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<tr>
<td>Category</td>
<td>Agriculture</td>
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<tr>
<td>Publisher</td>
<td>American Society for Horticultural Science</td>
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<tr>
<td>Publication Date</td>
<td>1983</td>
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Carbon Balance of *Peperomia obtusifolia* Plants during Acclimatization to Low PPFD

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Abstract. The CO₂ exchange rates of *Peperomia obtusifolia* A. Dietr. plants (tops and roots) were measured for 12-hour light and 12-hour dark cycles during 5 weeks of acclimatization at 30 μE m⁻² s⁻¹. A carbon balance analysis of the data indicated that the growth conversion efficiency (Yg) remained constant (0.73 ± 0.1 and 0.77 ± 0.04 before and after acclimatization, respectively). The daily rate of substrate production from photosynthesis (ΔWIΔt) remained constant at 18 ± 2 mg C plant⁻¹ 24 hr⁻¹ at the acclimatization photosynthetic photon flux density (PPFD), but the daily rate of synthesis of carbon into new material (ΔWIΔt) increased by 55% within the first week. The maintenance coefficient (m) decreased from 13.0 ± 0.9 to 7.4 ± 0.4 mg g⁻¹ 24 hr⁻¹, and change in m may be a criterion for selection of plants that can be adapted for use at low PPFD. The light compensation point (LCP) was reduced during acclimatization, but its use underestimated the PPFD required for 24-hour plant maintenance because of failure to account for night-time respiratory losses. It is suggested that the PPFD at which ΔWIΔt is zero or slightly above is more reliable than the light compensation point for determining PPFD required for plant maintenance.

The use of acclimatized foliage plants in interiorscaping has increased in recent years. Researchers would ultimately like to define the minimum PPFD at which various foliage plants can be maintained for extended periods of time, and also understand the important physiological processes that are involved in light acclimatization.

Light compensation point (LCP) studies have shown that reduced respiration rates are especially important in the acclimatization process (6, 14). Previous studies on light acclimatization have not accurately defined the minimum period required for acclimatization to take place because a time scale of 3 weeks to many months has been used (4, 6, 12). It seems likely that some acclimatization will occur in a few days (9, 11, 12). A preliminary study by the authors suggested that a large portion of acclimatization occurred with one week of exposure of *Peperomia obtusifolia* to 30 μE m⁻² s⁻¹. LCP were 55, 28, 33, 32, and 23 μE m⁻² s⁻¹ after 0, 1, 2, 3, and 4 weeks of acclimatization, respectively. One of the reasons for the popularity (3) of *P. obtusifolia* as a foliage plant may be due to its rapid rate of acclimatization when placed under low light conditions.

The LCP which has been used to define minimum PPFD for foliage plants does not take into account the respiratory losses at nighttime; it utilizes daytime instantaneous CO₂ exchange rate (CER) measurements, and in most studies does not consider the whole plant (tops and roots) (6, 14). LCP, therefore, will un-
deresist the required PPFD for whole plant transpiration over a 24-hour period. These limitations can be overcome by a carbon balance analysis.

The carbon balance analysis is a method of studying plant growth by the analysis of carbon gains and losses in a whole plant. 24-hour CER measurements are used. The carbon balance method has been used to analyze the growth of some crop plants (10, 11). We are not aware of any study of the carbon balance of a horticultural crop. From experience gained in past studies (11), P. obtusifolia (3) was selected as a good test plant.

The objectives of this study were to determine the parameters of the daily carbon balance equation for acclimatizing P. obtusifolia plants. The equation described by Thorne (11) was used:

\[ \Delta W/\Delta t = Y_r \Delta S/\Delta t - m W_i \]

The equation mathematically expresses that some of the substrate carbon produced by photosynthesis (\(\Delta S/\Delta t\)) will be consumed for maintaining existing biomass (\(m W_i\)) and the remainder will be converted to new biomass carbon (\(\Delta W/\Delta t\)) with the efficiency of \(Y_r\).

