Measurement of some relations between leaf resistance, CO_2-concentration and CO_2-assimilation in maize, beans and sunflower

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Summary

First some theoretical considerations are given which concern the relations between leaf resistances for CO_2 and water vapour, leaf transpiration, net CO_2-assimilation and external and internal CO_2-concentrations. The consequences of experimental errors for graphical representation are discussed. The experimental results indicate that for maize and beans under normal circumstances, the stomatal conductivity is controlled by the CO_2-concentration in the stomatal cavity and consequently by the rate of CO_2-assimilation.

At external CO_2-concentrations below 300 vpm the setpoint for the internal CO_2-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 CO_2-assimilation in sunflower responds more to external CO_2 than in maize and beans, but sunflower has also a less efficient water use. Maize uses water more efficient than beans, because it has a lower setpoint for the internal CO_2-concentration. When regulation is present, stomatal conductivity is best calculated as a function of net CO_2-assimilation and the setpoint for internal CO_2-concentration.

Introduction

A central problem in models concerning the growth, assimilation and transpiration of plants and crop surfaces is the quantitative description of stomatal behaviour. Sometimes the stomatal conductivity and with this the CO_2-assimilation appears to be controlled by the internal availability of water for transpiration; sometimes also by the humidity (Lange et al., 1971) of the external air. In some cases control of stomatal aperture seems to a large extent absent. In other cases the stomatal aperture and with this the rate of transpiration appears to be controlled by the CO_2-concentration within the stomatal cavity (Raschke, 1975) and consequently by the rate of CO_2-assimilation.

For this situation a description of stomatal behaviour is developed in this paper and evaluated by means of experiments and analyses. It reflects on one hand the most important aspects, but is on the other hand simple enough to be used

in simulation studies. The first part of this paper concerns theoretical considerations, pertinent for the analysis of experimental results. The experimental results and their interpretation are given next. In the last part some reflections are made about stomatal resistance as dependent on light, and on mesophyll resistance, and also about the transpiration coefficient.

Theoretical considerations

The CO_2 concentration within the stomatal cavity (C_i) cannot be measured directly, but must be computed from the net CO_2-assimilation P_n and the sum of resistances ΣR_c for CO_2 diffusion from the external source of CO_2 (C_e), according to the relation

$$P_n = \frac{(C_e - C_i)}{\Sigma R_c} . K \qquad (1)$$

The value of the conversion factor K at $20^\circ C$ is $1.83 \ 10^{-6}$ kg m^{-3} vpm^{-1} when the CO_2 concentrations are expressed in vpm, the net CO_2-assimilation in kg CO_2 m^{-2} s^{-1} and the resistances in s m^{-1}.

The net assimilation of a leaf can be measured in controlled assimilation chambers and the sum of resistances against CO_2-diffusion has to be calculated from simultaneous transpiration measurements.

Since accurate measurements of leaf temperature are difficult, at least under our experimental conditions (Louwerse and Van de Zweerde, 1976), leaf and boundary layer resistance were computed by using an expanded Penman equation for transpiration:

$$T = \frac{\Delta . N_r + \frac{V_d . \rho c_p}{R_{bh}}}{(\frac{R_{bv} + R_{lv}}{R_{bh}}) . \gamma + \Delta} . \frac{1}{L} \qquad (2)$$

In this equation T is the transpiration rate in kg H_2O m^{-2} s^{-1}, Δ the slope of the saturated vapour pressure curve at air temperature in mbar $^\circ C^{-1}$, V_d the vapour pressure deficit of the air in mbar, N_r the total absorbed radiative energy per leaf area in J m^{-2} s^{-1}, ρc_p the volumetric heat capacity of the air in J m$^{-3} {}^\circ C^{-1}$ (1240), γ the psychrometric constant in mbar $^\circ C^{-1}$ (0.67), and L the heat of vaporization of water in J kg^{-1} (2.45 10^6). R_{bv} and R_{lv} are the boundary layer resistance and leaf resistance for water vapour in s m^{-1}, and R_{bh} is the boundary layer resistance for heat in 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_{bv}/R_{bh} equals 0.93 (Monteith, 1973) when both sides of the leaves have stomata, as for maize, but for leaves with the stomata at one side only, as for beans, the ratio is twice this value.

The leaf resistance for water vapour remains as the only unknown in eq. 2, so that its value can be calculated from transpiration, air temperature and humidity measurements that are made simultaneously with the assimilation measurements.

The resistances for CO_2-diffusion can then easily be obtained since the ratio of leaf resistance against CO_2 and water vapour diffusion (R_{lc}/R_{lv}) equals 1.67, and the similar ratio for the boundary layer resistances (R_{bc}/R_{bv}) equals 1.42 (Monteith, 1973). This ratio is not affected by the geometrical distribution of the stomata on the leaves.

The ratio of 1.67 holds for the diffusion through the stomata, but not for the cuticula which is often assumed to be impermeable for CO_2. Hence the leaf resistance against CO_2-diffusion is underestimated in situations where the stomata are practically closed and most of the small transpiration takes place through the cuticula.

The assimilation chambers are thoroughly ventilated, which ensures that the CO_2-concentration in the chamber is the same as in the outgoing air. However, the CO_2-concentration in the ingoing air is in general higher. The ingoing (C_e) and the outgoing (C_o) CO_2-concentrations are related as

$$C_o = C_e - \frac{P_n}{K} \cdot \frac{A}{Q} \tag{3}$$

where P_n is again the net assimilation in kg CO_2 m^{-2} s^{-1}, A the leaf area in m^2 and Q the air flow through the chamber in m^3 s^{-1}. The ratio A/Q has the dimensions $s\ m^{-1}$ and may be considered a chamber resistance against turbulent transfer of CO_2 in series with the leaf and boundary layer resistance. For large A and small Q the resistance is large and thus also the drop in concentration, and vice versa. The chamber resistance against turbulent transfer of water vapour is numerically the same as for CO_2, but this has no further meaning since experiments with controlled humidity of the incoming air are not done.

