Plants subjected to drought at the vegetative stage apparently recovered quickly to show a greater rate of photosynthesis at anthesis. Table 1 shows that plants stressed at vegetative, but not stressed subsequently, gave a significantly high P_n rate at anthesis compared with well watered plants. This might be due to the adaptive mechanism of drought affected plants (Jones and Corlett, 1992). Interaction between cultivars and water regimes treatments was not significant.

Stomatal Conductance (g_s)

Cultivar difference in stomatal conductance (g_s) at the vegetative stage was not significant, but it was significant at anthesis (Table 1). C306 had the highest g_s at the anthesis stage, followed by Kanchan and Kalyansona, whereas Sonalika showed the lowest g_s among the cultivars. It was observed that g_s decreased with age of the leaves, except in the case of C306. The results are in general agreement with those of Uprety and Bhatia (1989), who reported that stomatal resistance in the leaves of mungbean increased with age and that the maximum values were obtained at pod development stage. The weak relationship (R^2=0.39) between P_n and g_s (Figure 1) indicates that reduction in Pn under drought stress conditions was regulated mostly by non-stomatal factors rather than stomatal closure.

Table 1. Net photosynthesis (P_n) and stomatal conductance (g_s) of four wheat cultivars in response to drought stress at two growth stages.

Treatment	Photosysnthesis rate (μmol m^{-2} s^{-1})		Stomatal conductance (mol m^{-2} s^{-1})	
	Vegetative	Anthesis	Vegetative	Anthesis
Cultivars				
Kanchan	13.42 A	12.22 B	1.176 A	0.671 B
Sonalika	15.68 A	11.42 B	1.334 A	0.298 C
Kalyansona	14.48 A	15.27 A	1.300 A	0.671 B
C306	9.25 B	10.54 B	1.118 A	1.140 A
Water regimes				
Control	19.59 A	19.57 B	1.735 A	0.847 B
Vegetative	6.82 B	21.63 A	0.729 B	1.027 A
Anthesis	–	3.99 C	–	0.425 C
Both	–	4.25 C	–	0.480 C
CV (%)	20.90	17.14	36.98	22.50

In a column, means followed by common letter(s) are not significantly different at the 5% level by DMRT.

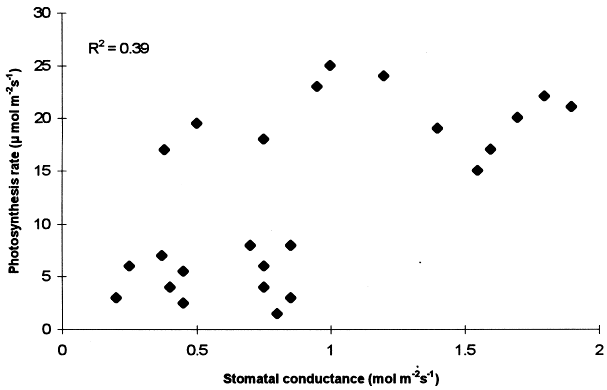

Figure 1. Scattered diagram showing relationship between stomatal conductance and photosynthesis rate of four wheat cultivars in response to drought stress at two growth stage.

Mesophyll Conductance (g_m)

Among the cultivars, Kanchan, Sonalika, and Kalyansona had statistically similar g_m rates at the vegetative stage which were significantly higher than C306 (Table 2). At anthesis Kalyansona showed the highest g_m rate, followed by Kanchan and Sonalika. The g_m rate was the lowest in C306 at the anthesis stage. Despite having a relatively higher g_s throughout and the highest g_s at anthesis, C306 showed the lowest mesophyll conductance (g_m) coupled with lowest rate of photosynthesis at both the growth stages. In contrast, Kalyansona maintained a higher P_n rate but had a significantly lower g_s rate than C306. Mesophyll conductance of Kalyansona was the highest. Our results suggest that gm rather than g_s had an overriding influence in regulating P_n. Earlier, there had been a suggestion that reduction in mesophyll photosynthetic capacity and reduction in stomatal conductance under water deficits may be coupled. The increased mesophyll resistance is generally associated with severe water stress (Begg and Turner, 1976), and under these conditions plants show a higher P_n rate in those having a higher g_m rate.

