PHOTOSYNTHETICA 34 (3): 473-476, 1997

BRIEF COMMUNICATION

Stomatal limitation of photosynthesis as affected by water stress and CO_2 concentration

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Abstract

A water stress effect on photosynthesis and transpiration of wheat seedlings at 50-500 μmol(CO_2) mol^{-1} was measured in an open gas exchange system. The limitation of photosynthesis by stomatal conductance was quantified by a stomatal control coefficient of the net photosynthetic rate. The stomatal control coefficient increased linearly as the water potential of root media decreased to -1 MPa, and it decreased with increasing CO_2 concentration.

Additional key words: irradiance; photon fluence density; stomatal conductance; transpiration; water potential.

Components of a complex process may limit its rate increase to various extents. Limitation of a process by a component is a measure of relative deficiency in the capacity of given component. Identification of the most limiting component may often be of practical importance (Jones *et al.* 1990).

The analysis of photosynthetic sensitivity to environmental and internal variables based on biochemical modelling (Giersch *et al.* 1990, Woodrow *et al.* 1990) may be used for determination of limitations. Control coefficients are defined as the ratio of the relative increase in the rate of the process to the relative increase in the capacity of the component. From the control theory it is apparent that the sum of all control coefficients should be 1.0 (Woodrow *et al.* 1990).

Stomata control the diffusive mass transfer of H_2O and CO_2 between environment and the leaf interior. Stomatal conductance (g_s) should be low to prevent an excessive water loss and hereby limit the CO_2 assimilation. The net photosynthetic rate (P_N) is

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Received 11 March 1996, *accepted* 10 June 1997.

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Abbreviations: PEG - polyethylene glycol; PFD - photon fluence density.

This work was partially sponsored by the Grant Agency of the Czech Republic, project number 501/93/0329.

a result of the interaction between source - ambient air plus stomata, and sink - assimilation processes in mesophyll. The demand function of mesophyll is P_N as a function of intercellular space CO_2 concentration, c_i (Farquhar and Sharkey 1982, see also Fig. 1*A*). The stomatal control coefficient of net photosynthetic rate, C_S, and the mesophyll control coefficient, C_M, may be calculated according to following formulae (Jones 1985, Woodrow *et al.* 1990):

$$C_S = \frac{g_S}{P_N}\frac{dP_N}{dg_S} = \frac{P_N'}{g_S + P_N'} \qquad C_M = 1.0 - C_S \tag{1}$$

where P_N is a function of intercellular concentration of CO_2, and P_N' is derivative of P_N with respect to c_i.

For evaluation of the derivative of P_N we have been using an analytical model of the demand function (Farquhar *et al.* 1980) which is approximately valid at limiting the photon flux density (Sage 1990):

$$P_N = \frac{P_{MAX}\left(c_i - \Gamma^*\right)}{c_i + 2.33\ \Gamma^*} - R_D \tag{2}$$

Γ^* is photocompensation concentration of CO_2, R_D is the dark respiration rate.

$$P_N' = \frac{P_{MAX}\ 3.33\ \Gamma^*}{\left(c_i + 2.33\ \Gamma^*\right)^2} \tag{3}$$

The value of Γ^* in C_3 plants as a function of temperature T [°C] may be calculated from a formula given by Brooks and Farquhar (1985):

$$\Gamma^* = 42.7 + 1.68\ (T - 25) + 0.0012\ (T - 25)^2 \tag{4}$$

The effect of CO_2 and water stress on stomatal limitation was estimated from the photosynthesis and transpiration measurements. Seedlings of winter wheat cv. Chlumecká 12 were grown at 20 °C, 200 μmol m^{-2} s^{-1} PFD, in Hoagland nutrient solution containing *PEG 8000* (osmotic potential -0.21 MPa), till the second leaf had been fully developed. The P_N response to CO_2 concentration from 100 to 800 μmol(CO_2) mol^{-1} was measured in an open gas exchange system with an infrared gas analyser (*URAS 3G*, *Hartman & Braun*, Germany) and a thermocouple psychrometer. The

Table 1. Results of fitting intercellular CO_2 [μmol(CO_2) mol^{-1}] responses of the net photosynthetic rate, P_N [μmol m^{-2} s^{-1}] by Eq. (2) and of stomatal conductivity, g_s [mmol m^{-2} s^{-1}] by the linear function ac_i+b.

	control						stress					
	P_{MAX}	R_D	R^2	a	b	R^2	P_{MAX}	R_D	R^2	a	b	R^2
1	20.7	1.1	0.98	-0.352	254	0.98	16.9	1.1	0.99	-0.052	81	0.84
2	22.6	0.1	0.96	-0.605	370	0.96	23.9	1.1	0.99	-0.099	103	0.74
3	17.7	1.3	0.99	-0.674	327	0.96	16.2	1.1	0.997	-0.137	108	0.96

PFD provided by a tungsten halogen lamp and filtered through a copper sulphate solution was 400 μmol m^{-2} s^{-1}. The leaf temperature ranged from 22.5 to 23.5 °C.

