Does variability in shoot carbon assimilation within the tree crown explain variability in peach fruit growth?

A. S. WALCROFT,1–3 F. LESCOURET,4 M. GÉNARD,4 H. SINOQUET,1 X. LE ROUX1,5 and N. DONÈS1

1 UMR 547 PIAF, INRA-Université Blaise Pascal, Domaine de Crouelle, 234 avenue du Brezet, 63039 Clermont-Ferrand Cedex 2, France
2 Present address: Landcare Research, Private Bag 11052, Palmerston North, New Zealand
3 Corresponding author (walcrofta@landcareresearch.co.nz)
4 INRA - PSH, Domaine St. Paul, site Agroparc, 84914 Avignon Cedex 9, France
5 Present address: Laboratoire d’Ecologie Microbienne (UMR 5557 CNRS-Université Lyon I, USC INRA), bat 741, 43 bd du 11 novembre 1918, 69622 Villeurbanne, France

Received May 9, 2003; accepted July 20, 2003; published online January 2, 2004

Summary  A three-dimensional model of radiative transfer and leaf gas exchange was used to quantify daily carbon (C) assimilation of all fruit-bearing shoots (FBS) in an early maturing 6-year-old peach tree (Prunus persica L. Batsch) with a heavy crop load. For a sample of FBS (n = 36), growth of fruit and leafy shoots was measured every 1–2 weeks from 24 days after bloom (DAB) until harvest, between 93–101 DAB. The objective was to relate shoot C assimilation with harvested fruit mass for each shoot to test the hypothesis that variation in C supply contributes significantly to variation in fruit growth within and among FBS. Mean C assimilation of the sampled shoots was 0.07 g C fruit−1 day−1, but varied between 0.014 and 0.32 g C fruit−1 day−1. This indicates that C availability for fruit growth would have varied significantly among individual FBS if they were autonomous. Mean fruit dry mass on each FBS varied between 0.716 and 7.68 g C at harvest, and most of the variation originated among, not within, individual FBS. However, there were no correlations between the mean and standard deviation of fruit mass and fruit relative growth rate when each was plotted against shoot C assimilation, indicating that factors such as those regulating C demand of fruit, or C transfer among individual FBS, may be more important in controlling variability in fruit growth than intra-crown variability in shoot C assimilation. Under the study conditions, FBS were non-autonomous for C, because a model of fruit and leafy shoot growth was unable to reproduce the observed growth without supplementary contribution of C from shoots without fruit.

Keywords: branch autonomy, photosynthesis, radiative transfer, three-dimensional modeling.

Introduction  Trees are composed of organs that may be either carbon (C) sources (photosynthesizing leaves and shoots) or C sinks (respiring tissue, fruit, growing shoots, cambium, stems, roots). Carbon sources and sinks are spatially distributed throughout the tree crown with varying distances between them, and are linked via phloem in the network of branches and stems. Carbon is thought to move between sources and sinks as a function of source supply, sink demand and distance between sources and sinks (DeJong and Grossman 1995). The capacity for C assimilation by photosynthesizing shoots varies throughout the crown as a function of leaf area, photosynthetic capacity and irradiance (Walcroft et al. 2002). Sink demand may also vary throughout the crown as a function of sink size (e.g., number or mass of fruit per shoot) and sink activity.

With respect to C balance, many tree species, both deciduous and evergreen, have been shown to comprise a collection of autonomous or semi-autonomous branches (Sprugel et al. 1991). In this case, C does not move among large branches, although there is generally a net export of C from branches to support cambial and root growth. For deciduous species, larger branches often become autonomous after shoot elongation has ceased (Lacointe et al. 2001), although branches can be induced to import C by experimental manipulation of branch source:sink ratios (Palmer et al. 1991).

Carbon source–sink relationships are important in controlling fruit growth, and may ultimately determine crop yield and fruit size distribution (Minchin et al. 1997). If branches are essentially autonomous for C, then the above-mentioned variabilities in C supply and demand throughout the tree crown may considerably influence fruit growth on individual branches throughout the crown. Variability in fruit growth is a significant problem for growers because it reduces the proportion of total fruit yield that satisfies market requirements for size and quality. This has led to much research aimed at identifying factors that influence the processes regulating fruit growth and quality (Robinson et al. 1983, Grossman and DeJong 1994, Fishman and Génard 1998, Lescourret et al. 1998, Bruchou and Génard 1999). Fruit growth, quality (fruit size and composition) and maturation are closely linked (Gé-
nard and Souty 1996, Génard et al. 1999, Souty et al. 1999), so optimal fruit growth management is a critical aspect for production of high quality table fruit.