Water deficit significantly decreased g_m both at the vegetative and anthesis stage. The reduction rate in g_m was greater than that of P_n and g_s when these were compared with control plants. The reduction in g_m due to drought stress was more severe at the anthesis (89%) than at the vegetative (66%) stage. The plants subjected to drought stress at the vegetative stage showed the highest g_m rate at anthesis under well-watered conditions. Plants subjected to repeated droughts, once at the vegetative stage and subsequently at anthesis, showed a g_m rate similar to that of the plants which encountered drought only at the anthesis stage. Interaction between cultivars and drought treatments was not significant. Under drought stress conditions, the reduction in P_n was accompanied by a parallel decrease in both g_s and g_m. This suggests that either g_s is dependent upon photosynthetic activity (Wong et al., 1979) or that both g_s and gm depend on leaf water potential or its components (Hanson and Hitz, 1982). In our experiment, it was observed that the reduction in g_m (66 to 89 %) was relatively higher than that of g_s (50 to 58 %), and there was a strong relationship (R^2=0.99) between P_n and g_m (Figure 2), indicating the dominance of mesophyll in reducing P_n rate in drought stressed plants.

Intercellular CO_2 Concentration

Among the cultivars C306 showed the highest intercellular CO_2 concentration (C_i) followed by Kanchan both at the vegetative and anthesis stage (Table 2). Cultivar Kalyansona showed the lowest C_i at both the growth stages. In general, there was a decreasing trend in C_i with an increase in P_n rate.

Water deficit significantly increased the C_i at both the vegetative and anthesis stage. The C_i of stressed plants were 5% and 16% higher at the vegetative and anthesis

Table 2. Mesophyll conductance (g_m) and intercellular CO_2 concentration (C_i) of four wheat cultivars in response to drought stress at two growth stages.

Treatment	Mesophyll conductance (mol $m^{-2} s^{-1}$) $\times 10^{-2}$		Intercellular CO_2 concentration (µL L^{-1})	
	Vegetative	Anthesis	Vegetative	Anthesis
Cultivars				
Kanchan	4.528 A	4.332 B	306.65 AB	301.55 B
Sonalika	5.347 A	4.528 B	298.79 B	270.85 D
Kalyansona	4.907 A	5.545 A	299.43 B	288.07 C
C306	3.042 B	3.481 C	310.63 A	315.81 A
Water regimes				
Control	6.632 A	7.229 B	296.20 B	272.18 B
Vegetative	2.279 B	7.944 A	311.55 A	274.33 B
Anthesis	–	1.303 C	–	316.67 A
Both	–	1.411 C	–	313.12 A
CV (%)	20.79	17.42	2.22	3.83

In a column, means followed by common letter(s) are not significantly different at the 5% level by DMRT.

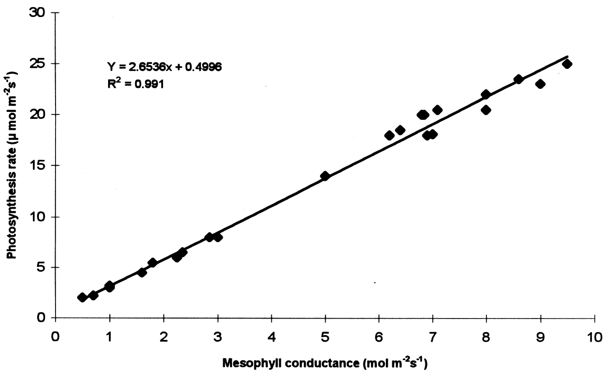

Figure 2. Relationship between mesophyll conductance and photosynthesis rate of four wheat cutivars in response to drought stress at two growth stages.

stages, respectively, than that of control plants. Our results regarding the effect of drought stress on the C_i were in agreement with Kicheva et al. (1994).

The responses of g_s, g_m and C_i in this study make clear that drought stress significantly decreases photosynthesis rates. Compared with g_s, g_m was found to be more sensitive to the drought stress. The weak relationship between P_n and g_s indicates that reduction in P_n under drought stress can not be attributed to the stomatal closure alone. Increased P_n at the anthesis of vegetative droughted plants under well-watered conditions might have occurred due to chemical changes in enzyme level or to drought hardening at the vegetative stage. However, this triggering effect of vegetative drought requires further investigation.

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乾旱逆境對小麥光合作用速率與葉片氣體交換之影響

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於半控制的條件下對小麥四種栽培品種，進行乾旱逆境影響光合作用速率與葉片氣體交換之評估。四種栽培品種 Kanchan、Sonalika、Kalyanosa 及 C306 皆種植於盆內以進行四個層次的水分逆境處理，在所有的栽培品種，Kalyansona於營養生長及開花時表現最高的光合作用速率。將植物曝露於乾旱逆境下，造成光合作用速率減少、氣孔及葉肉之導電度下降、以及細胞間二氧化碳濃度增加。植物於營養生長早期受乾旱處理，而後再生長於良好的灌溉條件下，發現其生理特性與未處理的對照組類似。光合作用速率減少通常伴隨氣孔導電度的下降，然而此種弱關聯性亦顯示非受氣孔限制的光合作用似乎已經在運作。

關鍵詞：乾旱逆境；光合作用；葉片氣體交換；小麥。