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Leaf gas exchanges and water relations affect the daily patterns of fruit growth and vascular flows in Abbé Fétel pear *(Pyrus communis* L.) trees

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ABSTRACT

Daily patterns of leaf and stem water potentials, leaf gas exchanges (net photosynthesis, stomatal conductance and transpiration), fruit growth, vascular (phloem and xylem) and transpiration in/outflows were determined in two subsequent years at regular time intervals during the season on pear trees of the cv. Abbé Fétel. Leaf gas exchanges showed higher values in the morning, while fruit shrank due to high transpiration water losses which were not balanced by xylem flows. Despite the high rates of transpiration, fruit were fully rehydrated in the afternoon thanks to high xylem flows, while phloem import occurred mostly in the midday hours. During most of the season, fruit growth was sustained above all by the xylem flux which represented upto 85% of fruit total inflows. Later, fruit growth rate decreased while dry matter accumulation increased following a rise in the phloem relative contribution to growth, which reached 50% of fruit total inflows. This is the first report to show how the biophysical mechanism of fruit growth in “Abbé Fétel” pear is based on high water exchanges by xylem and transpiration during most of the season. The simultaneous monitoring of leaf gas exchanges and fruit vascular flows during the day suggests how until about 95 days after full bloom (DAFB), leaves are stronger “sinks” for water in the morning while fruit import water mainly during the afternoon, thanks to the increase in leaf water potential following stomatal closure.

1. Introduction

Fruit quality and size depend on a large number of environmental, biophysical and biochemical factors leading to water and dry matter accumulation in fruit sinks. Canopy gas exchanges, carbohydrate translocation and partitioning and phloem unloading are just some steps in the complex network of interactive processes that leads to fruit growth.

Seasonal and circadian changes in the environmental conditions (photosynthetic photon flux density (PPFD), leaf-to-air vapour pressure deficit (VPD), etc.) highly impact on leaf functioning in terms of carbon assimilation and water use, which are known to follow daily patterns. On sunny days, canopy carbon assimilation rises quickly in the morning, reaching a maximum before midday, while it decreases in the afternoon due to partial stomatal closure (Giuliani et al., 1997); leaf transpiration instead remains high during the afternoon thanks to the high VPDs which are usually detected at this time of the day (Giuliani et al., 1997; Zibordi et al., 2009; Losciale et al., 2010). Besides gas exchanges, tree water relations also respond to diurnal changes of environmental conditions: stem, leaf and fruit water potentials always show a decrease at noon with a recovery during afternoon and night hours (McFadyen et al., 1996; Morandi et al., 2010a). The water potential gradients among these organs are responsible for driving phloem and xylem flows in the tree vascular path (Münch, 1930); therefore, changes in leaf water potential can indirectly affect the transport of water and assimilates to the growing fruit. In fact, stem water potential, and thus the stem-to-fruit water potential gradient, is affected by changes in leaf water status, with possible effects on fruit vascular flows. Fruit growth results from the balance between incoming and outgoing fluxes of water and dry matter: xylem and phloem flows

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Abbreviations: AGR, Absolute growth rate; DAFB, days after full bloom; PPFD, photosynthetic photon flux density; RGR, relative growth rate; VPD, vapour pressure deficit.

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represent the main sources for water and carbon, while fruit outflows mainly occur due to epidermis transpiration, although xylem backflows from fruit to leaves can also withdraw water from the fruit tissue (Lang, 1990; Fishman and Génard, 1998). When the balance between fruit in- and out-flows is positive, fruit diameter and weight increase. When it is negative, fruit shrink and loose weight. The alternation of periods of positive and negative balance in fruit in- and out-flows, determine circadian swelling/shrinkage cycles that characterize daily fruit growth in many species (Berger and Selles, 1993).

Fruit growth depends on its capacity to attract xylem and phloem flows (Fishman and Génard, 1998). Among other factors, this is related to its ability to (i) keep low water potentials and (ii) put in place an efficient strategy of phloem unloading (Patrick, 1997; Lalonde et al., 2003). The latter may rely on symplasmic or apoplasmic mechanisms, depending on whether carbohydrate transport to the fruit occurs via the symplast, thanks to turgor pressure and/or concentration gradients, or via the apoplast, thanks to specific carbohydrate transporters (Patrick, 1990; Patrick, 1997; Lalonde et al., 2003). When fruit water potential equals or exceeds stem water potential, xylem and phloem flows to the fruit may be reduced, and xylem backflows from fruit to leaves may easily occur in presence of negative stem-to-fruit water potential gradients.

Fruit epidermis transpiration, which depends on fruit surface area, surface conductance and environmental conditions (Jones and Higgs, 1982; Lescourret et al., 2001; Li et al., 2002; Gibert et al., 2005), may represent a very effective tool to keep fruit water potential low, thus favouring phloem and xylem imports to the fruit tissue (Fishman and Génard, 1998).

