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Relation between Mesophyll Surface Area, Photosynthetic Rate, and Illumination Level during Development for Leaves of *Plectranthus parviflorus* Henckel[1]

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ABSTRACT

The influence of illumination level during leaf development on the mesophyll cell surface area per unit leaf area (A^{mes}/A), CO_2 resistances, and the photosynthetic rate was determined for leaves of *Plectranthus parviflorus* Henckel. The relative importance of A^{mes}/A *versus* CO_2 resistances in accounting for observed changes in photosynthesis was quantitatively evaluated using equations based on analogies to electrical circuits.

When the illumination during development was raised from 900 to 42,000 lux, the leaves more than tripled in thickness as the mesophyll cells increased in size and frequency, which caused A^{mes}/A to go from 11 to 50. The net rate of photosynthesis at light saturation concomitantly increased 4-fold, reflecting a corresponding decrease in the total resistance for CO_2 movement per unit leaf area. However, the CO_2 resistance per unit area of mesophyll cells remained about 580 seconds per centimeter for leaves grown under 900 to 42,000 lux. Thus, for *P. parviflorus*, the increased photosynthetic rate for leaves developing under higher illuminations resulted from a higher A^{mes}/A, not from changes in the CO_2 resistances within individual mesophyll cells, expressed per unit area of cell surface. Results are discussed in terms of previously observed increases in thickness, internal leaf area, and photosynthetic rates for sun *versus* shade leaves on various plant species.

The internal leaf morphology of many plant species varies from that characteristic of shade leaves at low light levels to that of sun leaves when development occurs at illuminations approaching full sunlight (1, 7, 10–12, 21–24). Not only do sun leaves tend to have more highly developed palisade and spongy mesophyll regions than shade leaves, but also they have higher photosynthetic rates at light saturation (1, 2, 6, 10). The higher assimilation rates have been suggested to result from changes in activity of enzymes involved in photosynthesis (1, 2, 9, 10, 14, 18) and to variations in the number of chlorophylls per photosynthetic unit (1, 2, 9, 17). However, the higher rates of photosynthesis could also be a consequence of the changes in internal leaf morphology caused by illumination, a matter which apparently has not been systematically investigated. This morphological aspect will be described here by A^{mes}/A, the total surface area of the mesophyll cells per unit area of one side of a leaf or the ratio of internal to external leaf area. Enzymic and other cellular factors relating to photosynthesis are combined into a single resistance expressed per unit area of the mesophyll cells ($R^{cell}_{CO_2}$). This study uses electrical circuit analogies to determine quantitatively the relative contributions of A^{mes}/A *versus* $R^{cell}_{CO_2}$ in leading to the higher photosynthetic rates for *Plectranthus parviflorus* Henckel leaves grown under higher illuminations.

Ignoring respiration and photorespiration, the net rate of photosynthesis per unit leaf area (J_{CO_2}) is

$$J_{CO_2} = c_{CO_2}/R_{CO_2} = c_{CO_2}/(1.56\ R_{wv} + R^{int}_{CO_2}) \quad (1)$$

where c_{CO_2} is the CO_2 concentration outside the leaf, and R_{CO_2} is a total resistance for CO_2 fixation expressed per unit leaf area (3, 4, 8, 13, 15, 16, 20). As equation 1 indicates, R_{CO_2} has a gaseous phase component in common with the water vapor pathway, the factor 1.56 accounting for the ratio of the diffusion coefficient of water vapor to that of CO_2 in air at 20 C (16). In the liquid phases, the resistance to CO_2 movement ($R^{int}_{CO_2}$) is composed of contributions from cell walls, plasmalemmas, cytoplasm, chloroplast membranes, and the resistance associated with the carboxylation reaction (3, 4, 8, 14, 15, 20). This internal resistance, expressed per unit leaf area, is related to the resistance per unit area of mesophyll cells ($R^{cell}_{CO_2}$) as follows:

$$R^{cell}_{CO_2} = R^{int}_{CO_2}\ A^{mes}/A \quad (2)$$

If changes in photosynthetic rates between sun and shade leaves are dependent only on the internal leaf surface area as measured by A^{mes}/A, then $R^{cell}_{CO_2}$ should remain constant, indicating over-all similarity per unit area of mesophyll cells as far as net CO_2 uptake is concerned. On the other hand, enzymic, pigment, or other intracellular adjustments could cause $R^{cell}_{CO_2}$ to vary more than A^{mes}/A, in which case intracellular factors would contribute more than anatomical ones to the observed photosynthetic differences.

