

## Source and sink limitations in vascular flows in peach fruit

By B. MORANDI\* and L. CORELLI GRAPPADELLI

Dipartimento Colture Arboree, University of Bologna, Via Fanin 46, 40127 Bologna, Italy

(e-mail: bmorandi@agrsci.unibo.it)

(Accepted 6 September 2009)

### SUMMARY

The daily patterns of vascular and transpiration flows to and from peach fruit were compared between heavily-thinned (LCL) and unthinned (HCL) trees, in order to assess when these flows were limited by resource availability (source-limited) or by the genetic potential of the fruit (sink-limited) during the day. Minute variations in fruit growth and in phloem, xylem, and transpiration flows were determined at cell division (stage I) and at cell expansion (stage III) during fruit development on several fruit per treatment, using highly sensitive fruit gauges. During cell expansion, the thinning treatments were also compared for their effects on fruit water potential. At stage I, no difference between treatments was found in any of the flows, suggesting that fresh matter (FM) import from phloem and xylem is sink-limited during early fruit development. At stage III, HCL fruit were smaller and had higher specific transpiration rates during the day. Xylem flow did not show any source limitations due to high crop load. However, it was “sink-strengthened” in the afternoon, in HCL, as these fruit reached lower water potentials during the day. Phloem flow to HCL fruit was source-limited during the afternoon, and at night, due to fruit-to-fruit competition. However, HCL fruit appeared to take advantage of their lower water potential at midday, when they showed higher rates of phloem flow. Although daily growth in HCL fruit undergoes periods of source limitation, this study showed how, at certain times of day, fruit may be more active sinks in attracting resources in high cropping conditions than at low crop loads.

Water, carbohydrates, and mineral elements represent the main resources required for fruit growth. They reach the fruit *via* phloem and xylem flows and determine the accumulation of fresh matter (FM) and dry matter (DM) in fruit tissues. Vascular flows respond to hydrostatic pressure gradients along the vascular path (Minchin and Thorpe, 1987; Minchin *et al.*, 1996), whereas phloem unloading to the fruit may occur through passive or active mechanisms, depending on whether assimilate transport to sink cells occurs due to water potential gradients or to specific carbohydrate transporters, respectively (Patrick, 1990; 1997; Lalonde *et al.*, 2003). Water may also leave the fruit by epidermal transpiration and/or xylem backflow from the fruit to the leaves. When these outflows exceed FM imports, the fruits shrink, as often occurs in many species such as apple (Lang, 1990), peach (Huguet *et al.*, 1998; Morandi *et al.*, 2007a), and tomato.

Peach fruit growth is characterised by having large quantities of water move from tree to fruit, and from fruit to atmosphere. This is due to increasing epidermal permeability and xylem functioning during the season (Morandi *et al.*, 2007a). At stage III, fruit water losses appear to be important in peach growth, as they induce a decrease in midday fruit water potential (McFadyen *et al.*, 1996), thus facilitating possible passive phloem unloading, according to the Münch law of translocation (Patrick, 1997). Also, at stage III, xylem import to the fruit tends to occur with low values during the morning and can not balance the high transpirational water losses, causing the fruit to shrink (Morandi *et al.*, 2007a), increasing their osmotic concentration, and decreasing their turgor pressure (McFadyen *et al.*, 1996). Subsequently, xylem flow increases during the afternoon

and at night, thus causing increases in fruit volume. The proper functioning of this mechanism may depend on resource availability, environmental conditions, and genetic background, and is fundamental to peach fruit development.

Fruit growth has been defined as “source-limited” when it is reduced by a lack of resources, and as “sink-limited” when it is limited by the genetic background of the fruit (Wareing and Patrick, 1975; Patrick, 1988). Crop load strongly affects resource availability, as the source organs may not be able to supply sufficient resources to all growing sinks (Pavel and Dejong, 1993; Grossman and Dejong, 1995). Assuming there was no source limitation for fruit on heavily-thinned trees, Pavel and Dejong (1993) found that, in high cropping trees, the DM gain in fruit was source-limited during stages I and III, and sink-limited during stage II. Furthermore, several studies have reported negative effects of crop load on leaf, stem, and fruit water potentials (Naor *et al.*, 1999; 2001; McFadyen *et al.*, 1996), with possible changes in hydrostatic pressure gradients along the vascular path. This would affect vascular flows to and from fruit on both a seasonal and a daily scale, but little is known about how phloem and xylem flows respond to water and carbon limitations due to high cropping levels.

This study shows how inter-fruit competition, generated by different levels of thinning, affected daily patterns of phloem, xylem, and transpiration flows to and from peach fruit at stage I and stage III of fruit development.