However, as fruit species differ in fruit anatomical features (i.e. shape, size, surface conductance, and xylem conductivity), their physiological strategy to attract resources and grow will change. In apple and kiwifruit for example, surface conductance decreases during the season, and so do their water losses by transpiration (Jones and Higgs, 1982; Hallett and Sutherland, 2005; Montanaro et al., 2006). During the later stages of fruit development, this condition may keep fruit pressure potential relatively high with a subsequent reduction of fruit xylem import, which can also be caused by the presence of anatomical disruptions in the fruit xylem vessels determining significant increases in the fruit hydraulic resistance (Lang, 1990; Drazeta et al., 2001; 2004; Dichio et al., 2003; Clearwater et al., 2012; Mazzeo et al., 2013). Furthermore, low fruit water exchanges towards the atmosphere may imply a difficulty in maintaining the necessary hydrostatic pressure gradients for passive phloem unloading to occur (Minchin and Thorpe, 1987; Patrick, 1990; 1997), so that carbohydrate transport into the fruit must be mediated by specific carbohydrate transporters (Patrick, 1997).

During the first stages of growth, kiwifruit berries and apple show instead higher transpiration and xylem flows thanks to their higher surface conductance and xylem functionality (Lang, 1990; Morandi et al., 2010a). This is similar to peach, whose fruit show high water exchanges (by transpiration and xylem fluxes) during the cell expansion stage and seem to exploit the daily decrease in fruit pressure potential for some passive phloem unloading to occur (Morandi et al., 2007a). Indeed, peach fruit whose transpiration was reduced by bagging showed decreased phloem daily imports and growth (Morandi et al., 2010b).

Pear is a pome fruit species where Zangh et al. (2013) have recently identified specific sucrose transporters in the fruit apoplast, which is normally related to active phloem unloading. This might lead to hypothesize that pear share the same mechanism of fruit growth as apple (which maintains active phloem unloading during the whole season) (Zhang et al., 2004), although until now this has not been elucidated, either on a seasonal or on a daily basis.

This paper investigates the biophysical mechanism adopted by pear fruit to expand its size and gain dry matter daily and reports how leaf performances and water relations affect these processes during the day.

2. Materials and methods

2.1. Plant material and experimental set up

This study was conducted during 2011 and 2012 at the “F.lli Navarra” Experimental Farm, close to Ferrara, Italy (44°51′33.0“N 11°39′22.4“E). Seven-year-old pear trees of the cv. Abbè Fétel grafted on Sydo quince were used. The trees were spaced 3.3 × 0.8 m, corresponding to a planting density of 3787 trees ha^{-1} and they were trained as central leaders. The orchard, North-South oriented, was managed according to standard cultural practices in terms of fertilization, thinning and pruning. Irrigation was scheduled according to the regional web-based platform ‘Irrinet’ (Consorzio per il Canale Emiliano Romagnolo – CER – www.irriframe.it). ‘Irrinet’ provides irrigation scheduling (based on the Penman–Monteith equation) which takes into account orchard-specific parameters (soil, training system, density, cultivar, rootstock, irrigation system, etc.) and meteorological data collected by weather stations located in the proximity of the orchard. Soil water content was monitored at 20, 40 and 60 cm depth using tensiometers; data for the three depths were then averaged.

Full bloom occurred on March 27th in 2011 and on April 1st in 2012, while fruit were harvested on September 1st, 158 days after full bloom (DAFB) in 2011 and on September 7th, 159 DAFB in 2012.

In 2011, leaf gas exchanges and leaf and stem water potentials were monitored on four periods during the season, at 20, 50, 95 and 145 DAFB. Fruit growth and the vascular and transpiration flows to/from the fruit were also monitored in all periods except at 20 DAFB. In 2012, the same parameters were measured at 40, 65 and 115 DAFB. During this year, a further measurement of gas exchanges was performed at about 130 DAFB.

2.2. Water relations

In both years, and at all dates of measurement, stem and leaf water potentials were monitored on four trees at about 10.00, 12.00 and 15.00 h using a Scholander (Soilmoisture Equipment Corp. Santa Barbara, U.S.A.) pressure chamber. Stem water potential was also measured pre-dawn.

Leaf water potential was measured on one well exposed leaf per tree (four leaves per treatment), covered by aluminum foil just before excision (Turner and Long, 1980). Stem water potential was measured on the same trees: one leaf per tree placed in the inner part of the canopy, very close to the trunk, was chosen and covered with aluminium foil at least 90 min prior to measurement to allow equilibration with the stem according to the methodology described by McCutchan and Shackel (1992) and by Naor et al. (1995).

For all times of measurements, stem-to-leaf water potential gradient was calculated as the difference between leaf and stem water potentials.

At 40 DAFB in 2012, fruit pressure potential was also measured on one fruit per tree at 10:00, 12:00 and 15:00 hours. Unfortunately, these measurements couldn’t be repeated on the following dates as, because of the curved, lignified petiole of this species, the fruit couldn’t fit in the chamber anymore.

With the Scholander technique, the pressure potential recorded on leaf and stem can be assumed to be equal to the water potential as the concentration of the xylem sap is almost null for these organs. On the contrary, fruit pressure potential may not coincide with its