PHOTOSYNTHETICA 38 (3): 429-432, 2000

Gas exchange of spring barley and wheat grown under mild water shortage

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Abstract

During mild water stress (decrease of full water capacity from 60 to 35 %) net photosynthetic rate (P_N) of four spring barley and wheat genotypes was about twice lower than that for unstressed plants and was mainly limited by non-stomatal factors. Availability of CO_2 from intercellular spaces did not change significantly when stomatal conductance (g_s) decreased from 0.25-0.35 to 0.15-0.20 mol(H_2O) m^{-2} s^{-1}. There may be two main processes leading to similar intercellular CO_2 concentration (c_i) in stressed and unstressed seedlings despite of twice lower P_N under mild water stress: (*a*) lower diffusion of CO_2 through stomata represented by lower g_s, (*b*) lower consumption of CO_2 by photosynthetic apparatus of stressed plants. Last factor is partially pronounced by lower response of P_N to c_i observed for stressed than for control plants.

Additional key words: *Hordeum*; intercellular CO_2 concentration; photosynthesis; stomatal conductance; *Triticum*.

Introduction

Soil water is one of the main factors changing P_N and g_s. Photorespiration and dark respiration are relatively less sensitive to water shortage than photosynthesis and even under water stress an increase of photorespiration as a result of lower supply of CO_2 to ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) was observed in barley plants (Lal *et al.* 1996).

Photosynthetic apparatus of crop plants is relatively resistant to water deficit and decrease of photosynthesis under water stress is believed to be a result of lower g_s (Barrs 1968, Cornic and Massacci 1996) or that non-stomatal factors inhibit P_N (Boyer 1976, Farquhar and Sharkey 1982). During water stress abscisic acid (ABA) is produced in root system and transported to the leaves; it decreases g_s (Davies and Zhang 1991). Under mild water stress RuBPCO activity and contents of proteins and their transcripts are not much inhibited and P_N is usually quickly restored after stress cessation (Dreesmann *et al.* 1994). Indirectly, water deficit decreases P_N by decreasing assimilatory area of leaves.

The aim of this study was to determine the effects of increasing soil drought on stomatal and non-stomatal limitations of gas exchange parameters and to find the relative importance of these limitations to P_N in cultivars of wheat and rye.

Materials and methods

Two cultivars of spring wheat (*Triticum aestivum* L.) Hera and Omega and two cultivars of spring barley (*Hordeum vulgare* L.) Orlik and Polo were used. Plants were grown in Wagner pots filled with 6 kg of soil and 2 kg of sand, and 1.07 g KNO_3, 1.08 g NH_4NO_3, 0.74 g K_2SO_4, 0.65 g $MgSO_4 \times 7 H_2O$, 0.575 g KH_2PO_4, 0.888 g $Ca(H_2PO_4)_2$. Full water capacity of the soil mixture was 20 % of dry matter of soil with sand. Control plants were watered everyday to 60 % of full water capacity, stressed plants during the first 20 d were watered to 60 and from 21st to 30th day to 35 % of full water capacity. Plants were grown in the growth cabinet *KTLK-20000* (Germany) under 12-h photoperiod. Irradiance was 19.44 mol(PAR) d^{-1} (450 μmol m^{-2} s^{-1}). Temperature

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Received 22 May 2000, *accepted* 11 October 2000.

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during day and night was 22 and 12°C, respectively.

Gas exchange was measured with photosynthetic system *LI-6200* (*LI-COR*, Lincoln, Nebraska, USA) working in the closed mode. For measurements of CO_2 curves, leaf chamber was accurately tightened to prevent leakage. Fully developed intact young leaves having the highest P_N were used (Suzuki *et al.* 1987). Measurements were done in growth cabinet and temperature and irradiance were the same as these for growth.

All values are averages of five measurements. Results were statistically treated using variance analysis.

Results and discussion

There were rather small differences between P_N of all unstressed spring cereal genotypes at the beginning of water shortage and their P_N was in the range of 9.5-12.9 μmol(CO_2) m^{-2} s^{-1} (Fig. 1*A*,*B*). Following 3-10 d of water shortage, P_N of water stressed plants was always lower than that in control plants (Fig. 1*A*,*B*). At the last day of the experiment P_N was approximately two folds lower than that of controlled plants. The effect of water stress was the most pronounced for wheat cv. Omega and the smallest for barley cv. Polo. Generally, cultivars having the most lowered P_N after 5 d were also the most affected ones after 10 d of water stress. Transpiration rate (*E*) of all studied genotypes was also reduced during water stress (values not shown). Observed lower P_N under water stress could be an effect of changes in water status of the leaves and an effect of hormone signals sent from roots to the leaves (Davies and Zhang 1991).

