

Relations between Leaf Resistance, CO₂-Concentration and CO₂-Assimilation in Maize, Beans, Lalang Grass and Sunflower*

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Abstract

Theoretical considerations concern the relations between leaf resistances for CO₂ and water vapour, leaf transpiration, net CO₂-assimilation and external and internal CO₂-concentrations. Experiments with maize, beans and lalang grass show that the stomatal conductivity can be described as controlled by the CO₂-concentration in the stomatal cavity and consequently by the rate of CO₂-uptake. At external CO₂-concentrations below 300 vpm the internal CO₂-concentration is proportional to the external concentration, but above 300 vpm it no longer rises. In some cases the regulation disappears and in sunflower no regulation was found at all. Because of this, the CO₂-assimilation in sunflower responds more to external CO₂ than in maize and beans, but sunflower has also a less efficient water use. Maize uses water more efficiently than beans, because it has a lower setpoint for the internal CO₂-concentration. When regulation is present, stomatal conductivity is best calculated as a function of net CO₂-assimilation and the setpoint for internal CO₂-concentration.

The quantitative description of stomatal behaviour is a central problem in models concerning growth, photosynthesis and transpiration of plants and crop surfaces. Recently RASCHKE (1975) reviewed the literature on stomatal action. The effect of water on stomatal aperture is one of the most important, and overrules other internal and external influences in many cases. LANGE *et al.* (1971) reported a direct reaction of the stomata to the humidity of the ambient air, irrespective of the water status of the leaf. However, usually water acts as an internal factor, resulting in a feedback loop of leaf water content and stomatal aperture. Stomatal aperture limits the rate of net CO₂-assimilation (P_n), if the radiant flux densities are not too low. In this situation P_n can still be increased by raising the CO₂-concentration in the ambient air.

When water is not a limiting factor, two types of stomatal reaction may be distinguished (RASCHKE 1975): (1) The stomata apparently respond to the CO₂-concentration in the intercellular spaces. When the external CO₂-concentration is increased the stomata close, sometimes to such an extent that P_n remains constant even under saturation with radiant energy (GIFFORD and MUSGRAVE 1970). (2) The stomata remain just open and respond little to CO₂ and light. In this case the mesophyll resistance is the main limiting factor to P_n under high illuminance, so that the P_n should increase with external CO₂-concentration. Transition to the first type may be caused by

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242 abscisic acid, which is naturally produced when a slight water stress occurs. RASCHKE (1975) mentions some examples of both reaction types; *e. g.* (1) *Zea mays* (GIFFORD and MUSGRAVE 1970). RASCHKE's quotation of experiments of WHITEMAN and KOLLER (1967) with *Helianthus annuus* is not correct, since their data show a negligible response of stomatal aperture to internal CO₂-concentration. (2) *Xanthium strumarium*.

Literature data sustaining RASCHKE's opinion are still scarce. In this paper more evidence will be given in favour of it. For the first reaction type a description is developed which can be used in models for growth, photosynthesis and transpiration of plants and crop surfaces.

Theoretical Considerations

The CO₂-concentration within the stomatal cavity, [C_i kg m⁻³] cannot be measured directly, but must be computed from P_n [kg CO₂ m⁻² s⁻¹] and the sum of resistances, Σr_c [s m⁻¹] for CO₂-diffusion from the external source of CO₂, C_e [kg m⁻³], according to the relation

$$P_n = \frac{(C_e - C_i)}{\sum r_c} \quad (1)$$

Since accurate measurements of leaf temperature are difficult to make, leaf and boundary layer resistance were computed by using an expanded Penman equation for transpiration:

$$E = \frac{sH + \frac{(e_s(T) - e)qc_p}{r_{b,h}}}{s + \gamma \frac{(r_{b,v} + r_{l,v})}{r_{b,h}}} \frac{1}{\lambda} \quad (2)$$

