Convexity of the Photosynthetic Light-Response Curve in Relation to Intensity and Direction of Light during Growth

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Photosynthesis in the intermediate light range is most efficient when the convexity of the photosynthetic light-response curve is high. Factors determining the convexity were examined for intact leaves using Salix sp. and for a plant cell culture using the green microalga Coccomyxa sp. It was found that the leaf had lower convexity than diluted plant cells because the light gradient through the leaf was not fully matched by a corresponding gradient in photosynthetic capacity. The degree to which the leaf gradients were matched was quantified by measuring photosynthesis at both leaf surfaces using modulated fluorescence. Two principal growth conditions were identified as those causing mismatch of leaf gradients and lowering of the convexity relative to cells. The first was growth under low light, where leaves did not develop any noteworthy gradient in photosynthetic capacity. This led to decreased convexity, particularly in old leaves with high chlorophyll content and, hence, steep light gradients. Second and less conspicuous was growth under high light conditions when light was given bilaterally rather than unilaterally, which yielded leaves of high photosynthetic capacity at both surfaces. Two situations were also identified that caused the convexity to decrease at the chloroplast level: (a) increased light during growth, for both leaves and cells, and (b) increased CO₂ concentration during measurement of high-light-grown leaves. These changes of the intrinsic convexity were interpreted to indicate that the convexity declines with increased capacity of ribulose-1,5-bisphosphate carboxylase/oxygenase relative to the capacity of electron transport.

\[ \Theta P^2 - (\Phi I + P_{\text{max}}) P + \Phi I P_{\text{max}} = 0 \]  

where \( P \) is the rate of photosynthesis (y variable), \( I \) is the irradiance (x variable), \( \Phi \) is the maximum quantum yield, \( \Theta \) is the convexity, and \( P_{\text{max}} \) is the light-saturated rate of photosynthesis. \( \Phi \) and \( \Theta \) are parameters of particular importance for photosynthetic productivity under natural conditions, because it is believed that the rate of photosynthesis is limited by light most of the time (Long, 1985; Ort and Baker, 1988). As can be seen in Figure 1, \( \Theta \) determines the photosynthetic efficiency in the intermediate light range above the linear part determined by \( \Phi \). The highest possible efficiency is attained when \( \Theta = 1 \), in which case the curve goes directly from the initial line set by \( \Phi \) to the plateau set by \( P_{\text{max}} \) (the so-called Blackman curve). This is never realized for cells and leaves that typically show \( \Theta \) values within the range of 0.7 to 0.99. It should be noted that \( \Theta \) does not follow a linear scale. Therefore, a curve of \( \Theta = 0.90 \) is more different from a curve of \( \Theta = 0.99 \) than it is from a curve of \( \Theta = 0.75 \) (Fig. 1).

Several investigators have tried to ascribe a physical meaning to \( \Theta \). They fall into two categories: those seeking a physiological description of \( \Theta \) at the chloroplast level and those dealing with the structural factors that have the effect that the intrinsic \( \Theta \) of the chloroplast is not realized for the leaf. The basis for the latter effect is steep light gradient through the leaf. This has been demonstrated by sectioning leaves (Terashima and Saeki, 1983), by inserting optical fibers into leaves (Vogelmann, 1989), and by modeling (Evans et al., 1993). For a leaf to realize the intrinsic \( \Theta \) of the chloroplast, the light-response curves of all chloroplasts must be in phase (Terashima and Saeki, 1985). Thus, there must be a gradient in \( P_{\text{max}} \) through the leaf that matches the gradient in light. With increasing mismatch, \( \Theta \) decreases more and more from its intrinsic value (Oya and Laisk, 1976; Terashima and Saeki, 1985; Leverenz, 1987; Evans et al., 1993). This situation might arise because of an insufficient acclimation potential of the chloroplast. This probably explains the observation that \( \Theta \) decreases when the light gradient is accentuated by increased Chl content (Leverenz, 1987). The light and \( P_{\text{max}} \) gradients may also diverge following acclimation to light of variable direction. For instance, a vertical leaf that receives direct sunlight on both surfaces will develop a high \( P_{\text{max}} \) at both surfaces (Evans et al., 1993). When measured under unilateral illumination, such a leaf will show lower \( \Theta \) than a horizontal leaf (DeLucca et al., 1991; Evans et al., 1993). However, when light conditions are changed, internal reacclimation immediately starts and any large, initial depression in \( \Theta \) is largely overcome within a few days (Leverenz, 1988), irrespective of the particular leaf anatomy (Ogren and Evans, 1993).