### MATERIALS AND METHODS

#### *Plant material and treatments*

This study was conducted in 2007 at the Experimental Farm of the University of Bologna, Cadriano, Bologna,

\*Author for correspondence.

Italy. All trials were carried out on the mid-season nectarine (*Prunus persica*) cultivar ‘Red Gold’, trained as an open-vase at a density of 545 trees ha<sup>-1</sup>. Standard cultural practices were applied for pruning, fertilisation, and irrigation. At 30 d after full bloom (DAFB), eight trees were selected and two levels of crop load were established, each on four trees, by applying heavy hand-thinning, leaving one fruit per shoot (the low crop load treatment; LCL), or leaving the trees unthinned (the high crop load treatment; HCL). Temperatures and relative humidities were available from a weather station (A840 Base Station; Adcon Telemetry GmbH, Klosterneuburg, Austria) located on the farm. Weather data were collected at 15 min intervals throughout the experiment, and vapour pressure deficits (VPD) were calculated.

#### Relative growth rate of fruit

Seasonal patterns in fruit diameter were monitored at regular intervals throughout the season. The maximum and minimum transverse diameters of 15 randomly-chosen fruit per treatment were measured using callipers, from 30 DAFB (18 April 2007) until 1 week before harvest (22 July 2007). These size data for each fruit were averaged and converted to fresh weight (FW) using a cultivar-specific conversion equation (Morandi *et al.*, 2007a). Daily relative growth rates (RGR<sub>t</sub>; in g g<sup>-1</sup> d<sup>-1</sup>) at each recording time (t) were calculated using the following equation:

$$RGR_{t_1} = (FW_{t_1} - FW_{t_0}) / (t_1 - t_0) \times FW_{t_0}$$

where  $FW_{t_1}$  and  $FW_{t_0}$  were the fruit FW (g) calculated on a given recording date ( $t_1$ ) and on the day before ( $t_0$ ), respectively.

#### Phloem, xylem, and transpiration flows

Fruit growth, phloem inflow, xylem inflow or outflow, and transpiration outflow were determined over 24 h according to Lang (1990). Continuous and precise monitoring of variations in fruit diameter over time were performed using custom-built gauges (Morandi *et al.*, 2007b), linked to a CR1000 data-logger (Campbell Scientific Ltd., Shepshed, UK) taking readings every 15 min.

Variations in fruit diameter over time were monitored at stage I and at stage III of fruit development on six and five fruit per crop load treatment, respectively. Each fruit was subjected to the following progressive sequence of different conditions: “intact” (with all normal vascular connections), “girdled” (with phloem connections severed), and “detached” (with all vascular connections severed). In “detached” fruit the surface of the peduncle was covered with hot-melt glue, to avoid any water loss and the fruit were hung in their original position using thin wires. From these data, phloem, xylem and transpiration flows to and from the fruit could be computed following Lang (1990).

Representative, well-exposed fruit on the east side of the row were measured. Measurements were performed a few days after thinning, between 35 and 43 DAFB, at stage I, and between 91 and 99 DAFB, at the beginning of stage III. At stage I, eight fruit per crop load treatment (16 fruit in total) were monitored simultaneously: six

were monitored for 1 – 2 d in each of the “intact”, “girdled”, and “detached” conditions, while the two fruit remaining were left intact and served as controls. At stage III, the experiment was repeated with five fruit per crop load treatment monitored simultaneously, four fruit were used for flow determinations and one was used as a control. At this stage, a second set of measurements was taken immediately after the conclusion of the first.

According to Lang (1990), the daily contribution of the phloem could be calculated as the difference in diameter changes between normal and girdled fruit. The same could be done for the xylem by subtracting the diameter changes of “detached” fruit from those of the “girdled” fruit. Only those data collected on clear and sunny days were used for analysis.

The fruit diameter data were converted to FWs, and growth, phloem, and xylem transport and transpiration rates min<sup>-1</sup> were calculated for each fruit over 24 h, and expressed as FW changes per g fruit FW (g g<sup>-1</sup>) to allow comparisons between different stages and crop loads. For each fruit, the data were averaged on an hourly basis, and the treatments were separated by Student’s *t*-test.

#### Fruit water potential

The daily pattern of fruit water potential was monitored at 97 DAFB. Measurements were performed at 05.00 h, 10.00 h, 13.00 h, 16.00 h, 19.30 h, and 23.30 h on four fruit per treatment, using a Scholander pressure chamber (Scholander *et al.*, 1964). All fruit were removed with approx. 50 mm of woody stem attached. The cut surface at one side of the stem was covered immediately with hot-melt glue, whereas the other side was used for measurements in the pressure chamber. Means ( $\pm$  SE) were computed for each recording time and the treatments were compared by Student’s *t*-test.