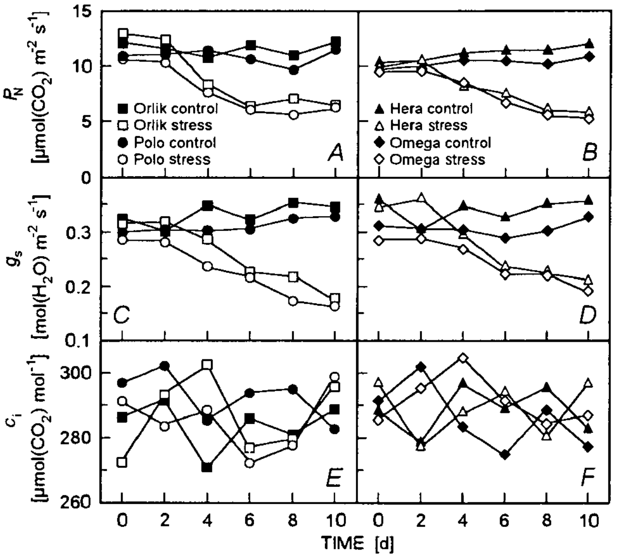

Fig. 1. Net photosynthetic rate, P_N (*A*, *B*), stomatal conductance, g_s (*C*, *D*), and intercellular CO_2 concentration, c_i (*E*, *F*) of two cultivars of barley (*A*, *C*, *E*) and two cultivars of wheat (*B*, *D*, *F*) grown under controlled and stressed conditions. In *A* and *B*, $LSD_{0.01}$ for time of measurement and for cultivars was 0.33, for water conditions 0.18, for interactions time of measurement×cultivars 0.91 and 0.82, for time of measurement×conditions 0.64 and 0.44. In *C* and *D*, $LSD_{0.01}$ for time of measurement and for conditions was 0.01, for interaction time of measurement×conditions 0.02 and 0.01. ■ - cv. Orlik, control; □ - cv. Orlik, stress; ● - cv. Polo, control; ○ - cv. Polo, stress; ▲ - cv. Hera, control; △ – cv. Hera, stress; ◆ - cv. Omega, control; ◇ - cv. Omega, stress.

Gummuluru *et al.* (1989) observed a decrease of P_N and *E* under water stress for hard wheat, and after re-watering rates of these processes returned to values found before stress. Loboda (1993) observed a decrease of P_N, g_s, and *E* and an increase of water use efficiency (WUE) for several spring cereal species. Also Johnson *et al.* (1974) found that during water stress P_N and *E* of flag leaf and ear of barley and wheat were inhibited. Rekika *et al.* (1998) observed that decrease in P_N in tetraploid wheat was due to stomatal and non-stomatal factors under mild and severe water stress which was concluded from the ratio of c_i to external CO_2 concentration. According to Kaiser (1987) there are no changes in P_N even during 50 % dehydration if saturated concentration of CO_2 is used.

Before water stress, g_s of all studied cultivars differed from about 0.29 for cvs. Polo and Omega to 0.36 mol(H_2O) m^{-2} s^{-1} for cv. Hera and was decreasing during water stress to 0.16-0.17 mol(H_2O) m^{-2} s^{-1} for cvs. Polo and Orlik (Fig. 1*C*,*D*). This decrease was the highest when soil water content dropped to 35 % of full water capacity.

According to Chaves (1991), under moderate water stress CO_2 assimilation is inhibited mainly as a result of stomata closure, and carbon assimilation may drop to zero without decreasing of potential possibilities of photosynthetic apparatus. When water content in plant decreased up to 30 %, irreversible damage of chloroplasts was observed and probably this damage took place not during dehydration but during rehydration (Kaiser 1987).

Although g_s was decreasing during water stress it probably was not responsible for decreasing photosynthetic activity although Yoshie (1986) found linear correlation between P_N and g_s for a number of temperate plants and the same phenomenon was observed by Gummuluru *et al.* (1989) for hard wheat. But sometimes non-stomatal factors can be responsible for lower P_N during water stress and, *e.g.*, Legg *et al.*

(1979) showed for spring barley that closure of stomata was responsible during water deficit only for a 6 % reduction of P_N.