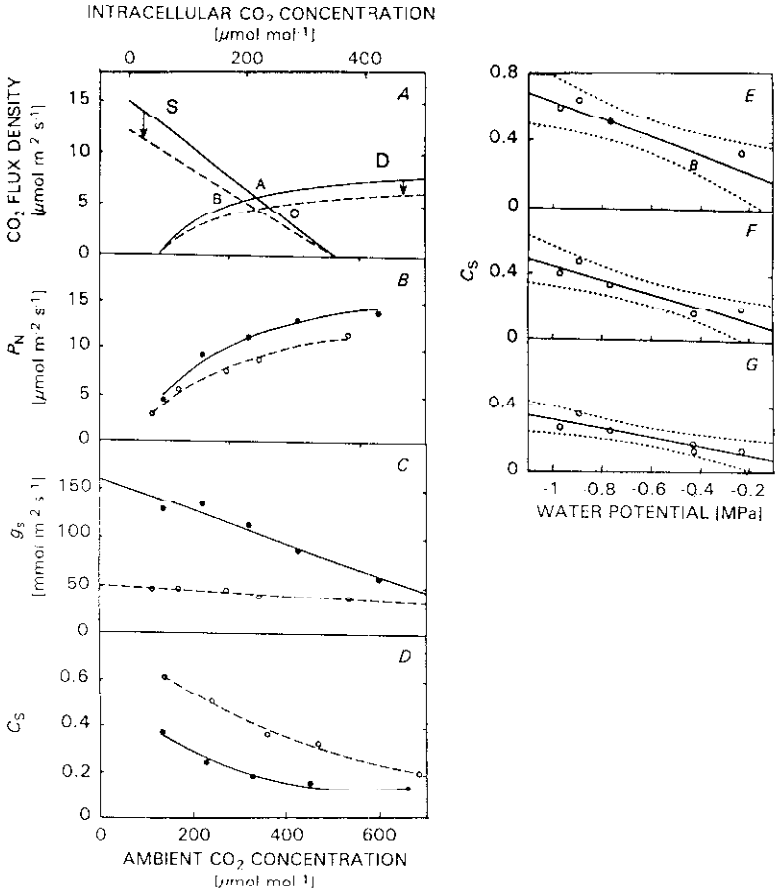

Fig. 1. *A*: Steady state net photosynthetic rate (P_N) is at the intercept of the source function, S, and demand function, D. The source function is linear with the slope equal to the negative stomatal conductance (g_s). The demand function is P_N as a function of the intercellular concentration of CO_2, c_i. As shown, stomatal limitation, defined as a sensitivity by Eq. (1), is larger than the mesophyll limitation. The same relative decreases in S and D cause different effects on P_N. D is less steep at point A than S, so a decrease in P_N caused by stomata closure (A→B) (proportional to the stomatal sensitivity coefficient C_s) is lesser than the decrease caused by mesophyll capacity (A→C). P_N (*B*) and g_s (*C*) of wheat *cv.* Chlumecká 12, second leaf, at PFD 400 μmol m^{-2} s^{-1}, 22 °C and either -0.23 MPa or -0.97 MPa water potential of nutrient solution; the P_N-c_i dependences were fitted by hyperbolic functions (2). The stomatal limitation of P_N at -0.23 MPa (*solid*) or -0.97 MPa (*dashed*) water potential of nutrient solution (*D*) was calculated from the fitted data in *B* and *C*. Stomatal limitation of wheat leaves was calculated at 150 (*E*), 350 (*F*) and 550 (*G*) μmol(CO_2) mol^{-1} and different water stresses imposed by lowered osmotic potential of nutrient solution.

The osmotic potential of the nutrient solution was measured with a thermocouple hygrometer (*HR-33T, Wescor*, USA) after the experiment. Water stress was imposed by lowering the water potential of nutrient solution with added PEG during measurement. The P_N as a function of c_i was fitted by Eq. (2), and the stomatal control coefficient was calculated according to Eqs. (1), (3), and (4).

Fit of experimental values by the model was close (Table 1, Fig. 1*B,C* for set 1). The stomatal control coefficient correlated well with the osmotic potential of the nutrient solution at a constant CO_2 concentration, and it decreased with increasing CO_2 concentration (Fig. 1*D-G*). The values of Pearson correlation coefficient [-0.91, -0.92, and -0.89 at concentrations 150, 350, and 550 μmol(CO_2) mol^{-1}] were highly significant.

The stomatal control coefficient value is not affected by paralel changes in both g_s and P_N. In our experiments, the decrease in g_s was higher than that in P_N which was typical for short-term water stress experiments. The stomatal control coefficient depended strongly on all factors directly affecting the stomatal closure, *e.g.*, the relative humidity of air (values not shown). It may be used as a simple measure of ratio of photosynthetic limitations by stomata and mesophyll.

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