## RESULTS

#### Relative growth rates of fruit

For both treatments (LCL/HCL), the RGR of fruit was high during stage I of growth and decreased sharply until approx. 60 DAFB. After this time, RGRs remained almost constant, at low values, until harvest. No differences in

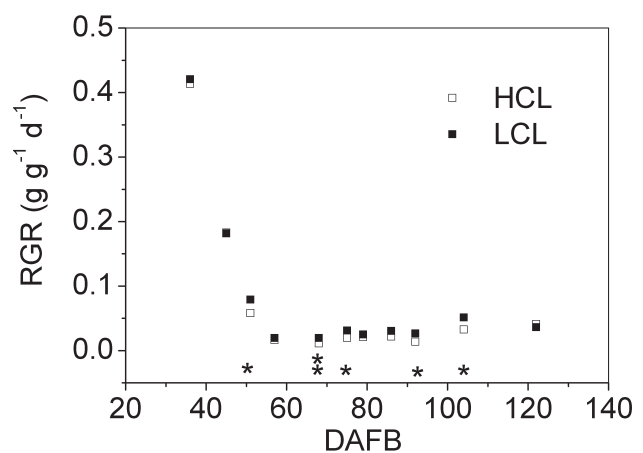


FIG. 1  
Seasonal patterns in the relative growth rates (RGR; g g<sup>-1</sup> d<sup>-1</sup>) of fruit in the LCL (closed symbols) and HCL (open symbols) treatments. Each datum point represents the mean value of 15 fruit. At each time point (days after full bloom; DAFB), treatments were compared by Student’s *t*-test. \*,  $P \leq 0.05$ , \*\*,  $P \leq 0.001$ .

TABLE I

Daily RGR, and transpiration, phloem and xylem flow rates per unit fruit FW ( $\text{g g}^{-1} \text{d}^{-1}$ ) for HCL (high crop load) and LCL (low crop load) peach fruit at stage I

Treatment	RGR ( $\text{g g}^{-1} \text{d}^{-1}$ )	Transpiration rate ( $\text{g g}^{-1} \text{d}^{-1}$ )	Phloem flow rate ( $\text{g g}^{-1} \text{d}^{-1}$ )	Xylem flow rate ( $\text{g g}^{-1} \text{d}^{-1}$ )
LCL	$0.158 \pm 0.054$	$-0.814 \pm 0.248$	$0.114 \pm 0.049$	$0.858 \pm 0.259$
HCL	$0.161 \pm 0.038$	$-0.822 \pm 0.210$	$0.117 \pm 0.033$	$0.867 \pm 0.215$
<i>P</i>	ns <sup>1</sup>	ns	ns	ns

<sup>1</sup>Treatments were compared by Student's *t*-test. ns, not significant. All values are means ( $\pm$ SE). *n* = 6.

RGR were recorded between treatments until 51 DAFB (stage I), when LCL fruit started to show higher RGR values than HCL fruit. Similarly, LCL fruit showed higher RGR values at 75 and 79 DAFB during stage II, and at 92 and 114 DAFB, during stage III (Figure 1).

#### Phloem, xylem and transpiration flows in Stage I

**Daily mass balance:** At 35 DAFB, measurements were performed on fruit that were, on average  $13.5 \pm 1.4$  or  $14.2 \pm 1.4$  mm in diameter and weighted  $2.35 \pm 0.53$  or  $2.79 \pm 0.65$  g for the HCL and LCL treatments, respectively. Both LCL and HCL fruit showed similar daily RGR values, vascular flows, and transpirational losses (Table I). The phloem and xylem accounted for 12% and 88% of the daily total inflow, respectively; while 87% of the water imported was lost by transpiration. A similar pattern was shown for daily growth, vascular and transpiration flows at the whole fruit level, with no differences recorded between the HCL and LCL treatments (Table I; Table II).

**Daily patterns of fruit RGR, phloem, xylem and transpiration flows:** The daily pattern of fruit RGR was similar for both the LCL and HCL treatments, with fruit growing at a constant rate of  $0.1 \text{ mg g}^{-1} \text{ min}^{-1}$  from 00.00 h to 15.00 h. After this time, the RGRs of fruit increased, reaching a maximum of  $0.2 \text{ mg g}^{-1} \text{ min}^{-1}$  at approx. 20.00 h, then decreasing to their initial value (Figure 2A).