MATERIALS AND METHODS

Cuttings from a single parent plant of *Plectranthus parviflorus* Henckel, a member of the Labiatae commonly known as "Creeping Charlie," were grown at 20 C and 55% relative humidity for 5 weeks in sterilized soil. The indicated illumination was provided for 12 hr each day using warm-white fluorescent tubes and neutral density screens (15,000 lux corresponded to 29 neinsteins $cm^{-2}\ sec^{-1}$ between 400 and 700 nm). Third node leaves approximately 15 cm^2 in area were used for measurements.

The A^{mes}/A ratio was determined using drawings prepared

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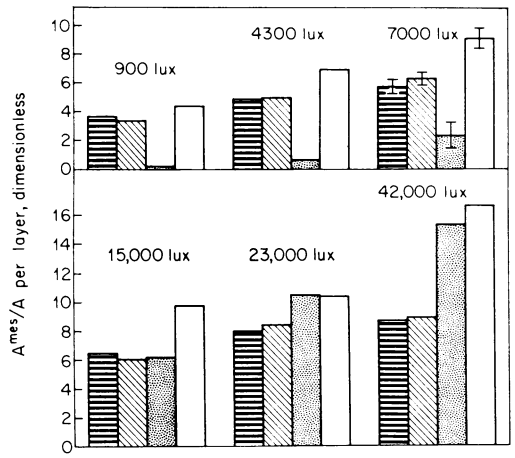

FIG. 1. Contributions of the palisade and spongy mesophyll to the internal area of leaves of *Plectranthus parviflorus* grown at the indicated illumination levels. ▤: A^{mes}/A for the uppermost palisade layer; ▧: the next palisade layer; ▨: lower palisade layers; □: A^{mes}/A for the spongy mesophyll. Representative standard errors of the mean obtained using six leaves are indicated for data at 7,000 lux.

with the aid of a camera lucida using an over-all magnification of 300 ×. Sections (500 μm × 500 μm) were taken from both sides of the central vein of a leaf, infiltrated with distilled H_2O, and the palisade and spongy mesophyll layers were drawn from paradermal views. Transverse sections 100 μm thick were then used to construct a three-dimensional model from which cell lengths and diameters were determined. Cell surface areas were calculated assuming that the mesophyll cells were cylindrical with hemispheres on each end.

To measure the net rate of photosynthesis (J_{CO_2}), detached leaves were placed in a 500-cm^3 chamber at 20 C through which 200 ml min^{-1} of 300 μl l^{-1} of CO_2 in N_2 was passed. Based on leaf anatomy, *P. parviflorus* is a C-3 plant (photorespiring) and so N_2 instead of air was used in order to minimize photorespiration (20). To minimize the relative contribution of respiration, a saturating illumination (50,000 lux or 130 neinsteins cm^{-2} sec^{-1} from 400 to 700 nm) was provided by a General Electric Cool-Beam 300-w tungsten lamp filtered through 10 cm of water. Lower illuminations were obtained using neutral density screens. The CO_2 concentrations in the gases entering and leaving the leaf chamber, which were averaged to obtain c_{CO_2}, were determined with a Beckman Model 215A infrared gas analyzer calibrated with CO_2 standards obtained from Liquid Carbonic Corp.

