



Physiology

Fruit calcium accumulation coupled and uncoupled from its transpiration in kiwifruit

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ARTICLE INFO

Article history:

Received 16 February 2015

Received in revised form 15 April 2015

Accepted 16 April 2015

Available online 23 April 2015

Keywords:

Fruit water budget

Microenvironment

Nutrient transport

Phloem

VPD

Water loss

Xylem

ABSTRACT

Accumulation of Ca in several fleshy fruit is often supposed to depend, among others, by climatic variables driving fruit transpiration. This study tests the whole causal chain hypothesis: $VPD \rightarrow$ fruit transpiration \rightarrow Ca accumulation. Also there are evidences that relationship between fruit transpiration and Ca content is not always clear, hence the hypothesis that low VPD reduces the fraction of xylemic water destined to transpiration was tested by examining the water budget of fruit.

Attached fruits of *Actinidia deliciosa* were subjected to Low (L) and High (H) VPD. Their transpiration was measured from early after fruit-set to day 157 after full bloom (DAFB). Fruits were picked at 70, 130 and 157 DAFB for Ca and K determinations and for water budget analysis.

Cumulative transpired water was ~ 70 g and ~ 16 g $H_2O\ f^{-1}$ in H_{VPD} and L_{VPD} , respectively. Calcium accumulated linearly ($R^2 = 0.71$) with cumulative transpiration when VPD was high, while correlation was weaker ($R^2 = 0.24$) under L_{VPD} . Under low VPD the fraction of xylem stream destined to transpiration declined to 40–50%.

Results suggest that Ca accumulation is coupled to cumulative transpiration under high VPD because under that condition cumulative transpiration equals xylem stream (which carry the nutrient). At L_{VPD} , Ca gain by fruit is uncoupled from transpiration because $\sim 60\%$ of the xylemic water is needed to sustain fruit growth. Results will apply to most fruits (apples, tomatoes, capsicum, grapes etc.) since most suffer Ca deficiency disorders and grow in changing environments with variable VPD, also they could be supportive for the implementation of fruit quality models accounting also for mineral compositions and for a reinterpretation of certain field practices aimed at naturally improve fruit Ca content.

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Introduction

Many fleshy fruits (e.g. apple, avocado, tomato, grape) including kiwifruit suffers physiological disorders during storage and, sometimes, also pre-harvest. Such disorders can be associated with low calcium (Ca) content (Saure, 1996; Ferguson and Watkins, 1989; Cutting and Bower, 1989; Witney et al., 1990; Ho and White, 2005; Thorp et al., 2003; Ferguson et al., 2003; Ciccarese et al., 2013).

Optimal Ca content of fruit and vegetables at harvest is generally found to improve their storability, probably because of its role in maintaining tissue mechanical strength (Hirschi, 2004). Improved storage is associated with reduced costs along the supply chain and therefore application of Ca-based foliar spray (field) or adoption of specific preconditioning protocol (packhouse) are common in fruit industry (Crisosto et al., 1997; Alcaraz-Lopez et al., 2003; Gerasopoulos and Drogoudi, 2005), even though natural friendly increased Ca is highly desirable.

Internal and external factors affecting the accumulation of Ca in fleshy fruit have been reported by Saure (2005). More recently, a review examined the factors (and their interactions) operating along the soil-to-fruit pathway in kiwifruit (Montanaro et al., 2014). In the light of the causal chain hypothesis: weather \rightarrow fruit transpiration \rightarrow Ca accumulation (Montanaro et al., 2012), among the external factors affecting fruit Ca accumulation in kiwifruit are the meteorological variables affecting fruit transpiration.

Abbreviations: DAFB, day after full bloom; E, daily transpiration rate; G, fruit growth; H_{VPD} , high vapour pressure deficit; L_{VPD} , low vapour pressure deficit; P, phloem water inflow; T, cumulative transpiration; X, xylem water inflow.

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Predominantly, these are those contributing to atmospheric vapour pressure deficit (*VPD*)—namely temperature and humidity.

Vapour pressure deficit may also affect fruit mineral nutrition indirectly through its effect on leaf transpiration (Lang and Volz, 1998). For example, studies have shown that reducing leaf transpiration by reducing *VPD* can also reduce the import of Ca by leaves. Assuming a constant uptake rate of Ca by the plant from the soil, a reduced leaf import, may favour an increased fruit import (Guichard et al., 2005; de Freitas et al., 2011).

The period of early fruit developmental is the most critical for Ca accumulation in most fleshy fruit including in kiwifruit. Principally, this seems to be because Ca is xylem mobile but phloem immobile (Bukovac and Wittwer, 1957), so it is the xylem sap inflow rate to the fruit, that determines the Ca import rate. In most fleshy fruits, the inflows of xylem sap and phloem sap are fairly similar in the early season (Lang, 1990), whereas the total sap inflow in the late season is strongly dominated by the phloem, with xylem sap inflow being negligible because of strongly reduction of transpiration (Saure, 2005; Montanaro et al., 2014). Thus, during the early stages of kiwifruit development (roughly from day 10 to day 50 after fruit set) a reduction in atmospheric *VPD*, reduces fruit transpiration, fruit xylem sap inflow, and supposedly Ca import (Morandi et al., 2012).

It appears that concurrent measurements of fruit transpiration and of fruit Ca accumulation along a relatively wide range of water loss have not been made. Therefore, this paper tests the hypothesis that if the *VPD* is the principle driver of fruit transpiration (Montanaro et al., 2012) and if fruit transpiration is the principle determinant of fruit Ca import, then fruit Ca import will be increased by rises in the cumulative fruits' transpiration as driven by increased *VPD*. Meanwhile, the xylem- and phloem-mobile nutrient potassium (K) will be much less affected by the increased *VPD*. To test this hypothesis, fruit transpiration, and the imports of Ca and K were assessed in fruit grown under high (H_{VPD}) and low *VPD* (L_{VPD}) conditions.