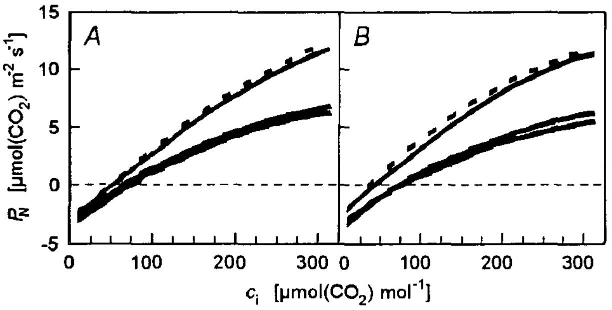

Fig. 2. The most representative CO_2 curves of two cultivars of barley (*A*) and two cultivars of wheat (*B*) grown under controlled and stressed conditions. LSD was not calculated. —— cv. Orlik, control (*A*) or cv. Hera, control (*B*); — — cv. Orlik, stress (*A*) or cv. Hera, stress (*B*); • • • - cv. Polo, control (*A*) or cv. Omega, control (*B*); — • — - cv. Polo, stress (*A*) or cv. Omega, stress (*B*).

In non-stressed barley plants P_N and g_s were higher than in non-stressed durum wheat plants and both parameters decreased with lowering water availability (Rekika *et al.* 1995). Under water stress g_s was more affected than P_N for barley and durum wheat (Rekika *et al.* 1995).

Wheat cultivars with large root growth had large leaf growth rate and large leaf area ratio and they had high WUE and low ratio of intercellular to ambient CO_2 partial pressure. This was a result of large differences in g_s associated with small differences in P_N (Boogaard *et al.* 1996).

Lower g_s under water stress is probably a result of higher production of ABA in root system, and this hormone is transported to leaves and causes stomata closure (Zhang and Davies 1989). ABA produced in mesophyll chloroplasts during water stress diffuses to stomatal cells and causes their closure. Stomatal sensitivity increases with leaf temperature (Cornic and Ghashghaie 1991) or with water potential of the leaves (Tardieu and Davies 1992), and depends on degradation of transported ABA in mesophyll (Trejo *et al.* 1993).

There were no significant differences in c_i between studied species and cultivars and its value was similar [270-300 μmol(CO_2) mol^{-1}] both for control and stressed plants during the studied period (Fig. 1*E,F*). According to Lawlor (1995), during water shortage c_i does not change or decreases. In wheat and barley seedlings c_i did not change under mild water stress, but increased under moderate and severe stresses for mulberry plants (Ramanjulu *et al.* 1998). On the other hand, Lal *et al.* (1996) found under first stages of water stress a low c_i due to partial stomatal closure and after that c_i remained constant or increased, what authors explained as decreasing of mesophyll conductance. Also the ratios of P_N to g_s and c_i to ambient CO_2 concentration were probably connected with non-stomatal effects for barley plants grown at 75, 35, 25, and 15 % of total available soil water (Arnau *et al.* 1997).

Under all studied c_i [0–300 μmol(CO_2) mol^{-1}] P_N was much higher in unstressed than in stressed plants and at 300 μmol(CO_2) mol^{-1} was about 11-12 μmol m^{-2} s^{-1} for unstressed plants and about 5.2-6.5 for stressed plants, respectively (Fig. 2). CO_2 compensation concentration of studied seedlings was 30-50 and 70-75 μmol(CO_2) mol^{-1}, respectively, for controlled and stressed plants (Fig. 2). Higher CO_2 compensation concentration under water stress observed for all studied genotypes may suggest higher contribution of photorespiration to gas exchange (Fig. 2). Usually the ratio of photorespiration to P_N is higher for dehydrated plants than for plants having enough water (Tourneux and Peltier 1995). Decrease of *E*, P_N, and dark respiration rate and increase of photorespiration rate for wheat cv. Courtot under water stress was observed by Renou *et al.* (1990): they found decrease of CO_2 concentration in chloroplasts of stressed plants but c_i did not change. Low CO_2 concentration in chloroplasts during water stress favours oxygenic RuBPCO activity because of rise of O_2/CO_2 and decrease of temperature optimum of photosynthesis (Cornic and Ghashghaie 1991).

Although g_s decreased during water stress, c_i was similar for stressed and control seedlings and was not limiting for P_N. Thus, decrease of g_s under stress could not be the cause of drop of P_N for the studied seedlings and P_N was rather limited by non-stomatal factors.

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