The resistance to water vapor loss from the leaves was measured with a Lambda Instruments Model LI-60 diffusive resistance porometer. Since water vapor came from both sides of a leaf, R_{wv} equaled R^u_{wv} $R^l_{wv}/(R^u_{wv} + R^l_{wv})$ where u and l refer to the upper and lower surface, respectively. Based on the leaf dimensions and the ambient wind velocity, the resistance of the unstirred air boundary layer was estimated to be 0.2 sec cm^{-1} (16) and this has been included to give the actual value of R_{wv} (this correction is small, because R_{wv} was generally about 3 sec cm^{-1}).

RESULTS

The illumination level during growth had a major influence on the internal leaf morphology of *Plectranthus parviflorus*. Figure 1 summarizes A^{mes}/A for individual layers of mesophyll cells for leaves developing at six different illuminations. The A^{mes}/A contribution from the upper two palisade layers more than doubled when the illumination was raised from 900 lux to 42,000 lux, primarily because of an increase in the over-all average length of the cells from 51 μm to 112 μm (the mean diameter remained near 40 μm). The A^{mes}/A ratio for the lower palisade layers went from 0.52 at 4300 lux to 6.15 at 15,000 lux to 15.42 at 42,000 lux (Fig. 1). A large increase in A^{mes}/A also occurred for the spongy mesophyll region, attributable to a rise in average cell area from 4900 μm^2 to 7800 μm^2 and a 2.4-fold increase in the number of such cells per unit leaf area as the illumination went from 900 lux to 42,000 lux.

Because the A^{mes}/A affecting CO_2 movement within a leaf includes only that part of the mesophyll cell surface area directly exposed to the intercellular air spaces, the percentage touching for the mesophyll cells was also determined from camera lucida drawings. The fraction of the surface area of the mesophyll cells touching adjacent cells averaged about 6% for the palisade region and 3% for the spongy region. Therefore the values given in Figure 1 overestimate the effective A^{mes}/A by this amount. However, the geometrical model used to calculate cell surface area does not include local surface irregularities, which leads to a potentially compensating underestimate of the A^{mes}/A involved in CO_2 diffusion. The intercellular air spaces in the palisade region averaged about 29% by volume for all illuminations, but decreased from 62% at 900 lux to 36% at 42,000 lux in the spongy mesophyll region.

The over-all A^{mes}/A continuously increased from 11.3 for leaves developing at 900 lux to 37.3 at 23,000 lux (Fig. 2). Figure 2 also shows that there was a parallel rise in the net rate of photosynthesis at light saturation (50,000 lux). Thus the change in photosynthetic capacity apparently reflected the increase in surface area within the leaf, a matter which can be quantitatively evaluated using equations 1 and 2. Table I summarizes the measured values for J_{CO_2}, c_{CO_2} (1 μl l^{-1} CO_2 at 20 C corresponds to 41 nmoles cm^{-3}), R_{wv}, and A^{mes}/A as well as the calculated resistances. Although R_{wv} had no apparent trend, $R^{int}_{CO_2}$ decreased nearly 5-fold as the illumination during leaf development was raised from 900 to 42,000 lux. This decrease occurred together with a nearly 5-fold increase in A^{mes}/A (Table I). Consequently, $R^{cell}_{CO_2}$, the resistance per unit area of the mesophyll cells, remained at about 580 sec cm^{-1} from 900 lux to 42,000 lux. In particular, the regression line for $R^{cell}_{CO_2}$ *versus* illumination was as follows: $R^{cell}_{CO_2}$ in sec cm^{-1} = 592 ± 38 − (0.74 ± 2.5) × illumination in kilolux; because the confidence interval for the slope contains zero, $R^{cell}_{CO_2}$ was indistinguishable at the

