RESEARCH PAPER

Vascular flows and transpiration affect peach (Prunus persica Batsch.) fruit daily growth

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Abstract
The relative contributions of xylem, phloem, and transpiration to fruit growth and the daily patterns of their flows have been determined in peach, during the two stages of rapid diameter increase, by precise and continuous monitoring of fruit diameter variations. Xylem, phloem, and transpiration contributions to growth were quantified by comparing the diurnal patterns of diameter change of fruits, which were then girdled and subsequently detached. Xylem supports peach growth by 70%, and phloem 30%, while transpiration accounts for ~60% of daily total inflows. These figures and their diurnal patterns were comparable among years, stages, and cultivars. Xylem was functional at both stage I and III, while fruit transpiration was high and strictly dependent on environmental conditions, causing periods of fruit shrinkage. Phloem imports were correlated to fruit shrinkage and appear to facilitate subsequent fruit enlargement. Peach displays a growth mechanism which can be explained on the basis of passive unloading of photoassimilates from the phloem. A pivotal role is played by the large amount of water flowing from the tree to the fruit and from the fruit to the atmosphere.

Key words: Fruit growth, fruit transpiration, peach, phloem, xylem.

Introduction
Fruit growth is the result of biophysical and biochemical events that allow water and dry matter to accumulate in fruit tissues. The rate of mass accumulation in the fruit depends on the balance between incoming and outgoing fluxes (Fishman and Génard, 1998). Water and assimilates are translocated to the fruit via phloem and xylem streams, while fruit epidermis transpiration and fruit respiration are the main outgoing fluxes. A reverse water flow from fruit to leaves is also possible via xylem backflow, as shown in some fruit species, including citrus (Mantell et al., 1980) and apple (Lang, 1990).

Fruit diameter variation in a finite time interval can be viewed as the net contribution of phloem import, which is always positive; xylem flow, which may be positive or negative; and transpiration through the cuticle, which is always negative. The effects on fruit diameter variation of dry matter gain and loss from fruit photosynthesis and respiration can be considered negligible on a daily scale (Blanke and Lenz, 1989).

Phloem and xylem flows are driven by turgor pressure and osmotic concentration gradients along the vascular path from source to sink organs (Münch, 1930; Minchin and Thorpe, 1987; Patrick, 1990, 1997; Minchin et al., 1996). In peach, diurnal patterns of leaf and fruit water potentials have been reported by McFadyen et al. (1996), who related changes in fruit growth rate over 24 h to shifting water potential gradients between fruit and leaves. In apple, Higgs and Jones (1984) and Jones and Higgs (1985) showed a close relationship between shrinkage (occurring in the middle of the day) and environmental conditions. In general, fruit shrinkage may occur as a consequence of fruit transpiration and seems to have an important role in lowering fruit water potential, thus creating the conditions for subsequent dry matter unloading to the fruit (Jones and Higgs, 1982; Berger and Selles, 1993; McFadyen et al., 1996).

Fruit transpiration is a physical process strictly dependent on both environmental conditions and epidermal features. It is driven by vapour pressure deficit (VPD), and it is proportional to fruit surface area and the skin
permeability coefficient (Lescourret et al., 2001; Wu et al., 2003). In apple, specific transpiration is greatly reduced near harvest, when the cuticle becomes much thicker (Jones and Higgs, 1982; Lang, 1990). In peach during stage III, the fruit lose water at higher specific rates than apple (Lescourret et al., 2001; Li et al., 2002; Wu et al., 2003).

Lang and Thorpe (1989) and Lang (1990) have developed a method to assess the relative contributions of phloem, xylem, and transpiration to daily fruit growth. Using this technique, they revealed important features of fruit growth and fresh matter balance in apple and grape where the xylem inflow is greatly reduced towards the end of the season and fruit growth is the result only of the phloem stream during cell expansion. While for apple recent studies report xylem disruption (Drazeta et al., 2001, 2004), in grape this phenomenon is not the cause of the observed reduction in the contribution of the xylem to fruit growth, which is rather the result of diminished hydraulic pressure driving xylem water flux (Bondada et al., 2005; Keller et al., 2006).