In relatively few studies has the physiological nature of \( \Theta \) been considered. Although they share the view that \( \Theta \) is determined by the transition from one major rate limitation

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of photosynthesis to another as light is increased, they disagree about the identity of these limitations. The widely used model of Farquhar et al. (1980) predicts that the rate limitation at high light is exerted by Rubisco. We (Ögren and Evans, 1993) have used this model to explain a variation in $\Theta$ produced by a range of CO$_2$ concentrations and suggested the following: the lower capacity of Rubisco relative to that of electron transport, the earlier the transition to $P_{\text{max}}$, and the higher the $\Theta$. There was a small difference between model and data that, however, could be accounted for by considering the light activation of Rubisco. Other workers have suggested that $\Theta$ is determined by the rate of PSII turnover relative to that of plastocynone reoxidization (Zvalinskii and Litvin, 1988; Leverenz et al., 1990). This model, however, cannot account for $\Theta$ being dependent on CO$_2$. In effect, it cannot easily handle any situation in which $\Theta$ departs from a value close to unity, because this model is based on the assumption that the turnover of PSII is invariably much faster than any other step in photosynthesis. Although $\Theta$ values approaching unity have been reported for shade-grown conifers (Leverenz, 1988) and some other C$_3$ plants (Prioul and Chartier, 1977), there are also reports of much lower values (Evans and Terashima, 1987; Ögren and Evans, 1993). Also, fluorescence analysis has revealed that PSII turnover is not constantly high but is gradually down-regulated as light is increased (Weiss and Berry, 1987).

In the present work I further address the questions as to what extent $\Theta$ varies and for what reasons. To study the intrinsic $\Theta$ independently of structural complications of a leaf, I have used a green unicellular alga belonging to the genus Coccomyxa. As shown by Palmqvist (1993), this alga lacks the carbon-accumulating mechanism present in most other green microalgae such as Chlamydomonas, Dunaliella, and Scenedesmus (Badger, 1987), which in itself may affect $\Theta$ (Falk and Palmqvist, 1993). Coccomyxa, therefore, has a photosynthetic apparatus more closely related to that of the C$_3$ plant (Palmqvist, 1993), which makes it particularly useful as a model system for the plant cell. It will be shown that the intrinsic $\Theta$ not only depends on CO$_2$ but also on irradiance.

A high $\Theta$ was found exclusively in shade-acclimated cells and leaves. As will be discussed below, these results are fully consistent with the previous hypothesis that the relative capacity of Rubisco is the main physiological factor determining $\Theta$.

To study the influence of leaf structure on $\Theta$, a fluorescence technique was used that allows top and bottom parts of the leaf to be analyzed separately for their photosynthesis rates. We (Evans et al., 1993) have previously used this technique to verify models of gradients in photosynthetic characteristics of leaves. Different case studies will be presented in which either the light or the $P_{\text{max}}$ gradient was varied.

