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III. Influence of leaf curvature and self-shading

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Abstract

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The diurnal pattern of absorbed solar radiation of curved sun leaves of *Solanum melongena* and *Ficus carica* was modeled by means of the computing program ECOSOL (Flach and Eller 1990) and its influence on photosynthesis was studied. The diurnal pattern of CO_2-uptake of the naturally curved lamina was modeled by means of the calculated quantum fluxes absorbed and the measured photosynthetic saturation curves of the leaves. Predicted values were compared to the measured patterns of photosynthesis of the leaves. Good correlation is achieved between measurement and calculation if the physiological state of the leaves during the measurements of the naturally curved lamina and the measurements of the saturation curves were comparable. The daily courses of CO_2-uptake and quantum fluxes absorbed of the naturally curved blades were compared to hypothetically flat, but otherwise identical, leaves with the same midrib orientation. For the naturally curved leaves the maxima of absorbed quantum flux lie much nearer to the saturating value for net photosynthesis than the maxima of flat leaves. Quantum use efficiencies were calculated and *Solanum melongena* shows a clear improvement for the case of the curved leaf.

Key words: Ficus carica, leaf curvature, optical properties, photosynthesis, *Solanum melongena,* solar radiation.

Introduction

The leaves of the sunlit portion of the crown of trees frequently have concave upwardly curved laminae, in contrast to the usually flat shade leaves (Wiesner 1899). These leaf morphologies can be observed in lilac (*Syringa vulgaris* L.), fig (*Ficus carica* L.), chestnut (*Castanea sativa* Mill.), horse-chestnut (*Aesculus hippocastanum* L.), apple (*Malus silvestris* Mill.) and many other species. This phenomenon can also be observed for herbaceous and woody plants like the egg-plant (*Solanum melongena* L.), potato (*Solanum tuberosum* L.), sage (*Salvia officinalis* L.) and ivy (*Hedera helix* L.). McMillen and McClendon (1979) also described it for mulberry (*Morus rubra* L.) and wild plum (*Prunus americana* Marsh.).

If this curvature tends to put the lamina in a more vertical position, the overall effect is comparable to an increased erectness of a flat leaf. The investigations of Ledent (1976) concerning the effect of twisted leaf surfaces on beam light interception showed that for the canopy as a whole, it is similar to a steeper inclination of the leaves. This results in less light interception at small solar zenith angle and more light interception when the sun is low (Ledent 1976). The same phenomenon is mentioned for leaves folded about the midrib (Ehleringer and Comstock 1987). It is frequently observed for mediterranean-climate and desert plants. A reduced amount of absorbed solar radiation around midday means lower leaf temperatures compared to a more horizontally positioned leaf (Gates 1980). In his investigations Vogel (1970) observed the maximum of heat dissipation for a sun leaf when it was oriented obliquely to a free or forced airstream. In an earlier study, Vogel (1968) showed that sun leaves are more effective heat dissipators than shade leaves.

The diurnal pattern of global radiation impinging on a leaf is obviously different for a curved sunlit lamina in comparison to that of a flat sunlit leaf with the same orientation of the midrib. Ross (1975) mentions three categories of interactions between a plant and the (global) radiation absorbed by it:
1) thermal effects
2) photosynthetic effects
3) morphogenetic effects.

Changes in the diurnal pattern of absorbed radiation will, therefore, give rise to changes in these three categories. The above mentioned studies concern predominantly the first point. The purpose of this paper is to investigate effects on photosynthesis. In order to put the diurnal pattern of global radiation in a proper relation to that of net CO_2-uptake, it must be taken into account that the net CO_2-uptake of most plants depends on the incoming or absorbed radiation in a non-linear way (Björkman 1981). As a consequence, the photosynthetic response of a curved leaf, in general, can not be estimated from its mean absorbed radiation. The curvature of the leaf blade must, rather, be approximated; e.g. by a set of flat contiguous triangles. With the diurnal pattern of global radiation incident on or absorbed by each of these subareas and the known functional relationship between the net CO_2-uptake and the incoming or absorbed radiation the net CO_2-uptake of each triangle can be determined. Subsequently the diurnal pattern for the whole leaf can be calculated by its weighted mean.

For the relatively small leaves of the trees and plants mentioned above it is impracticable to measure simultaneously the diurnal pattern of global radiation of each subarea. The computing program ECOSOL which was presented in Flach and Eller (1990) is a suitable appliance for modeling direct and diffuse radiation for any inclined plane. This modeling is based on actual irradiation measurements of a horizontally exposed pyranometer or quantum sensor. In Flach and Eller (1990) it was shown by comparisons of measured and calculated global and diffuse radiation, and their spectral distributions, that ECOSOL gives realistic values for modeling actual solar energy input.

In this paper the effects of the natural curvature of leaf blades on the diurnal pattern of incoming and absorbed radiation and of net CO_2-uptake in comparison to flat leaves are investigated. The measured and calculated time courses of net CO_2-uptake of the naturally curved leaves are compared. The relation of the measured saturation curve of net CO_2-uptake to the diurnal courses of the curved and evenly laid out leaves is studied, and their quantum use efficiency compared. The investigations were carried out for egg-plant and fig.

Material and methods

Plant material: Eggplants, *Solanum melongena* L., were grown from seed (Blue King F-1 Hybrid). Cuttings of fig, *Ficus carica* L., were taken from an outdoor tree in June of the year preceding the investigations. After rooting in the greenhouse at 25 °C they were cultivated outdoors for the rest of the vegetation period. End of May the pots with figs and eggplants were brought outdoor near the measuring site. Care was taken that the individual plants always maintained the same orientation and the pots were never moved. At the onset of the measurements the plants had a height of 40–60 cm.

Spectral properties of leaves: Spectral properties were determined using an integrating sphere and two spectroradiometers, a spectroradiometer LICOR LI 1800 (LICOR inc., Lincoln, Nebraska, USA) in the range 380–1050 nm as described by Tanner and Eller (1986) and a spectroradiometer ISCO SR (ISCO, Lincoln, Nebraska, USA) in the range 1050–1500 nm as described by Eller (1972). Between 300 and 400 nm a constant absorptivity was assumed, which was determined as the mean of the measured values between 380 and 400 nm. Between 1350 and 2300 nm a linear approximation was made according to Eller (1979) and for the wavelengths equal to or greater than 2300 nm a constant absorptivity of 0.96 was assumed.