where *E* is the transpiration rate [kg H₂O m⁻² s⁻¹], *s* the slope of the saturated vapour pressure curve at air temperature [mbar °C⁻¹], *e* the actual vapour pressure of the air [mbar], and *e_s(T)* the saturated vapour pressure at air temperature [mbar], *H* is the available absorbed radiative energy per leaf area [J m⁻² s⁻¹], *qc_p* the volumetric heat capacity of the air [J m⁻³ °C⁻¹] (1240), *γ* the psychrometric constant [mbar °C⁻¹] (0.67), and *λ* the heat of vaporization of water [J kg⁻¹] (2.45 × 10⁶); *r_{b,v}* and *r_{l,v}* are the boundary layer resistance and leaf resistance for water vapour [s m⁻¹], and *r_{b,h}* is the boundary layer resistance for heat [s m⁻¹]. The boundary layer resistances are found from similar measurements with a wet piece of filter paper of the same shape and size as the leaf, assuming a zero "leaf resistance" for this paper. The ratio *r_{b,v}/r_{b,h}* equals 0.93 (MONTEITH 1973) when both sides of the leaves have stomata (*e. g.* maize), but for leaves with the stomata on one side only (beans), the ratio is twice this value.

The leaf resistance for water vapour remains the only unknown in Eq. (2), so that its value can be calculated from transpiration, air temperature and humidity measurements made simultaneously with P_n measurements.

The resistances for CO₂-diffusion can then easily be obtained since the ratio of leaf resistance against CO₂ and water vapour diffusion (*r_{l,c}/r_{l,v}*) equals 1.67, and the similar ratio for the boundary layer resistances (*r_{b,c}/r_{b,v}*) equals 1.42 (MONTEITH 1973). This ratio is not affected by the geometrical distribution of the stomata on the leaves.

The assimilation chambers are thoroughly ventilated, which ensures that the CO₂-concentration in the chamber is the same as in the outgoing air. However, the CO₂-concentration in the ingoing air is in general higher. The ingoing (C_e) and the outgoing (C_a) CO₂-concentrations are related by the dilution equation

$$C_a = C_e - \frac{A}{Q} P_n \quad (3)$$

where A is leaf area [m²] and Q the air flow through the chamber [m³ s⁻¹]. The ratio A/Q [s m⁻¹] may be considered a chamber resistance to turbulent transfer of CO₂ in series with the leaf and boundary layer resistances. It is introduced because in our equipment the concentration of the ingoing air C_e , and not of the outgoing air C_a , is kept constant.

The sum of resistances to diffusion of CO₂ can thus be set equal to

$$\sum r_c = 1.67r_{i,v} + 1.42r_{b,v} + A/Q \quad (4)$$

The value of A/Q ranges between 50 and 150 s m⁻¹.

MATERIAL AND METHODS

The maize plants (*Zea mays* L. cv. civ. 7) were four weeks old, the bean plants (*Phaseolus vulgaris* L. cv. Berna) two weeks old and the sunflower plants (*Helianthus annuus* L. cv. INRA 65.01) three weeks old. The seeds were germinated in perlite and after a week the seedlings were transferred to pots with a "half Hoagland" solution, iron being added as ferric sodium-EDTA. The plants were grown under controlled conditions at a temperature of 20 °C and irradiance (*HPL-400* lamps) of about 60 W m⁻². The beans were aerated.

The lalang grass (*Imperata cylindrica*) had been growing in pots with soil. From 8 till 12 weeks before the measurements the sods were torn and transferred to pots with a "whole Hoagland" solution. Until the measurements they stayed in greenhouse under natural light conditions (summer). The sixth (full grown) leaf of maize, the primary leaves of beans, the second leaf of sunflower and arbitrary leaves of lalang grass, all attached to the plants, were used for the measurements. These were done at irradiances up to about 400 J m⁻² s⁻¹ (400–700 nm), CO₂-concentrations 50–1200 vpm, and at a temperature of 25 °C. The equipment used to measure net CO₂-assimilation, transpiration and irradiance was described by LOUWERSE and VAN OORSCHOT (1969). Some measurements near the compensation point were made with the equipment described by CHALLA (1976).