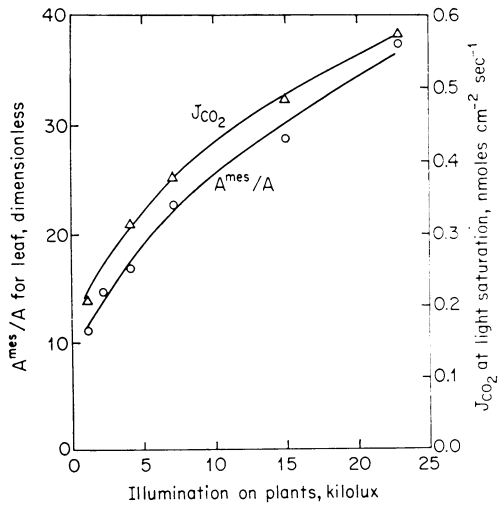

FIG. 2. Effect of illumination level during growth on the internal leaf area per unit surface area (A^{mes}/A) and the photosynthetic rate of detached leaves at light saturation (J_{CO_2}).

95% significance level from being constant for the range of illuminations tested. Thus the higher photosynthetic rates at light saturation for leaves of *P. parviflorus* grown at higher illumination levels could be accounted for by increases in A^{mes}/A without any apparent contribution from changes in $R^{cell}_{CO_2}$.

Leaves that developed under higher illuminations had a lower total resistance for CO_2 fixation at light saturation (Table I). Because of this lower R_{CO_2}, they would be expected to have higher photosynthetic rates at other light levels than do leaves developing under lower illuminations. Figure 3 shows that this was the case for leaves that developed at 25,000 lux compared with those from 4,000 lux. Equation 1 also indicates that J_{CO_2} should vary directly with c_{CO_2} (to be discussed below). The range of validity of this convenient simplification was checked for leaves developing at 4,000 or 25,000 lux by varying the external CO_2 concentration at 50,000 lux. Measured values of net photosynthesis agreed within ± 5% with equation 1 from 150 to 450 $\mu l\ l^{-1}$ of CO_2, which represented a 3-fold range in J_{CO_2}.

Although A^{mes}/A is an appropriate parameter for interpreting effects of leaf morphology on photosynthetic rate, it was rather time consuming to determine. Thus, the relationship between A^{mes}/A and leaf thickness was established for *P. parviflorus*. As A^{mes}/A increased, the leaf thickness of course increased, but not in a completely linear fashion (Fig. 4). The intercept on the ordinate is approximately 40 μm, a reasonable estimate of the thickness of the upper plus lower epidermis for *P. parviflorus* (an A^{mes}/A of zero corresponds to a "leaf" with no mesophyll region). As A^{mes}/A went from 6 to 50, the leaf thickness monotonically increased from under 200 μm to over 1,000 μm. Measurement of leaf thickness is therefore a convenient means of estimating A^{mes}/A for *P. parviflorus*.

Table I. *Resistances Involved in Photosynthesis for Plectranthus parviflorus Grown under Various Illuminations and Assayed at Light Saturation*

Illumination on Plants	J_{CO_2}	c_{CO_2}	R_{CO_2}	R_{wv}	$R^{int}_{CO_2}$	A^{mes}/A	$R^{cell}_{CO_2}$
lux	*nmoles cm^{-2} sec^{-1}*	*$\mu l\ l^{-1}$*	*sec cm^{-1}*				*sec cm^{-1}*
900	0.207	296	58.6	3.5	53.1	11.3	600
4300	0.314	295	38.5	3.8	32.6	17.0	554
7000	0.378	293	31.8	2.8	27.4	22.9	627
15,000	0.486	291	24.5	3.3	19.4	28.7	557
23,000	0.572	287	20.5	3.1	15.7	37.3	586
42,000	0.734	279	15.6	2.8	11.2	49.9	560

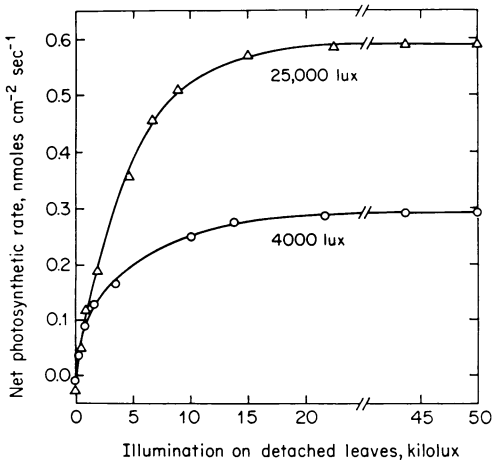

FIG. 3. Photosynthetic rates measured at various illuminations for leaves from plants grown at 4,000 or 25,000 lux.