Fruit transpiration rates followed the VPD with  $R^2$  values  $\geq 0.99$  for both treatments (data not shown). Fruit transpiration increased after 05.00 h, reaching a maximum of approx.  $1.75 \text{ mg g}^{-1} \text{ min}^{-1}$  after 12.00 h and decreasing thereafter (Figure 2B). The rate of phloem inflow increased from 00.00 h to approx. 18.00 h, reaching a maximum of approx.  $0.15 \text{ mg g}^{-1} \text{ min}^{-1}$ , then decreasing again to approx.  $0.05 \text{ mg g}^{-1} \text{ min}^{-1}$  until 00.00 h (Figure 2C). In both treatments, xylem inflow mirrored the transpiration flow, with a direct linear relationship between these two parameters ( $R^2 > 0.99$  in both treatments; Figure 2D). No diurnal differences in transpiration, xylem and phloem flows were found between treatments.

#### Phloem, xylem and transpiration flows in Stage III

**Daily mass balance:** At 91 DAFB, average fruit FWs ( $\pm$  SE) were  $103 \pm 8$ , and  $57 \pm 4$  g for LCL and HCL fruit, respectively. Daily growth rates in LCL fruit were two-and-three times higher than in HCL fruit, when expressed on a per unit of fruit, or on a whole fruit basis, respectively (Table III; Table IV). Phloem and xylem accounted for 20% and 80% of the total daily inflows, respectively; while 82% of the water was lost by transpiration in HCL fruit. In LCL fruit, transpiration

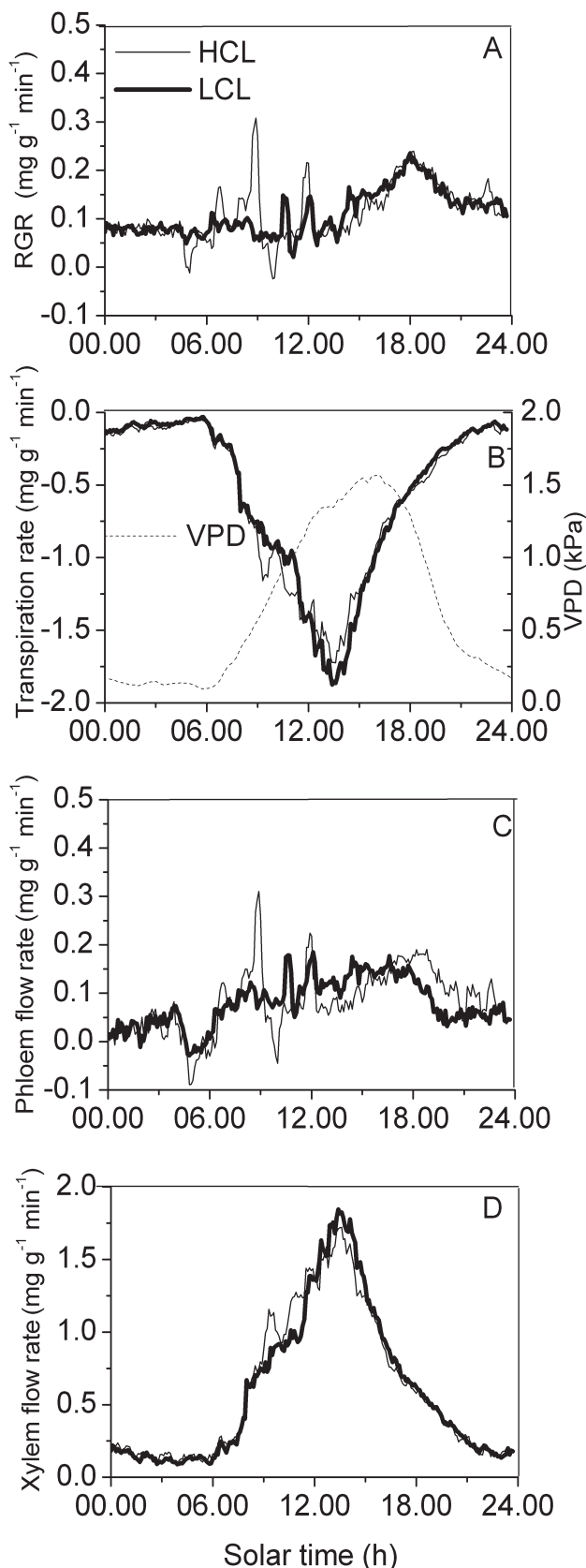


FIG. 2 Diurnal patterns in mean relative growth rates (RGR; Panel A), transpiration flow rates (Panel B), phloem flow rates (Panel C), and xylem flow rates (Panel D) (all in  $\text{mg g}^{-1} \text{ min}^{-1}$ ) for LCL (bold lines) and HCL (normal lines) peach fruit at 35–43 DAFB (stage I). The average vapour pressure deficit (VPD; kPa; dashed line) for the period considered is shown in Panel B. Treatments were compared by Student's *t*-test each hour and no significant differences appeared between treatments.

