Calcium-Related Plant Physiological Disorders©

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Calcium (Ca) is dependent on xylem translocation; it moves with the transpiration stream and binds with polysaccharides to strengthen cell walls, needed to produce firm fruit tissue, good quality and a long shelf life. Calcium prevents cell wall degradation, "leaky" membranes and premature senescence. Calcium deficiency disorders include "brown fleck" and poor keeping quality of potatoes, weak flower stems, blackheart in celery, bitter pit in apple and bract necrosis in poinsettia. Blossom-end rot (BER) is a Ca-deficiency disorder affecting tomatoes, peppers and watermelons. High temperatures (>30°C), high radiation levels (>300 $W \cdot m^{-2}$ or >1400 $J \cdot cm^{-2}$ per day), or low RH values (<50%) may trigger the development of BER. Three strategies may be followed to limit Ca deficiencies: (1) Improve conditions that enhance the uptake of Ca. (2) Improve the allocation of Ca to sensitive organs by improving xylem flow to these organs. (3) Avoid excessive growth where Ca ions are used to neutralise organic acids and insoluble oxalates are formed.

INTRODUCTION

Calcium (Ca) moves with the transpiration stream and binds with polysaccharides to strengthen cell walls, is needed to produce firm fruit tissue, and is associated with a good shelf life. Although Ca is generally associated with good quality, too much Ca may also create problems since stiffening of cell walls may limit the ability of fruits to expand, inducing fruit cracking (Combrink et al., 1995a). A lack of elasticity is a quality problem in cured tobacco leaves, grown at high Ca levels (Combrink and Davies, 1987).

When lettuce is grown under hot summer conditions with high radiation levels, it may develop tip-burn on the inner immature leaves, a well-known Ca-deficiency disorder. According to Collier (1982), interacting factors affect the development of tip-burn in lettuce. Factors associated with the development of Ca-related disorders were classified into three scenarios by Napier and Combrink (2006):

1) Factors affecting Ca uptake.
2) Factors affecting water and Ca movement to plant organs.
3) Intra plant factors, associated with rapid growth and insufficient functional Ca.

STRATEGIES TO DEAL WITH CA-RELATED DISORDERS

Insufficient Calcium Uptake

Several conditions affect the uptake of Ca such as root zone moisture levels, the presence of young and healthy root tips, the concentration of other cations, and the salinity of the root zone solution.

1. Root Zone Moisture. Calcium ions are passively taken up with water and move within the plant with the transpiration stream (Wiersum, 1966). Conditions that may suppress the uptake of water should thus also limit the uptake of Ca. Benoit and Ceustermans (2001) compared irrigation systems on peppers. Using a system with a constant flow of nutrient solution, almost no blossom-end rot (BER) was found compared to BER problems with a frequently dripped rock-wool substrate. By using a special moisture sensor, placed into the substrate to control the irrigation frequency, both the substrate EC and the incidence of BER decreased.

2. Root Tips. Calcium uptake is confined to young root tips (Robards et al., 1973) and is transported across the root through the apoplast, which is blocked when the endodermis becomes suberized in older tissue. The lateral transport of Ca does not occur in the more mature areas of the root where the endodermis is suberized. Scaife and Clarkson (1978) state that Ca uptake may be restricted when, for some reason, root growth is impeded and there is very little new root growth that is not suberized. This means that damage to young roots will prevent Ca-uptake. Roots and root hairs should be protected against drying, exposure to high salt concentrations or other factors that may damage young root tissue, since such damage results in limited uptake of water and Ca.

3. Available Calcium and Competing Cations. Low nutrient solution Ca levels will invariably lead to Ca deficiencies. It is also well known that the ratio between cations affect their uptake (Steiner, 1984). The uptake of Ca can easily be restricted in the presence of high levels of other cations, relative to Ca. An extremely strong suppressor of Ca uptake is the NH_4 ion. In the Netherlands, de Kreij (1997) showed that BER developed on peppers with as little as 0.5 $mmol_c \cdot L^{-1}$ NH_4 in the nutrient solution. With NH_4 at 1.0 $mmol_c \cdot L^{-1}$, the incidence of BER increased to about 60%. Gosselin and Trudel (1986) demonstrated that the uptake of K is favoured to the detriment of Ca at higher root zone temperatures. With extremely high Ca-levels, fruit cracking may occur due to a loss in elasticity in the fruit-peel cell walls (Combrink et al., 1995a). Using high Ca levels under low RH conditions to grow oven-cured tobacco, brittle and bulky leaves lacking elasticity were produced (Combrink and Davies, 1987). On the other hand, it is beneficial to grow bulky and crispy lettuce leaves, implying that lettuce needs relatively high Ca levels.