It follows from the foregoing that the sum of resistances against diffusion of CO_2, which is used in equation 1, can be set equal to

$$\Sigma R_c = 1.67\ R_{lv} + 1.42\ R_{bv} + A/Q \tag{4}$$

A few remarks have to be made regarding presentation of the experimental results. According to eq. 1, observational results may be presented in graphs with the

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net assimilation and the conductivity ($1/\Sigma R_c$) for CO_2 transfer along the axes.
If the leaf adjusts its stomatal aperture in such a way that a constant
internal CO_2-concentration (C_i) is maintained, the observational results at one
constant external CO_2-concentration (C_e) are then arranged along a straight
line (fig. 2a). This way of presentation has the advantage that the error in
the graph is almost independent of the magnitude of net assimilation and con-
ductivity. Both net assimilation and transpiration rate are measured by
differences in ingoing and outgoing air and so their absolute errors are about
constant.

If on the other hand the internal CO_2-concentration is directly calculated
by means of eq. 1, its error can be expressed as

$$\frac{\Delta C_i}{C_e - C_i} = \frac{\Delta P_n}{P_n} + \frac{\Delta \Sigma R_c}{\Sigma R_c} \qquad (5)$$

The relative error in ΣR_c is in first approximation equal to the relative
error in the transpiration rate. Therefore the error in C_i is larger at low
assimilation and transpiration rates, or at low light intensities. It also
appears that the absolute error in C_i is proportional to the difference between
external and internal concentration, so that the error is generally large at
high external concentrations. This has a detrimental effect on the graphical
representation, which is illustrated in graph 2c.

In graph 2a all points have the same weight, which facilitates the fitting
of a line. The slope of the line is related to the internal CO_2-concentration
according to

$$C_i = C_e - (K.S)^{-1} \qquad (6)$$

where the CO_2-concentration is expressed in vpm, the slope S in $m^3 kg^{-1}$ and K
in $kg\ m^{-3}\ vpm^{-1}$.

The straight line does not pass through the origin. The length of the
ordinate provides with an estimate for the cuticular conductivity for water
vapour, if this conductivity for CO_2 is assumed to be negligible.

Material and methods

The experiments were done in a light range (400-700 nm) up to about
400 $J\ m^{-2}\ s^{-1}$ at CO_2-concentrations ranging from 50-1200 vpm, and, unless stated
otherwise, at a temperature of 25^oC.

The maize plants (Zea mays var. civ. 7) were 4 weeks old, the bean plants
(Phaseolus vulgaris var. Berna) 2 weeks old and the sunflower plants (Helianthus
annuus, var. INRA 65.01) 3 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 $20^{\circ}C$ and a light intensity (HPL-400W) of about 60 J m^{-2} s^{-1}. The beans were aerated. The sixth (full grown) leaf of maize, the primary leaves of beans and the second leaf of sunflower, all attached to the plants, were used for the measurements.

The used equipment to measure CO_2-assimilation and transpiration is described by Louwerse and Van Oorschot (1969). Some measurements near compensation point were done with another equipment that is described by Challa (1976).

Results and interpretation

Results of a series of measurements, kindly provided by Mr. Louwerse, with beans of different age at an external CO_2-concentration of 300 vpm and at a range of light intensities are given in fig. 1a and 1b. Two conductivities for CO_2 are given in relation to the net assimilation. These are the inverse of the leaf resistance $(1/(1.67\ R_{1v})$, and of leaf plus boundary layer plus chamber resistance $1/(1.67\ R_{1v} + 1.42\ R_{bv} + A/Q)$. There is a close relation between net assimilation and conductivity in both cases, but in the case where the total resistance (fig. 1b) is considered, the relation is much closer to a straight line. This indicates that the opening of the stomata is regulated in such a way that the internal CO_2-concentration varies little with net assimilation and light intensity. The much more than proportional increase of the stomatal conductivity with increasing net assimilation in fig. 1a is then a direct consequence of the decrease of the CO_2-concentration at the leaf surface with increasing assimilation.

The results of light intensity series at a range of CO_2-concentrations for maize and beans in another experiment denoted by beans II are presented in fig. 2a and 2b. The lower graphs present the light response curves at different CO_2-concentrations and the upper graphs the relation between net CO_2-assimilation and the conductivity for CO_2. Linear relations appear to exist which means that the regulatory mechanism operates at all CO_2-concentrations, both in case of maize and beans. The average internal CO_2-concentration C_i at each external concentration may be calculated from the slope S of the lines (eq. 6). For beans at 1000 vpm external the computed internal concentration is negative, so that this set is obviously in error. Therefore this series at 1000 vpm is omitted in the next graphs. In fig. 3 the value of C_i is given for maize, beans and sunflower in dependence of the external CO_2-concentration. The error in the computed internal CO_2-concentration increases with the difference between external and internal concentration. Essentially the graph has the same disadvantage as fig. 2c, but

now a group of values at one external CO_2-concentration is averaged.