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RESULTS

Sunflower

The maximum CO₂-assimilation $P_{n,max}$, generally increased with the CO₂-concentration (Fig. 1, *bottom*). There was no relation between $1/\sum r_c$ and P_n (Fig. 1, *top*). In all cases the stomata were wide open, the leaf resistance for water vapour $r_{i,v}$ varying from 20 to 160 s m⁻¹, so that the internal CO₂-concentration was only slightly less than the external, even for the highest irradiances. The high correlation between the internal and the external CO₂-concentration is here a consequence of the absence of regulation of the stomata which remain open even in the dark or in high CO₂-concentrations. Clearly sunflower belongs to the second reaction type as mentioned in the introduction. The same conclusion can be derived from the work of WHITEMAN and KOLLER (1967) who also studied sunflower.

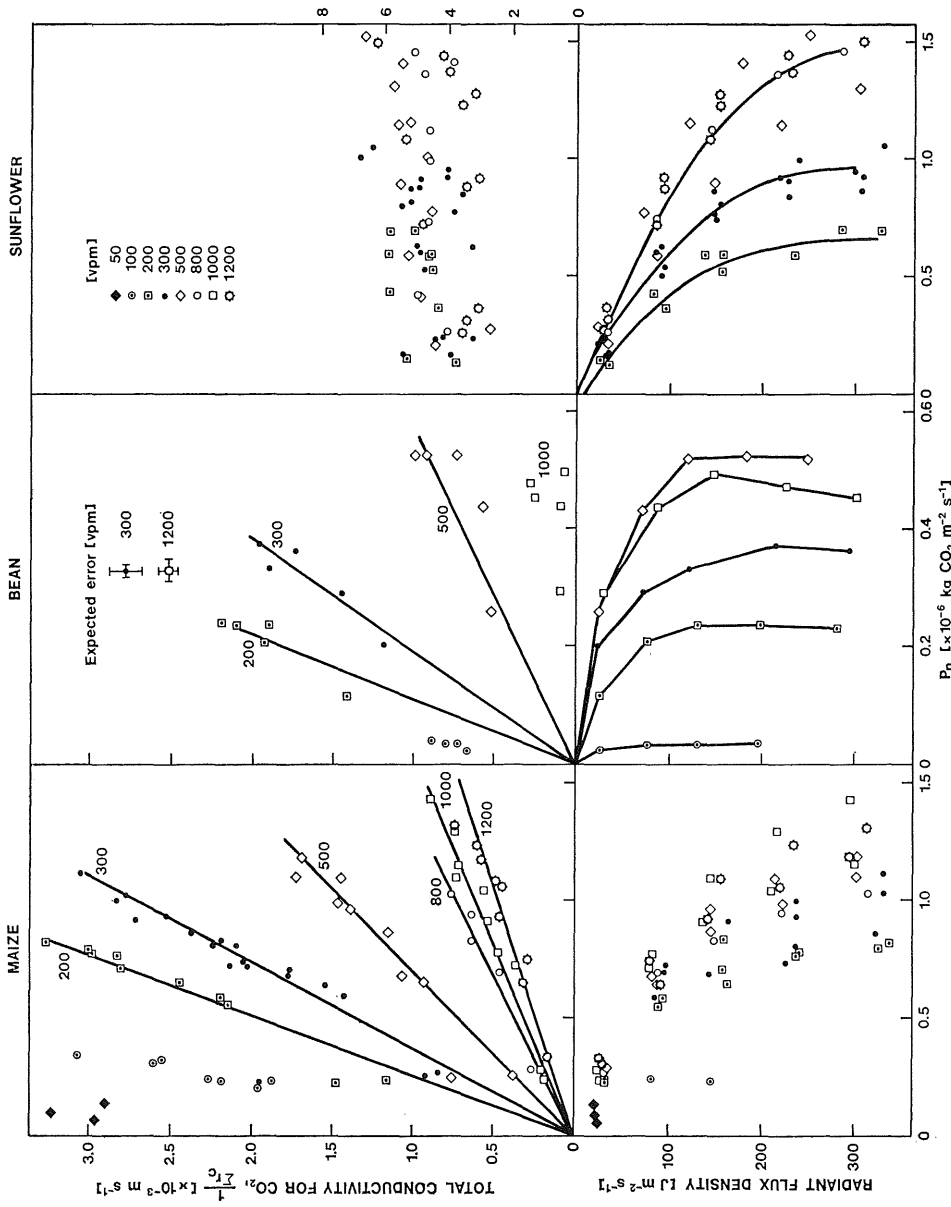


Fig. 1. Net CO₂-assimilation versus incident radiant flux density or total conductivity for CO₂ in maize, beans and sunflower for different external CO₂-concentrations.