Although for transpiring organs, their transpiration probably remains the main driver for Ca accumulation, within-plant transport and partitioning of Ca and other minerals are also known to be affected by “transpiration-independent” factors. For example, calcium demand by an organ and the physicochemical features of the conducting tissues (e.g. ion adsorption and desorption occurring at exchange sites along the walls of the xylem pathway) are likely to influence the metabolic movement of Ca (McLaughlin and Wimmer, 1999). Also the action of specialised transfer cells and the higher expression of Ca transporters and Ca binding proteins may promote accumulation of Ca into fruit independently of its transpiration (Pate and Gunning, 1972; Park et al., 2005).

This anticipates that Ca accumulation could be uncoupled from transpiration and encourages a slight reinterpretation of the *transpiration* → *Ca accumulation* element of the earlier causal chain relationship, at least for low-transpiring organs such as fruit. Here, to explain uncoupled Ca we would evoke the water budget (*sensu* Lang, 1990) of fruit as possibly modulated by *VPD*.

The various components of the fruit water budget (xylem, phloem, transpiration and growth) have been analysed in detail (Lang and Thorpe, 1989; Fishman and Génard, 1998) also in relation to the functionality of the vasculature (Clearwater et al., 2012) and, interestingly, to the *VPD* of the surrounding environment even if with contrasting conclusions. For example, in tomato increased *VPD* reduced fruit xylem inflows while phloem flow was almost unaffected, similarly, in young kiwifruit, increased *VPD* increased xylem and transpiration, but does not affect phloem imports (Guichard et al., 2005; Morandi et al., 2012). In peach fruit, both phloem and xylem fluxes were reduced under low *VPD* (Morandi et al., 2010b). Unfortunately, the physiological

significance in terms of Ca accumulation of that *VPD*-induced variations on water budget was not explored.

Considering that (i) Ca is carried by the water sourced by xylem which is then evaporated (transpiration) or alternatively stored to allow fruit growth, and (ii) that the partitioning amidst transpiration and growth may change under different *VPD*, it is proposed that assessing the components of fruit water budget under different *VPD* may help to explain the non-linearity existing between Ca and transpiration. There is a general consensus that growth of fruit integrates fluxes *in* and *out* of fruit (Lang and Thorpe, 1989) and that reduced *VPD* doesn't impact neither fruit growth nor phloem inflow (Guichard et al., 2005; Morandi et al., 2012). Therefore, it was hypothesised that under reduced *VPD* to adequately sustain fruit growth, the fraction of xylem flux destined to transpiration is reduced causing Ca accumulation to be uncoupled from transpiration.

To test this hypothesis, sources (xylem, phloem) and destiny (transpiration, growth) of the components of fruit water balance were analysed in fruit grown under H_{VPD} and L_{VPD} conditions.

Materials and methods

Study site and plant material

The experiment was carried out during the 2011 season in southern Italy (N40°25'19.24"; E16°44'3.03") on mature, own-rooted Hayward kiwifruit vines (*Actinidia deliciosa* var. *deliciosa*, C.F. Liang et A. R. Ferguson) planted at 625 plants ha⁻¹ and trained to a pergola. The orchard was managed to local commercial practice. Nitrogen was supplied through fertigation approximately every 20–30 days from April to July to reach a total of about 50 kg ha⁻¹ N, additional 50 kg ha⁻¹ N are supplied through organic fertiliser distributed in winter. No phosphorous, potassium or calcium were applied because the soil was already sufficient in these elements. The plants were regularly drip-irrigated (2 drippers per plant, 10 L h⁻¹ each) during the season on an approximately weekly basis. Bloom occurred during the last week of May (full bloom on May 24, 2011) and natural bee pollination ensured normal fruit-set.

Differentiating *VPD*

On day 7 after full-bloom (DAFB), when fruit had a length (\pm SE) of about 13 ± 0.3 mm, 100 attached fruit were enclosed with a closable (Ziploc®) transparent polyester bag (80 × 120 mm, 0.06 mm thick, Carlo Erba Reagents, Italy), an additional clip was used to ensure bag closure (see Fig. 1). Fruit were selected on 50 terminating fruiting canes from 15 randomly chosen vines.

To create two levels of *VPD*, half of the bagged fruit were loaded with 5 silica-gel sachets (Carlo Erba, cod. 345,702, 93 × 37 mm) each containing 5 g of desiccant. Silica gel can absorb up to 30% of its weight of water while maintaining the relative humidity of the atmosphere well below 80%, hence this treatment was labelled High-*VPD* (H_{VPD}). In bagged fruit without silica gel, the relative humidity of the air surrounding the fruit was near saturation (Montanaro et al., 2010), therefore that treatment was labelled Low-*VPD* (L_{VPD}). To minimise shoot-to-shoot variability, pairs of L_{VPD} and H_{VPD} fruit were selected on the same fruiting shoots. The Figure 1 reports the bag treatment design.

Temperature and relative humidity inside the bags ($\times 2$ per treatment) were measured through a digital probe (mod. CS215, Campbell Scientific Inc., Utah, USA) connected to a datalogger (CR10X, Campbell Scientific Inc., Utah, USA), which was programmed to record at 60 s intervals and to compute and store averages at 15 min intervals. To avoid possible direct contact of the probe with droplets of condensed water vapour, the probe

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