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Review

Calcium and the physiology of sweet cherries: A review

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ABSTRACT

Growing interest in the commercial production of sweet cherries around the world has stimulated research on the potential for supplementary applications of calcium (Ca) as a way to mitigate the risk of catastrophic crop loss, to improve fruit quality at harvest and to extend postharvest shelf life. The objective of this review is to summarize current information, to identify knowledge gaps and to help define future research needs. We focus on (1) analysis and uptake of Ca, (2) Ca effects on rain cracking and (3) Ca effects on postharvest quality.

Preharvest Ca sprays and postharvest Ca dips sometimes increase fruit Ca levels; but at other times these are ineffective. Similarly, Ca applications by overhead sprinkling during rain or by spraying or by immersion, sometimes reduce rain cracking; but not always. Reduced fruit cracking is usually accounted for as due to improvements in the mechanical properties of the skin - the fruits structural backbone. Calculation shows that osmotic effects of Ca that reduce fruit water uptake are an unlikely explanation. Preharvest or postharvest applications of Ca may also improve fruit firmness, decrease pedicel shriveling and reduce the incidence of fruit rots. The studies reviewed indicate that (1) little is known about the mechanisms and pathways of Ca uptake into the fruit and (2) Ca applications have the potential to reduce cracking and to help retain postharvest quality; but these looked-for effects are often illusive. The lack of consistent behavior is likely due to erratic movement of the polar Ca ion through the cuticle. Future studies should focus on the mechanisms and pathways of Ca penetration into developing sweet cherry fruit and on its final location at both tissue and cellular levels.

1. Introduction

Calcium plays important roles in the pre- and postharvest physiology of most plant organs and tissues – and particularly of fruit. The range of critical physiological functions affected by Ca is diverse and includes: signal transduction as a secondary messenger (Hardingham and Bading, 1999; Steinhorst and Kudla, 2014), the control of gene expression and protein regulation (Kudla et al., 2018; Webb et al., 1996), the maintenance and regulation of membrane permeability (Poovaiah and Leopold, 1973; van Steveninck, 1965) and the cross-linking and structural reinforcement of cell-wall constituents (Chan et al., 2017; Demarty et al., 1984). For general information on the functions and functionality of Ca in plants we refer the reader also to the reviews of Bangerth (1979); Dodd et al. (2010); Gilliham et al. (2011); Hocking et al. (2016); Kirkby and Pilbeam (1984); Kudla et al. (2010) and White and Broadley (2003).

Calcium is considered the critical nutrient in determining fruit quality. The reasons for fruit being particularly susceptible to an insufficiency of Ca are several-fold (Marschner, 1995). First, Ca competes with other cations for negative charges during nutrient uptake and is therefore subject to cation uptake antagonism. Second, Ca movement within the plant is limited to the xylem (it is not transported in the phloem). Third, Ca taken up from the soil solution is transported in the xylem stream predominately to the leaves due to their high transpiration. Compared to fruit, leaves have much larger surface area to volume ratios and also much higher stomatal densities. Fifth, in many fruitcrop species, the fruit xylem loses functionality during development, like in apple (Drazeta et al., 2001); grape (Bondada et al., 2005; Chatelet et al., 2008a, b; Choat et al., 2009; Düring et al., 1987; Findlay et al., 1987; Keller et al., 2006; Knipfer et al., 2015); kiwifruit (Mazzeo et al., 2013) and sweet cherry (Brüggenwirth et al., 2016; Winkler et al., 2016a). And, finally, fruit have high volume-growth rates until late in development and this causes their Ca concentrations to decrease (by dilution).