The relation between $1/\Sigma r_c$ and P_n was entirely different from that for sunflower (Fig. 1). At each external CO₂-concentration there was a practically linear relation between them, indicating that C_i remained at an approximately constant level. This result can be used for a computation of stomatal resistance from P_n or *vice versa*, once C_i is known.

There are objections to the calculation of C_i for each observation separately. C_i can be better calculated from the slope, S , of the lines in Fig. 1, according to

$$C_i = C_e - 1/S \quad (5)$$

For maize and beans (Fig. 2) the internal CO₂-concentration is about proportional to the external concentration below 300 vpm ($0.549 \times 10^{-3} \text{ kg m}^{-3}$). Above 300 vpm saturation occurs

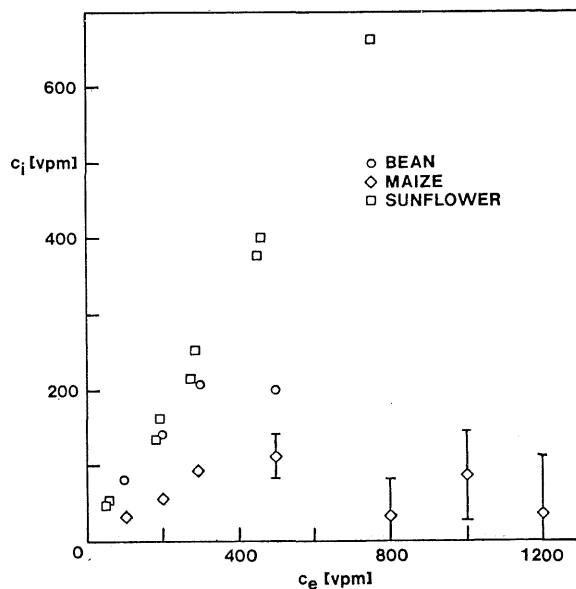


Fig. 2. Computed internal CO₂-concentrations, C_i , versus external, C_e , in maize, beans and sunflower. For computation the lines in Fig. 1 were used (for sunflower only the highest irradiance $330 \text{ J m}^{-2} \text{ s}^{-1}$).

and C_i stabilizes at about 120 vpm ($0.22 \times 10^{-3} \text{ kg m}^{-3}$) in maize and 210 vpm ($0.384 \times 10^{-3} \text{ kg m}^{-3}$) in beans. The series at $1.83 \times 10^{-3} \text{ kg CO}_2 \text{ m}^{-3}$ (1000 vpm) in beans is omitted, because of an error in the measuring of transpiration.