Fluctuations in environmental conditions, as occur daily or during the season, and specific genetic features may turn on and off each flow of matter (xylem, phloem, and transpiration), i.e. the fruit can adopt different modes of growth. In apple, grape, and citrus, among other species, fruit growth mechanisms have been investigated largely on a seasonal, but not a daily scale, from both the biophysical and biochemical points of view. In peach, many models have been developed to explain quantitatively several aspects of fruit growth in variable conditions of water stress and crop load during stage III (Fishman and Génard, 1998, 1999; Huguet et al., 1998; Génard et al., 2003). However, further experimental data are needed to validate them, particularly those that focus on the diurnal pattern of fruit growth.

The objective of the present study was to determine the daily processes permitting peach fruit to maintain its strength as a sink in relation to the changing tree and environment conditions. Mass balance was investigated on a daily basis and partitioned into phloem, xylem, and transpiration components during the two stages of fast diameter growth (cell division or stage I, and cell expansion or stage III) to understand better their roles and interactions in peach fruit growth dynamics.

Materials and methods

Plant material and environment data

Studies were conducted over three seasons: 2003, 2004, and 2005. In the first and last years, trials were conducted in Cadriano, Bologna, Italy, on the mid-season nectarine ‘Red Gold’, grafted on A6 clonal seedlings, trained as a Y trellis at a density of 1274 trees ha⁻¹. Standard cultural practices were applied for pruning, fertilization, and irrigation.

In 2004, the experiment was carried out at the Horticultural Research Farm of the University of Georgia, Watkinsville, GA, on ‘Redhaven’ peaches on Lovell rootstock. Trees were trained as a perpendicular V at a density of 512 trees ha⁻¹. Standard management was applied, according to the Georgia Cooperative Extension Service guidelines.

In 2003 and 2004, temperature data were collected at 6 min intervals with a thermocouple positioned in a shaded part of the canopy, and interfaced to a CR10 data-logger (Campbell Scientific Ltd, Leicestershire, UK). In 2005, temperature and relative humidity were available from a weather station (A840 Base Station–Adcon Telemetry GMBH, Klosterneuburg, Austria) placed on the farm. With these data, the VPD was calculated in 2005.

Phloem, xylem, and transpiration flows

In all the three seasons, fruit growth, phloem inflow, xylem in/outflow, and transpiration outflow were determined on a daily scale following Lang (1990). Continuous and precise monitoring of fruit diameter variations over time was performed using custom-built gauges (Morandi et al., 2007b), consisting of a light, stainless steel frame supporting an electronic sensor (Megatron Elektronik AG & Co., Munich, Germany). The resolution attained was in the order of 3–4 μm. The gauges were interfaced to a CR10 data-logger and readings were taken every 6 min.

Diameter variations over time were monitored on several fruit, all subjected to the same sequence of treatments: ‘intact’ (with normal vascular connections), ‘girdled’ (with the phloem connection severed), and ‘detached’ (with all vascular connections severed). In ‘detached’ fruit, the peduncle surface was covered with glue, to avoid any water loss, and fruit were hung in their original position using thin wire. With these data, phloem, xylem, and transpiration contributions to fruit growth can be computed following Lang (1990). Representative, well-exposed fruit placed on the east side of the row were measured.

In the first year (2003), the experiment was performed only at stage III, while in 2004 and 2005 measurements were carried out at both stage I and stage III.

In the first year (2003), 115 days after full bloom (DAFB), five fruit were selected: three of them were subjected to the sequence of treatments (‘intact’, ‘girdled’, ‘detached’) while the remaining two were left intact and served as controls. All treated fruit were measured for 3 d in each of the three different treatments, and the whole experiment lasted 9 d. In the second year (2004), the experiments were set similarly to 2003 with more replications: at both stage I and stage III, four treated fruit and three control fruit were monitored starting at 32 and 96 DAFB, corresponding to cell division and expansion. In the third year (2005), yet more fruit were measured, for shorter periods of time: 2 d in the ‘intact’ and ‘girdled’ treatment and only 1 d in the ‘detached’ treatment. Seven treated and three control fruit were monitored at stage I (44 DAFB), and 13 treated and five control fruit at stage III (105 DAFB).

Data were averaged for each fruit during each treatment condition (normal, girdled, and detached). Only data collected on clear and sunny days were used.