**MATERIALS AND METHODS**

**Plant Material**

Plants of a single clone of Salix sp. (No. 75 in the Swedish Energy Project, Swedish University of Agricultural Sciences) were grown to a height of approximately 1 m in pots of soil. They were watered daily with a complete nutrient solution and kept in a growth room at 20 to 30°C, 50 to 80% RH, and at an irradiance of about 200 $\mu$mol m$^{-2}$ s$^{-1}$ (17-h photoperiod) provided by metal halogen lamps (HQL-TS 400 W; Osram, Berlin, Germany). Leaves exposed to this irradiance on upper surfaces exclusively were taken to represent the low-light-acclimated state. High-light-acclimated leaves were obtained by enclosing a pair of opposite, nearly fully expanded leaves in separate water-jacketed clamp-on cuvettes. They were exposed to 1400 $\mu$mol m$^{-2}$ s$^{-1}$ (17-h photoperiod) from metal halogen lamps (described above). The cuvettes were maintained at 25°C and flushed with humidified air (18°C dew point temperature) through inlet manifolds that were designed for maximal air turbulence. The cuvette interior was painted matt black to minimize diffuse illumination. A 5-mm thick glass pane and a layer of heat-reflecting filters (Balzer Calfix-C; Lichtenstein) were placed in front of the cuvette glass window to reduce heat radiation. The leaves were held in the cuvettes for four to five consecutive photoperiods. This was followed by a 7-h period of low light to allow any photoinhibition to be fully repaired before measurements started. In one experiment, the leaves were flipped over once a day and thus illuminated alternatingly on upper and lower surfaces.

A canopy of the same Salix clone was growing outside the laboratory. Mature leaves positioned within the sector E-W on main shoots were excised in the morning while they were still in the shade. After being recut under water, they were transferred to vials of water and used immediately. The leaves were acclimated to a period of mainly clear days with maximum air temperatures in the range of 20 to 25°C.

Leaf Chl contents were determined as described by Arnon (1949) using two leaf discs (1.1 cm$^2$) per leaf.

A single strain of a unicellular green alga (Coccomyxa sp.) was grown axenically in a liquid medium, with the major composition as for BG11 (Ripka et al., 1981), trace elements according to the formula of Surzycki (1971), and a pH of 6.8 buffered with 10 mm bis-Tris propane (Sigma). The alga was isolated from the lichen Peltigera aphthosa (L.) Willd, in which it is the primary photobiont. The procedure for isolation was.
Described by Palmqvist (1993). The cultures, in cylindrical flasks of 35 mm diameter, were bubbled with air, continuously illuminated by a metal halogen lamp (specified above), and kept in a clear water bath maintained at 25°C. They were diluted daily to give a Chl concentration of about 5 µg mL⁻¹. Chl concentration of pelleted cells was determined according to the method of Ronen and Galun (1984).

Measurement of CO₂ Exchange

Exchange of CO₂ and H₂O by individual leaves was measured in an open system (Compact Minicuvette System 400, gas mixing unit GMA1 and cuvette GK-022; H. Walz, Effeltrich, Germany) complemented with an absolute CO₂ analyzer (LCA-3; ADC Ltd., Hoddesdon, UK). The differential CO₂ analyzer was calibrated against a range of CO₂ standards. Illumination was provided by a studio lamp (model HMV 1200; Pani, Vienna, Austria) with a size of 5° as seen from the cuvette. The beam was attenuated by a set of neutral density filters (Kodak Wratten Gel) and confined to the cuvette window using opaque frames. To further reduce diffuse illumination the exterior of the transparent cuvette was covered with black tape. The irradiance close to the leaf was measured with a GaAsP diode (model G1125-02; Hamamatsu, Ichinocho, Japan) sensitive to white only. It was read by a voltmeter (model 195A; Keithley, Cleveland, OH) across a 1-kΩ resistor. The set-up was calibrated against a quantum sensor (Li-189; Li-Cor, Inc., Lincoln, NE). A photosynthetic light-response curve was measured with the upper leaf surface illuminated. The leaf was gradually brought to the highest irradiance during a period of 1 to 2 h. A series of readings were then taken at stepwise decreased irradiance while the leaf temperature was held at 27 ± 0.1°C as measured with a thermocouple pressed onto the lower leaf surface. The water vapor pressure deficit was ±0.4 kPa. Rates and conductances were calculated according to the method of von Caemmerer and Farquhar (1981).