All the observations of Fig. 1 can be reduced to one line with a slope of unity when the variable

$$P_c = (C_s - C_r)/r_{l,c} \quad (6)$$

is plotted versus P_n (Fig. 3). Here C_s is the CO₂-concentration at the leaf surface and C_r , an assumed regulatory, internal CO₂-concentration. According to Fig. 2, C_r is best estimated as a Blackman type saturation function of C_e . The saturation levels are 120 and 210 vpm, and the proportionality factors at low external concentrations 0.4 and 0.7 for maize and beans, respectively. C_r is here related to C_s and not to C_e , since the latter cannot be detected by the leaf. Most of the scatter in Fig. 3 can be ascribed to the experimental error. For low CO₂-concentrations (50–300 vpm or $0.091\text{--}0.549 \times 10^{-3} \text{ kg m}^{-3}$) the internal CO₂-concentration is a fraction of the external CO₂-concentration (Fig. 4). The results are plotted in the same way as in Fig. 3 and with C_r

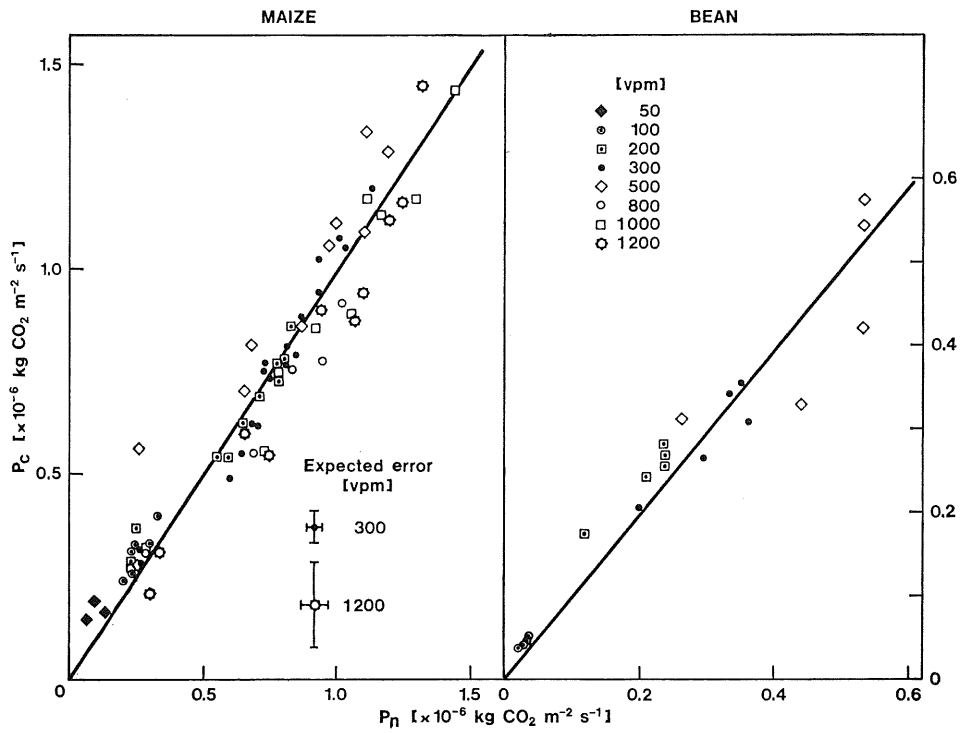


Fig. 3. Computed CO_2 -fluxes across the leaf resistance (leaf conductivity for CO_2 times the difference between the computed concentration at the leaf surface, C_s , and the assumed internal CO_2 -concentration, C_i) versus measured net CO_2 -assimilation for maize and beans at different external CO_2 -concentrations.

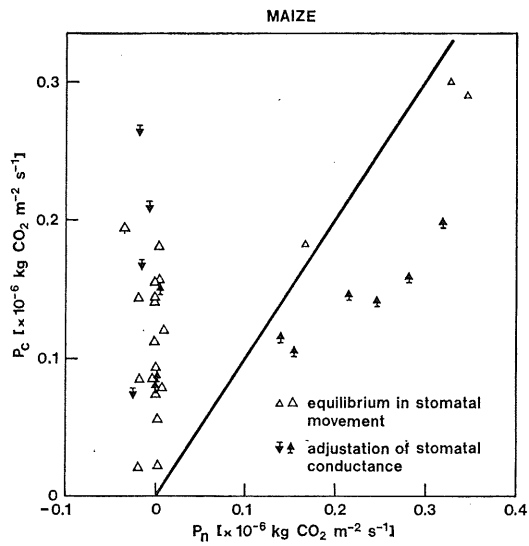


Fig. 4. Same variables as in Fig. 3 for some measurements with maize near compensation point at external CO_2 -concentrations ranging from 50 to 300 vpm. In a few cases the irradiance was increased to obtain positive CO_2 -assimilation.