According to Lang (1990), the daily phloem contribution can be calculated as the difference between the diameter changes of normal and girdled fruit; the same can be done for the xylem by subtracting the diameter changes of detached fruit from those of the girdled fruit. For each fruit diameter, data were converted to weight according to cultivar-specific conversion equations (reported below).

Phloem, xylem, and transpiration transport, and transpiration rates per minute were calculated for each fruit during 24 h, and expressed as weight changes per unit of fruit weight (g g⁻¹) to allow comparisons between years, stages, and cultivars. At each recording time, means and standard errors were computed for all the parameters considered.
Subsidiary determinations

Diameter–weight conversion equations: Diameters (D) were converted to weights (W) using the following equation:

\[ W(g) = a \times D \text{ (mm)}^b \]  

where a and b were 0.0023 (SE ± 0.00025) and 2.7734 (SE ± 0.032) for ‘Red Gold’, and 0.0011 (SE ± 0.0004) and 2.8169 (SE ± 0.048) for ‘Redhaven’, respectively. These equations were obtained by regressing diameter and weight data of a large number of fruit from the orchards where the experiments were set. The \( R^2 \) of the relationship was >0.99 for both cultivars.

Phloem sap concentration: The average concentration of the phloem sap was estimated in the third year (2005) at both stage I and stage III, by dividing the mean daily dry matter (DW) gain (g DW fruit\(^{-1}\) d\(^{-1}\)) by the mean daily amount of fresh matter (FW) imported via phloem (g FW fruit\(^{-1}\) d\(^{-1}\)). The mean daily DW gain was calculated simultaneously with these experiments by consecutively harvesting at 3–5 d intervals of 10 comparable fruit from at least six trees of the same orchard whose dry matter content was estimated as the average weight difference between the two measurements. Measurements were repeated on four clear, sunny days.

Daily fruit transpiration: A parallel, independent measurement of daily fruit transpiration was carried out in the third year (2005) at both stages. Ten fruit comparable with those monitored by the gauges were detached and their fresh weight and diameter immediately measured. Peduncles were then covered with glue, and fruit were hung with thin wire as close as possible to their original position. Twenty-four hours later the weight and diameter measurements were repeated and daily transpiration was estimated as the average weight difference between the two measurements. Measurements were repeated on four clear, sunny days.

Results

In 2004 and 2005, data at cell division were collected 10–15 d before the end of stage I, when fruit were 16–18 mm in diameter and weighed 3–4 g. At stage III in all years, fruit ranged from 50 mm to 55 mm in diameter and from 80 g to 100 g in weight.

Stage I: mass balance in peach daily growth

‘Redhaven’ fruit gained ~0.16 g g\(^{-1}\) fresh matter d\(^{-1}\), corresponding to 0.88 g fruit\(^{-1}\) d\(^{-1}\). This growth was the result of 0.37 g g\(^{-1}\) total inflow (xylem+phloem), of which 59% was lost by transpiration. Phloem and xylem relative contributions to growth were 38% and 62%, respectively (Tables 1 and 2).

‘Red Gold’ fruit grew 0.14 g g\(^{-1}\) d\(^{-1}\) or 0.56 g fruit\(^{-1}\) d\(^{-1}\). Fruit total inflows were 0.42 g g\(^{-1}\) fresh matter d\(^{-1}\) with relatively similar transpiration losses (64% of total inflows) (Tables 1 and 2). In 2005, these transpiration losses were quite similar to those of the fruit that were detached and left in the same place in the canopy (data not shown). Phloem sap concentration was calculated at 16.4%.

Stage I: relative growth rate and daily phloem, xylem, and transpiration flows

Early in the season, daily fruit relative growth rate (RGR) followed similar patterns for both cultivars. Minimum values were recorded a few hours after dawn and remained low through the first half of the morning. Afterwards, RGR began to increase, reaching a maximum

### Table 1. Daily specific growth (g g\(^{-1}\) d\(^{-1}\)) for intact (G) and girdled (A) fruit, and the contribution to growth of transpiration (T), phloem (P), and xylem (X), recorded at stage I in 2004 and 2005 and at stage III in 2003, 2004, and 2005