Measurement of O₂ Exchange

Exchange of O₂ by algae was measured using an O₂ electrode (Hansatech Ltd., King’s Lynn, UK) maintained at 25°C. Illumination from a voltage-stabilized projector lamp was changed by varying the lamp-cuvette distance or by inserting white nylon screens into the optical path. The irradiance was measured at the cuvette center using the diode described above. An algal sample of 1 mL was transferred directly from the culture flask, and bicarbonate was added from a fresh stock solution to give a final concentration of 4 mM. A sequence of readings were then made by stepwise increases in the irradiance. When this exceeded approximately 200 µmol m⁻² s⁻¹, a new sample was taken for each new point. This was done to ensure that photosynthesis was not limited by increased O₂ tension, photoinhibition, or carbohydrate accumulation. The O₂ signal was displayed on a strip-chart recorded. A linear trace over a minimum of 4 min was taken to indicate a stable rate. A complete light-response curve containing 14 to 22 data points took about 1.5 h. The Chl content of samples taken from the culture during this interval was calculated by interpolation from determinations made at the start and the end of the interval using samples of 10 mL.

Modeling of Photosynthetic Light-Response Curve

The photosynthesis versus irradiance data were fitted to Equation 1. In the present study, I represents incident irradiance, and Φ, thus, represents apparent Φ. R was added to P to obtain a correct intercept on the y axis. All data presented show the sum of R and Φ, i.e. the gross rate of photosynthesis. This was done to facilitate direct comparison of curves with different R. Data below an irradiance of 50 µmol m⁻² s⁻¹ were excluded to avoid distortion of the curve due to the Kok effect (Sharp et al., 1984). The data were fitted and the parameters estimated using a statistical package based on the Marquardt algorithm (Regression; Blackwell Scientific Publications, Oxford, UK).

Measurement of Chl Fluorescence

Fluorescence was measured using a computerized set-up of two fast modulation fluorometers (PAM; H. Walz, Effeltrich, Germany). The leaf was placed in a water-jacketed clamp-on cuvette held at 25°C. The cuvette was flushed with a gas stream of desired CO₂ content, supplied from a cylinder or the gas-mixing unit described above, and humidified to a dew point temperature of 20°C. The two fiber ends were held on opposite sides of the leaf 3 mm from the surface. The leaf remained attached, except when field-grown leaves that had petioles in water were measured. Continuous illumination, provided by a projector lamp and a set of neutral density filters (Schott), was passed to either leaf surface through the corresponding fiber. Fluorescence was assayed at 100-s intervals at both surfaces simultaneously (measuring irradiance = 2 µmol m⁻² s⁻¹): the steady-state fluorescence, FS, and following addition of 2-s flashes, the maximum fluorescence, Fm'. The continuous irradiance was 500 µmol m⁻² s⁻¹ at the start. Upon stabilization of Fm' at both surfaces, it was raised to 1000 µmol m⁻² s⁻¹. Upon return of steady state, the flash irradiance was increased from 5 to 10 mmol m⁻² s⁻¹ for the illuminated surface and from 3 to 6 mmol m⁻² s⁻¹ for the shaded surface. The readings subsequently made were used to calculate the quantum yield of PSII at both surfaces: ΨPSII = (Fm' - Fs)/Fm' (=ΔF/Fm') (Genty et al., 1989).

RESULTS

Typical photosynthetic light-response curves of algal cells grown under different light regimens are shown in Figure 2. It appears that cells grown under low light have a higher Φ and a lower Pmax than those grown under high light, with intermediate values found under intermediate light. These findings are verified by the data summarized in Table I: from a value of 0.98 in low-light-grown cells, Φ decreased to 0.83 when irradiance increased 6-fold and the Pmax increased by a factor of 2.4. It should be noted that this Φ decline was not the result of any high-light stress, i.e. photoinhibition. Although this may cause decreased Φ (Leverenz et al., 1990; Ögren and Sjöström, 1990), the major effect of photoinhibition is rather a decreased Φ (Powles, 1984). This was clearly not observed here (Table I). As will be discussed below, the Φ decline reflects an adaptive response where the capacity of Rubisco is increased relative to that of electron transport. (It is surprising that low light-grown cells showed somewhat...
The dashed curve would have been observed had a corresponding gradient in terms of lighttif-minated. In the leaf, however, this condition is only met when the steep light gradient through the leaf is matched by a strong coupling of PSII electron transport to carbon reduction (Seaton and Walker, 1991; Öquist and Chow, 1992), which appears to be independent of the position of the chloroplast within the leaf (Evans et al., 1993). Measurements of \( \Phi_{\text{PSII}} \) were carried out at both leaf surfaces when the upper surface was illuminated by near-saturating light. In young, low-light-grown leaves, \( \Phi_{\text{PSII}} \) was an average of 1.8 times higher at the lower than at the upper surface (Table II), indicating that photosynthesis was operating further down on the light-response curve at the lower surface (higher \( \Phi \) = steeper tangent to the curve); the rate at the upper surface must have been close to \( P_{\text{max}} \) under the particular light used. We can, therefore, conclude that the gradients in light and \( P_{\text{max}} \) did not match. It is most likely that this is the major, if not the whole, explanation for \( \Theta \) being lower in low-light-grown leaves (0.91) than in corresponding cells (0.98).