Modeling of the irradiation on individual leaves: Radiation was measured with a horizontally exposed pyranometer (CM-5, Kipp and Zonen, Delft, NL) and a quantum sensor LI-190S (LICOR inc., Lincoln, Nebraska, USA), which were placed near the cuvette for the CO_2 gas exchange measurement. These data served as described (Flach and Eller 1990) for the choice of the appropriate value for the sea-level meteorological range. The cuvette was specially constructed for this investigations. It is revolving about two axes (i.e. polar and declination axis), so that the frontside of the cuvette can follow the sun's track by steps of 15°, while the leaf and with it the entire plant in the pot remain in their original position. The direct solar radiation falls, therefore, always nearly perpendicular through the front side of the cuvette and the irradiation conditions for the direct radiation remain the same during the day. The walls of the cuvette were manufactured of 10 mm plexiglas. Their transmissivity was measured as described for the spectral properties of the leaves. The values between 1550 nm–3000 nm were drawn from the technical notes of the manufacterer (Röhm GmbH, Darmstadt, FRD, 1971). The data obtained served as input data set for the transmission calculation of the modeled incoming radiation.

Analysis of the curvature of the leaf blade: To model the irradiation on the curved leaf blade, the lamina was approximated by a set of contiguous triangles. The cartesian coordinates of the apices were then determined by means of a pointed rod, which was connected to a coordinate system formed by three perpendicular scales. The z-axis pointed to the zenith, i.e. the x-y-plane was parallel to the horizontal plane. At culmination the azimutal direction of the x-axis was determined. The spatial coordinates of the apices define the positions of the triangles in the space. Together with the azimutal direction of the x-axis the zenith angles and azimuths of the normals to the triangular planes can be derived.

Shading and sky obstructions: Every quarter of an hour the leaf was photographed to determine the shading periods for each leaf section during the day. The percentage of sky obstruction was estimated by means of fish-eye photographs, taken from the place of the leaf in the cuvette, and a sextant. The estimated 9% were taken into account for the modeling.

Modeling of the reflected radiation by the environment: for the upper leaf surfaces the reflection properties of the leaves themselves were used as for both leaves, i.e. eggplant and fig, the blades were curved concavely upward. For the lower leaf surfaces the dataset ALLSOIL, the average reflection properties for different types of soil (Flach and Eller 1990) were used.

Measurement of CO_2 gas exchange: CO_2 gas exchange and transpiration were measured with a fully climatized cuvette system at constant air temperature (22 °C) and dew point (10.5 °C for eggplant and 12.5 °C for fig). The system is described in detail by Seibert (1984) and Flach (1986). Leaf temperature was measured with a copper-constantan (Cu-CuNi) thermocouple with a wire diameter of 0.07 mm, which was inserted into the midrib on the lower leaf side. Data acquisition was made with a data transfer unit (ORION 3530A, Schlumberger, Farnborough, UK) combined with an APPLE II personal computer (APPLE Computer Inc., California, USA).

Performing of the experiments: One of the fully developed leaves of the plant was inserted for acclimatization into the gas exchange cuvette some days prior to the measurements. Care was taken that the plant and its leaves retained the same orientation as during precultivation. In this way the irradiation conditions during the day did not change except for the unavoidable alterations caused by the cuvette walls. Gas exchange measurement for the curved leaf blade were performed on the first day with very clear weather conditions. Immediately afterwards, the subdivision of the leaf surface into triangles was marked on a photograph and the cartesian coordinates of the angles determined. The leaf blade was then spread out evenly by means of a support which was tied down with a nylon thread. Care was taken that the midrib maintained the same orientation and inclination. The cartesian coordinates of four to five points along the midrib and on the blade were measured to determine its spatial orientation.

Gas exchange measurements to determine the saturation function were carried out on the first day with clear weather conditions but not later than a week. Thereafter, the leaf was harvested and its spectral optical properties and the areas of the leaf sections and of the total leaf were determined.

Light saturation curves: The functional relationship between the measured CO_2-uptake and the irradiation or the absorbed quanta was described by a rectangular hyperbola:

$$(1) \qquad J_{CO_2} = b\,G/(1+a\,G) - r$$

with G = irradiation or absorbed quanta, a and b = parameters of the hyperbola, r = respiration rate. The parameters a, b and r were derived empirically by variation. The relationship (1) is somewhat simplified and no special attention was paid to obtain realistic values for the respiration rate. To model the net CO_2-uptake of the curved leaf blade during the day, a good mathematical description of the measured saturation function for CO_2-uptake is sufficient.

Modeled irradiation, absorbed quanta and net CO_2-uptake of a whole leaf: The instantaneous value of irradiation or absorbed quantum flux per unit leaf area for the whole leaf is calculated by the weighted mean:

$$(2) \qquad \bar{G} = \frac{\sum\limits_{i=1}^{n} G_i \cdot A_i}{\sum\limits_{i=1}^{n} A_i}$$

with G_i = irradiance or absorbed quantum flux for the i-th leaf element, A_i = area of the i-th leaf element and $\sum\limits_{i=1}^{n} A_i$ = total leaf area. In the same way the instantaneous CO_2-uptake per unit leaf area of the whole leaf is calculated by

$$(3) \qquad \bar{J}_{CO_2} = \frac{\sum\limits_{i=1}^{n} J_{CO_2}(G_i) \cdot A_i}{\sum\limits_{i=1}^{n} A_i}$$

with $J_{CO_2}(G_i)$ = instantaneous CO_2-uptake of the i-th leaf element.

Results and discussion

The measurements were performed on October 20 and 25 for eggplant and July 29/30 and 31 for fig. The first data corresponds to the measurements for the curved lamina and the second to the collection of the data for the saturation curve as mentioned in the preceding chapter. Fig. 1 a and b show the measured spectral absorptivities of the upper and lower surfaces of the leaves of the eggplant and fig.