The daily rate of synthesis of carbon into new material (\(\Delta W/\Delta t\)) and the daily rate of substrate production from photosynthesis (\(\Delta S/\Delta t\)) were determined during acclimatization. The conversion efficiency \(Y_r\) and the maintenance coefficient \(m\) were determined before and after acclimatization.

Also, CER at varying PPFD and ICP were determined before and after acclimatization to see how closely the ICP can predict the minimum PPFD for plant survival. An important assumption for the use of the carbon balance equation is that the plant is in a steady state, which means that the substrate produced in photosynthesis is completely utilized in one day without any change in storage. The steady state condition was achieved in this study on the 4th day after exposure of the plants to the low PPFD.

**Materials and Methods**

Tip cuttings of P. obtusifolia plants were rooted in the greenhouse and then transplanted into 10-cm-diameter pots. Washed friable sand mixed with washed and graded fine sand was placed in the pot. The sand mixture was used as the growing medium. The sand mixture was used because it was found to be suitable for the propagation of the plants. The plants were grown in a growth chamber for 6 weeks before the acclimatization treatment was imposed. The light source in the growth chamber was a mixture of eighteen 100W incandescent bulbs and thirty 9W fluorescent tubes. PPFD at initial plant height was 250 \(\mu\) E m\(^{-2}\) s\(^{-1}\). Air temperature was maintained at a relative humidity was 78 ± 5% and the photoperiod was 12 hr. Plants were watered twice daily with a modified Hoagland's solution until adequate roots were formed, and then watered once daily. A section of the growth chamber was shaded with neutral density red screen to obtain a low PPFD of 5.94 \(\mu\) E m\(^{-2}\) s\(^{-1}\) for 5 weeks of acclimatization. Other environmental conditions were the same as during production of the plants. Four plant replicates were used in each experiment.

The first CER measurement was made at the high production PPFD, and the acclimatization treatment was started immediately. During the first 2 weeks, plants were enclosed in 2 plant assimilation chambers for whole plant CER measurements. The temperature inside the assimilation chamber was maintained at 29 ± 0.5\(^\circ\)C, and relative humidity was 75%. Copper-constantan thermocouples were used to monitor leaf and assimilation chamber air temperatures. The assimilation chambers were placed inside an environmental control chamber. An important feature of this chamber was that it had only a transparent top, thus extraneous light was excluded from the sides. Light source during CER measurements was a high-output fluorescent lamp. Outside air was passed continuously through the assimilation chamber. At regular intervals, air from a compressed air cylinder was passed through the assimilation chamber, and the CO\(_2\) concentration difference between air entering and that leaving the assimilation chamber was monitored with an infrared gas analyzer (IRGA). (Beckman model 865). CER measurements were made for 12-hr light and 12-hr dark periods. The first 2 plants were then removed to the acclimatization area and 2 other plants were enclosed for CER measurements.

CER measurements were made at the high PPFD of 250 \(\mu\) E m\(^{-2}\) s\(^{-1}\) before the start of acclimatization, day 0. Then, at the low PPFD of 30 \(\mu\) E m\(^{-2}\) s\(^{-1}\) on days 1, 2, 4, 7, 14, 21, and 28. Plants were then exposed to high PPFD for 3 days, for redetermination of CER at this high PPFD. This was necessary for calculating \(Y_r\) after acclimatization. CER was calculated as follows:

\[ CER = C \times CO_2 \times FR \]

where \(CER\) = CO\(_2\) exchange rate (mg CO\(_2\) plant\(^{-1}\) hr\(^{-1}\)),
\(C\) = Conversion factor (1.82 × 10\(^{-2}\) mmol ppm\(^{-1}\) liter\(^{-1}\)),
\(CO_2\) = concentration difference between incoming and outgoing air in the assimilation chamber (ppm),
\(FR\) = Flow rate (liters hr\(^{-1}\)).