For maize and beans the internal CO_2-concentration is independent of the external CO_2-concentration above a value of 300 vpm for the latter. The relation for sunflower will be discussed later. Below 300 vpm the internal CO_2-concentration decreases with decreasing external CO_2-concentration. Although large accuracy may not be expected, the proportionality between internal and external concentrations near the origin of the graph in fig. 3 indicates that in this region the setpoint is a fraction of the CO_2-concentration on the leaf surface C_s. All the observations given in fig. 2 are presented again in fig. 4, but this time along the vertical axis:

$$(C_s - C_i)/1.67 R_{lv})$$

where C_s is the calculated CO_2-concentration at the leaf surface and C_i the regulatory CO_2-concentration. This variable is a CO_2-flux (vpm m s^{-1}) across the stomatal resistance as computed from an external CO_2-concentration and an assumed internal CO_2-concentration. For C_s below 300 vpm C_i is estimated as f.C_s and above 300 vpm C_i is fixed at 120 and 210 vpm for maize and beans, resp. The proportionality factors (f) are estimated at 0.4 for maize and 0.7 for beans. All observations arrange now along the straight line with slope K^{-1}, K being the conversion factor in eq. 1. To illustrate the influence of the choice of C_i two other graphs are given for maize. In fig. 4c C_i equals f.C_s over the whole range and in fig. 4d C_i is taken as a constant value of 120 vpm. By combining these dependences to a Blackman type saturation curve the graphs of fig. 4a and 4b are obtained with considerably less scatter. Above external CO_2-concentrations of about 300 vpm the internal concentration is regulated at a constant level, which is estimated about 120 vpm for maize and 210 vpm for beans. Most of the scatter in the results may now be ascribed to the experimental error, as follows from the error in reading the recorded output, indicated in the figures. Hence further improvements of interpretation cannot be achieved with the equipment presently in use.

There is still more evidence that the setpoint of the internal concentration is not constant, but a fraction of the external concentration when this is low. In fig. 5b the results of some observations at low CO_2-concentrations are plotted in the same way as in fig. 4a, whereby C_i is given a value of 0.4 C_s. The observations at a positive net assimilation up to 0.35x10^{-6} kg CO_2 m^{-2} s^{-1} arrange again close to the line with slope K^{-1}. These observations were done at external CO_2-concentrations varying between 50 and 300 vpm. At these low concentrations stomatal movement becomes slow so that in many cases equilibrium was not yet reached. The other observational points in fig. 5b represent measurements near compensation point, at various CO_2-concentrations. As follows from eq. 5

the internal CO_2-concentration C_i can be determined most accurately near compensation point. If a constant setpoint of internal concentration exists, the results of a series of measurements near compensation point at various external CO_2-concentration should unambiguously reflect the dependency of the stomatal conductivity on the CO_2-concentration. In fig. 5a the stomatal conductivities in the same series of measurements are given versus internal CO_2-concentration, but it appears that no such relation exists. There is no clear rule for the value of the stomatal conductivity, probably because the required energy for normal regulation is lacking. However, even when the net assimilation is only slightly positive, the regulatory mechanism becomes operative again, and can be well explained by regulation at a fraction of external CO_2-concentration when this is low.

The results of the experiments with sunflower, given in fig. 6, indicate no regulation at all. In fig. 3 the relation is given between internal and external CO_2-concentration for the highest light intensity of the light series. In all cases the internal CO_2-concentration is only slightly less than the external, because the stomata are wide open. For lower light intensities the difference between external and internal CO_2-concentration was even less. Therefore the high correlation between internal and external CO_2-concentration for high irradiance in fig. 3 only means that in sunflower regulation of the stomatal aperture is absent. The same conclusion follows from the work of Whiteman and Koller (1967) who also studied sunflower. It is consistent with the absence of regulation that the maximum photosynthetic rate of sunflower continues to increase above 300 vpm with the external CO_2-concentration. Although a C_3-plant, it reaches the same level as maize at high external concentrations of CO_2. Raschke (1975) mentions that the regulatory mechanism only starts to function after the plants have been exposed to some water stress. Experiments to induce the regulatory mechanism with sunflower have not been executed, and it has not been tried yet to grow beans and maize under conditions where the regulatory mechanism is absent. Under field conditions, it is impossible to avoid water stress completely, so that it may be that the regulatory mechanism will always become operative.

Discussion

In view of the application of the described results in models for CO_2-assimilation and transpiration, an important aspect is the consistency of the found relationships, especially of the rule for the internal regulatory concentration.

The results for bean plants in fig. 1 indicate an apparent internal CO_2-concentration of only 160 vpm. This is considerably less than the 210 vpm which was found in the other bean plants, for which data are presented in fig. 2.

For maize plants Raschke and Dunn (1971) found also a value of about 0.4 for the ratio of the internal and external CO_2-concentrations, but they report that this proportionality holds up to 1000 vpm external. On the other hand they do mention other experiments indicating a constant internal CO_2-concentration.

Although regulation at a constant internal CO_2-concentration is evident in many cases, the value of the setpoint seems to vary with the history of the environmental conditions of the plant and may be with different genotypes.

Moreover the cuticular conductivity for water is not regulated by internal CO_2, which causes a parallel upward shift of the lines in fig. 1a and 1b. Some cuticular conductivity for CO_2, about which not much is known, would cause a similar shift in the opposite direction. A further investigation of these effects seems worthwhile, but was not done in the scope of this paper.

The net CO_2-assimilation P_n is often presented as a hyperbolic function of absorbed light intensity (I).

$$P_n = (P_m + R) \frac{I}{I + I_h} - R \tag{7}$$

in which P_m is the maximum net CO_2-assimilation, R the dark respiration and I_h the half value point. Eq. 1 and 4 may be combined to

$$R_{1c} = (C_e - C_i).K/P_n - R_{bc} - A/Q \tag{8}$$

Substitution of P_n results in the following equation for R_{1c}

$$R_{1c} = \frac{(C_e - C_i).K}{(P_m - R.\frac{I_h}{I})} . \frac{(I + I_h)}{I} - R_{bc} - A/Q \tag{9}$$

Since the difference between external C_e and internal C_i is independent of light intensity, there exists then also a hyperbolic relation between stomatal resistance and light intensity. This is in accordance with the data of Kuiper (1961) and others.