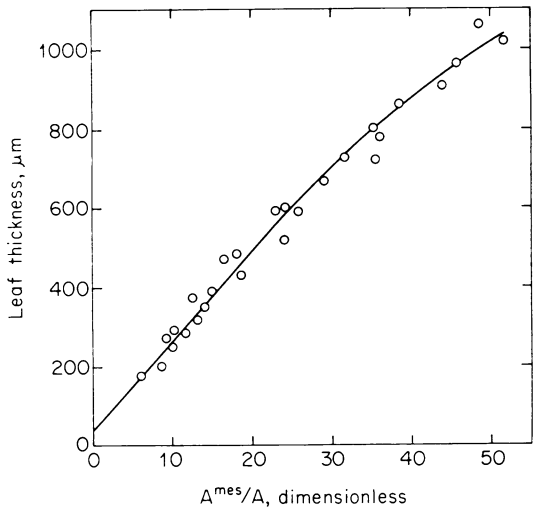

FIG. 4. Relation between A^{mes}/A and leaf thickness.

DISCUSSION

Previous investigations have related the higher photosynthetic rates of sun leaves compared with shade leaves on the same plant to elevated enzymic activities or changes in pigment amounts caused by the higher illuminations (1, 2, 9, 10, 14, 17, 18). However, it has not been clear whether such alterations per unit leaf area reflect changes per unit area of mesophyll cells. The present study indicates that for *Plectranthus parviflorus* all of the observed increases in photosynthesis at higher illuminations can be accounted for by accompanying increases in internal leaf area. Specifically, as the illumination during growth was raised from under 1,000 lux to over 40,000 lux, the surface area of mesophyll cells exposed to the intercellular air spaces per unit area of one side of a leaf (*i.e.*, A^{mes}/A) increased from 11 to 50 (Table I). A^{mes}/A increased because of a lengthening of cells in the upper two palisade layers, the development of additional palisade layers, and an increase in size and frequency of spongy mesophyll cells. However, the resistance per unit area of mesophyll cells at light saturation encountered by CO_2 moving across the cell walls and membranes into the chloroplasts plus the carboxylation resistance remained at about 580 sec cm^{-1} for all growth illuminations tested. Such a high resistance per unit area of mesophyll cell surface makes it mandatory for the leaves to have a large internal surface area in order to maintain substantial rates of photosynthesis. In summary, leaves of *P. parviflorus* developing under high illumination were able to take advantage of the increased light level not by changing the net photosynthetic properties per unit cell wall area, but by increasing the area of mesophyll cells exposed to the intercellular air spaces per unit leaf area.

Electrical circuit analogies can be valuable for analyzing the relative importance of various components in the CO_2 fixation pathway, but they must be employed with caution. For example, equation 1 implicitly assumes that the CO_2 concentration becomes zero as a result of the carboxylation resistance (4, 14, 15). Other investigators (6, 8, 20) view the CO_2 concentration after the carboxylation resistance as non-zero but negligible at light saturation compared with c_{CO_2}, in which case equation 1 is still valid. This condition becomes less tenable as the illumination on the detached leaves is reduced and respiration (and photorespiration) also cannot then be ignored. Therefore equation 1 is

not really applicable below about 10,000 lux on the detached leaves of *P. parviflorus* (Fig. 3). Moreover, the higher light compensation point generally observed for shade compared with sun leaves (2, 10, 12, 23) is undoubtedly related to the increasing relative importance of respiration at low illuminations as well as to additional complications resulting from possible changes in the carboxylation resistance and increases in the CO_2 concentration in the chloroplasts. In short, based on the lower R_{CO_2} at light saturation, a higher photosynthetic rate is generally expected for leaves developing at 25,000 lux compared with 4,000 lux (Fig. 3). However, without knowing the actual CO_2 resistances, fluxes, and concentrations within the mesophyll cells, the exact shape of the curve cannot be predicted, especially at the lower illuminations.