The calculated CER was converted to mg CO\(_2\) plant\(^{-1}\) hr\(^{-1}\) by a factor of 0.27 (the proportion of CO\(_2\) in CO\(_2\) and integrated over a 12-hr day period to obtain D and a 12-hr night period to obtain W\(_d\)) and the carbon balance parameters (11) were then calculated as:

\[ \Delta S/\Delta t = \text{Daily rate of substrate C production} \]
\[ = D - N \text{ (mg C plant}^{-1}\text{ 24 hr}^{-1}\text{)} \]
\[ \Delta W/\Delta t = \text{Daily rate of synthesis of C into new material} \]
\[ = D + N \text{ (mg C plant}^{-1}\text{ 24 hr}^{-1}\text{)} \]

At the end of the 5 weeks of acclimatization, the plants were harvested (leaves, stems, and roots), dried in an 80\(^\circ\)C oven for 3 days, and the dry weight (W\(_d\)) was determined. The carbon equivalent of dry weight (W\(_d\)) was calculated using 0.594 CO\(_2\) dry weight as conversion factor (12). Values of \(Y_r\) and \(m\) were calculated as follows (12):

\[ Y_r = (\Delta W/\Delta t_1 - \Delta W/\Delta t_2)/(\Delta S/\Delta t_1 - \Delta S/\Delta t_2) \]

Subscripts 1 and 2 refer to high and low PPFD, respectively.

\[ m = (\Delta S/\Delta t - (1/Y_r)\Delta W/\Delta t)/W_i \]

In the calculation of \(m\) before and after acclimatization, the same value of \(W_i\) was used.

In the 2nd experiment, 4 plants produced under identical conditions to those in exp rt. 1 were used to measure instantaneous CER at varying PPFD before acclimatization and after 5 weeks

of acclimatization. CER per unit leaf area in mg CO₂ dm⁻² hr⁻¹ was plotted against PPFD. The light compensation point, which is that PPFD at which there is zero CER, was determined graphically. Leaf area (one side only) was determined by measuring length and maximum width of each leaf and using a predetermined equation (8) to calculate the leaf area.

Results

The changes in the rate of substrate production from photosynthesis (ΔS/Δt) and rate of synthesis of carbon into new material (ΔW/Δt) are shown in Fig. 1. At the high PPFD, (ΔS/Δt) was 97 mg C plant⁻¹ 24 hr⁻¹ and it was 15 mg C plant⁻¹ 24 hr⁻¹ at the low PPFD before acclimatization. After one week of acclimatization, (ΔS/Δt) was still 15 mg C plant⁻¹ 24 hr⁻¹ at the low PPFD. Subsequent weeks of acclimatization did not show substantial changes in (ΔS/Δt). At the end of 5 weeks of acclimatization, (ΔS/Δt) was 18.7 mg C plant⁻¹ 24 hr⁻¹.

The rate of synthesis of carbon into new material (ΔW/Δt) exhibited a large increase during acclimatization. The largest increase occurred within the first week, from −33 mg C plant⁻¹ 24 hr⁻¹ to −15 mg C plant⁻¹ 24 hr⁻¹ (55% increase). Subsequent increase was at a slower rate. It was −5 mg C plant⁻¹ 24 hr⁻¹ after 5 weeks of acclimatization.

Integrated daytime (D) and nighttime (N) CER are shown in Fig. 2. The daytime total was negative at the low PPFD up to the 4th day of acclimatization. After one week, D was positive. N totals also exhibited the greatest rise during the first week. Yₑ did not change significantly after acclimatization (Table 1). On the average, Yₑ was 0.73 ± 0.04 before and 0.77 ± 0.04 after acclimatization. The maintenance coefficient (m) changed considerably, values before and after acclimatization being 13 ± 0.9 and 7.4 ± 0.4 mg g⁻¹ day⁻¹, respectively.

The CER response curve to varying PPFD before and after acclimatization is shown in Fig. 3. There was a decrease in the dark CER and LCP. A regression analysis done on CER at 0, 93, and 164 μE m⁻² s⁻¹, indicates that initial slopes were 0.0176 before and 0.0219 after acclimatization, and the correlation coefficient was 0.989 before and 0.988 after acclimatization.