<table>
<thead>
<tr>
<th>Stage</th>
<th>Year</th>
<th>G</th>
<th>A</th>
<th>T</th>
<th>P</th>
<th>X</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>2004</td>
<td>0.156±0.022</td>
<td>0.013±0.005</td>
<td>-0.217±0.026</td>
<td>0.143±0.021</td>
<td>0.230±0.023</td>
</tr>
<tr>
<td>I</td>
<td>2005</td>
<td>0.144±0.031</td>
<td>0.047±0.007</td>
<td>-0.273±0.015</td>
<td>0.097±0.026</td>
<td>0.320±0.020</td>
</tr>
<tr>
<td>III</td>
<td>2003</td>
<td>0.041±0.005</td>
<td>0.014±0.006</td>
<td>-0.065±0.010</td>
<td>0.027±0.002</td>
<td>0.079±0.014</td>
</tr>
<tr>
<td>III</td>
<td>2004</td>
<td>0.044±0.001</td>
<td>0.015±0.004</td>
<td>-0.051±0.005</td>
<td>0.029±0.005</td>
<td>0.066±0.005</td>
</tr>
<tr>
<td>III</td>
<td>2005</td>
<td>0.044±0.002</td>
<td>0.013±0.003</td>
<td>-0.058±0.005</td>
<td>0.031±0.005</td>
<td>0.070±0.006</td>
</tr>
</tbody>
</table>

### Table 2. Daily growth (g fruit\(^{-1}\) d\(^{-1}\)) for intact (G) and girdled (A) fruit, and the contribution to growth of transpiration (T), phloem (P), and xylem (X), recorded at stage I in 2004 and 2005 and at stage III in 2003, 2004, and 2005

<table>
<thead>
<tr>
<th>Stage</th>
<th>Year</th>
<th>G</th>
<th>A</th>
<th>T</th>
<th>P</th>
<th>X</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>2004</td>
<td>0.876±0.138</td>
<td>0.066±0.022</td>
<td>-1.222±0.190</td>
<td>0.810±0.132</td>
<td>1.288±0.172</td>
</tr>
<tr>
<td>I</td>
<td>2005</td>
<td>0.558±0.127</td>
<td>0.181±0.030</td>
<td>-1.055±0.062</td>
<td>0.378±0.105</td>
<td>1.236±0.081</td>
</tr>
<tr>
<td>III</td>
<td>2003</td>
<td>3.62±0.451</td>
<td>1.25±0.561</td>
<td>-5.92±1.142</td>
<td>2.37±0.117</td>
<td>7.17±1.464</td>
</tr>
<tr>
<td>III</td>
<td>2004</td>
<td>3.65±0.142</td>
<td>1.26±0.358</td>
<td>-4.30±0.529</td>
<td>2.41±0.409</td>
<td>5.56±0.554</td>
</tr>
<tr>
<td>III</td>
<td>2005</td>
<td>3.61±0.251</td>
<td>0.98±0.248</td>
<td>-4.74±0.512</td>
<td>2.63±0.435</td>
<td>5.72±0.474</td>
</tr>
</tbody>
</table>
in late afternoon (Figs 1a and 2a). Limited shrinkage occurred in 2004, while in 2005 fruit RGR was always positive. Night-time growth rates were higher than during the day on average (Figs 1a and 2a).

In both years, peach and nectarine fresh matter flows immediately after dawn showed minimum rates in xylem and phloem unloading, and very low, if any, transpiration loss (Figs 1a and 2a). In 2004, morning transpiration losses were not balanced by xylem inflow, which remained low (on average 0.05 mg g\(^{-1}\) min\(^{-1}\)) until midday, causing a slight shrinkage, with fruit RGR showing negative values of \(-0.03\) mg g\(^{-1}\) min\(^{-1}\). At the same time, phloem inflow increased to 0.17 mg g\(^{-1}\) min\(^{-1}\) around midday, partially offsetting transpiration losses and inducing the increase of fruit RGR during the late morning (Fig. 1a).

In 2005, the morning xylem inflow (on average 0.25 mg g\(^{-1}\) min\(^{-1}\)) was sufficient to balance water losses, while the phloem inflow, despite increasing slightly after dawn, remained lower (\(-0.05\) mg g\(^{-1}\) min\(^{-1}\)) than in 2004 (Fig. 2a).