Under light saturation the maximum rate of net CO_2-assimilation P_m can be described in terms of internal CO_2-concentration (C_i), compensation point for CO_2 (Γ) and mesophyll resistance (R_m)

$$P_m = (C_i - \Gamma).K/R_m \qquad (10)$$

For maize and beans the internal CO_2-concentration hardly increased above 300 vpm external. This means that also the maximum net CO_2-assimilation should be insensitive to the external CO_2-concentration above 300 vpm. In fig. 2a and 2b there is still some increase noticeable from 300 to 500 vpm external, but at higher concentrations the maximum assimilation does not reach higher values. The compensation concentration of CO_2 (Γ) for maize and beans was 10 and 80 vpm in our experiments, as derived from a graph of net assimilation at high light intensity versus external CO_2-concentration, extrapolation of the graph to P_m is zero giving an estimate for Γ. Hence, the mesophyll resistance, according to eq. 10, was 150 and 450 s m^{-1} for maize and beans resp.

Below 300 vpm external, the internal CO_2-concentration is a fraction f of the external CO_2-concentration C_o, which can be concluded from the slopes of the lines in fig. 2a. It also appears in the graph that in this region the stomatal conductivity reaches a maximum. At first sight it seems plausable that this should be attributed to physical constraints on the maximum stomatal aperture. However, if that were the case one would expect that the top part of the curves would bend to the right. The regulatory mechanism being then no longer operative, because it has reached its limits, ~~so that~~ the internal concentration would drop to values lower than the setpoint. In reality the regulatory mechanism is still at work in the top part of the curves. Therefore the constant minimum resistance below 300 vpm external must be explained by means of the regulatory mechanism, which can be done as follows. Combining eq. 1 and eq. 10 gives for the minimal total resistance

$$\Sigma R_c(min) = \frac{(C_e - C_i)}{(C_i - \Gamma)} \cdot R_m \qquad (11)$$

In the fictive simplified situation with Γ at zero and $R_{bc}+A/Q$ at zero eq. 11 would result in

$$R_{c(min)} = (\frac{1-f}{f}) R_m \qquad (12)$$

Hence a constant $R_{c(min)}$ proves that both f and the mesophyll resistance R_m are independent of the CO_2-concentration. The more general expression for $R_{c(min)}$, including Γ and $R_{bc}+A/Q$ is

$$\Sigma R_{c(min)} = \frac{(1-f)C_e}{(fC_e-\Gamma)} (R_m + f(R_{bc} + A/Q)) - f (R_{bc} + A/Q) \qquad (13)$$

The addition of R_{bc} +A/Q changes nothing in the reasoning, but the non-zero compensation point effectuates an increase of the minimum resistance when C_e decreases. For maize with Γ at 10 vpm this effect is largely negligible but with beans it should show up. The maximum conductivity at 100 vpm is indeed much less than those at 200 and 300 vpm (fig. 2b). Thus assuming a constant $R_{c(min)}$ with a correction for the effect of the compensation point, regulation of internal concentration at a fraction of the external CO_2-concentration at the leaf surface, and a constant mesophyll resistance are consistent with each other.

The observation that maximum net assimilation hardly increases with increasing CO_2-concentration above 500 vpm seems contradictory with the experience in greenhouses where CO_2 fertilization up to at least 1000 vpm is practiced to increase production. It may be that this practice only succeeds with some species or when the plants are grown in absence of water stress, so that the regulatory mechanism does not become operative. A further analysis of this aspect of the problem seems worthwhile.

It is well known that the transpiration coefficient of C_4-plants is about half of that of C_3-plants, both at low and high light intensities (De Wit, 1958; De Wit and Alberda, 1961). This can now be sufficiently explained as an effect of the regulatory mechanism that maintains the difference between external and internal CO_2-concentration (C_e-C_i) in C_4-plants about twice as large as in C_3-plants, under normal CO_2-concentrations of about 300 vpm. At low light intensities the assimilation rate of C_4-plants is only slightly higher than in C_3-plants, so that the difference in transpiration coefficient shows mainly up in a two times larger rate of transpiration for C_3-plants. At high light intensities, however, the assimilation rate of C_4-plants may reach twice the value of C_3-plants, which then results in transpiration rates that are about equal.

At high temperatures and radiation levels the regulatory mechanism would have a devastating effect, since beyond the temperature optimum of net assimilation a further temperature increase would result in a decrease of assimilation and hence in a closure of stomata. This would again increase leaf temperature and because of this positive feedback the assimilation would soon collapse. However, according to the literature reviewed by Raschke (1975), the regulatory mechanism is no longer operative at high temperatures.

Our measurements with maize at a low temperature (fig. 7) indicate that the regulation mechanism is not operative at low light intensities. The stomatal conductivity and so the internal CO_2-concentration are higher than in accordance with the regulation. With increasing radiation the regulation is gradually restored. This may be a direct light effect, but more likely it is a result of the increased leaf temperature under high irradiation, at the end of a light

series the temperature being as high as $19^{\circ}C$. These scarce data indicate that in plants which normally possess regulation, this mechanism gradually disappears for lower temperatures.

The well known increase of stomatal resistance with increasing age of the leaf may be considered as a consequence of the decrease of photosynthesis. In fig. 1 the results are presented for beans of 2, 3 and 4 weeks old. The ageing of the plants shows up in a simultaneous decrease of photosynthesis and leaf conductivity. Within the experimental scatter of the results no tendency can be found of a change of internal CO_2-concentration with age.

Water stress may overrule the regulation by internal CO_2-concentration, which may then drop to values somewhere between the setpoint and compensation point. For C_4-plants this effect can enhance the difference between external and internal concentration with at most a factor 1.6 and for C_3-plants with a factor 2.7. Observed reductions of the transpiration coefficients are in general smaller, because plants under water stress transpire most of their water during periods that this stress is not manifest, and also because of the increased relative importance of cuticular transpiration.

From literature data and our own experiments it appears that the presence of regulation of internal CO_2-concentration by the stomatal resistance depends on the plant species, but also on the way the plants are grown and on their actual environmental conditions. The regulation mechanism may improve the water use efficiency, but absence of regulation may improve the actual rate of net CO_2-assimilation because the internal CO_2-concentration can be higher when the stomata are open.

