Seasonal courses of CO2 exchange and carbon balance in fruits of *Cinnamomum camphora*

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Summary  Carbon dioxide exchange in fruits of *Cinnamomum camphora* Sieb. was followed over a growing season from July to December 1992. Dark respiration was exponentially related to temperature, with a \( Q_{10} \) value near 2. Light dependence of photosynthetic CO2 refixation, i.e., the ratio of gross photosynthesis to dark respiration, was approximated by a hyperbolic function. Seasonal variation in maximum CO2 refixation capacity ranged between 52 and 174%, reaching a maximum in early August. Daily photosynthetic CO2 refixation ranged between 17 and 51% over the growth period. We evaluated seasonal variation in translocation rate to the fruit on the basis of the seasonal rates of gross photosynthesis, dark respiration and increase in fruit dry weight, and used the results to develop a simple carbon flow model of fruit development. Seasonal changes in translocation rate paralleled those in fruit growth rate, with two peaks during the periods before and after September. Seed formation took place in the period between the two peaks. The relationship between fruit growth rate and translocation rate was approximated by a linear function. The carbon flow model estimated that, over the reproductive period, the amount of assimilate translocated to each fruit was 377.2 mg dry weight, of which 58.5% was accounted for by weight growth and 41.5% was consumed by net respiration. Carbon dioxide refixation accounted for 22.9% of the carbon balance of the fruit.

Keywords: carbon flow balance, fruit development, photosynthetic CO2 refixation, translocation.

Introduction  There are several reports describing the occurrence of photosynthesis in reproductive tissues of various tree species (Dickmann and Kozlowski 1970, Rook and Sweet 1971, Bazzaz et al. 1979, Linder and Troeng 1981, Koppel et al. 1987, Ogawa et al. 1988, Whiley et al. 1992). These studies suggest that the photosynthetic contribution of developing fruits to their own dry matter demands is significant. However, it has also been reported that fruiting depresses tree growth (Eis et al. 1965, Tappeiner 1969, Teich 1975, Ogawa et al. 1988), which implies that carbohydrates are translocated from other organs for the production of fruits. Early studies showed that developing fruits preferentially mobilize current photosynthetic leaves (Dickmann and Kozlowski 1968, Rook and Sweet 1971).

Although translocation plays an important role in fruit growth and seed formation, the process is poorly understood. Quantitative analysis of translocation to fruits could help elucidate the physiological controls on the regulation of distribution and translocation of photosynthates within the tree.

We followed the time course of CO2 exchange in fruits of *Cinnamomum camphora* Sieb. over an entire growing season and developed a simple carbon flow model from the results. The model estimates daily and seasonal translocation of photosynthates to a fruit. A quantitative relationship between translocation and dry weight increment of a fruit was also derived.

Materials and methods  

Plant material  

Between 31 and 42 fruits from a *Cinnamomum camphora* tree growing on the campus of Nagoya University were sampled on 11 occasions between July 11 and December 29, 1991. In December 1991, the height of the sample tree was 11.0 m and stem diameter at breast height was 29.3 cm. The tree flowered in early June, fruited in early July, and dropped all fruits in late December.

Measurements  

Rates of CO2 exchange were measured in an open gas-exchange system with an infrared gas analyzer (URA-2S, Shimadzu, Kyoto, Japan). Air was stored in an air bag and supplied to the assimilation chamber at a rate of 0.5 l min\(^{-1}\). The CO2 concentration in the air averaged 392.1 ± 13.6 (SD) ppm throughout the experimental period.

The assimilation chamber was immersed in a thermoregulated water-bath with 1.5-cm layer of water above the chamber surface. Chamber air temperature was maintained by circulating air through copper tubes in the water-bath, with the desired temperature being maintained by means of a temperature controller (TE-106S, Toyo, Chiba, Japan). Air temperature in the assimilation chamber was measured with a copper-constantan thermocouple. Air temperature inside the chamber was ad-
justed to the mean air temperature in the field at the beginning of each measurement day. Mean air temperature in the field varied from 11.0 to 29.9 °C during the measurement period from July to December.

Light was provided by two 500-W incandescent flood lamps, and a 1.0-cm thick water filter was placed between the lamps and the assimilation chamber to absorb excess infrared radiation. Various photon flux densities were achieved by changing the voltage supplied to the lamps. The photon flux density (PFD) on the outside top surface of the chamber (PFD_o, µmol m^{-2} s^{-1}) was measured with a quantum sensor (LI-190SA, Li-Cor, Inc., Lincoln, NE), and PFD inside the assimilation chamber (PFD_i, µmol m^{-2} s^{-1}) was calculated from the equation: PFD_i = 0.908 PFD_o^{0.999} (determination coefficient = 1.00). In addition, daily irradiance outdoors beside the experimental tree was measured with a photometric sensor having a spectral sensitivity in the range of 400 to 680 nm (IKS-15, Koito, Tokyo, Japan) (Hagihara et al. 1987).

Fruits with attached peduncles were removed from the tree and taken immediately to the laboratory where the end of each peduncle was recut under distilled water. The peduncles were placed in vials containing distilled water. For each CO_2 measurement, there were between 31 and 42 fruits in the assimilation chamber.

