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# Increasing water stress negatively affects pear fruit growth by reducing first its xylem and then its phloem inflow

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SUMMARY

Drought stress negatively affects many physiological parameters and determines lower yields and fruit size. This paper investigates on the effects of prolonged water restriction on leaf gas exchanges, water relations and fruit growth on a 24-h time-scale in order to understand how different physiological processes interact to each other to face increasing drought stress and affect pear productive performances during the season. The diurnal patterns of tree water relations, leaf gas exchanges, fruit growth, fruit vascular and transpiration flows were monitored at about 50, 95 and 145 days after full bloom (DAFB) on pear trees of the cv. Abbé Fétel, subjected to two irrigation regimes, corresponding to a water restitution of 100% and 25% of the estimated $Et_c$, respectively. Drought stress progressively increased during the season due to lower soil tensions and higher daily vapour pressure deficits (VPDs). Stem water potential was the first parameter to be negatively affected by stress and determined the simultaneous reduction of fruit xylem flow, which at 95 DAFB was reflected by a decrease in fruit daily growth. Leaf photosynthesis was reduced only from 95 DAFB on, but was not immediately reflected by a decrease in fruit phloem flow, which instead was reduced only at 145 DAFB. This work shows how water stress negatively affects pear fruit growth by reducing first its xylem and then its phloem inflow. This determines a progressive increase in the phloem relative contribution to growth, which lead to the typical higher dry matter percentages of stressed fruit.



## Introduction

It is well known how orchard performance in terms of yield and quality of production is related to water availability: trees subjected to prolonged water stress usually present smaller fruit and lower yields (Behboudian et al., 1994; Naor et al., 2001; Naor, 2001; Lopez et al., 2011) and, sometimes, higher quality traits, such as soluble solid contents (Lopez et al., 2011) and dry matter percentages.

Drought stress affects many biophysical, biochemical and molecular processes in the tree but it is difficult to have an overview of how they: (i) are related to each other, and (ii) integrate in modifying tree physiology and crop productivity. Long periods of drought may also induce anatomical modifications at various levels; for example, changes in leaf mesophyll structure have been found in olive and avocado trees subjected to water stress with consequent decreases in their gas exchanges (Chartzoulakis et al., 1999, 2002).

Depending on a wide range of species specific hydraulical features such as vessels size, density etc. (Fernandez et al., 2001; Dichio et al., 2013; Lo Gullo et al., 2003), the onset of drought conditions quickly modifies tree water relations by decreasing either leaf or/and stem water potentials (McCutchan and Shackel, 1992; Naor et al., 1995; Marsal et al., 2008). These changes can affect the water potential gradients between the various tree organs with consequences on xylem and phloem flows within the tree (Münch, 1930; Minchin and Thorpe, 1987).

At leaf level, ABA and other molecules are transported from the roots as signals to reduce stomatal conductance and prevent leaves from excessive water losses by transpiration (Davies and Zhang, 1991; Hare et al., 1997). This causes a decrease in the sub-stomatal

*Abbreviations:* AGRa, bsolute growth rate; DAFB, days after full bloom; RGR, relative growth rate; VPD, vapour pressure deficit.

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$CO_2$ concentration and a consequent reduction in leaf assimilation rates, although some species can improve their photosynthetic efficiency via osmotic adjustment.

Drought-induced changes in the vascular flows within the tree can readily affect also fruit development. In fact, fruit volume growth results from the balance among phloem, xylem and epidermis transpiration in/outflows (Fishman and Génard, 1998) and changes in this balance are readily reflected by fruit net growth (Greenspan et al., 1994). Fruit transpiration responds both to surface conductance and environmental conditions (i.e. air vapour pressure deficit) (Jones and Higgs, 1982). Fruit surface conductance can be modified depending on fruit development conditions (Aloni et al., 1998; Leonardi et al., 1999), although the effect of prolonged drought stress on this anatomical trait has not been documented yet. Fruit transpiration has been found to positively affect fruit quality in some species like kiwifruit (Montanaro et al., 2012; Clark and Smith, 1988) and peach (Morandi et al., 2010b), so that high seasonal vapour pressure deficits (VPDs) may be related to the development of positive quality traits in the fruit. This effect is attributed to the decreased cell turgor, which follows water losses by transpiration, and increases the fruit potential to attract xylem and phloem flows via hydrostatic pressure gradients (Münch, 1930; Minchin and Thorpe, 1987; Patrick, 1997). However, in some fruit species, like apple and kiwifruit, xylem conductivity is highly reduced during the season with a consequent stop in fruit xylem import (Dichio et al., 2003; Drazeta et al., 2001, 2004; Clearwater et al., 2012). Furthermore, as demonstrated by Mazzeo et al. (2013) in kiwifruit and by Choat et al. (2009) in grape berry, xylem fruit resistance can increase during the season, with consequent negative effects on fruit xylem inflows.