When regulation is present, stomatal conductivity can be best calculated as function of the net CO_2-assimilation and the setpoint for internal CO_2-concentration. When there is no regulation, the stomatal conductivity can have any value between the upper and the lower boundary. The upper boundary is dictated by the water status of the plant. The lower boundary is given by the requirement that the internal CO_2-concentration can not be negative.

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Fig. 1   Stomatal conductivity (1a) and total conductivity (1b) for CO_2 versus net assimilation in beans of different age (beans I).

Fig. 2 (a, b) Net CO_2-assimilation in maize and beans (II) for different external CO_2-concentrations.
        (c) Total conductivity for water vapour versus computed internal CO_2-concentration in maize, measured at different external CO_2-concentrations .

Fig. 3   Computed internal CO_2-concentrations versus external CO_2-concentrations in maize, beans (I and II) and sunflower. The points for sunflower hold for the highest light intensity only (330 J m^{-2} s^{-1}).

Fig. 4 (a, b) Computed CO_2 flux across stomata (leaf conductivity for CO_2 times the difference between computed concentration at leaf surface and assumed internal CO_2-concentration) versus measured net CO_2-assimilation for maize and beans II at different external CO_2-concentrations.
        (c) Same as 4a, but C_i assumed as $f.C_s$ (f=0.4).
        (d) Same as 4a, but C_i assumed constant at 120 vpm.

Fig. 5   (a) Leaf conductivity for water vapour versus computed internal CO_2-concentration for some measurements near compensation point at CO_2-concentrations below 300 vpm. For the encircled points some light was given, so that net assimilation was positive. Triangles indicate equilibrium, an upward or downward arrow indicates the direction of stomatal movement for non-equilibrium situations.
        (b) Same measurements as in 5a. Same coordinates as in fig. 4a and 4c (f=0.4).

Fig. 6   Net CO_2-assimilation versus incident light, and total conductivity for CO_2 versus net CO_2-assimilation in sunflower for different external CO_2-concentrations (compare fig. 2a, 2b).

Fig. 7   Computed CO_2 flux across stomata versus measured net CO_2-assimilation for maize at 300 vpm external, and at different temperatures.