In Figs. 2, 3a and b the saturation curves are shown together with the adjusted rectangular hyperbola. The values of the parameters a, b and r are given in the same
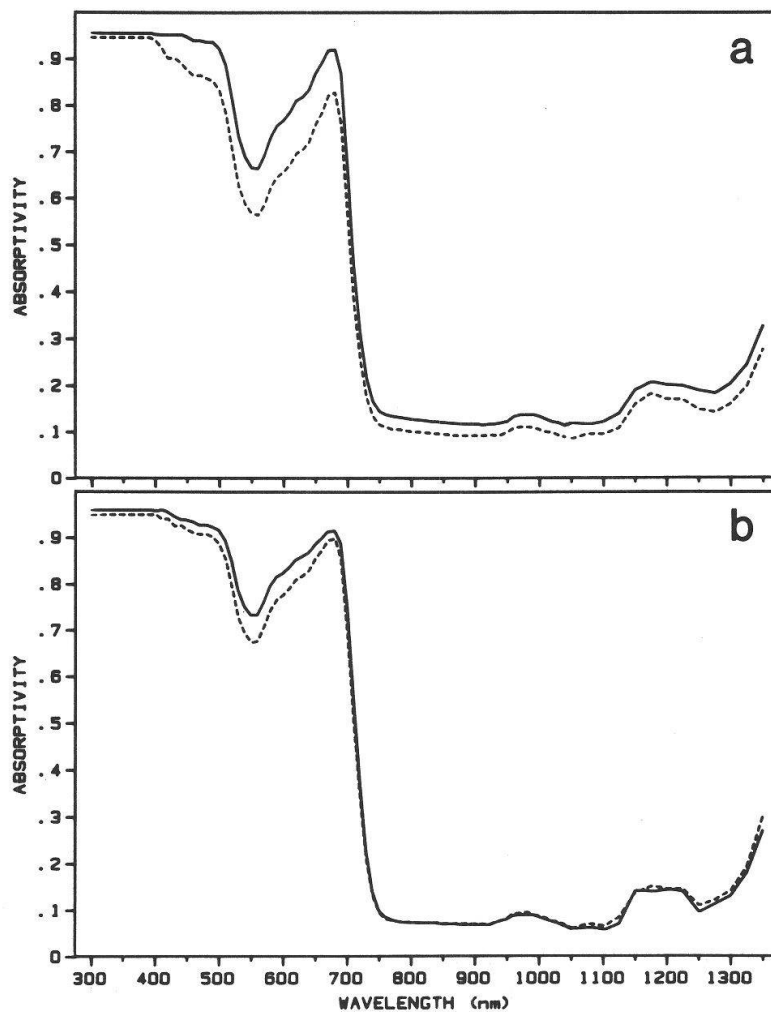
Fig. 1 a, b. Measured spectral absorptivity of the adaxial (——) and abaxial (———) leaf surface of *Solanum melongena* (a) and *Ficus carica* (b).

figures. The fig leaf in the morning followed a somewhat different saturation curve than in the afternoon. The leaf temperature was clearly higher in the afternoon for the same amount of absorbed quanta than in the morning. This was caused by the increasing ambient air temperature and with this, increasing temperatures of the cuvette walls (maximum: $+12.5$ K above cuvette air temperature in the afternoon). The warmer cuvette walls caused an uptake of longwave radiation energy by the leaf. This effect is negligible for the leaf of the eggplant, because the ambient air temperature was only slightly different from the cuvette air temperature (maximum: -3 K in the morning).

The net CO_2-uptake of the naturally curved leaf blades and the evenly spread out leaf were measured as described in the preceding chapter. Fig. 4a and b show both leaves together with their subdivisions of the lamina. The net CO_2-uptake was calculated separately for each triangle or subarea by means of its calculated diurnal pattern of the absorbed quantum flux under consideration, of the shading periods and the modeled saturation function. The net CO_2-uptake for the whole leaf was then determined as weighted mean, corresponding to the proportion of each subarea, i.e. triangle and, if necessary, parts of the border.
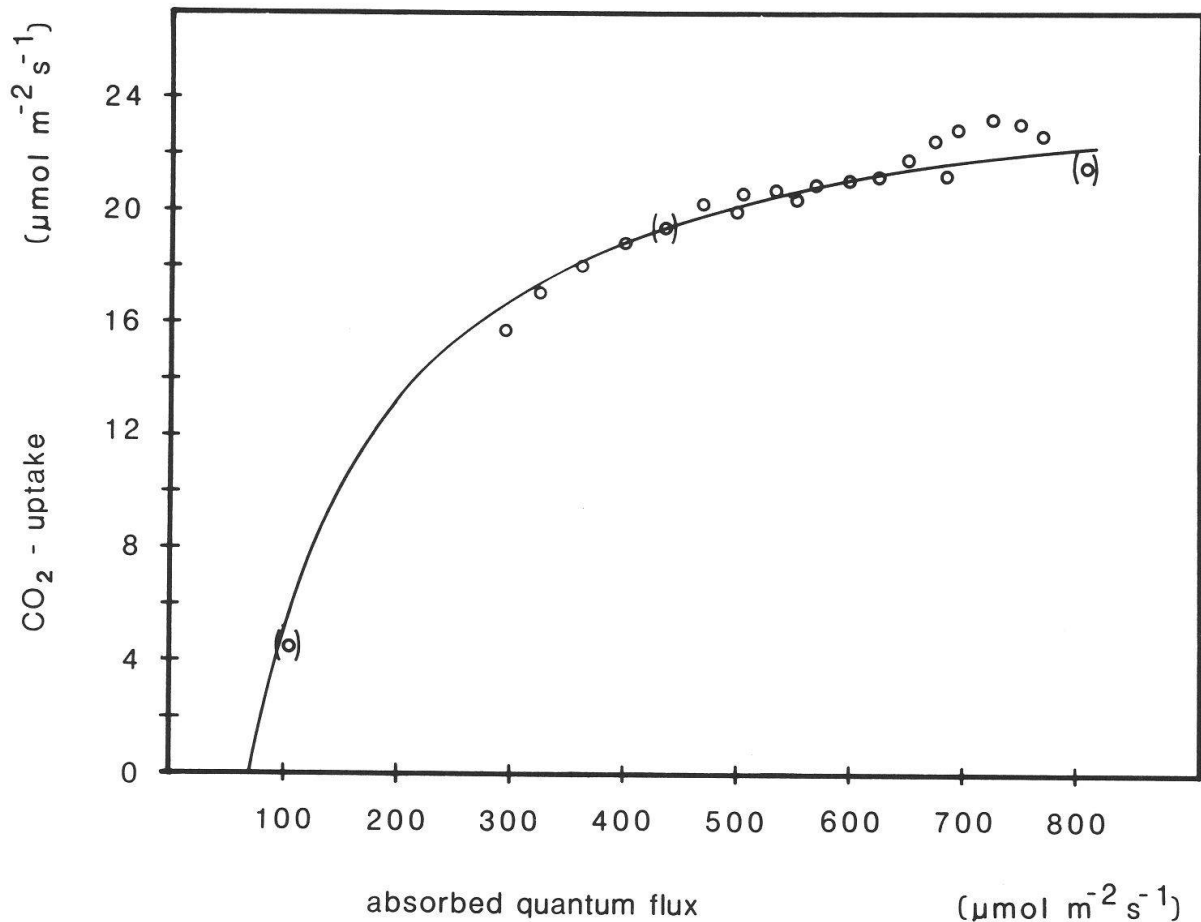
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Fig. 2. Measured saturation curves (o) of CO_2-uptake of *Solanum melongena* leaf with the adjusted rectangular hyperbola (parameters: a = 0.01825, b = 1.0805, r = 33.21).