Variability in fruit growth can emerge at several scales: among orchards as a result of climatic and soil differences, among trees as a result of local soil patterns, planting regimes and shading from shelterbelts, and among and within shoots in a single tree as a result of physiological and micro-environmental factors. For peach trees (Prunus persica L. Batsch), the processes most likely to influence variability in fruit growth occur at the scale of the fruit-bearing shoot (FBS, Lescourret et al. 1998). The FBS are 1-year-old stems that bear fruit as well as current-year leafy shoots. Leafy shoots carry out gas exchange, thus providing the FBS with C, so it might be expected that variability in leafy shoot C assimilation would contribute significantly to variability in fruit growth if FBS are autonomous for C. The FBS may therefore be the logical target of management intervention designed to minimize fruit growth variability.

Our study objective was to quantify the variability in C assimilation of all FBS within a single peach tree, and to determine the degree to which the observed variation in fruit growth of a sample of FBS from the tree could be explained by variation in C assimilation of these shoots. We hypothesized that mean fruit mass would be greater in shoots with greater C assimilation per fruit because of the greater local C availability. In addition, variability in individual fruit mass would be less in shoots with greater C assimilation because any individual fruit would be less likely to be C limited. These hypotheses imply some degree of shoot autonomy for C, because free C translocation among shoots (i.e., a common C pool for fruit growth) would smooth out differences in fruit growth induced by differences in C assimilation among shoots.

To test the hypotheses, a three-dimensional model of radiative transfer and leaf gas exchange (Sinoquet et al. 2001) was parameterized and evaluated for peach, then used to compute the daily C assimilation rate of each FBS within the experimental tree over the main period of fruit growth. A sample of 36 FBS distributed throughout the tree crown was selected for biweekly measurements of fruit and leafy shoot growth. Observed fruit and shoot growth were compared with simulations by a model describing growth processes in isolated FBS (Lescourret et al. 1998), where shoot C assimilation was calculated from the 3-D model. The degree to which shoots were autonomous for C was determined based on an approach that compared the amount of C needed to grow fruit to the observed size with the amount of C supplied by the FBS for fruit growth (shoot C assimilation plus reserve mobilization minus C use for growth and maintenance respiration of the FBS). The quantity of C required to meet the total C deficit of FBS that were not autonomous for C was determined, and the ability of current-year and 1-year-old non-FBS, as a nearby potential source of C to meet this shortfall, was quantified.

Materials and methods

Plant material

Measurements were made during 1999 on a 6-year-old peach tree growing in a research orchard near Avignon, France (43.9° N, 4.8° E). The tree was of the early maturing ‘Alexandra’ variety planted at 5 x 5 m spacing on a silt–clay soil. The tree was goblet-pruned, fertilized and periodically irrigated. Full bloom for this cultivar occurred around March 15. In contrast to normal horticultural management practices, no winter pruning occurred and fruits were not thinned so that a relatively high fruit yield resulted and the conditions of the study were closer to natural situations (wild fruit trees) than to cultivated situations.

Fruit and leafy shoot growth measurements

A sample of 36 FBS that represented about 26% of the total number of FBS (140) was selected from within the tree crown for measurements of fruits and leafy shoot growth. On each FBS, the numbers of fruits and leafy shoots were recorded, and the diameter and length of fruit and leafy shoots, respectively, were measured every 1–2 weeks from around 24 days after bloom (DAB) until harvest, between 93–101 DAB. Fruit diameter was converted to fruit dry mass (DM) based on an allometric relationship for the cultivar ‘Alexandra’ presented in Ben Mimoun et al. (1996). Leafy shoot length (m) was converted to dry mass (g) based on an allometric relationship derived from data collected between 1997 and 1999 (DM = 15.9 x length, n = 215, r² = 0.95). Fruit and leafy shoot DM were converted to mass C by assuming the C content of fruit to be 42% (Lescourret et al. 1998), and that of leafy shoot DM to be 45% (Grossman and DeJong 1994).

Growth data of a sample of individual fruit were analyzed to determine the approximate timing of the two main phases of fruit growth commonly observed in peaches—cell division/differentiation followed by cell expansion/maturation (DeJong and Goudriaan 1989). This biphasic growth system results in a double-sigmoid growth pattern, in which growth is divided into three stages. Stages I and III describe periods of rapid increase in fruit mass associated with cell division/differentiation and cell expansion/maturation, respectively, whereas Stage II describes a period of slow growth between Stages I and III that is apparently a function of the length of time until onset of cell expansion/maturation (DeJong and Goudriaan 1989).

To simulate C assimilation processes at the scale of FBS, measurement of the three-dimensional spatial location of all leafy elements was required, taking account of crown growth over time (Walcroft et al. 2002). The tree crown architecture was therefore measured twice, at 45 and 65 DAB, to capture most of the shoot elongation. The technique is described in detail by Sinoquet et al. (1997) and uses 3A software (Adam et al. 1999). At the same time, tree topology was recorded as a multi-scale tree graph following Godin et al. (1999). This system allows the tree to be analyzed later at a range of scales, and links components in terms of branching or succession. The
tree was divided into components consisting of current-year vegetative shoots that bear foliage (leafy shoots), 1-year-old FBS, and older woody branches, noting branching and succession between individual shoots and branches.