The ratio of \( \Phi_{\text{PSII}} \) of lower surface to upper surface thus provides a measure of the degree of match between gradients in light and \( P_{\text{max}} \): the closer the ratio is to unity the closer the match. Different types of leaves were examined. Those grown under high light showed a closer match than did those grown under low light (\( \Phi_{\text{PSII}} \) ratios of 1.4 and 1.8, respectively, Table II). Because they had the same low Chl content and the same light environment until a late stage of leaf growth, and, therefore, probably very similar leaf anatomy, we expect them to have the same light gradient. Hence, they must differ with respect to the \( P_{\text{max}} \) gradient. This was also confirmed by an analysis that took advantage of the fact that \( P_{\text{max}} \) is proportional to \( \Phi_{\text{PSII}} \) under saturating and direct illumination. As can be seen from the near-light-saturated values of \( \Phi_{\text{PSII}} \) in Table II, \( P_{\text{max}} \) was higher at the upper than at the lower surface in high-light-grown leaves (\( \Phi_{\text{PSII}} \) = 0.42 and 0.31, respectively), whereas upper and lower surfaces were identical in low-light-grown leaves (\( \Phi_{\text{PSII}} \) = 0.21 and 0.20, respectively). This absence of a \( P_{\text{max}} \) gradient in low-light-grown leaves is also reflected by the \( \Theta \) data: low-light-grown leaves deviated more from corresponding cells (\( \Theta = 0.91 \) and 0.98, respectively) than did high-light-grown leaves (0.78 and 0.83, respectively; Tables I and II). In fact, in the former case the actual difference is larger than the numerical values indicated because of the nonlinear scale of \( \Theta \).

As the low-light-acclimated leaf grew older and the Chl concentration increased (47%), the gradients between light and \( P_{\text{max}} \) diverged further (\( \Phi_{\text{PSII}} \) ratio increased from 1.8 to 2.5; Table II). This was largely attributed to an increased light gradient because the \( P_{\text{max}} \) of the respective surfaces did not change much (Table II). As a result, \( \Theta \) decreased from 0.91 to 0.82 (Table II).

When leaves developed under bilateral rather than unilateral light, the Chl content was acclimated to 7-fold increases at 600 as at 25°C. We can, therefore, conclude that the gradients in light and \( P_{\text{max}} \) did not match. It is most likely that this is the major, if not the whole, explanation for \( \Theta \) being lower in low-light-grown leaves (0.91) than in corresponding cells (0.98).

The same trend in \( \Theta \) was observed for leaves. When young leaves of low Chl content were acclimated to 7-fold increases in light, \( \Theta \) decreased from 0.91 to 0.78, whereas \( P_{\text{max}} \) increased 1.5-fold (Table II).