List of symbols

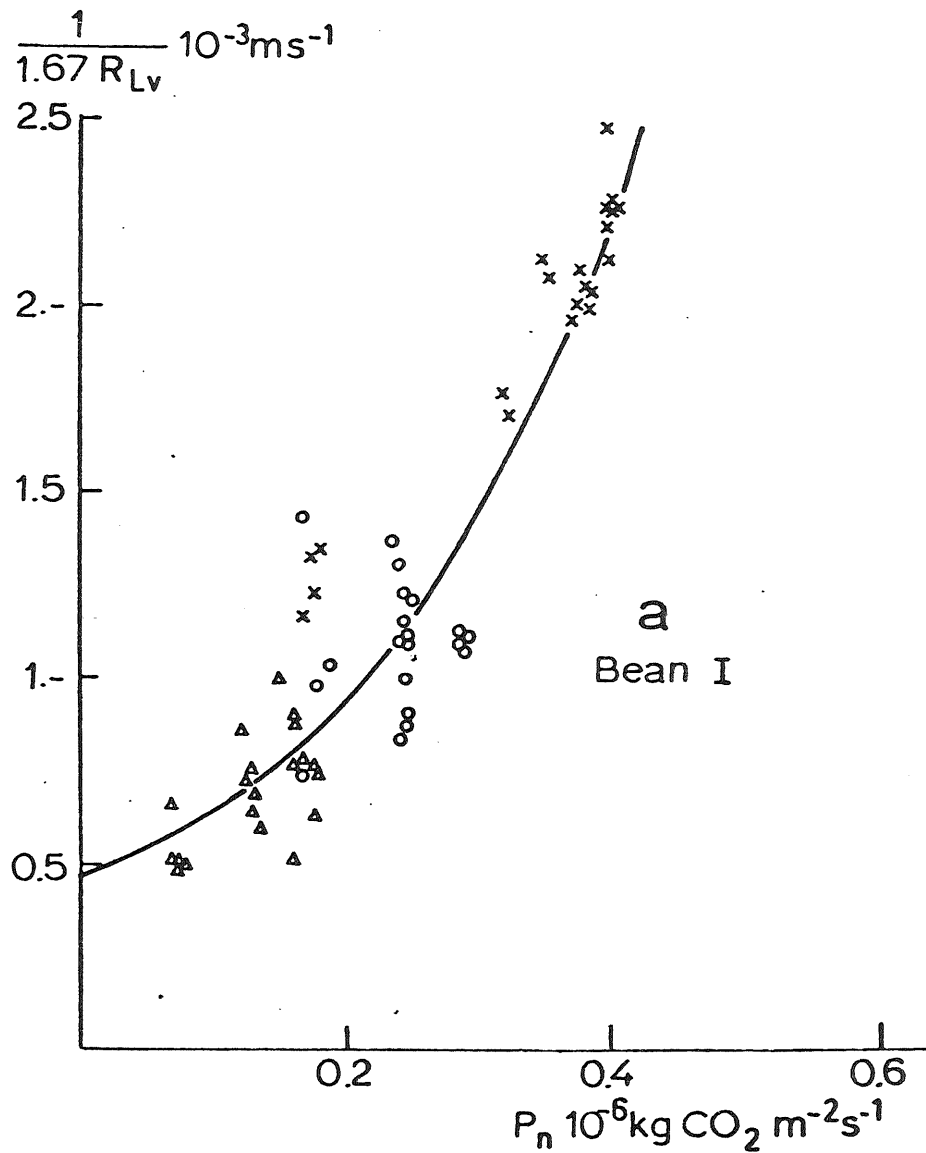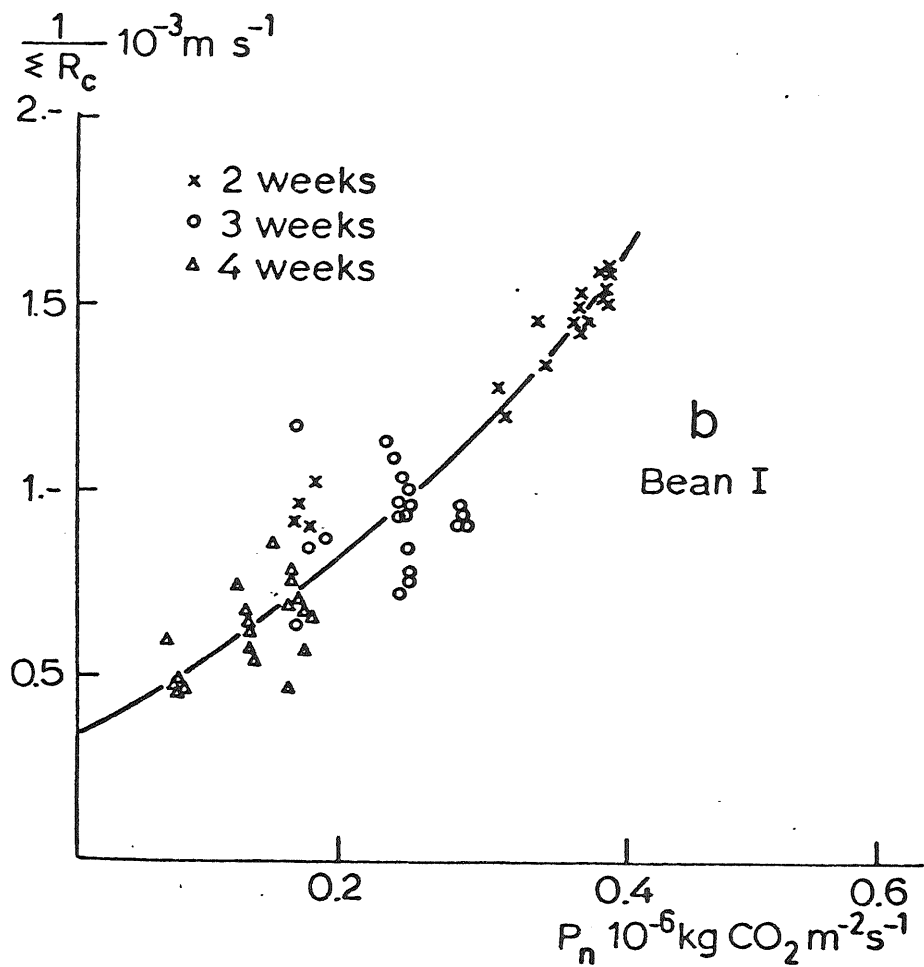| Symbol	Description	Units
A	leaf area	m^2
C_e	CO_2-concentration in the ingoing air	vpm
C_i	CO_2-concentration in stomatal cavity	vpm
C_o	CO_2-concentration of the outgoing air	vpm
C_s	CO_2-concentration at leaf surface	vpm
f	ratio of internal and external CO_2-concentrations	-
I^m	absorbed visible radiation	$J\ m^{-2}\ s^{-1}$
I_h	half saturation point of the radiation I	$J\ m^{-2}\ s^{-1}$
K	conversion factor	$kg\ CO_2\ m^{-3}\ vpm^{-1}$
L	heat of vaporization of water	$J\ kg^{-1}$
N_r	absorbed radiative energy per leaf area	$J\ m^{-2}\ s^{-1}$
P_n	net CO_2-assimilation	$kg\ CO_2\ m^{-2}\ s^{-1}$
P_m	maximum net CO_2-assimilation	$kg\ CO_2\ m^{-2}\ s^{-1}$
Q	air flow	$m^3\ s^{-1}$
R	dark respiration	$kg\ CO_2\ m^{-2}$
R_c	resistance for CO_2	$s\ m^{-1}$
R_m	mesophyll resistance	$s\ m^{-1}$
R_{bc}	boundary layer resistance for CO_2	$s\ m^{-1}$
R_{bh}	boundary layer resistance for heat	$s\ m^{-1}$
R_{bv}	boundary layer resistance for water vapour	$s\ m^{-1}$
R_{lc}	leaf resistance for CO_2	$s\ m^{-1}$
R_{lv}	leaf resistance for water vapour	$s\ m^{-1}$
S	slope of line in graph	$m^3\ (kg\ CO_2)^{-1}$
T	transpiration rate per leaf area	$kg\ H_2O\ m^{-2}\ s^{-1}$
V_d	vapour pressure deficit of the air	mbar
γ	psychrometric constant	$mbar\ ^oC^{-1}$
Γ	compensation point of CO_2	vpm
Δ	slope of saturated vapour pressure curve	$mbar\ ^oC^{-1}$
ρc_p	volumetric heat capacity of the air	$J\ m^{-3}\ ^oC^{-1}$

