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Epidermal Diffusive Conductance as Related to Leaf Water Potential and Photon Flux Density

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Abstract. Response of epidermal diffusive conductance to simultaneous changes in leaf water potential and photon flux density was studied in primary bean leaves. Values of epidermal conductance corresponding to every photon flux density decreased with decreasing leaf water potential below -6.9×10^5 Pa; slight decrease was followed by a rapid one at water potential ranging from -8.0 to -10.5×10^5 Pa. In the leaves with water potential lower than -10.5×10^5 Pa neither the saturated photon flux density (1200 μeinstein $m^{-2}s^{-1}$) induced photoactive stomatal opening.

Negative influence of one factor could be partially compensated by positive influence of the other. These results were in good agreement with the considered mechanism of action of leaf water potential and photon flux density on epidermal conductance.

Stomatal functioning reflects a compromise between the conflicting requirements for controlling water use and the development of plant water deficit, while maintaining adequate levels of photosynthesis and evaporative cooling. Under field conditions such factors as irradiance, ambient humidity and CO_2 concentration, air and leaf temperature, leaf water status *etc.* often change simultaneously. Therefore in addition to direct effects of each of these factors on epidermal conductance, also their interactions must be taken into account (HALL *et al.* 1976).

The aim of this work was to study influence of simultaneous changes in photon flux density and leaf water potential as the effects of these two factors separately on epidermal diffusive conductance in primary bean leaves were discussed in previous papers (SOLÁROVÁ *et al.* 1977, ŠESTÁK *et al.* 1978).

Material and Methods

Seedlings of French bean (*Phaseolus vulgaris* L. cv. Jantar) were grown in plastic pots with coarse sand and nutrient solution in an air conditioned cabinet (CEL 37—14, Sherer, Michigan, USA; photon flux density (400 to 700 nm) 300 μeinstein $m^{-2}s^{-1}$, 16 h day including two twilight periods, day/night temperature and relative humidity 25/16 °C and 60/80%, respect-

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ively. Water stress in whole plants was induced by cessation of watering. During the following five days water potential in primary leaves decreased on the average from -4 to -11×10^5 Pa (for details see POSPÍŠILOVÁ *et al.* 1976, SOLÁROVÁ *et al.* 1977). Water potential was measured with a droplet thermocouple psychrometer. The conductance of epidermes was determined by a diffusion porometer Lambda LI-60 with chamber 15 S and lithium chloride Hydrosensor 4-4817. The porometer was calibrated by metal plates with varying numbers of holes. The temperature during exposure was 25 °C, relative humidity 70% and photon flux densities 60, 120, 400, 750 and 1200 μeinstein $m^{-2}s^{-1}$. The length of exposure necessary for setting up equilibrium epidermal conductance for different photon flux densities and leaf water potentials was determined in preliminary experiments.

Results and Discussion

Under saturated photon flux density epidermal diffusive conductance (g_{ep}) with increasing water stress slightly increased, at optimum values of water potential (ψ_w from -6.0 to -7.0×10^5 Pa) it reached a maximum and with further decrease in ψ_w decreased slightly and then sharply to very low value (Fig. 1, for details see also SOLÁROVÁ *et al.* 1977). Under lower photon flux densities this shape of response curve became less expressive than under higher photon flux densities. However, the ranges of ψ_w where dominating decrease in epidermal conductance occurred were similar (approximately from -8.0 to -10.5×10^5 Pa) under all photon flux densities (Fig. 1).