Although qualitatively similar to the algal data, the whole \( \Theta \) range of leaves was shifted toward lower values. The intrinsic value of \( \Theta \) is only realized when all cells operate on the same relative positions of the light-response curve all the way up to \( P_{\text{max}} \). This must have been the case for the algal cultures that were highly diluted and, hence, uniformly illuminated. In the leaf, however, this condition is only met when the steep light gradient through the leaf is matched by a corresponding gradient in \( P_{\text{max}} \). The degree to which this occurred was estimated using a fluorescence technique that discriminates between photosynthesis at upper and lower leaf surfaces (Evans et al., 1993). Although fluorescence measures the quantum yield of PSII, \( \Phi_{\text{PSII}} \), rather than the quantum yield of CO2 assimilation (Genty et al., 1989), there is a strong coupling of PSII electron transport to carbon reduction (Seaton and Walker, 1991; Öquist and Chow, 1992), which appears to be independent of the position of the chloroplast within the leaf (Evans et al., 1993). Measurements of \( \Phi_{\text{PSII}} \) were carried out at both leaf surfaces when the upper surface was illuminated by near-saturating light. In young, low-light-grown leaves, \( \Phi_{\text{PSII}} \) was an average of 1.8 times higher at the lower than at the upper surface (Table II), indicating that photosynthesis was operating further down on the light-response curve at the lower surface (higher \( \Phi \) = steeper tangent to the curve); the rate at the upper surface must have been close to \( P_{\text{max}} \) under the particular light used. We can, therefore, conclude that the gradients in light and \( P_{\text{max}} \) did not match. It is most likely that this is the major, if not the whole, explanation for \( \Theta \) being lower in low-light-grown leaves (0.91) than in corresponding cells (0.98).

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When leaves developed under bilateral rather than unilat-
eral high-light illumination, $\Theta$ decreased from 0.78 to 0.72 when measured under unilateral illumination (Table II). This small, although statistically significant, effect is likely to be mediated by an increased mismatch between light and $P_{\text{max}}$ gradients as revealed by an increased $\Phi_{\text{PSII}}$ ratio (from 1.4 to 1.6). In contrast to the situation in which the Chl content and the light gradient increased, the increased mismatch was caused by a flattening of the $P_{\text{max}}$ gradient upon development of an equally high $P_{\text{max}}$ at the lower as well as the upper surface ($\Phi_{\text{PSII}} = 0.36$ and 0.37, respectively; Table II).

Field-grown leaves most closely resembled high-light-acclimated leaves because they had similar values of $\Theta$ and the $\Phi_{\text{PSII}}$ ratio. This was found to be 1.43, 1.38, and 1.35 at CO$_2$ partial pressures of 12, 34, and 90 Pa, respectively (mean values of three high-light-grown leaves, $se \leq 0.05$). Thus, the interrelationship between light and $P_{\text{max}}$ gradients was independent of CO$_2$.

**DISCUSSION**

$\Theta$ of high-light-grown leaves was decreased as the CO$_2$ concentration was increased (Fig. 3). This reflects a change in the intrinsic $\Theta$ because the interrelationship between leaf gradients in light and $P_{\text{max}}$ did not change (data in text). The same trend was observed in *Eucalyptus* leaves and when analyzed indicated that $\Theta$ is governed by the relative capacity of Rubisco (Ogren and Evans, 1993). According to the model of Farquhar et al. (1980), CO$_2$ assimilation is limited at low light by the rate of electron transport and at high light by the capacity of Rubisco. The position of the breaking point between these two limitations determines $\Theta$. Because the electron transport per se appears to follow a curve of low $\Theta$ (Ogren and Evans, 1993), the Rubisco limitation must set in at low light to obtain a combined curve of a high $\Theta$. If the light activation of Rubisco proceeds over an extended light range (Portis, Jr., 1992), the transition becomes more gradual, and $\Theta$ will become somewhat lower than expected given a
sharp truncation of the electron transport curve by Rubisco (Ogren and Evans, 1993). Still, the simplified model of Farquhar et al. (1980) provided good qualitative agreement with the experimental data.

The electron transport of PSII, measured by Chl fluorescence, also showed a light-response curve in which Θ was dependent on CO₂ (Ogren and Evans, 1993). This is consistent with the idea that the activity of PSII is down-regulated to match slower steps in photosynthesis (Weiss and Berry, 1987). If the intrinsic, very rapid turnover of PSII would be realized over the whole light range, we would expect a sharp transition of the photosynthetic light-response curve from a limitation exerted by PSII at low light to one exerted by the reoxidation of plastoquinone at high light. In this hypothetical case, later steps in photosynthesis would have little influence on Θ.