**Shoot C assimilation model**

Carbon assimilation was simulated over the main fruit growth period by a process-based model (RATP, Sinoquet et al. 2001). The model simulates the spatial distribution of radiation and leaf gas exchange, taking into account tree architecture (spatial location of foliage elements), tree crown microclimate, and leaf physiological and physical properties. The tree crown is represented in the model as a three-dimensional array of cubic cells, each with dimensions of 0.2 m$^3$. Each cell is characterized by a leaf area density (m$^2$ m$^{-3}$) computed from tree architecture measurements (length of leafy shoots) based on an allometric relationship between leafy shoot length and leaf area. Parameters for the model were derived from measurements of photosynthetic capacity and stomatal conductance within the tree crown (Le Roux et al. 2001, Walcroft et al. 2002). The model was run continuously over the main period of fruit growth, between 49 and 106 DAB, by assuming that leaf area increased linearly with time between the two dates of architecture measurement, then remained constant until fruits were harvested. Calculations were performed half-hourly and integrated to give daily fluxes for each shoot.

**Branch-bag photosynthetic measurements**

To validate the shoot C assimilation model, photosynthetic measurements were made on six shoots throughout the tree crown using branch bags. Three shoots were predominately shaded and three shoots relatively exposed to direct sunlight. The system design was open-flow, and each bag consisted of a clear plastic sheet rolled into a tube and heat-sealed along the crown using branch bags. Three shoots were predominately enclosed several leafy shoots. Ambient air was pumped into each bag at between 50 and 120 l min$^{-1}$, depending on bag size and enclosed leaf area, so the residence time of gas in the bag was between 15 and 30 s. Flow rate to each bag was measured with a flow meter (FC 260, Tylan, CA). Gas was sampled from the ambient air as well as from the outlet of each bag, measured for water vapor concentration (RHT-2, General Eastern Instruments, MA), then drawn through desiccant before passage through a differential CO$_2$ analyzer (BINOS-100, Rosemount, Germany). Shoot C assimilation rate ($A$, mol CO$_2$ m$^{-2}$ s$^{-1}$) was calculated as:

$$A = \frac{F(C_r - C_s)}{S} \tag{1}$$

where $F$ is molar flow rate of gas into the bag (mol s$^{-1}$), $C_r$ and $C_s$ are the CO$_2$ mole fractions (mol CO$_2$ mol air$^{-1}$) in the ambient and bag outlet, respectively, and $S$ is one-sided surface area of foliage inside the bag (m$^2$).

The system was fully automated, and cycled between each bag at about 5 min intervals. After each complete cycle, analyzer stability was checked by passing ambient air through both the reference and sample analyzers. Thus, a gas exchange measurement for each bag was recorded about every 35 min. Measured daily integrals were calculated on the assumption that the measured rate represented the mean rate between measurements, and converted to g C shoot$^{-1}$ day$^{-1}$ by multiplying by shoot leaf area and converting molar to mass units. After measurements were completed, the sampled shoots were harvested to determine leaf surface area with a leaf area meter (LI-3100, Li-Cor, Lincoln, NE). Leaves were dried, then analyzed for nitrogen concentration with an elemental analyzer (Carlo-Erba, Milan, Italy). Nitrogen content (g N m$^{-2}$) was computed from leaf mass-to-area ratio and N concentration. Leaf-level photosynthetic capacity was then determined based on the relationship between N content and photosynthetic capacity presented in Walcroft et al. (2002), and the data were used as inputs to the 3-D shoot C assimilation model.

Shoot C assimilation measurements were made over one day that was clear during the morning and partly cloudy during the afternoon. The shoot C assimilation model was run over the same period as the measurements. Climatic variables (solar irradiance, air temperature and air humidity) measured at 5-min intervals within 30 m of the studied tree were used in the model.

**Fruit-bearing shoot model**

To quantify the total C requirements of FBS, and the potential contribution of shoots without fruit to the C requirements of shoots with fruit, the tree was divided into three zones (basal, middle and peripheral) according to radial distance of each shoot from a central axis point on the main stem. The C dynamics of the mean fruit-bearing shoot within each zone were simulated with the model of Lescourret et al. (1998). This model uses a C balance method to compute dry mass growth increments of the fruit-bearing 1-year-old stem, the leafy shoots, and the fruit.

