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BRIEF COMMUNICATION

Hydraulic conductance, stomatal conductance, and maximal photosynthetic rate in bean leaves

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Abstract

A positive correlation was found between steady state values of hydraulic (L_{pA}) and stomatal conductance (g_s) of French bean leaves: both were lower in the dark than in the light and lower in water-deficient plants than in the well-watered ones. The relative rate of stomatal opening after a pressure rise in the xylem was also positively related to L_{pA}. The L_{pA} and g_s were both related to the maximal photosynthetic rate at saturating CO_2 concentrations.

Additional key words: *Phaseolus vulgaris* L.; plant watering; stomatal opening.

Several papers describe changes in hydraulic conductance of the xylem of different plants (especially in trees) as being caused by embolism in the xylem of branches and trunk (Sperry and Tyree 1988, Cochard *et al.* 1992, Zotz *et al.* 1994). Little is known about hydraulic conductance in leaves (L_{pA}), in which water flows through smaller vessels and through cell walls to the sites of evaporation. There is some evidence that L_{pA} in herbaceous species is higher at higher transpiration rates (Hailey *et al.* 1973, Black 1979, Boyer 1985). This suggests a correlation between L_{pA} and stomatal conductance (g_s). The evaporation from epidermis is considerable in some species (Shackel and Brinckmann 1985), or epidermis is in a close hydraulic contact with the sites of evaporation of the mesophyll in other species (Nonami *et al.* 1991). Low L_{pA} can limit water flow to the sites of evaporation and thus g_s. In whole sugarcane plants the changes in vapour phase and liquid phase conductances are coordinated (Meinzer and Grantz 1991). In this work, L_{pA}, g_s and the maximal photosynthetic rate (P_{max}) were measured simultaneously in bean leaves.

Dwarf bean (*Phaseolus vulgaris* L.) cv. Oregon plants were grown in a growth chamber (for details see Moldau *et al.* 1993). Two series of experiments (in spring and in autumn) were carried out in which leaves from 30 different plants were

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measured. Some plants were measured after being kept in a darkened leaf chamber for one hour, and some plants when they were not watered for 2 d.

The method used involves the application of pressure to leaf petioles in water in a pressure chamber, simultaneous measurement of the infiltration rate, measurement of the transpiration rate and of leaf temperature to estimate g_s (Sôber 1996), and measurement of radiant energy- and CO_2-saturated photosynthetic rate with the gas-analyser *LI-6262*. Leaf parameters were measured in a special leaf chamber (Sôber and Moldau 1977) at photon flux density of 1010 µmol m^{-2} s^{-1}, CO_2 concentration 300 or 1200 µmol mol^{-1}, and relative humidity 40-50 %. The g_s and relative rate of its increase per unit pressure (P) increase,

$$v = \Delta g_s \, \Delta t^{-1} \, g_s^{-1} \, \Delta P^{-1} \qquad (1)$$

were calculated using air humidity and leaf temperature data. [The relative rate was involved, because it was equal to coefficient k in the exponent, if g_s changed exponentially between two steady state values g_{s1} and g_{s2}: $g_s = (g_{s2} - g_{s1})\,e^{-kt}$. The coefficient k depended on the process of opening and not on absolute values of g_s.]

Infiltration of leaves was initiated by a pressure rise in the pressure bomb with the leaf petiole under water, and the change in leaf water content was monitored by β-gauge technique (Mederski 1961, Sôber 1996). The water potential in intercellular spaces of infiltrating leaves was assumed to be equal to zero. The L_{pA} was defined and calculated per leaf area by the formula

$$L_{pA} = F_w \, \Delta P^{-1}, \qquad (2)$$

where F_w was the flow rate of liquid water through the petiole and the leaf into intercellular spaces per leaf area, and ΔP was the pressure difference between the ends of liquid water pathways. The F_w was calculated from the infiltrating water flow rate F_i, measured by the β-gauge technique and corrected by the transpiration rate, E (the actual liquid flow rate was higher than the measured F_i, by E and $E < 0.2\ F_i$ in our experiments):

$$F_w = F_i + E. \qquad (3)$$

The infiltration rate

$$F_i = \Delta w / \Delta t \qquad (4)$$

where leaf water content per leaf area, w, was determined through relative difference of leaf wet mass per area, x, from its final value, x_e:

$$w = x_e[1 + (x - x_e)/x_e] - x_d \qquad (5)$$

where $(x-x_e)/x_e$ was determined by β-gauge techniques:

$$(x - x_e)/x_e = (\ln I_e - \ln I)/(\ln I_0 - \ln I_e) \qquad (6)$$

I and I_e in Eq. (6) are current and final values of β-irradiance, respectively, and I_0 is β-irradiance in the absence of the leaf in the leaf chamber. The leaf dry and wet masses per area, x_d and x_e, in Eq. (5) were obtained immediately after measurement of each leaf. [As the absorption of β-radiation is described by the equation

$$I = I_0 e^{-nx} \tag{7}$$

the relative changes in x could be calculated independently of variable coefficient n in Eq. (7), which was different in different leaves, but did not change during the infiltration of one leaf.] As the L_{pA} decreased some time after pressure rise (Sôber 1996) and g_s increased, only the initial values are presented in this work.