TABLE II

Daily RGR, and transpiration, phloem and xylem flow rates ( $\text{g fruit}^{-1} \text{d}^{-1}$ ) for HCL (high crop load) and LCL (low crop load) peach fruit at stage I

Treatment	RGR ( $\text{g fruit}^{-1} \text{d}^{-1}$ )	Transpiration rate ( $\text{g fruit}^{-1} \text{d}^{-1}$ )	Phloem flow rate ( $\text{g fruit}^{-1} \text{d}^{-1}$ )	Xylem flow rate ( $\text{g fruit}^{-1} \text{d}^{-1}$ )
LCL	$0.285 \pm 0.060$	$-1.390 \pm 0.120$	$0.209 \pm 0.047$	$1.467 \pm 0.133$
HCL	$0.284 \pm 0.058$	$-1.385 \pm 0.076$	$0.193 \pm 0.059$	$1.476 \pm 0.008$
<i>P</i>	ns <sup>1</sup>	ns	ns	ns

<sup>1</sup>Treatments were compared by student's *t*-test. ns, not significant. All values are means ( $\pm$ SE). *n* = 6.

losses were 60% of the daily total inflow, while phloem and xylem flows accounted for 32% and 68%, respectively (Table III; Table IV). No differences were found between treatments for the vascular and transpiration flows per unit fruit FW (Table III); however, LCL fruit had a higher daily phloem flow at the whole fruit level (Table IV).

**Daily patterns of fruit RGR, phloem, xylem and transpiration flows:** Daily patterns of fruit RGR were similar in HCL and LCL trees. Fruit shrank in the morning and grew during the afternoon and at night. However, LCL fruit maintained higher RGRs during the whole day, especially during the late afternoon and at night (Figure 3A).

In both treatments, specific transpiration rates were positively related to VPD, with *R*<sup>2</sup> values of 0.64 and 0.88 for LCL and HCL fruit, respectively. Water losses increased in the morning, and reached their maximum at around 15.00 h, then decreased in the evening and remained low during the night (Figure 3B). Differences between the LCL and HCL treatments appeared during the morning and late afternoon, when the smaller HCL fruit maintained higher specific transpiration rates (Figure 3B). Xylem flow per unit fruit FW was low during the morning in both treatments. It increased during the afternoon, and reached a maximum between 18.00 – 20.00 h. At this time, the xylem flow to HCL fruit was > 50% higher than to LCL fruit, and maintained a significant difference until 23.00 h (Figure 3D).

During the day, phloem flow was lower than xylem flow in both treatments. HCL and LCL fruit maintained low phloem flows during the night and the early morning; thereafter HCL fruit showed a midday peak in phloem flow, with statistically higher values than LCL fruit. After 12.00 h, the phloem flow to HCL fruit remained constant, at approx.  $0.03 \text{ mg g}^{-1} \text{ min}^{-1}$ , until 18.00 h, then it decreased to almost zero (which was significantly lower than in LCL fruit) for the rest of the day and at night. Phloem flow to LCL fruit increased in the afternoon, reached a maximum of approx.  $0.04 \text{ mg g}^{-1} \text{ min}^{-1}$  in the evening, and maintained these high rates until the end of the day (Figure 3C).

TABLE III

Daily RGR, and transpiration, phloem and xylem flow rates per unit fruit FW ( $\text{g g}^{-1} \text{d}^{-1}$ ) for HCL (high crop load) and LCL (low crop load) peach fruit at stage III

Treatment	RGR ( $\text{g g}^{-1} \text{d}^{-1}$ )	Transpiration rate ( $\text{g g}^{-1} \text{d}^{-1}$ )	Phloem flow rate ( $\text{g g}^{-1} \text{d}^{-1}$ )	Xylem flow rate ( $\text{g g}^{-1} \text{d}^{-1}$ )
LCL	$0.036 \pm 0.005$	$-0.053 \pm 0.012$	$0.029 \pm 0.005$	$0.060 \pm 0.012$
HCL	$0.018 \pm 0.003$	$-0.083 \pm 0.011$	$0.020 \pm 0.004$	$0.081 \pm 0.013$
<i>P</i>	0.007 <sup>1</sup>	ns	ns	ns

<sup>1</sup>Treatments were compared by Student's *t*-test. ns, not significant. All values are means ( $\pm$ SE). *n* = 5.