After an early morning minimum, fruit transpiration increased, reaching maxima of 0.32 mg g\(^{-1}\) min\(^{-1}\) and 0.45 mg g\(^{-1}\) min\(^{-1}\) in ‘Redhaven’ and ‘Red Gold’, respectively, at about 17.00 h. In both years, the xylem flow increased in the afternoon, following a pattern symmetrical to that of transpiration. Maximum rates of xylem inflow were attained shortly after transpiration started to decrease. In 2004, the maximum xylem inflow was \(-0.44\) mg g\(^{-1}\) min\(^{-1}\); in 2005 it peaked at 0.48 mg g\(^{-1}\) min\(^{-1}\). Phloem inflow remained high after midday and, together with the increased xylem flow, it allowed the afternoon increase in fruit RGR to 0.23 mg g\(^{-1}\) min\(^{-1}\) and 0.17 mg g\(^{-1}\) min\(^{-1}\) in ‘Redhaven’ and ‘Red Gold’, respectively. In both 2004 and 2005, the maximum fruit RGR was recorded around 18.00 h as the result of the highest xylem inflow and the decrease in transpiration (Figs 1a and 2a).

In both cultivars, xylem and transpiration flows decreased gradually during the night. However, the balance of these flows was always in favour of the xylem. Phloem inflow maintained quite stable values throughout the night but tended to decrease near dawn. The water uptake from the xylem and the phloem inflow allowed maintenance of high RGRs, leading to large specific gains of fresh matter during the night (Figs 1a and 2a).

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**Fig. 1.** Diurnal courses of fruit RGR, specific phloem, xylem, transpiration flow rates (mg g\(^{-1}\) min\(^{-1}\)), and temperature for ‘Redhaven’ in 2004, during stage I (a) and stage III (b) of fruit development. Maximum SEs at stage I were 0.051, 0.046, 0.056, and 0.070 for RGR, phloem and xylem inflows, and transpiration rates, respectively, while at stage III they were 0.011, 0.025, 0.023, and 0.020 for RGR, phloem and xylem inflows, and transpiration rates, respectively. Data were recorded at 6 min intervals, during the 2004 season.

**Fig. 2.** Diurnal courses of fruit RGR, specific phloem, xylem, transpiration flow rates (mg g\(^{-1}\) min\(^{-1}\)), and VPD (kPa) for ‘Red Gold’ in 2005, during stage I (a) and stage III (b) of fruit development. Maximum SEs at stage I were 0.044, 0.052, 0.093, and 0.088 for RGR, phloem and xylem inflows, and transpiration rates, respectively, while at stage III they were 0.007, 0.012, 0.016, and 0.012 for RGR, phloem and xylem inflows, and transpiration rates, respectively. Data were recorded at 6 min intervals during the 2005 season.
Stage III: mass balance in peach daily growth

At stage III, the mean daily RGR for the three experiments was 0.043 mg g\(^{-1}\) d\(^{-1}\), corresponding to \(\sim 3.6\) g fruit\(^{-1}\) d\(^{-1}\) (Tables 1 and 2).

Daily specific growth was supported by average total inflows of 0.1 mg g\(^{-1}\) d\(^{-1}\), corresponding to 8-9 g of fresh matter unloaded daily to each fruit. Phloem and xylem relative contributions to daily total inflow were \(\sim 30\%\) and 70\%, respectively, in both 2004 and 2005, while in 2003 the phloem contribution was 5\% lower. Specific transpiration was similar over the three years, although slightly higher in 2003. Mean daily water loss was 0.058 mg g\(^{-1}\) d\(^{-1}\), corresponding to 4-6 g fruit\(^{-1}\) d\(^{-1}\) (Tables 1 and 2). Data on fruit transpiration measured with the gauges were similar to those obtained by weighing fruit immediately and 24 h after detachment (data not shown). Phloem concentration calculated at stage III was 16.3\%.

Stage III: relative growth rate and daily phloem, xylem, and transpiration flows

At stage III, fruit always grew at their maximum rates during late afternoon and the night, and at the lowest around midday (Figs 1b and 2b). In 2003 (data not shown) and 2004, fruit shrinkage was clearly detected during the middle of the day, but very little negative growth was recorded in 2005 (Figs 1b and 2b).