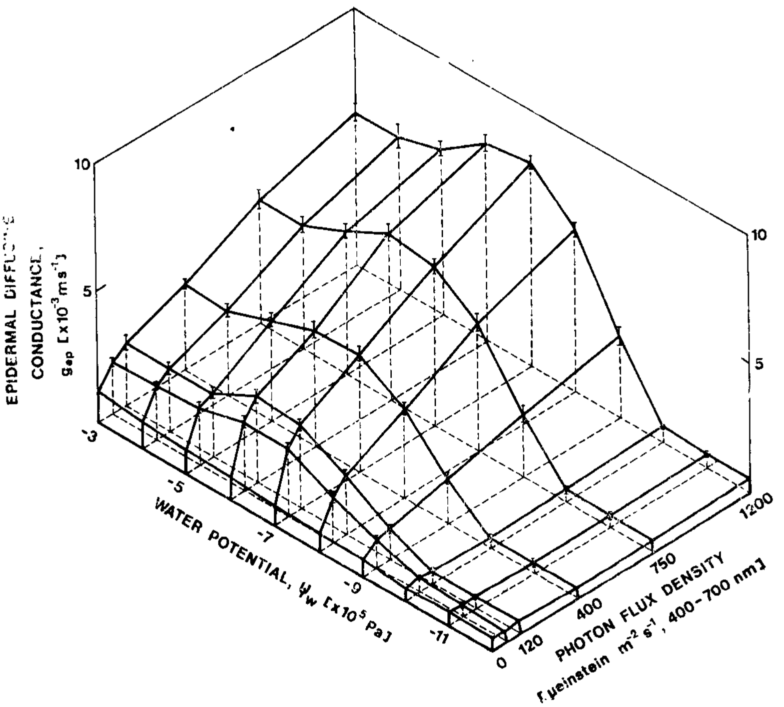

Fig. 1. Effect of photon flux density and water potential of primary bean leaves on diffusive conductance of their epidermes.

The effect of photon flux density on the dependence of leaf resistance (leaf resistance $= 1/g_{ep}$) on ψ_w was studied by MAKKING and VAN HEEMST (1972) in French bean, by BEADLE *et al.* (1973) in maize and sorghum and by KASSAM (1973) in broad bean. While in French bean, maize and sorghum photon flux density influenced only the resistance of leaves with ψ_w higher than that which induced conspicuous increase in leaf resistance, in broad bean also this „critical" value of ψ_w changed and under lower photon flux densities the leaf resistance responded to any decrease in ψ_w. Our results were rather in agreement with the results of MAKKING and VAN HEEMST (1972) and BEADLE *et al.* (1973), as the range of ψ_w where closing reactions of stomata appeared was practically the same under all photon flux densities.

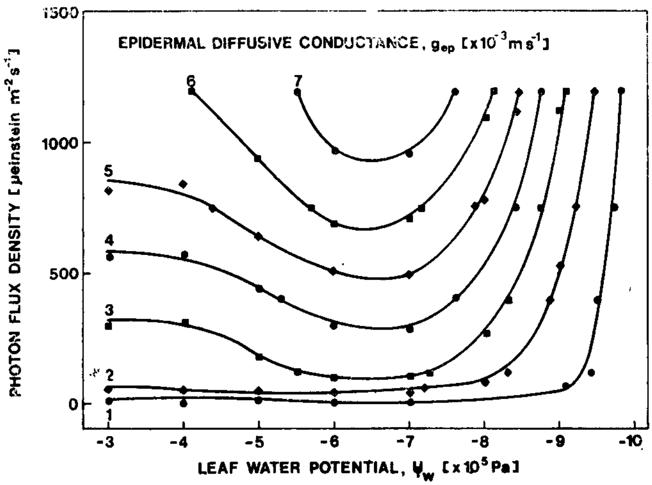

Fig. 2. Isogram of epidermal diffusive conductance as a function of photon flux density and leaf water potential.

Epidermal diffusive conductance of intact leaves increases in response to increasing photon flux density. There are usually two phases in the response curve: a rapid increase over low photon flux densities followed by a gradual increase over higher ranges (for review see *e.g.* BURROWS and MILTHORPE 1976). Water stress induced changes of both these phases but not to the same extent. Thus the shape of curves expressing dependence of epidermal conductance on photon flux density changed (Fig. 1). With the decrease in leaf ψ_w the photon flux density necessary for significant increase in epidermal conductance due to photoactive stomatal opening increased, and in the leaves with ψ_w lower than -10.5×10^5 Pa neither the highest photon flux density (1200 µeinstein $m^{-2}s^{-1}$) induced photoactive stomatal opening. The values of g_{ep} corresponding to every measured photon flux density (including saturated one) decreased with the decrease in ψ_w below optimum; slight decrease was followed by a rapid one when ψ_w reached values from -8.0 to -10.5×10^5 Pa.