Under normal production conditions, Ca deficiencies rarely occur in fruit but imbalances in nutrient supply causing 'relative Ca deficiencies' are common and well known. These include blossom-end rot in tomato (Ward, 1973), pepper (Marcelis and Ho, 1999) and water melon (Scott et al., 1993), bitter pit in apple (Ferguson and Watkins, 1989; Vang-Petersen, 1980) and cork spot in 'Anjou' pear (Richardson and Lombard, 1979). In these fruit crops, special measures are routinely taken to decrease the incidence of these disorders by increasing tree and

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fruit Ca supply. These interventions include foliar sprays and the adjustment of greenhouse microclimates. In other fruit crop species, such as in kiwifruit and grape, Ca is used to improve fruit firmness and to decrease the incidence of rots (Antunes et al., 2005; Ciccarese et al., 2013).

In recent years, the economics of sweet cherry production have become highly attractive. Here, Ca is used to mitigate the risk of preharvest rain-cracking of fruit and to increase postharvest fruit firmness and shelf-life. A large number of studies have now emerged that report on the effects of Ca treatments on pre- and postharvest performance. However, the associated gains are not consistent. In some studies, Ca applications were found beneficial while in others there was no significant effect. The reason for the lack of consistency in the Ca response is unknown.

The objective of this review is to summarize the literature, identify gaps in knowledge and define future research needs. We focus on sweet cherry and on the following areas: (1) analysis and uptake of Ca, (2) Ca effects on rain cracking and (3) Ca effects on postharvest behavior.

2. Calcium analysis and uptake

2.1. Analysis of Ca

Studying Ca uptake in the absence of radiolabeled ^{45}Ca requires classical mineral analysis by atomic absorption spectrometry (AAS) or inductively coupled plasma based systems, like inductively coupled plasma optical emission spectrometry (ICP-OES) or inductively coupled plasma atomic emission spectroscopy (ICP-AES). An AAS is often used when single-element analysis is required, whereas ICP used in multiple element analyses can quantify up to 70 elements in a single sample. Prior to Ca analysis, any Ca residues on the fruit surface must be washed off. This can be done reliably by incubating fruit in low concentrations of acids (e.g. citric acid or hydrochloric acid). Fruit is then prepared for analysis by depitting and drying and grinding (freeze-drying (Lidster et al., 1978; Measham et al., 2017); or oven-drying (Tsantili et al., 2007)). Subsequently, the material is ashed in an oven or digested using acids (Campbell and Plank, 1998). It is important to note, that Ca and phosphate interfere with one another in AAS when using an air-acetylene flame leading to error (Bhattacharya et al., 1979; Fishman and Downs, 1966; Trudeau and Freier, 1967; Yofé and Finkelstein, 1958). Interference is eliminated by using a nitrous oxide-acetylene flame (Bhattacharya et al., 1979) or by adding lanthanum at a concentration of 1% as a releasing agent (Fishman and Downs, 1966). Unfortunately, this interaction has not always been recognized, so leading to a significant underestimation of the Ca content by about 50% (0.65 ± 0.07 vs. 0.32 ± 0.03 mg g^{-1} dry matter for samples with lanthanum vs. without lanthanum, respectively) in mature field-grown 'Staccato' sweet cherry (Winkler, unpublished data).

2.2. Ca uptake in sweet cherry

Surprisingly few studies have focused on Ca uptake by sweet cherry fruits. In principle, uptake may occur via two parallel pathways, through the xylem of the vascular system and/or through the fruit skin.

2.2.1. Vascular penetration

The Ca concentration in the phloem is very low, such that Ca is considered phloem immobile (Marschner, 1995). Thus, any Ca inflow to the fruit through the vasculature must take place via the xylem. In plants, the driving force for xylem transport is a gradient in water potential between the soil solution and the distal plant tissues where transpiration is occurring. Soil water potential is usually (relatively) close to 0 MPa while that of the apoplast of a transpiring tissue (e.g. of a leaf) is commonly around -0.8 MPa (Taiz and Zeiger, 1991). Thus, the xylem transport of water (and Ca) into the fruit is in direct competition with that into the leaves, where the latter have much higher surface areas and much higher transpiration rates than fruits (Hocking et al., 2016). Under high-transpiration conditions (e.g. high irradiance, low humidity, wind and high air temperature) tree water potential will often fall to a point at which some fruit water may be transferred 'backwards' out of the fruit into the tree – so-called negative xylem flow (Lang, 1990).