The comparisons between the measured and calculated values of the CO_2 gas exchange are given in Figs. 5 and 6, together with leaf temperature, water vapour pressure difference between leaf and air, and leaf conductance. The values of the last three parameters are given as a function of day time for the curved leaf blade in the same manner as those of the CO_2-uptake. The values of the flattened leaf blade were determined for the same amount of absorbed quantum flux. This kind of comparison is necessary for judging the conformity of the measured and calculated diurnal courses of the net CO_2-uptake. Differences in these three parameters would indicate that differences in the calculated and measured CO_2-uptake could be expected which are not directly related to different absorbed quantum fluxes. As Figs. 5 and 6 show the conformity is always good provided there is conformity in these three parameters. This is the case for the eggplant and the morning values of fig. In the afternoon, during the fig measurement, there obviously occurs a partial stomatal closure of the naturally curved leaf, in spite of good water supply. This stomatal closure could not be observed for the flat leaf blade.

The accuracy for the measurements and the calculations lies between 5 and 10%, except for the marginal hours in the morning and evening, where the uncertainty for both increases quickly.

To examine the effect of the curvature of the leaf blades on the diurnal pattern of the absorbed quantum flux and the net CO_2-uptake, these two parameters were modeled for
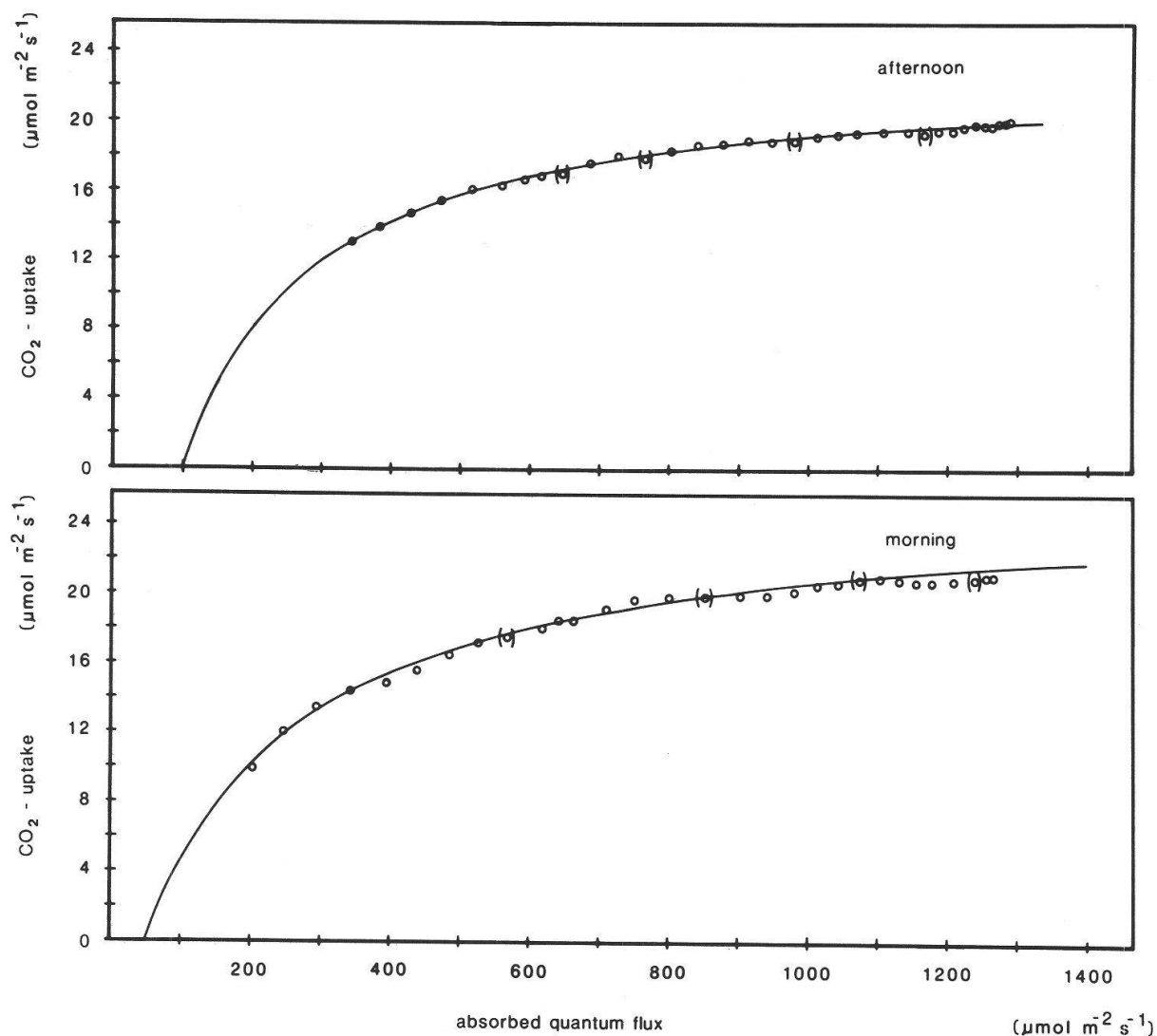
Fig. 3. Measured saturation curves (o) of CO_2-uptake in the afternoon and morning of the *Ficus carica* leaf with the adjusted rectangular hyperbola (parameters in the afternoon: a = 0.01190, b = 0.5998, r = 27.38; parameters in the morning: a = 0.005577, b = 0.1816, r = 7.103).