Differences in response of leaf resistance to increasing photon flux density were found by HANSEN (1971) among sugar beet leaves with relative water contents 85, 75 and 57 %, and by BEHBOUDIAN (1977) among leaves of cucumber, pepper and tomato with water potentials from -3.2 to $-18.4 \times$

$\times 10^5$ Pa. ČATSKÝ *et al.* (1973) and ALLEN *et al.* (1975) also determined a higher minimum resistance in leaves of unirrigated than of irrigated maize or peanut plants, but the shape of photon flux density response curves for both variants was uniform.

Maximal values of g_{ep} were reached only under saturated photon flux density (1200 μeinstein $m^{-2}s^{-1}$) and optimal leaf ψ_w (from -6.0 to -7.0×10^5 Pa). With the decrease in any of the two factors g_{ep} decreased. The negative influence of one factor on g_{ep} could be partially compensated by positive influence of the other. Thus the same values of g_{ep} were found under

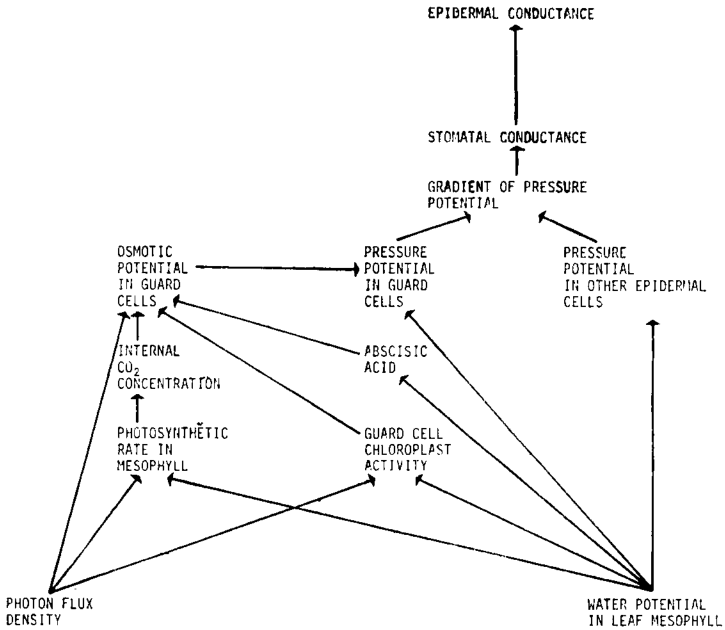

Fig. 3. Possible ways of affecting epidermal diffusive conductance by leaf water potential and photon flux density.

Epidermal conductance is mainly determined by the degree of stomata opening and thus by the gradient of pressure potential between guard cells and other epidermal cells. The corresponding gradient of osmotic potential due to accumulation of K^+ and organic anions in guard cells enables the equilibrium in water potential to be attained.

The response of stomata to water stress can be purely physical: decrease in pressure potential both in guard cells and other epidermal cells to zero as a consequence of a lowered water potential in the leaf. Abscisic acid which is rapidly formed in the leaf tissue under water stress has ability to cause stomatal closure probably by decrease in accumulation of K^+ in guard cells. Stomatal closure can be also mediated by changes in guard cells chloroplast activity, as cyclic photophosphorylation can provide energy for the accumulation of K^+ (for review see BOYER 1976).

Both, leaf water potential and photon flux density, can influence the activity of chloroplasts in leaf mesophyll and thus internal CO_2 concentration. Sensitivity to internal CO_2 concentration is a common feature of stomata. A direct stomatal response to irradiance was observed *e.g.* by ZEIGER *et al.* (1977).

higher photon flux density and lower ψ_w as under lower photon flux density and higher ψ_w (Fig. 2). These results were in good agreement with the mechanism of action of photon flux density and leaf ψ_w on g_{ep} considered in Fig. 3. Changes of any of these quite different factors evoke the pathways leading to the same final reaction: change in the gradient of pressure potential between guard cells and other epidermal cells. Some connections exist even between pathways leading to this final reaction.

When ψ_w decreased below -10.5×10^5 Pa, the stomata did not open at any photon flux density and therefore in this range of ψ_w epidermal conductance was limited by water stress. Epidermal conductance was limited also by very low values of photon flux density. Interactions between these two factors were not observed.

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