The potential contribution to fruit growth on FBS of C from non-FBS within each zone was determined by calculating the total C deficit for the mean FBS, and the daily assimilation of C in non-FBS, which accumulated in a pool and was assumed to be available for translocation to FBS. The total C required for one fruit of the mean FBS of a given zone was calculated as follows. The cumulative observed fruit growth was smoothed by a local regression procedure (Chambers and Hastie 1992) to give daily fruit dry mass W (g) as well as daily fruit dry mass growth rate $\Delta W/\Delta t$ (g day$^{-1}$). Daily maintenance respiration demand MR (g C day$^{-1}$) is a function of $W$, and varies with temperature according to the $Q_{10}$ concept:

$$MR = MR_{10} \cdot Q_{10}^{\theta / \theta_{10} / 10} W 3600H \tag{2}$$

where $MR_{10}$ is maintenance respiration rate (7.81 $\times$ 10$^{-9}$ g C g$^{-1}$ g$^{-1}$ day$^{-1}$) at the reference temperature $\theta_{10}$ (20°C), $Q_{10}$ is the rate at which MR increases with a 10°C increase in temperature (1.9), $\theta$ is the mean daily temperature (°C) and $H$ is day length (h). Daily growth demand $D$ (g C day$^{-1}$) was derived.
from:

\[ D = \frac{\Delta W}{\Delta t} (CC + GRC) \]  

where CC is C concentration of fruit dry mass (0.4242 g C g\text{DM}^{-1}) and GRC is growth respiration coefficient (0.0843 g C g\text{DM}^{-1}). Values for parameters MRR, \( \theta_0 \), \( Q_{\text{ref}} \), CC and GRC are taken from Lescourret et al. (1998).

The resulting daily quantities MR and D were then multiplied by the mean number of fruit per shoot. The total C deficit for the mean shoot was the difference between total C required for the observed fruit growth and C supplied to fruit as predicted by the fruit-bearing shoot model. Daily assimilation of C in non-FBS was deduced from the shoot C assimilation model. Carbon from the accumulated pool was provided to the mean FBS in each zone to meet the imbalance between C supplied by the FBS and that required according to:

\[ C_{\text{provided}} = \frac{C_{\text{pool}} D_i}{(D_1 + D_2 + D_3) n_i} \]  

where \( C_{\text{pool}} \) is the accumulated C pool in shoots without fruit, \( D_i \) is the total C deficit of all FBS in zone \( i \) (deficit of mean shoot multiplied by the number of shoots), and \( n_i \) is number of FBS in zone \( i \) (\( i = 1 \) to 3).

Results

Shoot C assimilation

Measured instantaneous shoot net C assimilation rates varied between –0.5 \( \mu \text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \) (nighttime values) and 9.0 \( \mu \text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \) (values for maximal irradiance on sunlit shoots) (Figure 1). Carbon assimilation rates in sunlit shoots were generally about three times greater than those in shaded shoots. Overall, the model performed well in predicting instantaneous \( \text{CO}_2 \) assimilation rates for sunlit and shaded shoots. The slope and intercept of the regression between measured and simulated rates were not significantly different from one and zero, respectively. The root-mean-squared error of simulated instantaneous \( \text{CO}_2 \) assimilation rates compared with measured rates was 1.23 \( \mu \text{mol m}^{-2} \text{ s}^{-1} \). On a daily basis, the three sunlit shoots assimilated between 0.4 and 0.5 g C day\(^{-1}\), whereas the shaded shoots assimilated about 0.1 g C day\(^{-1}\). The model performed well on a daily basis, predicting C assimilation for the six shoots with a root-mean-squared error of 0.03 g C day\(^{-1}\).

Carbon assimilation at the shoot scale varied widely throughout the tree crown (Table 1). The mean daily rate for all shoots was 0.66 g C day\(^{-1}\), and the range varied over 140-fold from a minimum of 0.025 g C day\(^{-1}\) to a maximum of 3.58 g C day\(^{-1}\) (Table 1). The distribution was highly skewed, with 50% of all shoots assimilating less than 0.38 g C day\(^{-1}\), and 75% of shoots assimilating less than 0.84 g C day\(^{-1}\). The mean C assimilation rate of the 36 sampled shoots was not significantly different from that of all shoots (\( P = 0.85 \)), indicating that the shoots selected for fruit and leafy shoot growth measurements were a representative sample of all shoots. Most of the variability in C assimilation per shoot originated from differences in shoot size—larger shoots had greater leaf area, and generally greater daily C assimilation rates per shoot (Figure 2). Examining shoot C assimilation per unit leaf area normalizes the effect of shoot size, so the remaining variability in C assimilation arises mainly from differences in shoot microclimate and leaf physiological properties. On a leaf area basis, mean shoot C assimilation was 2.20 g C m\(^{-2}\) day\(^{-1}\), and varied only 4.7-fold between 0.82 and 3.97 g C m\(^{-2}\) day\(^{-1}\) (Table 1). In contrast to whole-shoot C assimilation rate, the rate per unit leaf area was normally distributed, with a coefficient of variation of about 0.3.