Fruit growth began to decrease immediately after dawn, in response to a decrease in xylem inflow and a concurrent increase in transpiration outflow. The xylem inflow remained quite low in the morning (on average 0.015, 0.01, and 0.03 mg g\(^{-1}\) min\(^{-1}\) in 2003, 2004, and 2005), unable to balance the continuous rise in transpiration that was almost twice the xylem inflow at that time (Figs 1b and 2b). The minimum fruit growth rate was recorded around noon with values of \(-0.021\) mg g\(^{-1}\) min\(^{-1}\) in 2003, up to 0 mg g\(^{-1}\) min\(^{-1}\) in 2005. Daily phloem patterns were not constant over the three years. During the morning and afternoon, phloem inflow rose to values between 0.03 mg g\(^{-1}\) min\(^{-1}\) and 0.05 mg g\(^{-1}\) min\(^{-1}\) (Figs 1b and 2b). Transpiration rates reached their maxima between 15.00 h and 17.00 h in 2003 and 2005, but earlier in 2004. Rates of 0.067, 0.099, and 0.087 mg g\(^{-1}\) min\(^{-1}\) in the three years, respectively, were recorded. The increase in water loss was coupled to a sharp rise in xylem inflow, which peaked in late afternoon, at around 19.00 h, as soon as the transpiration rate began to decrease, as occurred in stage I. Xylem inflows achieved values of 0.09 mg g\(^{-1}\) min\(^{-1}\) that were similar for the three years. Maximum fruit growth of 0.06-0.07 mg g\(^{-1}\) min\(^{-1}\) was recorded for ‘Red Gold’ and ‘Redhaven’ in all three years.

Night phloem inflows averaged 0.015-0.02 mg g\(^{-1}\) min\(^{-1}\) for ‘Red Gold’ in 2003 and 2005 (Fig. 2b), and 0.006 mg g\(^{-1}\) min\(^{-1}\) for ‘Redhaven’ (Fig. 1b).

Discussion

During the cell division and cell expansion stages, similar relative contributions of phloem, xylem, and transpiration to growth were found: peach fruit growth is sustained by about 30\% from the phloem and 70\% from the xylem. Transpiration losses account for 55–65\% of total inflows. The small variations in relative contributions between years may depend on the environmental conditions and the two cultivars used.

The growth strategy of peach is very different from that of apple and kiwifruit, whose xylem and phloem contributions vary greatly during the season. In apple, the xylem contribution to growth decreases with the development of the fruit, coinciding with a total loss of xylem functionality near harvest (Drazeta et al., 2001, 2004). At the same time, phloem unloading becomes more important for apple fruit cell expansion (Lang, 1990). In kiwifruit, the xylem becomes dysfunctional at the beginning of the last fruit expansion stage (Dichio et al., 2003), and the fruit transpiration is greatly reduced at the same time (Morandi et al., 2007a).

The approach used in this work to elucidate the growth strategy of peach allows separation and quantification of diurnal flows, as well as detailed information about the hourly variation of those fluxes and their changing contributions to fruit growth rates during a day.

Patterns of daily fruit growth and flows are quite similar at cell division and expansion. Hourly transpiration follows air temperature and VPD (Figs 1a and 2a, b), in agreement with Lescourret et al. (2001), Wu et al. (2003), and Huguet et al. (1998). Positive linear relationships were found between fruit transpiration rate and VPD at both stage I (\(R^2 = 0.81\)) and stage III (\(R^2 = 0.92\)), demonstrating a tight coupling of fruit transpiration to environmental conditions.

In the morning, xylem flow is reduced to its minimum values, coincident with the time of maximum expansion of the fruit, i.e. when this organ probably attains its highest turgor, which might prevent further inflow to the fruit. As the day progresses and fruit transpiration increases, the xylem and phloem inflows are not able to match the instantaneous rates of water loss. When fruit transpiration is not balanced by xylem inflow, fruit growth slows down to about zero, as occurs at stage I during the morning (Figs 1a and 2a), or becomes negative causing fruit shrinkage, as at stage III around noon (Figs 1b and 2b). These reductions in diameter are due only to transpiration losses and not to xylem backflows, since negative values in xylem flow rates were never detected during the two stages in all the studies carried out. In peach, the active transpiration through the skin should allow the fruit to reduce its turgor and to increase the osmotic concentration of its tissues.