Leverenz (1988) found an invariably high Θ in shade-acclimated shoots of Pinus even under high CO₂ concentration. What appears to be a conflicting result at first sight may be misleading because, according to the present study, shade-acclimated leaves are bound to have a high Θ that is only marginally altered by CO₂ (Fig. 3A). Also, the particular high CO₂ treatment used by Leverenz, 200 Pa, could have been superoptimal and could have led to a situation resembling that at normal CO₂. At least this was the case in Eucalyptus, in which Θ decreased with increased CO₂ content up to 100 Pa but beyond that point began to increase back to high values (Ogren and Evans, 1993).

Θ also decreased with increased light during growth (Table II). Leaf structural factors were not involved because the effect was equally evident in algal cells (Table I). In fact, the structural factors acted in the opposite direction because the leaf gradients in light and P_max were less closely matched in low-light- than in high-light-grown leaves of the same Chl content (Φ_max ratios in Table II). Neither was photoinhibition involved, although this has been demonstrated to cause decreased Θ in other situations (Leverenz et al., 1990; Ogren and Sjöström, 1990). In agreement, DeLucia et al. (1991) reported higher Θ values in shade- than in sun-acclimated leaves analyzed for O₂ evolution.

Like the situation with CO₂, the decline in Θ upon high-light acclimation was paralleled by an increased P_max. These changes are most likely associated with an increased capacity of Rubisco. Numerous reports have demonstrated a strong correlation between P_max and the leaf content of Rubisco (Björkman, 1981). Flux control analysis has also revealed that this enzyme is the principal limitation to CO₂ assimilation at saturating light in both shade- and sun-acclimated leaves (Woodrow and Mott, 1988). Of particular interest are data showing that the capacity of Rubisco is increased relative to that of electron transport as growth irradiance is increased (Sukenik et al., 1987). Thus, the hypothesis that Θ decreases with increased relative capacity of Rubisco (Ogren and Evans, 1993) is consistent with the literature data and is applicable for changes in CO₂, as well as light, and probably also for other factors known to involve Rubisco, such as nitrogen and temperature.

Leaves have lower Θ than chloroplasts for two main reasons. First, they may be unable to develop a P_max gradient that exactly matches the light gradient. Second, they may have developed a P_max gradient under one particular light direction but are analyzed for another one. The latter situation is illustrated by leaves that develop under bilateral illumination but are measured under unilateral illumination. In the present study, this caused a relatively small decrease in Θ in comparison with what was found for Eucalyptus leaves (Evans et al., 1993), presumably because the latter were denser and, therefore, had steeper light gradients. The discrepancy between P_max and light gradients becomes even larger when horizontal leaves are illuminated from below, an effect that has been demonstrated for many different species (Oya and Laik, 1976; Terashima, 1986; DeLucia et al., 1991; Evans et al., 1993).

The other reason for leaves having lower Θ than chloroplasts, an incomplete internal acclimation, is illustrated by low-light-grown leaves. In the young stage, these leaves did not show any gradient in P_max despite a significant gradient in light (Table II). When old, they were still lacking any noteworthy P_max gradient, although the light gradient had become considerably steeper as a result of increased leaf Chl content. Consequently, Θ was decreased further. This effect of increased Chl content on Θ has also been demonstrated for shade-grown conifers (Leverenz, 1988). It is tempting to speculate that this is because the chloroplast has a fairly narrow acclimation range. Indeed, Terashima and Inoue (1985) found only a 2-fold range in Rubisco content when comparing top and bottom layers of leaves. Similarly, P_max for the individual leaf surface (proportional to Φ_max; Table II) as well as for cells (Table I) varied by a factor of 2.4 when irradiance varied between the extremes. This is to be compared with the more than 10-fold variation in internal light found in typical leaves (Terashima and Saeki, 1985; Evans et al., 1993).

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LITERATURE CITED


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