Phloem flow to the fruit is driven by hydrostatic pressure gradients in the vascular path (Minchin and Thorpe, 1987; Patrick, 1990, 1997) although carbohydrate unloading from the phloem may also depend on the activity of specific carbohydrate transporters (Patrick, 1997). Besides being affected by drought conditions, the mechanisms of fruit growth and the relative contribution of phloem and xylem flows can change depending on the species and on the phenological stage, as demonstrated from studies carried out in apple (Lang, 1990), kiwifruit (Morandi et al., 2010a; Clearwater et al., 2012), peach (Morandi et al., 2007a, 2010b), grape (Greenspan et al., 1994) and tomato (Ho et al., 1997; Guichard et al., 2005). It follows that these species may show different physiological responses to drought, although most of them end up with decreased fruit size and higher dry matter percentages at harvest (Naor et al., 1997; Miller et al., 1998). Besides, fruit growth rate also depends on carbon availability, which can be reduced because of the lower photosynthetic rates typical of drought stressed leaves (Teng et al., 1999). However, carbon partitioning among the different sink organs may change depending on sink priority: as this latter changes with species and phenological stage (Minchin et al., 1996), the application of drought stress at specific times during the season can modify carbon partitioning to vegetative or reproductive sinks and thus the source–sink ratio within the tree (Escobar-Gutierrez et al., 1998; Arndt et al., 2000; Dichio et al., 2007).

Although the daily mechanisms of pear fruit growth have not been documented yet, some papers report a negative effect of water stress either on pear fruit size and on tree water relations, with reduced leaf and stem water potentials, leaf turgor pressure and gas exchanges (Marsal and Girona, 1997; Naor et al., 2001; O'Connell and Goodwin, 2007; Sharma and Sharma, 2008). Among these parameters stem water potential appears to be the most sensitive to soil water conditions and it can be useful to detect upcoming stresses (McCutchan and Shackel, 1992; Naor et al., 1995). Besides, midday stem water potential during the season has been found to be positively related to final fruit weight in apple (Naor et al., 1997) and nectarine (Berman and Dejong, 1996; Naor et al., 1999) but the reasons of this relationship have not been fully documented yet. Pear carbon assimilation has been found to be reduced as well in response to stress (Behboudian et al., 1994, while this species does not appear to adopt osmotic adjustment mechanisms to increase its water use efficiency (Behboudian et al., 1994; Marsal and Girona, 1997).

Water is a limited resource and in some regions its availability for irrigation is becoming more and more critical. Pear is a species which is often cultivated in regions with high water deficits ($Et_0$—precipitations), where growers have difficulties in coping with water scarcity. Therefore, it is important to develop strategies to guarantee pear orchard productive performances and quality standards, even in conditions of limited water supply.

This work reports on the effects of prolonged water scarcity on pear water relations, leaf gas exchanges and on the biophysical mechanisms of fruit growth and focuses on how all these parameters interact daily in determining the decreases in yield and fruit size which are typical of trees subjected to drought stress.

## Materials and methods

### *Plant material and experimental set*

This work was carried out on eight pear trees of the cv. Abbè Fétel, grafted on Sydo and located at the "F.lli Navarra" Experiment Farm, close to Ferrara, Italy. Trees were spaced $3.3 \times 0.8$ m, with a density of 3787 trees $ha^{-1}$ and trained as slender spindle. The orchard was managed according to standard cultural practices in terms of fertilization, thinning and pruning.

Full bloom occurred on March 27th 2011 and fruit where harvest on September 1st, 158 days after full bloom (DAFB).

Starting about 40 DAFB, two irrigation regimes, corresponding to 100%, and 25% of the estimated evapo-transpiration ($Et_c$) were imposed, on four trees each, until harvest. Daily evapo-transpiration ($Et_c$) was obtained from the Irrinet irrigation scheduling system developed and made available over the Internet by the "Consorzio per il Canale Emiliano Romagnolo (CER)" of the Emilia-Romagna Region (www.irriframe.it). The environmental parameters needed by this software were collected by a weather station located near the orchard. For each treatment, soil water content was monitored 20, 40 and 60 cm depth using tensiometers; data for the three depths were then averaged.

In four periods during the season, corresponding to fruit-set (20 DAFB), cell division (50 DAFB), beginning (95 DAFB) and end (145 DAFB) of the cell expansion stages, respectively, leaf gas exchanges and stem water potentials were monitored during the day and compared among the two treatments. Leaf water potential was also monitored on the same dates except at 20 DAFB. Fruit growth and the vascular and transpiration flows to/from the fruit were also monitored in all periods except at fruit set.

### *Water relations*

Stem and leaf water potentials were monitored at about 10.00, 12.00 and 15.00 h, on four trees per treatment using a Scholander (Soilmosture 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 shoot leaf per tree, covered by aluminium 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 main stem, was chosen and covered with aluminium foil at least 90 minutes prior to measurement to allow equilibration with