Following the daily diameter reduction (occurring mainly at stage III), fruit resume their growth, reaching...
the highest rates of fruit enlargement in late afternoon. This growth depends mainly on xylem inflow (Figs 1a, b and 2a, b), which in the afternoon increases quickly and more than balances instantaneous transpiration water losses. As indicated above, the turgor increase caused by water entering the fruit is probably responsible for the reduction in xylem inflow, and thus the reduction of fruit growth observed in the early morning (Figs 1a, b and 2a, b).

However, if fruit are to gain weight (~0.65 g d\(^{-1}\) at stage I and 3.6 g d\(^{-1}\) at stage III), daily xylem and phloem inflow must exceed the amount lost via transpiration. To achieve this, fruit water potentials need to be maintained low enough to attract more water into the fruit, either by a decrease in fruit turgor pressure or by an increase in osmotic concentration. The cell expansion process can contribute to maintain turgor low enough for water and solutes to enter the fruit (Schmalstig and Cosgrove, 1990). Cosgrove (1993a, b) reported that the high turgor pressure reached by growing cells (as peach fruit cells rehydrate during late afternoon and night) may induce cell wall relaxation, with a reduction in the symplast turgor pressure. This would allow further inflows to the fruit which restore turgor and drive cell wall expansion. A further mechanism of turgor regulation relies on the export of small amounts of solutes from the cytoplasm to the cell wall, which greatly reduces apoplasmic osmotic potential and decreases the symplast turgor pressure (Patrick, 1990, 1997). This mechanism might be active in peaches where it might favour the bulk flow of xylem and phloem sap into the fruit, similarly to what was reported for post-veraison grapes by Matthews and Shackel (2005).

Diurnal phloem inflow rates are lower than xylem inflows, and their patterns more variable among years. However, phloem inflow is more constant and less dependent on temperature changes within a given season. Appreciable rates of phloem unloading during the central hours of the day and the early afternoon are, however, common to all the studies. These flows are observed especially when fruit shrink or decrease their growth rate, which is also the time when fruit show the lowest water potential, as reported by McFadyen et al., (1996). The transpiration loss, lowering fruit osmotic potential and turgor pressure with the likely formation of a pressure gradient between phloem and sink tissues, should favour passive phloem unloading. Therefore, for bulk flow phloem unloading, diurnal shrinkage may be a necessary step to allow dry matter accumulation in the fruit. Carbohydrates imported daily from the phloem into the fruit symplast can play a role alongside the other turgor-controlling mechanisms in reducing water potential, with the result that an amount of water exceeding that lost by transpiration can enter the fruit from the xylem.

Phloem dry matter contents calculated in the two stages are quite similar (~16.3% and 16.4%, respectively) in the present studies. These concentrations match data reported by Escobar-Gutierrez et al., (1995), who found seedling phloem concentrations of 14%. Values between 9% and 17% were adopted for fruit on medium cropped trees in the peach model developed by Fishman and Génard (1998). Furthermore, phloem concentrations around 17% have been reported for various plant species. (Van Bel, 1993; Ruan and Patrick, 1995). Close agreement between the calculated phloem concentration and independent data reported by other authors provides support for the present method of studying the relative contributions of phloem, xylem, and transpiration to fruit growth.

The present data suggest that transpiration, responding to environmental conditions, lowers fruit water content and thus water potential, via a loss of turgor and an increase in solute concentration (Jones and Higgs, 1982; Berger and Selles, 1993; McFadyen et al., 1996). This favours both xylem and phloem flows to the fruit (Lang and Thorpe, 1986; Minchin and Thorpe, 1987; Patrick, 1990, 1997; Minchin et al., 1996). Xylem inflow, in response to cuticle water losses, delivers water at rates high enough to support fruit enlargement. Phloem flows fit the hypothesis of transpiration lowering fruit water potentials; passive unloading can then be considered the main driver of fruit growth, without excluding active mechanisms, which have been reported for stage I, but not for stage III (Vizzotto et al., 1996).

Fruit growth mechanisms in peach are based on large quantities of water moving from tree to fruit and from fruit to atmosphere. This rather massive water exchange is central to the strategy developed by this species to accumulate fresh matter passively, yet in quantities larger than apple, on a whole fruit basis (DeJong and Goudriaan, 1989; Lakso et al., 1995). The main features of this strategy are the high permeability of the fruit epidermis and the full functionality of the xylem until harvest.

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