Using linear variable displacement transducers (LVDTs), Brüggenwirth et al. (2016) quantified the water flows in the xylem and phloem of the fruit stalks of developing sweet cherries, and also that due to transpiration through the fruit skin. Flows along the individual pathways were obtained using the method of Lang (1990) and Lang and Thorpe (1989). Up to stage III, the xylem contribution to the vascular flow into a sweet cherry fruit is more than 80% of total inflow. However, from stage III onwards, this portion decreases progressively, falling at maturity to almost zero % of the total vascular inflow. The reason for the decrease in xylem inflow is decreased xylem conductivity (Grimm et al., 2017; Winkler et al., 2016a). Experiments using acid fuchsin and gadoteric acid (Gd DOTA) as tracers and fluorescence microscopy and magnetic resonance imaging reveal a progressive shutdown of the xylem flow during stage III. Shutdown begins at the stylar end of the fruit and proceeds towards the pedicel end. Initially, just the minor veins in the flesh become dysfunctional, later the major veins and last the large bundles. At maturity, only the small portion of the fruit xylem directly distal to the pedicel remains conductive. The occurrence of intrafascicular cavities indicates the reason for decreased xylem conductance is rupture of vessels due to excessive, growth-induced straining, rather than to vessel blockage (Grimm et al., 2017). The decreased conductance has three consequences for fruit Ca supply: first, the temporal pattern of Ca import by the fruit will mirror that of the declining xylem conductance. Second, based on the observed pattern of progressive xylem dysfunction in the fruit, a gradient in Ca content from the proximal end of the fruit (high) to the distal end (low) is expected. Third, the Ca content per unit fresh or dry weight is expected to decrease due to the marked increase in fruit volume during stage III (Facteau, 1982). Unfortunately, direct evidence is lacking for some of these predictions.

2.2.2. Uptake via the fruit surface

Uptake via the fruit surface is the second possible route for entry of (anthropogenic) Ca to the fruit. Preharvest, Ca penetrates either from concentrated dried-down spray residues after 'foliar' Ca applications or, postharvest, from bathing in dilute Ca solutions in the packhouse - for example during hydro-cooling (Zoofoli et al., 2017). The most common procedure is the spray application of Ca salts, mostly $CaCl_2$, in the field. Such Ca uptake has been quantified in only a limited number of studies (Table 1). Unfortunately, there is not sufficient detail on the application to allow calculating the amount and concentration of the Ca applied, which makes comparisons across studies difficult. Moreover, the results obtained are not consistent. Thus, Wójcik et al. (2002) observed a 26% increase in the Ca content of 'Merton Premier' over three years after spraying three times each season with 0.5% $CaCl_2$. In a similar trial, the Ca content of 'Burlat' increased statistically significantly in two years at two sites, following three or five applications of 0.5% $CaCl_2$ during stage III (Wójcik et al., 2013). Similarly, Ca content of 'Vogue' cherry increased after application of 45 mM or 58.5 mM $CaCl_2$ at the stage II/III transition and early stage III. Landi et al. (2016) applied 1% $Ca(OH)_2$ and two commercial formulations (both CaO based and hence, forming $Ca(OH)_2$ in solution) after fruit-set and after pit hardening in 'Grace Star' and 'Sweetheart'. They obtained increased Ca content for only one of the commercial products and for only one of the cherry cultivars - 'Sweetheart'. Demirsoy and Bilgener (1998) sprayed 0.7% $Ca(OH)_2$ with a non-specified surfactant once or three times in '0900 Ziraat', 'Lambert' and 'Van'. The fruit Ca content was extremely variable. Significant uptake occurred only in 'Van' sprayed three times. Koffmann et al. (1996) applied $CaCl_2$, $Ca(OH)_2$ and Ca polyphenate chelate with different surfactants up to three times in the cultivars 'Ron's Seedling'