A^{mes}/A for *P. parviflorus* varied from 6 to 50 (Fig. 4). Although no other species has been reported to have such a wide range for internal leaf area per unit surface area, the values are similar to previous determinations of this or equivalent parameters (6, 7, 10, 21, 22). For example, Turrell (22) summarized data up to 1965 on 17 species and reported that A^{mes}/A ranged from 9 for *Ginkgo biloba* up to 77 for *Catalpa speciosa*. El-Sharkawy and Hesketh (6) found that A^{mes}/A varied from 12 to 31 for the 14 species they considered. For *Medicago sativa* leaves from 120 to 260 μm thick, Turrell (22) established a linear relationship between A^{mes}/A and leaf thickness (although his calculated regression equation does not agree with the data given). Figure 4 indicates a linear relation between A^{mes}/A and leaf thickness for mature third-node leaves of *Plectranthus parviflorus* up to nearly 700 μm thick, *viz.*, $A^{mes}/A = 0.44 \times$ (leaf thickness in μm: 40). Above 700 μm, the leaf thickness tends to increase less rapidly for a given increment in A^{mes}/A, primarily attributable to a tighter packing of the spongy mesophyll cells.

P. parviflorus and over 30 other species vary internal leaf morphology in response to illumination (2, 7, 10–12, 21–24). This is most readily apparent from the generally observed 2- to 4-fold increase in thickness for sun *versus* shade leaves on the same plant. Turrell, who noted that A^{mes}/A went from 14 for shade leaves of *Syringa vulgaris* to 26 for sun leaves, felt the great increase in internal leaf area would increase transpiration (21, 22). However, experiments of Tanton and Crowdy (19) indicate that the transpiration rate would be essentially independent of A^{mes}/A; nearly all of the water evaporated from leaves of *Hordeum vulgare* L., *Plantago major* L., *Prunus laurocerasus* L., and *Phaseolus vulgaris* L. actually comes from the inner sides of the guard cells and other epidermal cells (5, 19), and so the water vapor flux in the intracellular air spaces would be relatively small. Changes in A^{mes}/A would therefore have their major direct influence on photosynthesis, not on transpiration. Leaves of many plant species develop at the top of the canopy exposed to higher illuminations and thus could develop a lower total CO_2 resistance compared with leaves differentiating at lower light levels. This may have evolved as an adaptation which takes advantage of elevated illuminations available during leaf development. The importance of A^{mes}/A and $R^{cell}_{CO_2}$ for photosynthesis has generally not been appreciated, and consequently these parameters have not been systematically studied for sun *versus* shade leaves or in other situations where there is a wide range of illumination levels during leaf development.

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CORRECTIONS

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Nobel, Park S., Lawrence J. Zaragoza, and William K. Smith. Relation between Mesophyll Surface Area, Photosynthetic Rate, and Illumination Level during Development for Leaves of *Plectranthus parviflorus* Henckel.

Page 1070, column 1, paragraph 1, lines 13 to 16 should be corrected to read: Figure 4 indicates a linear relation between A^{mes}/A and leaf thickness for mature third-node leaves of *Plectranthus parviflorus* up to nearly 700 μm thick, *viz.*, $A^{mes}/A = 0.044 \times$ (leaf thickness in μm: 40).

Vol. 56: 579-583. 1975

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Page 581, Table III, column 7, the activity of bound UDP glucose starch synthetase 21 days after flowering should be corrected to read: 0.

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Page 41, line 3 should be corrected to read: Received for publication August 11, 1975 and in revised form September 19, 1975.

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Page 344, column 2, line 5 should be corrected to read: as follows: fractional horsepower motor, type NS1-13, with 1/40 hp, ...