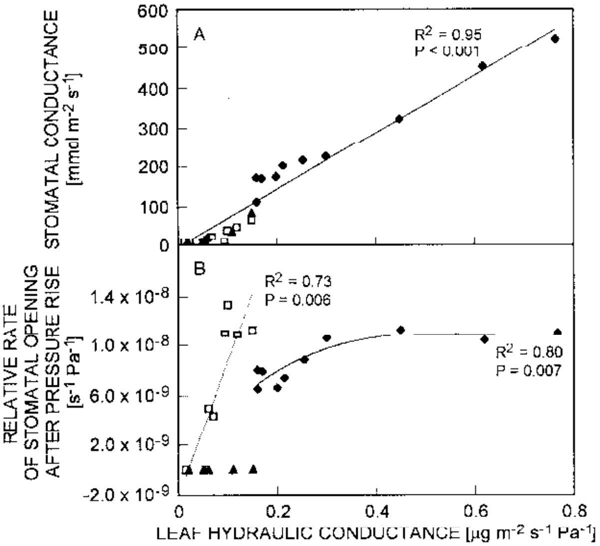

Fig. 1. Relationships between leaf hydraulic conductance (L_{pA}) and stomatal conductance, g_s, (*A*) or between L_{pA} and relative rate of stomatal opening after equal pressure rise in the pressure chamber, v (*B*). Initial values of L_{pA}, g_s, and v are used. ◆ - well-watered plants, □ - water-deficient plants, ▲ - plants, kept in the dark for 1 h. Different points represent leaves from different plants.

The measured initial values of L_{pA} varied greatly (values between 0.03 and 0.80 μg m^{-2} s^{-1} Pa^{-1}) and did not depend on the pressure applied in the pressure chamber. The highest values of L_{pA} calculated per area of intercellular spaces are (Sôber 1996) similar to those reported for most cells of higher plants (Steudle *et al.* 1983). The other measured values of L_{pA} were up to 30 times lower but never higher than the values of hydraulic conductance of individual cells. Thus the measured hydraulic resistance must be located in cells and not in infiltrating intercellular spaces. The initial L_{pA}, L_{pA0} correlated with the initial g_s, g_{s0} estimated before the pressure rise (Fig. 1*A*). All values of L_{pA0} and g_{s0}, measured in the dark or on the leaves of water-deficient plants, were low in comparison to those measured in the light on the leaves of watered plants. The initial relative rate of stomatal opening per unit pressure increase, v_0, was also related to L_{pA} (Fig. 1*B*), especially in water-deficient plants.

One possible explanation of the observed relationships is that relatively high and variable hydraulic resistance is located in the bundle sheath and/or mesophyll tissue. The rate of water flow both to intercellular spaces and to epidermis is then regulated by this resistance. If water transport to the epidermis is improved, its water potential increases, causing stomatal opening. The rate of this response at the same L_{pA} (Fig. 1*B*) can depend on water deficit because pH and abscisic acid concentration of the apoplastic compartment of leaves are changing under water stress (Wilkinson and Davies 1997).

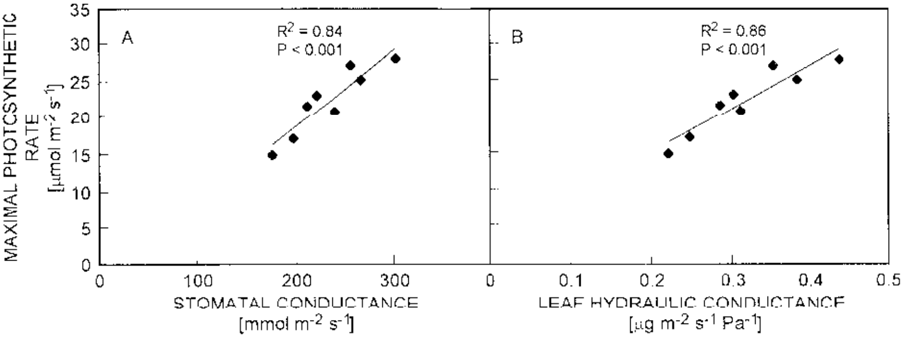

Fig. 2. Relationships between stomatal conductance (g_s) and CO_2- and radiant energy-saturated photosynthetic rate (P_{max}) (*A*) or between leaf hydraulic conductance (L_{pA}) and CO_2- and radiant energy-saturated photosynthetic rate, P_{max} (*B*) in well-watered plants.

The factors which determine the variability in L_{pA} are unclear. The lower L_{pA} under water deficit can be caused by air blockage in the leaf xylem (Cochard *et al.* 1992). However, differences in L_{pA} in light and dark can not be explained in this way and deserve a more detailed study. On the other hand, the steady state values of g_s and photosynthetic rate are often correlated (Wong *et al.* 1985, Ball *et al.* 1987). This was also the case in our experiments (Fig. 2*A*). In addition, the P_{max} was positively related with L_{pA} (Fig. 2*B*). L_{pA} can be different in different areoles between veins (this was confirmed by the patchy infiltration seen in water-deficient leaves) and can be a primary cause of the patchy distribution of g_s and photosynthetic rate discussed by different authors (Terashima 1992, Mott 1995).

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