the naturally curved leaf and a flat leaf of the same midrib orientation and inclination. The modeling could also be done for the entire day for the eggplant, as the daily pattern of shading was recorded. The results for both leaves, i.e. from eggplant and fig are given in Figs. 7 and 8. The horizontal lines at 850 $\mu mol_Q \, m^{-2} \, s^{-1}$ for eggplant and 1000 and 1050 $\mu mol_Q \, m^{-2} \, s^{-1}$ for fig mark the saturation values of photosynthesis. The criterion for these values was chosen as follows: the absorbed quantum flux is saturating photosynthesis if, by an additional absorption of 100 $\mu mol_Q \, m^{-2} \, s^{-1}$, the rate of photosynthesis increases less than 2%.

Figs. 7 and 8 show two interesting features. The maximum of the daily course of irradiation for both eggplant and fig lies much nearer to the saturation value for the curved leaf blade than for the flat leaf. On the other side the radiation is better utilized in the marginal hours of the morning and evening. This effect is much more distinct for the eggplant as a result of the stronger curvature of the leaf blade. It is fundamentally the same effect as obtained for the differences in the daily pattern of absorbed quantum
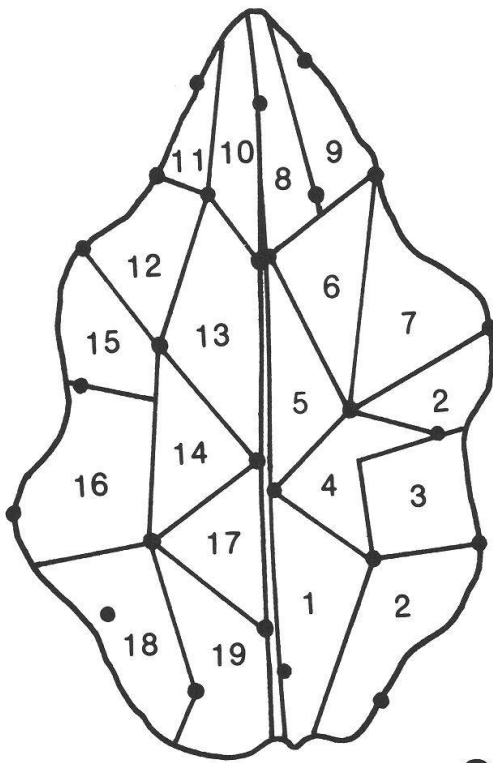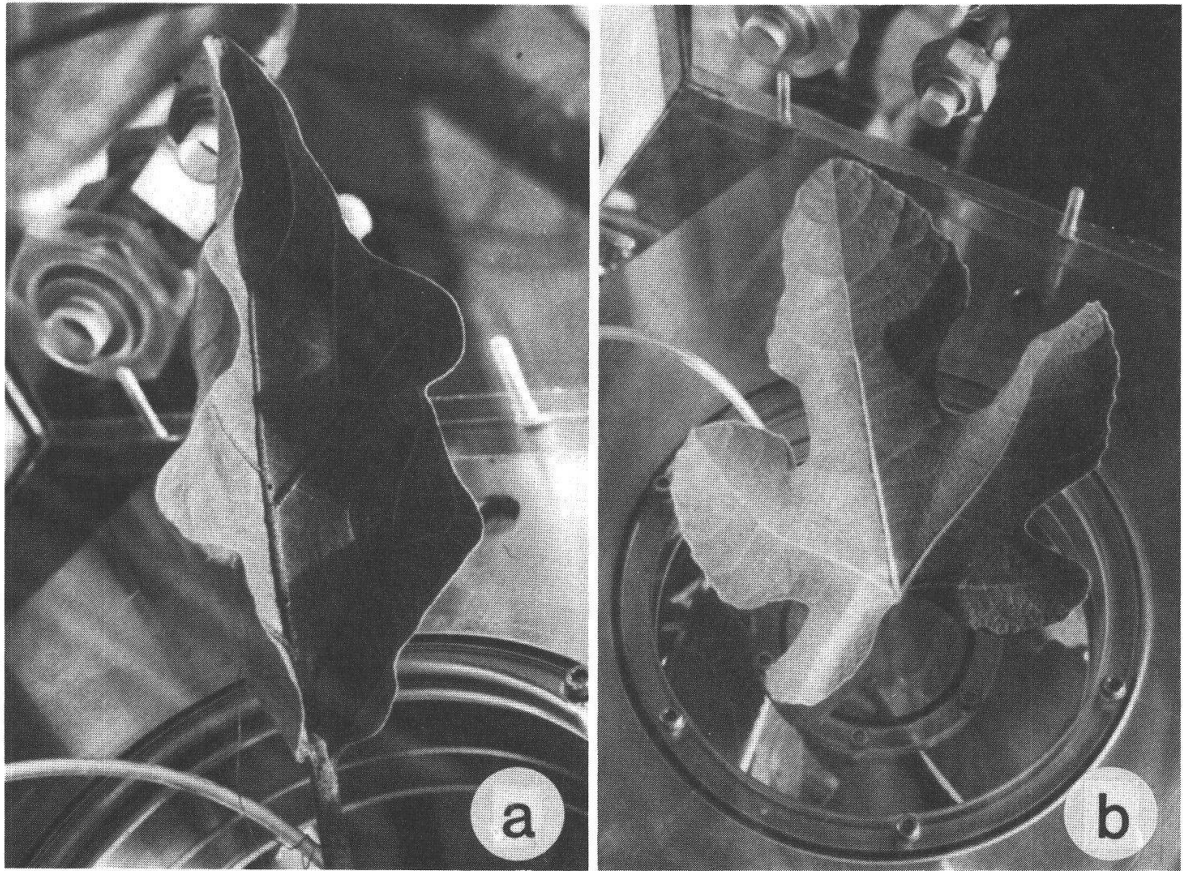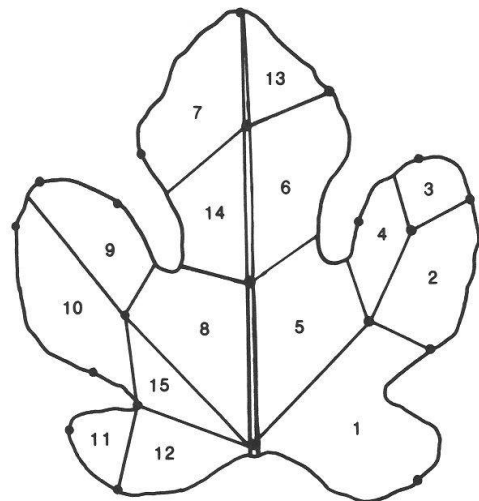
Fig. 4a, b. *Solanum melongena* (a) and *Ficus carica* leaf (b) with their subdivision of the leaf area (c) and (d) respectively.
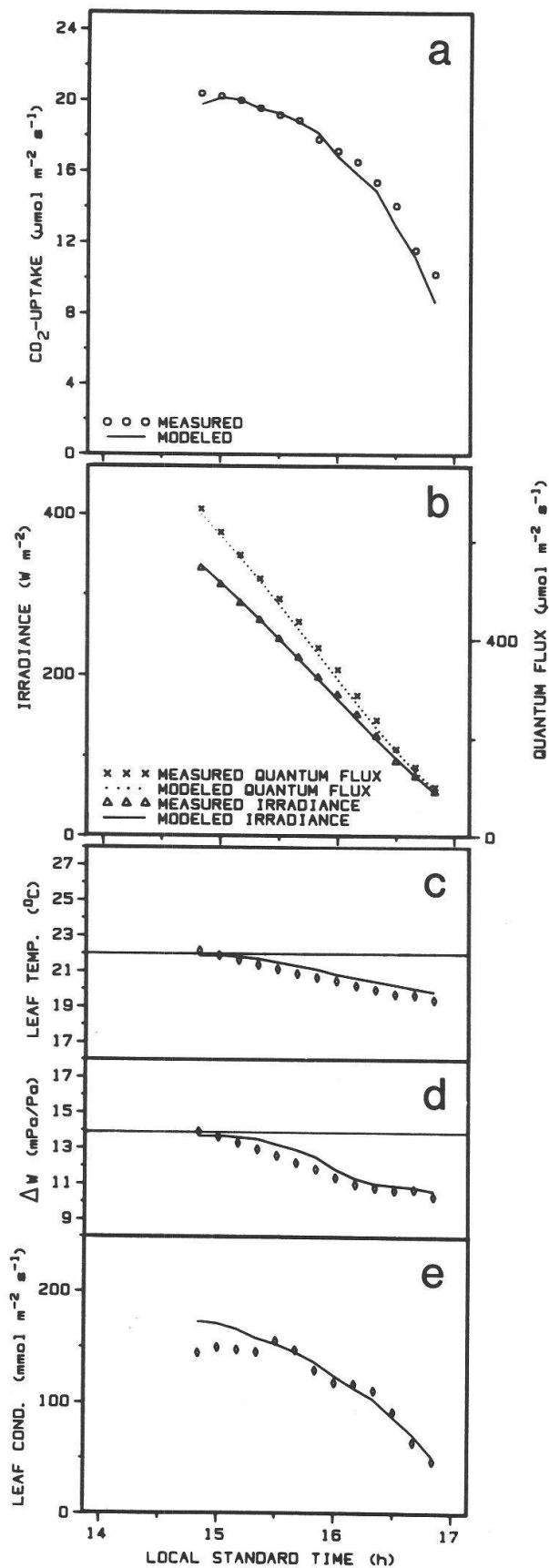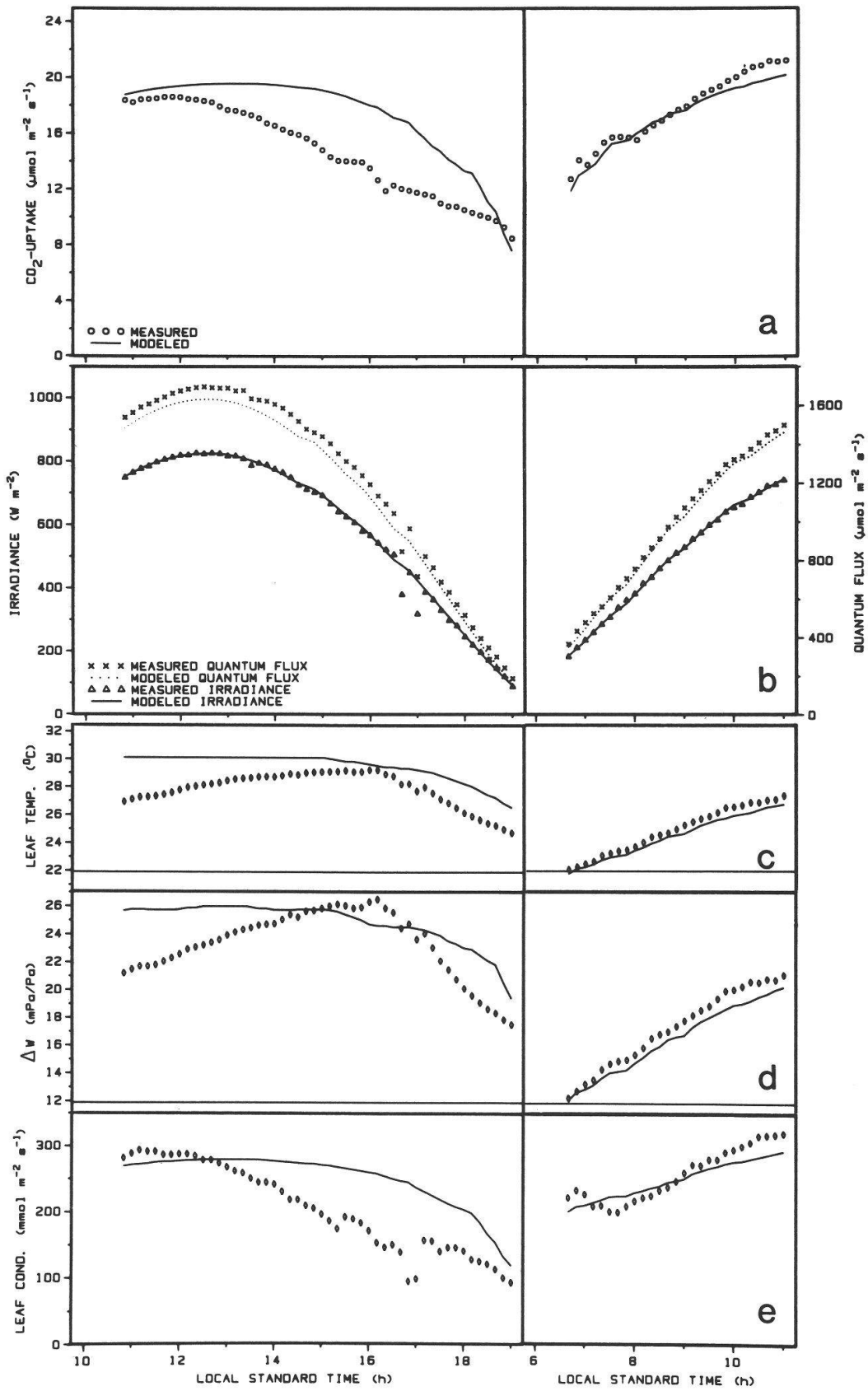
Fig. 5a–e. Modeled and measured CO_2-uptake (a) for the *Solanum melongena* leaf with the naturally curved lamina, measured and modeled horizontal irradiance and quantum flux (b), measured leaf temperature (c), water vapour pressure difference between leaf and air (ΔW) (d) and leaf conductance (e) of the naturally curved leaf ($\diamond$) and the flattened lamina (——) for the corresponding irradiance per unit leaf area. The horizontal lines at 22.0 °C and 13.9 mPa/Pa correspond to the clima of the gas exchange cuvette.
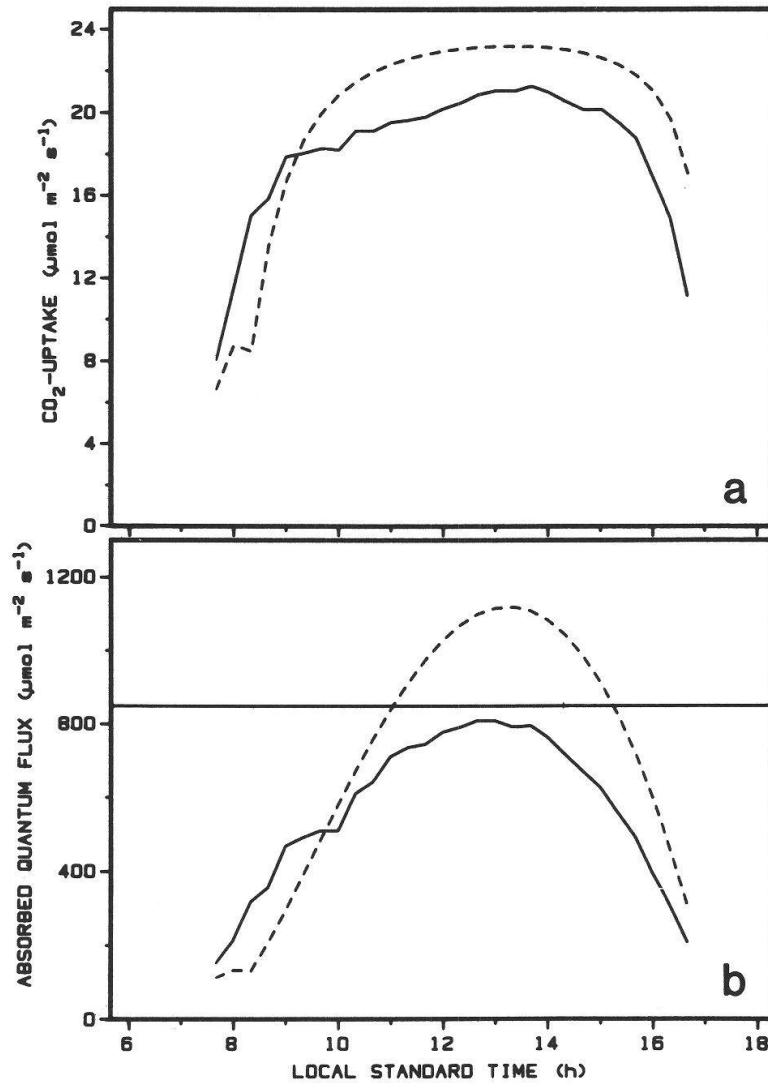
Fig. 7a, b. Modeled diurnal courses of CO_2-uptake (a) and the weighted mean of absorbed quantum flux (b) per unit leaf area for the naturally curved lamina (——) of *Solanum melongena* and a hypothetical flat leaf (– – –) with the same midrib orientation. The horizontal line at 850 μmol m^{-2} s^{-1} correspond to the saturating value of absorbed quantum flux.