chosen as $0.4 C_s$. The observational points appear to be ordered in two branches. For those at the compensation point (vertical branch) no clear rule can be derived for the value of the stomatal conductivity, probably because the required energy for normal stomatal functioning is lacking. However, at positive values of P_n , the relation with stomatal conductivity is restored and can be well described by regulation of the internal concentration at a fraction of the external CO₂-concentration. Because stomatal movements are very slow at low CO₂-concentrations, not all measurements reached equilibrium, as is indicated by an arrow in the direction of movement.

Ageing Beans

The well-known increase of stomatal resistance with increasing age of the leaf (Fig. 5) may be considered as a consequence of the decrease of photosynthesis. Within the experimental scatter of the results no tendency can be found for a change of internal CO₂-concentration with age. Therefore the decrease of P_n is due to simultaneous increase of the mesophyll resistance and stomatal resistance.

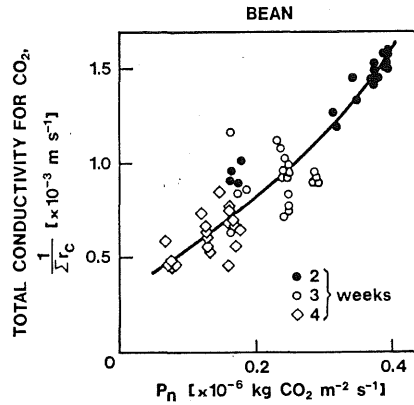


Fig. 5. Total conductivity for CO₂ versus net CO₂-assimilation in beans of different age. The external CO₂-concentration was 300 vpm, irradiances 100 – 400 W m⁻². (Experiments of W. LOUWERSE.)

Lalang Grass (*Imperata cylindrica*)

The curves of the response of net CO₂-assimilation to radiant energy were quite variable from plant to plant (Fig. 6, *bottom*). The relation between the conductivity for CO₂ and P_n for the same set was a straight line, and moreover, the variability was less (Fig. 6, *top*). The slope of the line shows that the internal CO₂-concentration, C_i , was maintained at about 140 vpm (0.256×10^{-6} kg m⁻³).

DISCUSSION

The constancy of the found relationships under various circumstances is important for their applicability in models for photosynthesis and transpiration.

For maize the internal CO₂-concentration (Fig. 2), and P_n (Fig. 1), hardly increased above 300 vpm external. This is in accordance with observations of GIFFORD and MUSGRAVE (1970), who proved that this effect is due to stomatal closure.