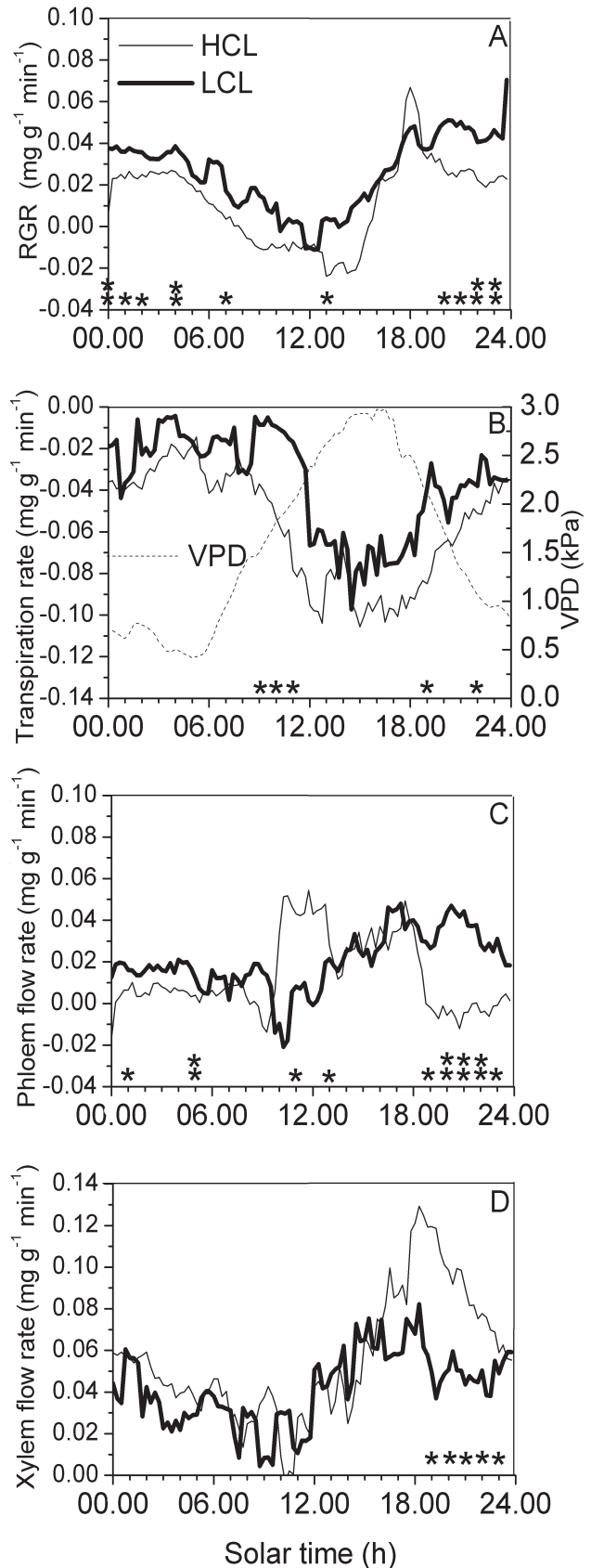


FIG. 3

Diurnal patterns in mean relative growth rates (Panel A), transpiration flow rates (Panel B), phloem flow rates (Panel C), and xylem flow rates (Panel D) (all in  $\text{mg g}^{-1} \text{min}^{-1}$ ) for LCL (bold lines) and HCL (normal lines) peach fruit at 91 – 99 DAFB (stage III). The average VPD (kPa; dashed line) for the period considered is shown in Panel B. Treatments were compared by Student's *t*-test each hour. Those means marked with asterisks were significantly different at  $P \leq 0.05$  (\*), or  $P \leq 0.001$  (\*\*).

TABLE IV

Daily RGR, and transpiration, phloem and xylem flow rates ( $\text{g fruit}^{-1} \text{d}^{-1}$ ) for HCL (high crop load) and LCL (low crop load) peach fruit at stage III

Treatment	RGR ( $\text{g fruit}^{-1} \text{d}^{-1}$ )	Transpiration rate ( $\text{g fruit}^{-1} \text{d}^{-1}$ )	Phloem flow rate ( $\text{g fruit}^{-1} \text{d}^{-1}$ )	Xylem flow rate ( $\text{g fruit}^{-1} \text{d}^{-1}$ )
LCL	$3.49 \pm 0.60$	$-4.95 \pm 1.12$	$2.87 \pm 0.66$	$5.57 \pm 1.06$
HCL	$1.02 \pm 0.20$	$-4.76 \pm 0.87$	$1.07 \pm 0.07$	$4.71 \pm 0.98$
<i>P</i>	0.004 <sup>1</sup>	ns	0.03	ns

<sup>1</sup>Treatments were compared by Student's *t*-test. ns, not significant. All values are means ( $\pm$ SE). *n* = 5.