Discussion

During the period of acclimatization, rate of substrate production (ΔS/Δt) changed very little, yet the rate of synthesis of carbon into new material (ΔW/Δt) increased substantially (55% the first week). This suggests an improvement in the utilization of new fixed carbon to protein and growth.

![Fig. 1. Daily rate of substrate production (ΔS/Δt) and daily rate of synthesis of carbon into new material (ΔW/Δt) at high day (0) low PPFD (day 1 to 35).](image1)

![Fig. 2. Total daytime CO₂ exchange rate (D) and total nighttime CO₂ exchange rate (N) at high PPFD (day 0) and low PPFD (day 1 to 35).](image2)

![Table 1. Growth conversion efficiency (Yₑ) and maintenance coefficient (m) of P. obtusifolia plants before and after 5 weeks of low light acclimatization.](table1)

**Significantly different at 1% level (ANOVA) ± s.d.
of available substrate and/or a reduction in the amount of sub- 
strate utilized for maintenance, so that more substrate was avail-
able for incorporation into new plant material. Since \( W \) was 
constant during acclimatization, the increased \( \Delta W/At \) was at-
tributed to a reduction in the maintenance term.

Increased \( D \) agrees with published data, showing increases in CO,
uptake in the light during acclimatization (6, 14). In our
study, \( D \) attained positive values after one week, but \( \Delta W/At \) 
did not become positive even after 5 weeks. This difference illus-
trates how \( D \) or CO,
uptake (6, 14) and \( \Delta W/At \) differ as estimates of
plant growth by use of CO,
flux measurements. The term
"net photosynthesis" has been used for \( D \) and its limitation of 
not accounting for all respiratory losses is known. However, no 
allowance has been made for this in previous studies (1, 6, 14).
On the other hand, \( \Delta W/At \), which does account for all respiratory losses and hence gives a true estimate of growth rate \( \Delta W/At \), has not been used in the study of acclimatization of foliage 
plants.

In the use of foliage plants indoors, the light level at which the
plant is capable of maintaining itself without excessive growth is 
ideal for prolonged use. The LCP is that light level at which CO,
uptake is zero. The LCP has been used to estimate the 
required PPFD for maintenance of foliage plants; however, de-
termination of LCP does not account for nighttime respiratory 
losses, and therefore will underestimate the PPFD for plant main-
tenance. Especially when whole plant CER (tops and roots) is 
measured. Since \( \Delta W/At \) overcomes these drawbacks, de-
termination of LCP does not account for all respiratory losses and hence gives a true estimate of growth rate \( \Delta W/At \), has not been used in the study of acclimatization of foliage 
plants. In practical terms, foliage plants can be 
maintained for prolonged periods at low PPFD when \( \Delta W/At \) is zero or slightly above. An LCP of 24 \( \mu E \) \( m^{-2} \) \( s^{-1} \) after five 
weeks of acclimatization confirms that the PPFD at which the
plant can maintain itself is underestimated by the LCP, since 
\( \Delta W/At \) was negative after 5 weeks of acclimatization at 30\( \mu E \) 
\( m^{-2} \) \( s^{-1} \).

Increased \( W \) at low PPFD and reduced \( D \) after accli-
matization have been interpreted as an increase in photosynthetic 
efficiency (6, 14); however, the constant \( \Delta W/At \) that was found 
in this study does not support this idea. Moreover, the constant 
initial slopes of CER measurements at low PPFD (Fig. 3) indicate 
that photosynthetic quantum efficiency was the same (6, 7).
Reduction in LCP and the apparent increase in CER were due 
to the reduction in dark respiration (7), resulting in an upward
shift of the CER response curve at varying PPFD. PPFD by continu-

In summary, growth and dark respiration might be affected differen-
tially during acclimatization. In this study, growth respiration was 
constant during acclimatization while maintenance respiration 
was reduced. This suggests that the amount of the dark balance 
curves that was affected in this study, could be used as a selection criterion for plants that can be adapted for use at 
low PPFD. The greater the reduction in \( m \), the more adaptable 
the plant would be.

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