The mean rate of C assimilation per fruit for all shoots was 0.14 g C fruit\(^{-1}\) day\(^{-1}\), and varied between 0.014 and 0.92 g C fruit\(^{-1}\) day\(^{-1}\) (Table 1). For the sampled shoots, the mean daily rate of C assimilation per fruit was lower than that for all shoots, but the coefficient of variation was similar. The distribution was highly skewed, with 75% of all FBS assimilating less than 0.08 g C fruit\(^{-1}\) day\(^{-1}\), whereas only 5% of all FBS assimilated more than 0.18 g C fruit\(^{-1}\) day\(^{-1}\).

Total daily C assimilation by the whole tree varied from 33 to 180 g C day\(^{-1}\), with a mean rate of 142 g C day\(^{-1}\) (Figure 3a). Most of the day-to-day variation was climate-driven, although there was a gradual increase between 50 and 70 DAB as a result of increasing leaf area (Walcroft et al. 2002). The FBS contributed around 65% of total daily C assimilation by the whole tree. Shoots without fruit contributed the remaining 35%, which amounted to about 60 g C day\(^{-1}\). The mean rate of C assimilation of FBS within three spatial zones was about 0.4, 0.7, and 1.0 g C day\(^{-1}\) in the basal, middle and peripheral zones, respectively (Figure 3b).
Fruit and leafy shoot growth variability
The mean number of fruit per FBS was 11.1 (SD 6.7), ranging from 2 to 25. Mean fruit mass per FBS at the beginning of measurements was 0.653 g C, and ranged between 0.01 and 1.08 g C (Table 2). At harvest, mean fruit mass per FBS had increased to 5.05 g C, and ranged between 0.716 and 7.68 g C. Analysis of variance indicated most variance in fruit mass originated among shoots, rather than within individual shoots (F-ratio > 1). Data on growth of individual fruits indicated that growth rates generally slowed between 55 and 75 DAB, typical of Stage II growth, but increased rapidly afterwards indicating the commencement of Stage III growth. Fruit mass during Stage II growth was closely related to fruit mass at the commencement of measurements (r² = 0.58, Figure 4). However, the relationship between fruit mass at Stage II and that at harvest was poor (r² = 0.05), indicating that most variability in fruit mass originated during Stage III growth.

The mean number of leafy shoots per FBS was 15.3 (SD = 5.4), and ranged from 6 to 30. Mean shoot leaf area increased from 0.19 to 0.28 m² between the two dates that tree architecture was digitized. When measurements began, mean leafy shoot mass was 0.32 g C, and this increased to 0.78 g C at harvest. Leafy shoot mass at harvest was highly variable among shoots, ranging from 0.007 to 5.60 g C, and was highly skewed so that 75% of all FBS had less than 1.2 g C in leafy shoots. As with the fruit, most of the variation in leafy shoot mass originated among FBS rather than within FBS.

**Table 1.** Statistics of C assimilation for all fruit-bearing shoots in the peach tree, and for sampled shoots on which fruit growth was measured. The significance of differences in rates between all shoots and sampled shoots was determined with a t-test. Data were log-transformed before the t-test because of the skewed distributions.

<table>
<thead>
<tr>
<th>C assimilation rate</th>
<th>C assimilation per unit leaf area</th>
<th>C assimilation per fruit</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All shoots (g C day⁻¹)</td>
<td>Sampled shoots (g C day⁻¹)</td>
</tr>
<tr>
<td>Mean</td>
<td>0.66</td>
<td>0.63</td>
</tr>
<tr>
<td>Maximum</td>
<td>3.58</td>
<td>2.23</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.025</td>
<td>0.093</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.74</td>
<td>0.48</td>
</tr>
<tr>
<td>Skewness</td>
<td>2.11</td>
<td>1.29</td>
</tr>
<tr>
<td>Number of shoots</td>
<td>140</td>
<td>36</td>
</tr>
</tbody>
</table>

| t-test | P = 0.29 | P = 0.90 | P = 0.001 |

**Figure 2.** Relationship between shoot leaf area and mean daily C assimilation for sampled shoots.

**Figure 3.** (a) Temporal course of simulated total daily C assimilation in fruit-bearing shoots, shoots without fruit and the whole tree. (b) Temporal course of simulated mean shoot C assimilation of shoots in the basal, middle and peripheral zones.
Simmulation per fruit on each FBS. Fruit relative growth rate and the variability in relative growth rate within a shoot were both unrelated to C assimilation per fruit on each FBS (Figures 5c and 5d).