Fig. 1

Fig. 2 a, b
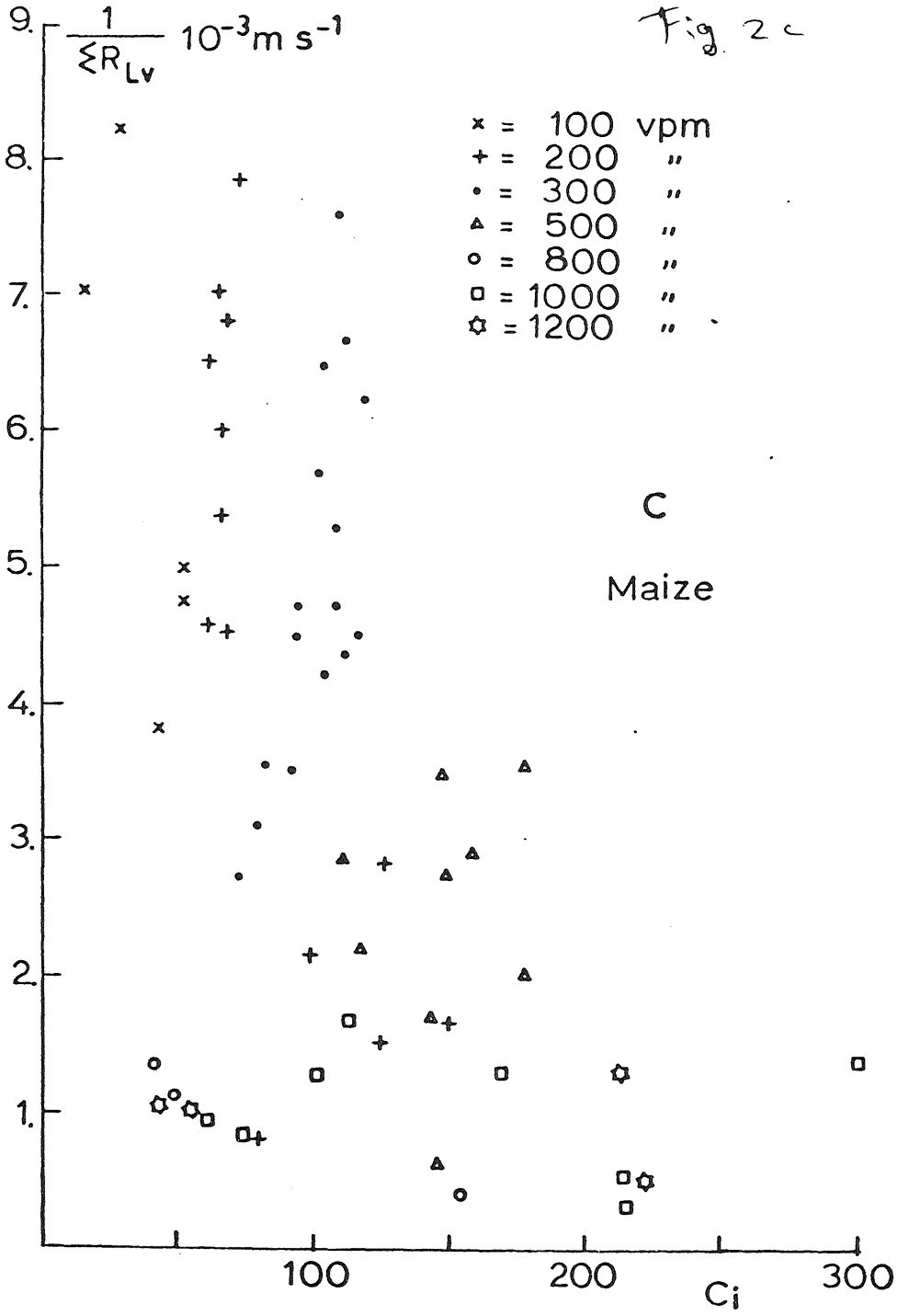
Fig. 2c

Fig. 3

Fig. 2c — Maize

$\dfrac{1}{\xi R_{Lv}}\ 10^{-3}\,m\,s^{-1}$ versus C_i

Legend:
- × = 100 vpm
- + = 200 "
- • = 300 "
- △ = 500 "
- ○ = 800 "
- □ = 1000 "
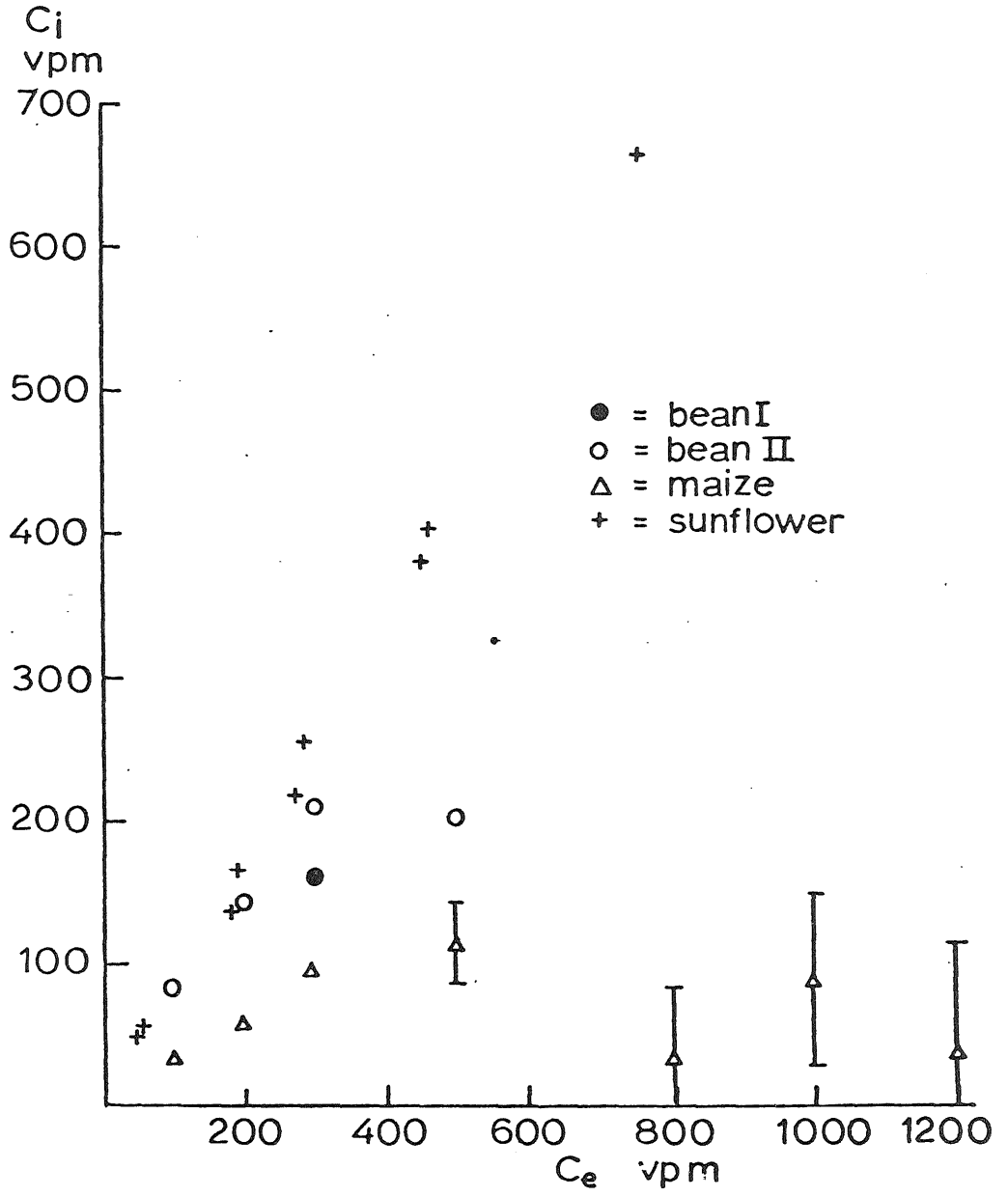- ✿ = 1200 "