Fig. 6a–e. Modeled and measured CO_2-uptake (a) for the *Ficus carica* leaf in the afternoon and morning with the naturally curved lamina, measured and modeled horizontal irradiance and quantum flux (b), measured leaf temperature (c), water vapour pressure difference between leaf and air (ΔW) (d) and leaf conductance (e) of the naturally curved leaf (◇) and the flattened lamina (——) for the corresponding irradiance per unit leaf area. The horizontal lines at 21.9 °C and 11.9 mPa/Pa and 22.0 °C and 11.8 mPa/Pa correspond to the clima of the gas exchange cuvette.
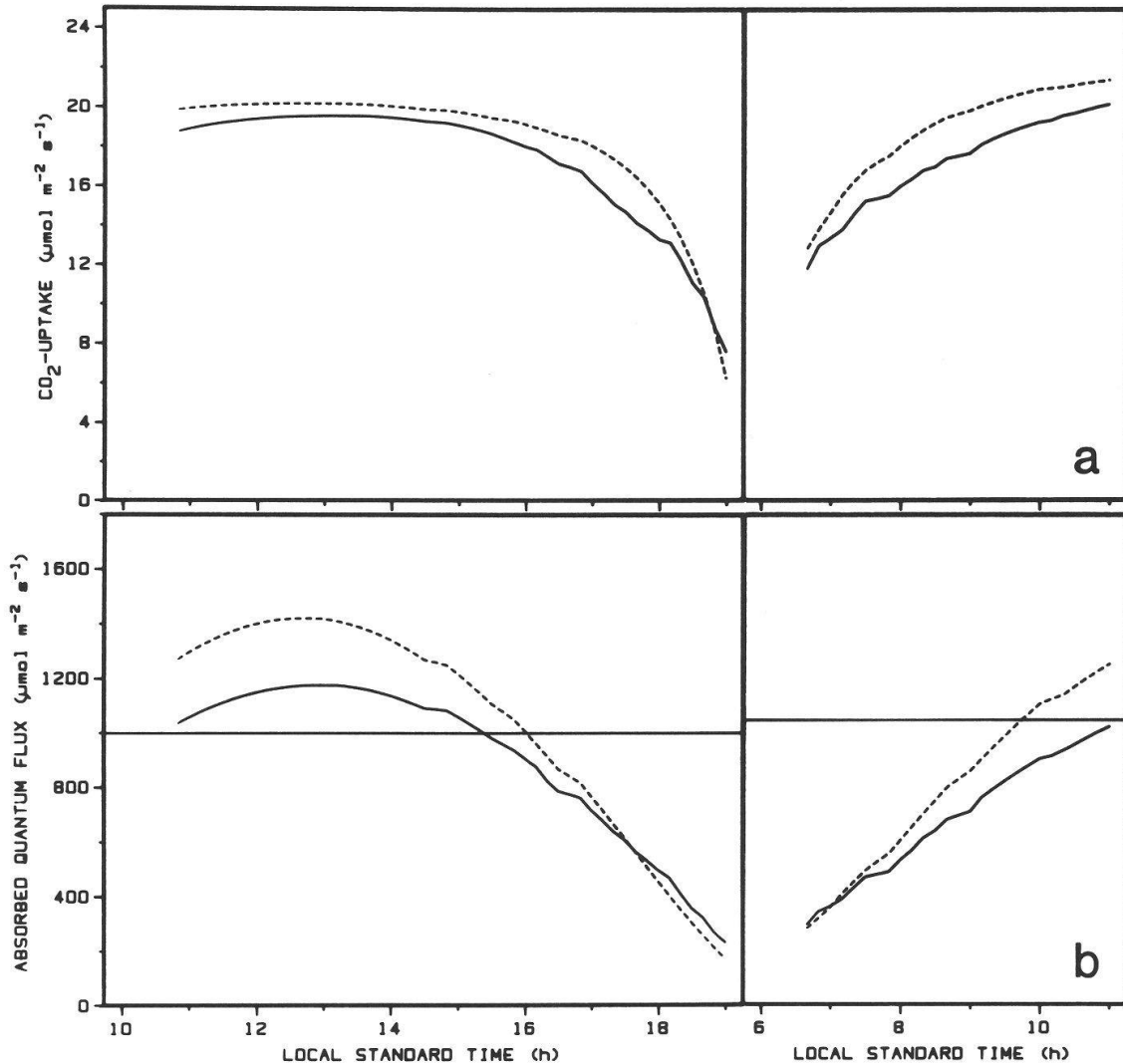
Fig. 8a, b. Modeled diurnal courses of CO_2-uptake (a) and the weighted mean of absorbed quantum flux (b) per unit leaf area for the naturally curved lamina (——) of *Ficus carica* and a hypothetical flat leaf (———) with the same midrib orientation. The horizontal lines at 1000 and 1050 $\mu mol\ m^{-2}\ s^{-1}$ correspond to the saturating values of absorbed quantum flux in the afternoon and morning respectively.