Photosynthetic response to light was determined by measuring CO_2 exchange at eight PFD values in the range of 25 to 800 µmol m^{-2} s^{-1}. Photosynthetic CO_2 refixation (p, %), was calculated as the difference between CO_2 release measured in the light and CO_2 release measured in the dark (Linder and Troeng 1981, Koppel et al. 1987). Dark respiration was measured at the same temperature as the photosynthetic measurements. The dark respiration response to temperature was assessed by measurements at six temperatures, from 10 to 35 °C.

After the CO_2 exchange measurements, fruit diameters were taken, and fruit dry weights were measured after oven-drying at 85 °C for 24 h. The dry matter/CO_2 conversion factor was assumed to be 0.614 (C_6H_{10}O_5/6CO_2) (Yoda 1983, Mariko and Koisumi 1993). Beginning in August, chlorophyll concentration of the fruits was determined spectrophotometrically by a modification of the method of Mackinney (1941).

Results

Diameter and dry weight growth
Fruit diameter increased until reaching 9 mm in late September. Fruit dry weight increased linearly before leveling off between late November and late December (Figure 1). The period of dry weight increase was about 2 months longer than the period of diameter growth, because diameter growth ceased at the onset of seed formation in September.

Temperature dependence of dark respiration
Dark respiration rate (r, mg CO_2 g dw^{-1} h^{-1}) was linearly related to air temperature in the assimilation chamber (θ, °C) when plotted on semi-log coordinates (Figure 2). The regression line was given by an exponential function,
where \( r_0 \) and \( k \) are coefficients.

The \( Q_{10} \) value (\( Q_{10} = \exp(10k) \)) for \( r \) ranged from 1.58 to 2.11 during the experimental period, except in December when the value increased to 2.7.

**Photosynthetic CO\(_2\) refixation**

The relationship between photosynthetic CO\(_2\) refixation (\( p \), %), and PFD\(_i\) (\( \mu\text{mol m}^{-2} \text{s}^{-1} \)) on log-log coordinates satisfied the hyperbolic formula,

\[
p = \frac{b \text{PFD}_i}{1 + a \text{PFD}_i},
\]

where \( a \) and \( b \) are coefficients specific to each season (Figure 3). The values of \( a \) and \( b \), which did not show clear seasonal changes, were in the range of 23 to 408 \( \mu\text{mol m}^{-2} \text{s}^{-1} \) and 0.44 to 2.35 to \( \mu\text{mol m}^{-2} \text{s}^{-1} \), respectively.

Table 1 shows the seasonal variation in maximum CO\(_2\) refixation capacity, \( p_{\text{max}} \), which is equivalent to the asymptote (\( b/a \)) in Equation 2. Maximum CO\(_2\) refixation capacity varied between 52 and 174%, reaching a seasonal maximum in early August.

**Relationship between CO\(_2\) refixation capacity and chlorophyll concentration**

Fruits were green after fruiting, but began to turn purplish-black in mid-November. All fruits were black after late November. The chlorophyll concentration ranged between 0.0680 and 0.662 \( \text{mg g}^{-1} \text{d.wt.} \), and decreased as the season progressed (Table 1). The relationship between maximum CO\(_2\) refixation capacity (\( p_{\text{max}}, \% \)) and chlorophyll (Chl) concentration (Figure 4) was approximated by the power function: \( p_{\text{max}} = 163.1 \text{Chl}^{0.437} \), indicating that maximum CO\(_2\) refixation capacity is roughly proportional to the square root of the chlorophyll concentration.

**Daily photosynthetic CO\(_2\) refixation**

We estimated daily photosynthetic CO\(_2\) refixation on the basis of Equation 2. As shown in Figure 5, estimated daily photosynthetic CO\(_2\) refixation increased during early fruit development, reached a maximum in early July, and decreased toward December. Estimated daily dark respiration was maximal in mid-August and decreased as the season progressed, reaching a
constant rate during the period from early September to late October. Daily photosynthetic CO$_2$ re fixation expressed as a percentage of daily dark respiration had a maximum of 51% in early August and decreased to a minimum of 17% in late December.

**Carbon balance**

Net translocation, which is defined as translocation of assimilates into a fruit minus assimilate translocation out of the fruit (Hozumi and Kurachi 1991), was estimated from a simple carbon flow model of a fruit before fruit fall. In the model, translocation into fruits from other tree parts ($\Delta T_i$, mg$_{dw}$/fruit$^{-1}$) at a given time interval ($\Delta t$, days) was expressed as,

$$\Delta T_i = \Delta r - \Delta p + \Delta w,$$

(3)

where $\Delta r$, $\Delta p$ and $\Delta w$ are dark respiration, photosynthetic CO$_2$ re fixation, and dry weight growth of a fruit, respectively. Seasonal trends in $r$, $p$ and $w$ are shown in Figure 6. Translocation rate ($\Delta T_i/\Delta t$) changed in parallel with the change in growth rate ($\Delta w/\Delta t$), exhibiting two peaks during the periods from early August to late August and from mid-October to late October. Seed formation began in September. Thus, we conclude that the decrease in the rates of $\Delta T_i/\Delta t$ and $\Delta w/\Delta t$ was related to the onset of seed formation. Although the ratio of $(\Delta w/\Delta t)/(\Delta T_i/\Delta t)$ was more or less constant throughout the growing season, ranging from 53 to 63%, it declined to 42% in December (Figure 6).