One possible explanation for the lack of correspondence between available C per fruit and fruit growth on a shoot is that C may be translocated among nearby FBS and shoots without fruit, thus reducing or eliminating differences in available C per fruit and therefore in fruit growth. To determine whether FBS could assimilate sufficient C to meet their own growth requirements, and to quantify any C deficit or excess, the mass of C assimilated in fruit and leafy shoots over the period in which C assimilation was simulated was plotted against total shoot C assimilation (Figure 6). Values above the 1:1 line indicate FBS in which there was a greater mass of C in fruit and leafy shoots than was assimilated by the FBS. In contrast, values beneath the 1:1 line indicate assimilated C in excess of requirements for fruit and leafy shoot growth. Just over half the FBS did not assimilate sufficient C to meet growth requirements, and must have imported C from neighboring FBS or non-fruiting shoots, or from C reserves in the trunk and roots. This analysis is conservative because maintenance respiration of the FBS during the growing period was not considered. The total C requirement of FBS during the growing period would have been greater than the growth C requirement, so it is likely that a larger proportion of FBS than that shown in Figure 6 would have imported C to meet these requirements.

Differences between local assimilation and fruit growth requirements were analyzed at the scale of three zones in the tree (basal, middle and peripheral). For the mean FBS in each zone,

Table 2. Statistics of fruit dry mass (g C) of sampled FBS when measurements commenced and at harvest, and relative growth rate (RGR; day\(^{-1}\)) during Stage III of fruit growth. Statistics of leafy shoot dry mass (g C) when measurements commenced and at harvest. ANOVA F-ratios indicate the ratio of sample variances among shoots to that within shoots. For each F-value, the associated probability was < 0.05.

<table>
<thead>
<tr>
<th></th>
<th>Initial fruit mass</th>
<th>Fruit mass at harvest</th>
<th>Fruit RGR Stage III</th>
<th>Initial leafy shoot mass</th>
<th>Leafy shoot mass at harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>0.653</td>
<td>5.05</td>
<td>0.0029</td>
<td>0.32</td>
<td>0.78</td>
</tr>
<tr>
<td>Maximum</td>
<td>1.08</td>
<td>7.68</td>
<td>0.0185</td>
<td>1.24</td>
<td>5.60</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.01</td>
<td>0.716</td>
<td>0.0015</td>
<td>0.004</td>
<td>0.007</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.153</td>
<td>1.30</td>
<td>0.0011</td>
<td>0.28</td>
<td>0.80</td>
</tr>
<tr>
<td>n</td>
<td>439</td>
<td>277</td>
<td>264</td>
<td>639</td>
<td>574</td>
</tr>
<tr>
<td>ANOVA F-ratio</td>
<td>2.32</td>
<td>2.67</td>
<td>2.22</td>
<td>2.60</td>
<td>2.13</td>
</tr>
</tbody>
</table>

Figure 4. Initial fruit mass plotted against estimated fruit mass at Stage II of growth (mid-fruit mass), and fruit mass at Stage II plotted against final mass at fruit harvest.
the daily C deficit was computed as described in the Methods section. These were integrated over the whole tree to give an estimate of the amount of C required each day from sources outside the FBS to meet any C deficit of FBS (Figure 7).

In this analysis, C is provided to FBS from non-FBS at a rate equivalent to the daily FBS C deficit provided there is sufficient C stored in, or being assimilated by, non-FBS. The preferred source of C for translocation is current assimilates of non-FBS. When daily assimilation of non-FBS exceeds the daily C deficit of FBS, then C accumulates in a storage pool. When the daily C deficit of FBS exceeds daily assimilation of non-FBS, C from the storage pool is utilized to meet the shortfall, and the pool size declines accordingly. When the C storage pool is exhausted, then the rate at which C is provided to FBS is limited by current assimilation of non-FBS. If the rate at which C is provided is less than the daily C deficit, then fruit growth will be source-limited.

Between 53 and 70 DAB, the total C deficit of FBS was low because most fruits were growing slowly (Stage II growth), and the deficit could be met from current assimilates of non-FBS. Because the C deficit of FBS was less than C assimilation of non-FBS, C accumulated in a storage pool that peaked at about 850 g C at 73 DAB. After 70 DAB, the daily C deficit of FBS increased as Stage III fruit growth began, eventually exceeding the daily rate of C assimilation in non-FBS. In meeting the growing C deficit, the C pool declined, and was fully depleted by about 87 DAB. At this point, the rate at which C was provided to FBS declined to equal the rate of current C assimilation in non-FBS, which was below that needed to meet the daily FBS C deficit. It is likely at this stage that fruit growth was limited by C supply, although sufficient C to meet the deficit may have been translocated to FBS from other reserves, such as older stems and roots.