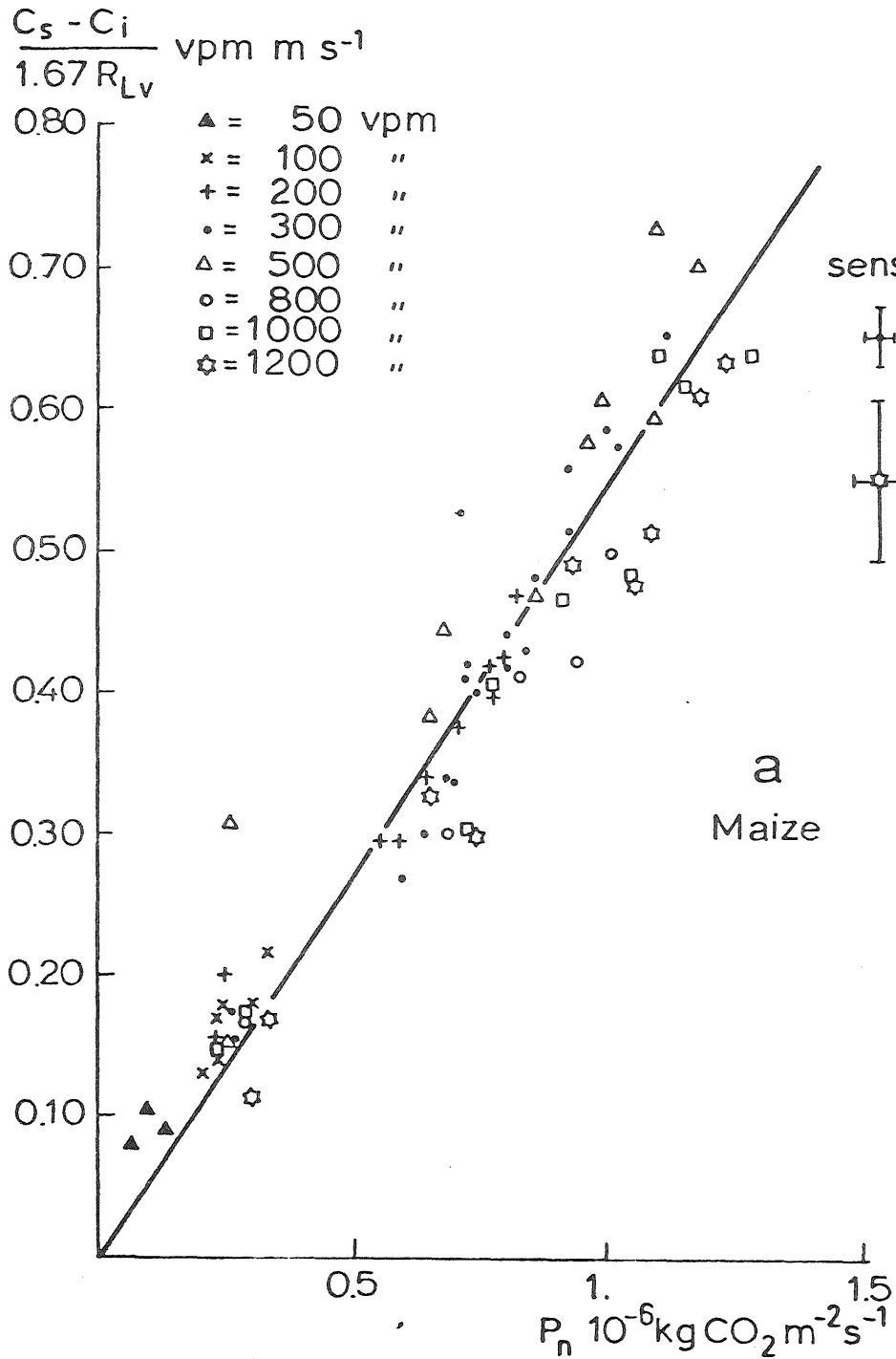**Fig. 3** — C_i vpm versus C_e vpm

Legend:
- ● = bean I
- ○ = bean II
- △ = maize
- + = sunflower

Fig. 4 a, b

Fig. 4 c,d

Fig 5ᵃ

Fig. 5b

a
Maize

Fig. 6

Fig. 7