### Fruit water potential

Both treatments showed a similar daily pattern of fruit water potential (FWP). FWP decreased after 05.00 h, showed the most negative values around 12.00 h, increased during the afternoon, and reached its highest daily values during the evening, and at night. However, from 10.00 – 06.00 h, HCL fruit maintained significantly lower FWPs than LCL fruit (Figure 4).

## DISCUSSION

### Stage I fruit

By assuming there was no source limitation in heavily-thinned (LCL) trees, Pavel and Dejong (1993) defined the cell division and cell expansion stages as periods of source-limited growth for peach fruit on high cropping (HCL) trees. Our results did not show any source limitation on fruit growth rates or vascular flows during the earliest stages of fruit development (35 - 45 DAFB) on a daily (Table I; Table II) or on an hourly (Figure 2) basis. However, limitations in the RGRs of HCL fruit appeared later, starting from 60 DAFB, when the fruit were towards the end of stage I (Figure 1). This may indicate that our flow measurements were conducted too early to detect any crop load effects on phloem and xylem flows during stage I.

During the day, fruit transpiration rate was driven by VPD and followed similar patterns in both LCL and HCL fruit. In both treatments, xylem flow mirrored fruit transpiration, as if the higher the rate of water loss, the greater the space for new xylem import to the fruit (Figure 2B, D). This direct and simultaneous response of the xylem to losses by transpiration suggests that, under our conditions, even in the HCL trees, water did not limit fruit growth at stage I and that the small fruit at this stage offered low resistance along the water pathway from stem to atmosphere. It is likely that the volume of water required by fruit at stage I is low and does not significantly affect the water balance of the tree, even in the presence of many fruit. It is also possible that more water was available to the tree at stage I of fruit growth, as leaf transpiration was certainly lower in the earlier, cooler part of the growing season. Phloem flow increased during the day, with no differences between LCL or HCL treatments (Figure 2C) and maximum values were reached at 18.00 h, after several hours of photosynthesis had elapsed.

### Stage III fruit

At cell expansion, inter-fruit competition determined the source limitations on fruit growth, with a lower daily RGR in HCL than in LCL trees (Table III). On a hourly scale, this difference appeared during the evening and at night, when fruit growth rates are usually higher in peach

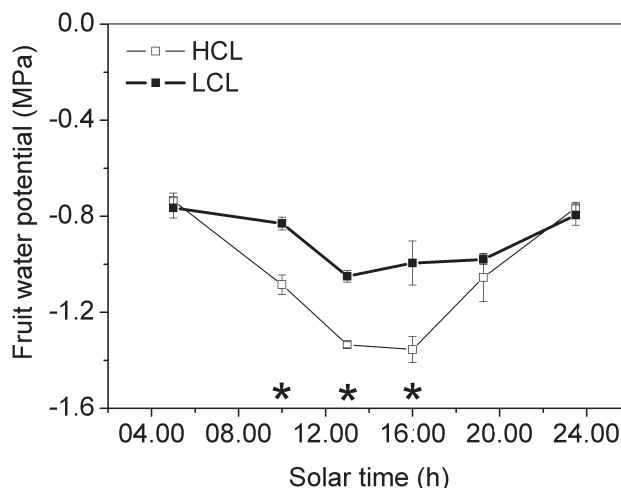


FIG. 4

Diurnal patterns in fruit water potential ( $\pm$  SE) in LCL (closed symbols and bold line) or HCL (open symbols and normal line) peach tree treatments. Each point is the average of four fruit. At each measurement, treatments were compared by Student's *t*-test. Those measurements marked with asterisks were significantly different at  $P \leq 0.05$  (\*).

(Morandi *et al.*, 2007a; Figure 3A). The daily patterns of transpiration, as well as phloem and xylem flows, can provide an explanation for such an influence of crop load on fruit RGR.

During the day, transpiration rate followed the VPD in both treatments; however, HCL fruit showed higher values than LCL fruit during the morning and late afternoon (Figure 3B). These differences were due to the higher surface-to-volume ratio of the smaller HCL fruit, and affected fruit water potential. Data collected from the same trees showed a negative relationship between fruit water losses and fruit water potential during the day (Morandi *et al.*, in press). As the smaller HCL fruit lost larger amounts of water at midday, their water potential reached more negative values than in LCL fruit (Figure 4), and increased their potential strength to import fresh matter *via* xylem and phloem flows.