Fruit mass at harvest was slightly lower in the basal zone, at around 4.5 g C, compared with the middle (5.5 g C) and peripheral (6.0 g C) zones (Figure 8). Simulations of fruit growth for the mean shoot within each zone showed that photosynthesis of autonomous FBS could not provide sufficient C to meet fruit growth requirements, and simulated growth therefore underestimated observed growth. The greatest underestimation occurred in the basal and middle zones, where simulated fruit mass at harvest was about 3 g C lower than observed. The model underestimated observed growth in the peripheral zone by about 2 g C, reflecting the greater C assimilation rate in this zone (Figure 3b). By allowing transfer of C to FBS from other sources or reserves, such as non-FBS, the model simulated well the observed pattern of fruit growth. A decline in fruit growth was evident in the middle and peripheral zones after 87 DAB (Figures 8c and 8f), which coincided with the period indicated in Figure 7 when the C reserve in shoots without fruit was exhausted, and fruit growth may therefore have been supply-limited. Although the close fit of simulated and observed growth was primarily a result of the method of determining C transfer to FBS (i.e., C was supplied at the rate required to meet the calculated C deficit, which was calculated from the observed fruit growth), the important conclusions that can be drawn from this result are that FBS could not have been autonomous for C, and that non-FBS were likely an important source of C for fruit growth on FBS.

Discussion

We combined a range of physiological and architectural measurements with state-of-the-art process-based models to quantify variability in C assimilation at the scale of individual FBS within a peach tree. This approach to modeling C assimilation has significant advantages over those in other studies. Our model is mainly process-driven, with a reduced reliance on empiricism. Thus, given the appropriate parameters, the same model can be applied to different species (e.g., walnut, Sinoquet et al. 2001) and in different locations (e.g., peach in Portugal, Le Roux et al. 2001). The model computes radiative
transfer and leaf-level fluxes in three dimensions, allowing shoot-level processes to be elucidated. This is important because most of the variability in fruit growth and quality appears to originate at the shoot scale within trees rather than among trees in an orchard (Génard and Bruchou 1993, Urban et al. 2003). Finally, the model can be validated directly against measurements of shoot C assimilation.

**Relationship between C assimilation and fruit growth within and among individual FBS**

Variability in mean fruit mass among FBS, and in individual fruit mass within each FBS, was unrelated to variation in C assimilation per fruit of the FBS. Similarly, variability in mean fruit relative growth rate (RGR) among FBS, and in individual fruit RGR within each FBS, was unrelated to variation in C assimilation per fruit of the FBS. Thus, the data do not support our hypothesis that variation in C assimilation at the FBS scale contributes significantly to variation in fruit growth and harvest mass. However, numerous studies have indirectly pointed to variation in local C gain as having a potential influence on fruit growth and quality. Génard (1992) showed that variation in the leaf area around peach fruit contributed to variability in fruit mass, presumably because of the close relationship between shoot leaf area and C assimilation (Figure 2). Similarly, Génard et al. (1998) showed that, on girdled shoots, mean peach fruit mass per FBS increased around 3-fold with an increase in the ratio of number of leaves to number of fruit from 6 to 30. Grossman and DeJong (1994) show that mean peach fruit mass was lower on unthinned trees, and increased with increasing severity of fruit pruning. Despite this indirect evidence for an effect of shoot C assimilation on fruit growth, our data show that other factors may be more important in regulating individual fruit growth on FBS, at least in situations close to natural situations (unpruned, unthinned trees).

It is possible that C translocation processes within an FBS are more important in regulating individual fruit growth than shoot C assimilation per fruit. Bruchou and Génard (1999) used a model to show that growth rate of individual peach fruit declines with increasing distance from photosynthesizing shoots, and this matched observations of individual fruit mass on isolated FBS. Marsal et al. (2003) showed that mean peach fruit mass was reduced when fruit grew in clumps, and suggested that this was caused by the greater resulting distance between fruits and the sources of C. An alternative mechanism that may operate within shoots is that C translocation to a fruit depends on C demand in addition to C supply (Pavel and DeJong 1993). In peach, as in most fruit, C demand is related to fruit (sink) size and activity (Grossman and DeJong 1994,

---

**Figure 8.** Observed (circles) and simulated (solid lines) growth of one average fruit on the average shoot in each zone. Plots a, c and e: no external C contribution. Plots b, d and f: include C contribution from shoots without fruit. Plots a and b: basal zone. Plots c and d: middle zone. Plots e and f: peripheral zone. Vertical dashed lines indicate the period when fruit growth was possibly limited by reduced C supply.
Lescourret et al. 1998). Larger fruit will demand more C, grow faster thereby demanding more C, and so on. Fruit that are initially larger should therefore grow more rapidly than fruit that are initially smaller, thereby increasing greatly the variability in fruit mass within an FBS. One might therefore predict a close relationship between initial fruit mass and fruit mass at harvest. In our study, the relationship between initial fruit mass and that at Stage II growth was strong (Figure 4), indicating that sink demand was the main determinant of fruit growth during the first growth stages. However, there was a poor relationship between fruit mass at Stage II growth and final harvest mass, indicating that larger fruit did not necessarily grow more rapidly than smaller fruit during Stage III of the growth pattern. In this case, it is possible that variations in C supply to individual fruit largely determined individual fruit growth.