flux caused by the different inclinations of the older and young leaf of *Aloe dichotoma* (Eller and Flach 1990). As a consequence of both features the absorbed energy is optimized, to improve the photosynthetic activity without loading the photosynthetic tissue by an excess of energy.

The calculated values of the quantum use efficiency

$$
(4) \qquad \Phi = \frac{\int_{t_1}^{t_2} \bar{J}_{CO_2} \, dt}{\int_{t_1}^{t_2} \bar{G}_a \, dt}
$$

with $\bar{J}_{CO_2}$ = net photosynthesis, $\bar{G}_a$ = absorbed quantum flux and $t_1 \ldots t_2$ = timespan, should also in part show the improved efficiency of the curved leaves. Table 1 shows the

Table 1. Quantum use efficiencies of the measured and calculated net photosynthetic rates (Φ_m...measured, Φ_c...calculated for the naturally curved leaf, Φ_{cm}...calculated for the flat leaf with the same midrib orientation)

Leaf	Timespan (t_1-t_2)	Φ_m	Φ_c	Φ_{cm}
Solanum melongena	7h30–17h00	–	0.032	0.028
Ficus carica (afternoon)	10h50–19h00	0.016	0.019	0.018
Ficus carica (morning)	6h40–11h00	0.026	0.025	0.023

values for the measured and calculated net CO_2-uptake for the curved and flat blades. A clear improvement of the quantum use efficiency is only given for the eggplant. This is partially due to the stronger upward curvature of the leaf of the eggplant compared to that of the fig (Fig. 4).

To understand the meaning of these effects as applied to a whole tree or a canopy, it is necessary to analyse them in their entirety. This could be done by a statistical treatment as, e.g., Kuroiwa (1970) predicts that the productivity is optimized in a canopy by a certain height-dependent distribution of leaf inclinations. But one has also to consider the expression and distribution of sun and shade leaves with their differences in the photosynthetic response to the incoming light. Likewise to answer the question, whether a whole egg- or fig plant is optimized concerning its productivity, would need more extensive investigations involving measurements of saturation curves and analyses of the leaf orientations for each individual leaf as outlined above.

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