During the day, the xylem flow to HCL fruit was never lower than in LCL fruit (Figure 3D), indicating that inter-fruit competition for water did not cause the "source limitation" for this flow. This lack of any difference between treatments might be due to the higher transpiration rates, and thus lower water potentials, of HCL fruit during the day. However, tree water availability may also be negatively affected by crop load, as reported by Naor *et al.* (1999; 2001) and by Matthews and Shackel (2005), who found lower midday stem water potentials in high-cropping peach trees. This effect of crop load on midday fruit and stem water potentials may ultimately reduce the difference between treatments in the resulting stem-to-fruit water potential gradient, and thus in xylem flow. In the morning, the xylem flow remained low for both treatments (Figure 3D). At this time, leaf transpiration increases quickly, with attendant reductions in leaf water potential (McFadyen *et al.*, 1996). This probably causes both HCL and LCL fruit to loose in the competition with leaves for water. Regardless of crop level, the morning xylem flow to peach fruit may thus be considered "source limited" (i.e., limited by water availability at the whole tree level). Later in the day, as leaf and stem water potentials rise

(Morandi *et al.*, in press), HCL fruit showed higher xylem flows. In the afternoon, the HCL fruit water potential was probably lowered by the assimilates unloaded in the preceding hours (Figure 4), as suggested by the midday peak in phloem flow to HCL fruit (Figure 3C). When leaves reduce their demand for water, more is available at the whole tree level and thus the xylem flow increased to both HCL and LCL fruit, although to lower values in the latter (Figure 3D). As LCL fruit did not reach such negative water potential values as those reached by HCL fruit (Figure 4), their xylem flow could be considered to be “sink-limited” in the afternoon. Conversely, we could define the afternoon xylem flow to HCL fruit as “sink-strengthened”.

The daily phloem flow in peach is generally lower than the xylem flow and contributes to fruit growth mainly around midday and in the afternoon (Morandi *et al.*, 2007a). Due to the lower absolute values of this parameter, any background noise in its measurement may affect its determination; therefore, occasional negative values should be ignored.

After 09.00 h, phloem flow to HCL fruit increased rapidly and reached a peak at midday (Figure 3C), following the decreasing (and lower overall) fruit water potential of these fruit that created the conditions for passive phloem unloading. Therefore, the midday phloem flow can be defined as “sink-strengthened” in HCL fruit, whereas in LCL fruit it appears to be “sink-limited”, as these fruit did not reach such negative water potentials (Figure 4) and accordingly show lower phloem imports. Later in the day, the phloem flow to HCL fruit decreased to values close to zero (Figure 3C), probably because of their sharp rehydration in the afternoon following the large xylem inflows which returned their water potential values back to those in LCL fruit (Figure 4). The availability of carbohydrates in LCL trees should be higher than in HCL trees, due to a lower inter-fruit competition for assimilates (Fishman and Génard, 1998). Therefore, in the late afternoon, at the end of the daily period of photosynthesis, LCL fruit maintained higher phloem flows (Figure 3C) while, for the same reason,

HCL fruit experienced a “source-limitation” which lasted through the night. This had a negative effect on the amount of FM received each day by HCL fruit, which was also shown as a negative daily balance between the water imported by the xylem and that lost by transpiration on a per unit of fruit basis and on a whole fruit basis (Table III; Table IV). The combination of these effects determined the difference in relative and absolute growth rates between treatments at stage III.

## CONCLUSIONS

Assuming there was no assimilate or water limitation for fruit growth on LCL trees, this work indicates when phloem, xylem or transpiration flows to or from peach fruit are source- or sink-limited during the day, and shows how such flows may even be “sink-strengthened” in some cases.

Early in the growing season, the import of FM *via* the phloem and xylem appears to be sink-limited throughout the day, with no difference in fruit RGR values between crop load treatments. In contrast, by stage III, phloem flow and fruit growth rates experienced periods of source limitation due to inter-fruit competition; however, at some times during the day, HCL fruit were able to “sink-strengthen” their phloem and xylem flows, due to their higher transpiration rate and lower water potential. These results suggest that, under high competition conditions, HCL fruit may have developed strategies to increase their activity as sinks, thus improving their ability to compete for resources.

This work was supported by the ISAFRUIT Project funded by the European Commission under Thematic Priority 5 – Food Quality and Safety of the 6th Framework Programme of RTD (Contract No. FP6-FOOD-CT-2006-016279).

Disclaimer: Opinions expressed in this publication may not be regarded as stating an official position of the European Commission.

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