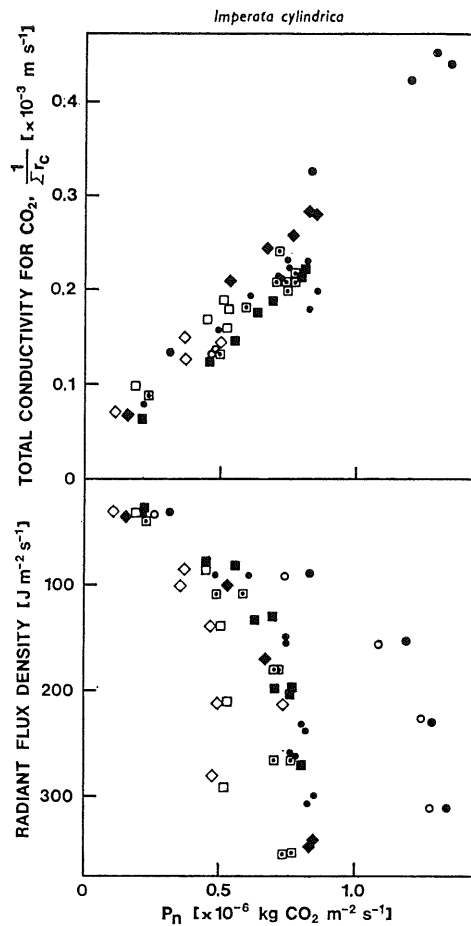


Fig. 6. Net CO₂-assimilation *versus* incident radiant flux density (*bottom*) or total conductivity for CO₂ (*top*) in lalang grass, measured at 300 vpm external CO₂-concentration 300 vpm and irradiance 100 to 400 W m⁻². (Experiments of J. L. P. VAN OORSCHOT.)

In another experiment we found that for maize the internal CO₂-concentration rises to about 220 vpm when the leaf temperatures are low (10–15 °C). Since both transpiration and assimilation are small then, this effect is of little quantitative importance.

The found results explain why the transpiration coefficient of C₄-plants is about half of that of C₃-plants, both at low and high irradiance (DE WIT 1958; DE WIT and ALBERDA 1971): C₄-plants are able to maintain a CO₂-concentration inside the stomatal cavity, which is two times lower with respect to the external CO₂-concentration, than C₃ plants are.

Since sunflower belongs to the second reaction type, a much higher transpiration coefficient can be expected. Indeed, according to a report of CETIOM (Information Techniques, 1975) sunflower has an exceptionally high transpiration rate under field conditions.

The presence of regulation of internal CO₂-concentration by the stomatal resistance depends on the plant species, but may also depend on the way the plants are grown and on their actual environmental conditions.

List of symbols

- A — leaf area [m²]
- C_a — ambient CO₂-concentration (outgoing air) [kg CO₂ m⁻³]

C_e	— external CO ₂ -concentration (ingoing air) [kg CO ₂ m ⁻³]
C_i	— internal CO ₂ -concentration [kg CO ₂ m ⁻³]
C_r	— internal regulatory CO ₂ -concentration [kg CO ₂ m ⁻³]
C_s	— computed CO ₂ -concentration at the leaf surface [kg CO ₂ m ⁻³]
E	— transpiration rate [kg H ₂ O m ⁻² s ⁻¹]
e	— pressure of water vapour in air [mbar]
$e_s(T)$	— saturation vapour pressure of air temperature [mbar]
H	— energy available for sensible and latent heat transfer [J m ⁻² s ⁻¹]
P_c	— net CO ₂ -assimilation calculated from assumed internal regulatory CO ₂ -concentration [kg CO ₂ m ⁻² s ⁻¹]
P_n	— net CO ₂ -assimilation [kg CO ₂ m ⁻² s ⁻¹]
$P_{n,max}$	— maximal net CO ₂ -assimilation [kg CO ₂ m ⁻² s ⁻¹]
Q	— air flow [m ³ s ⁻¹]
$r_{b,c}$	— boundary layer resistance to CO ₂ [s m ⁻¹]
r_c	— resistance to CO ₂ diffusion [s m ⁻¹]
$r_{b,h}$	— boundary layer resistance to heat [s m ⁻¹]
$r_{b,v}$	— boundary layer resistance to water vapour [s m ⁻¹]
$r_{l,v}$	— leaf resistance to water vapour [s m ⁻¹]
$r_{l,c}$	— leaf resistance to CO ₂ [s m ⁻¹]
S	— slope of graph of $1/\Sigma r_c$ versus P_n [m ³ (kg CO ₂) ⁻¹]
s	— slope of saturated vapour pressure curve [mbar °C ⁻¹]
γ	— psychrometer constant [mbar °C ⁻¹]
λ	— latent heat of vaporization of water [J (kg H ₂ O) ⁻¹]
ρc_p	— volumetric heat capacity of the air [J m ⁻³ °C ⁻¹]

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