The carbon flow model estimated total assimilate translocation to a fruit over the whole reproductive period to be 377.2 mg dry weight, of which 58.5% was distributed to dry weight increment, and the rest was consumed by dark respiration (i.e., net respiration not refixed by photosynthesis) (Linder and Troeng 1981, Koppel et al. 1987) (Table 2 and Figure 7). The model estimated that 22.9% of the carbon balance of a fruit was obtained by CO$_2$ re fixation, which reduced respiration loss by 35.6%.

**Table 2.** Translocation estimated on the basis of Equation 3: $\Delta T_i = \Delta r - \Delta p + \Delta w$ over the entire reproductive period from July 11 to December 19, 1991. The dry matter/CO$_2$ conversion factor was assumed to be 0.614 (Yoda 1983, Mariko and Koizumi 1993).

<table>
<thead>
<tr>
<th>Unit of expression</th>
<th>Photosynthetic CO$_2$ re fixation</th>
<th>Dark respiration</th>
<th>Net respiration</th>
<th>Dry weight increment</th>
<th>Translocation</th>
</tr>
</thead>
<tbody>
<tr>
<td>mg$_{dw}$/fruit$^{-1}$</td>
<td>86.4</td>
<td>242.9</td>
<td>156.6</td>
<td>220.7</td>
<td>377.2</td>
</tr>
<tr>
<td>%$^1$</td>
<td>22.9</td>
<td>64.4</td>
<td>41.5</td>
<td>58.5</td>
<td>100.0</td>
</tr>
<tr>
<td>35.6$^2$</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

$^1$ Amount relative to amount of assimilate translocated to the fruit.

$^2$ Photosynthetic CO$_2$ re fixation was calculated as a percentage of dark respiration (Linder and Troeng 1981, Koppel et al. 1987).
men t /translocation ratio of 41.5% in
ported for
than the ratios in
and Troeng 1981), but higher than the value of 1 6 -- 17% re-
comparable to the value of 30% for
the respiration loss by 36% for
rates. An analysis of the relationship between maximum CO

Figure 7. Relationships between daily rates of dry weight growth
tation rate (\(\Delta T_i / \Delta t\)) of C. camphora fruits. The two lines correspond to: \(\Delta w / \Delta t = q \Delta T_i / \Delta t\) (determination coefficient = 0.96) and \(\Delta w / \Delta t = (1 - q) \Delta T_i / \Delta t\) (obtained by substituting Equation 4 in Equa-
tion 3).

Discussion

Fruit coloration

Although fruit color changed from green to purplish-black or
black, the fruit contained chlorophyll and photosynthesized
over the entire growing season. Similarly, Koppel et al. (1987)
found that green and purple cones of Picea abies (L.) Karst.
had similar chlorophyll concentrations in the cone scales,
ranging from 0.2 -- 0.3 mg \(g_m^{-1}\), and similar photosynthetic
rates. An analysis of the relationship between maximum CO_2
refixation capacity and chlorophyll concentration indicated that
fruit photosynthesis is partly regulated by chlorophyll
concentration.

Fruit carbon balance

We estimated that maximum daily gain of photosynthetic CO_2
refixation in fruit was half of daily dark respiration. This value
is high compared with the maximum daily refixations of 40% in
Pinus sylvestris L. strobili (Linder and Troeng 1981) and
26 -- 34% in P. abies (Koppel et al. 1987). However, over the
entire growth period, photosynthetic CO_2 refixation reduced
the respiration loss by 36% for C. camphora fruit, which is
comparable to the value of 30% for P. sylvestris strobili (Linder
and Troeng 1981), but higher than the value of 16 -- 17% re-
ported for P. abies (Koppel et al. 1987). The dry weight incre-
ment/translocation ratio of 41.5% in C. camphora was lower than
the ratios in P. sylvestris (Linder and Troeng 1981) and
P. abies (Koppel et al. 1987), which we calculated to be 66.7%
and 60.6 -- 64.2%, respectively, whereas the CO_2 fixa-
tion/translocation ratio of 22.9% was higher than the corre-
sponding ratios in these two species (14.9% and 7.3 -- 7.4%,
respectively).

The relationship between \(\Delta w / \Delta t\) and \(\Delta T_i / \Delta t\), (Figure 7) fitted
the proportionality function,

\[
\Delta w / \Delta t = q (\Delta T_i / \Delta t),
\]

where \(q\) is a coefficient with a value of 0.595. This value shows
that over the entire growing season, an average of 59.5% of the
photosynthesize translocated to the fruit was used for dry weight
growth of the fruit and 40.5% was consumed by net respira-
tion.

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