Our study highlighted the requirement for translocation of C to FBS from external sources and reserves to meet the high C demand of fruit in the Stage III period of rapid growth. Thus, FBS could not be considered as autonomous for C. Of the FBS we sampled, over half did not assimilate sufficient C to meet the growth requirements of the fruit and leafy shoots they bore (Figure 6), and so must have imported C from alternative sources. An absence of shoot autonomy has been shown in many fruit tree species. Hansen (1969) showed that C is easily translocated among apple shoots, and the amount of C translocated is related to the leaf:fruit ratio of a shoot. Hansen and Christensen (1974) showed that C is transferred as much from non-FBS to FBS as from leaves to fruit within an FBS. Chalmers et al. (1975) showed that when the phloem of main branches on a peach tree was severed, fruit growth on shoots above the cut was enhanced whereas that on shoots below the cut was reduced, indicating that C would normally be translocated among shoots on a main branch. Roper et al. (1987) concluded that fruiting spur leaves of sweet cherry do not have the capacity to support fruit growth and so must be supplemented by C from other sources. Carbon was translocated between fruit-bearing and non-fruit-bearing parts of an apple tree (Palmer et al. 1991). Corelli-Grappadelli et al. (1996) showed that, in peach, C was translocated from non-fruiting shoots and extension shoots to FBS when fruits were rapidly expanding during Stage III of the growth curve. Based on an experiment where fruit distribution patterns were manipulated among FBS and main branches, Marsal et al. (2003) concluded that FBS were almost, but not completely, autonomous for C. The methods used in these papers allow C transfer among shoots to be determined in a qualitative sense. The novel aspect of our study is the ability to quantify any C deficit of FBS by a modeling approach, and thereby determine the extent of C translocation required to meet this deficit and satisfy fruit growth demands.

Quantifying C deficits of FBS has highlighted the importance of non-FBS to the C balance of the whole tree, and as a source of C potentially available to FBS during periods of rapid fruit growth. When FBS were considered autonomous for C, the fruit growth model was unable to reproduce the observed growth rates because of insufficient C supply by the FBS. Non-FBS contributed around 35% of the whole-tree C assimilation (Figure 3a), and for most of the fruit growth period this quantity of C would have been sufficient to meet the C deficit of FBS. During the early part of the season, when fruits were not growing rapidly, the model predicted a significant pool of excess C accumulated in non-FBS. This pool was then rapidly depleted as fruit growth rate increased, and was exhausted around 87 DAB. After this, the rate of simulated fruit growth slowed markedly, indicating that even the maximum possible contribution of C from non-FBS was still insufficient to meet the C deficit of FBS. At this point it is likely that other C sources, such as mobilization of reserves in the stem and roots, contributed to fruit growth. Alternatively, fruit growth may be periodically restricted by limited availability of C, particularly at high fruit crop load (Pavel and DeJong 1993, DeJong and Grossman 1995).

Carbon in excess of immediate requirements during the growing season is generally stored as nonstructural carbohydrates. Jordan et al. (2001) showed that the concentration of nonstructural carbohydrates (soluble sugars and starch) in 1-year-old shoots declines strongly after bud break, continues to decline over the period of fruit growth and then increases following fruit harvest. Similarly, Caruso et al. (1997) reported a rapid decrease in starch content of 1-year-old wood during peach fruit development. These studies indicate that a pool of stored nonstructural carbohydrates generally exists in peach trees at the beginning of the fruit growth period. This pool is depleted to meet the requirements of fruit growth later in the season, which is consistent with our modeling analysis.

Conclusions

We attempted to answer the question: does variability in shoot C assimilation within the tree crown explain variability in peach fruit growth? The modeling approach revealed large variability in shoot C assimilation rates within the crown. However, variations in fruit growth rate and mass among fruit-bearing shoots were unrelated to the large variations in shoot C assimilation. Thus, other factors that influence C translocation to individual fruits on an FBS are likely to be more important in determining variability in fruit growth and quality. Under the study conditions (unpruned, unthinned tree), the FBS were not autonomous for C. Shoots without fruit contributed a significant amount of C to FBS, but even this was insufficient to meet the needs of the rapidly expanding fruit late in the season and a period of supply-limited growth occurred.

Acknowledgments

The authors thank S. Ploquin, B. Adam, R. Laurent, A. Diaz-Espejo, E. Frak and B. Jaussely for their expert technical assistance in the field experiments. This work was funded by a grant from the Ministère de la Recherche, France, Grant No. 99 P 0497, and supported with fellowships provided by INRA (France) and the Trimble Agricultural Research Fund (New Zealand).
References