4. Salinity. A high EC in the root zone may induce BER problems, simply due to an osmotic effect restricting the uptake of water and Ca (De Krij et al., 1999). Belda and Ho (1993) reported that a low Ca supply restricts xylem development in the fruit placenta, further restricting the movement of water and Ca to the distal end of developing fruit. An elevated EC may thus directly restrict Ca uptake but may also indirectly restrict the translocation of Ca, due to inadequate xylem development. After reaching this stage, a lower EC will not save the fruit. To prevent the development of BER in tomatoes, the recommendation is to ensure that the EC in tomato root media be kept below 3 $mS \cdot cm^{-1}$.

Water Movement to Plant Organs

Calcium moves only in the xylem, directed by the transpiration stream (Wiersum, 1979). This is a problem during warm periods when leaves lose large volumes of water for evaporative cooling, limiting water movement to low transpiring fruits. In lettuce, the Ca in the tips of transpiring leaves was 10 to 15 fold higher than similar sections of inner non-transpiring leaves (Barta and Tibbitts, 1991). Once fixed to plant tissue, Calcium does not move to other organs due to its immobility in phloem (Epstein and Bloom, 2004).

1. Root Pressure. Under conditions where plant organs are permanently wilted or permanently turgid, a lack of diurnal fluxes may restrict movement of Ca-rich xylem sap into the organs (Collier, 1982). Root pressure can easily force water with Ca into moderately wilted organs at night, after a hot day, thus regaining turgidity in these organs and reducing Ca deficiency disorders. However, this root pressure can only develop in a moist but well-aerated root medium with moderate concentrations of absorbable ions at optimum temperatures (Epstein and Bloom, 2004). Australian growers are advised to ensure that lettuce crops are provided with adequate water overnight to limit the development of tipburn (www.dpi.vic.gov.au).

2. Root-Zone Temperature. The incidence of BER on peppers decreased significantly where the temperature of the nutrient solution was reduced in a NFT system, associated with a better oxygen supply to the roots and an improved Ca uptake relative to K at the lower root zone temperatures (Benoit and Ceustermans, 2001). Jackson (1980) reported that the need for oxygen in the root zone more than doubles when the root temperature rises from 20 to 30°C. At 20°C, the volume of root zone oxygen needs to be replaced five times per hour, compared to 12 replacements needed per hour at 30°C. High root-zone temperatures induce oxygen deficiencies that result in reduced water and Ca uptake.

3. Relative Humidity and Transpiration Rates. Because Ca moves with the transpiration stream its movement is dependant on environmental conditions (Adams et al., 1994). Combrink et al. (1995b) demonstrated that fruit transpiration and the translocation of Ca to developing melon fruit decreased by exposing isolated fruits to high relative humidity (RH) levels. Smit and Combrink (2004) induced BER on tomatoes with the same technique. An attempt to reduce the incidence of BER on peppers by reducing leaf transpiration with foliar sprays, also reduced pepper yields (Schon, 1993). By allowing the RH to drop below 50%, water movement to leaves increased to the detriment of developing pepper fruit (Benoit and Ceustermans, 2001). This problem could be reduced by increasing the minimum RH in the greenhouse to 60%. A pad and fan or foggers may be used to increase the RH during hot and dry South African summer days. Due to the high cost of a standard wet wall, a cheaper alternative was developed by Dr. Dreyer at Vredendal. Rather than using an expensive but perishable carton pad, micro jets are used to form a mist between two nets at the suction side of the greenhouse. While saline water cannot be used for overhead foggers, it is safe for use in this system.

Intraplant Factors

1. Insufficient Functional Calcium. Due to higher summer temperatures, an increase in respiration rate is associated with an increased concentration of carboxylic acids, all of which form stable complexes with Ca. This loss of functional Ca can induce the development of tipburn in lettuce (Misaghi and Grogan, 1978). By reducing the respiration rate, the risk that Ca-deficiency disorders may develop, can thus be lowered.

2. High Auxin Levels. Chlorogenic acid forms under long day conditions, inhibiting IAA oxidase (Collier, 1982). This leads to the accumulation of IAA, stimulating cell enlargement and increasing the incidence of tipburn in lettuce. According to Rayle and Cleland (1977), an increased hydrogen ion concentration results due to auxin action. Cell walls enlarge as a result of the increased hydrogen ion concentration, displacing Ca ions and loosening cell walls.

3. Calcium Supply via Xylem Tubes. The relative flow of Ca to developing plant tissue may decrease when growth rates increase. In summer, with optimum temperatures and light intensities, the production of photosynthates is optimised. These carbohydrates move into fruit via the phloem and increase cell expansion and growth, coinciding with movement of water and Ca in the xylem to transpiring leaves, rather than to the fruit. Rapid fruit development, coinciding with high leaf transpiration rates, aggravates Ca deficiencies in tomato and pepper fruit. Tipburn, affecting the inner leaves of cabbage, increased under conditions favouring transpiration, which tended to route the water to the wrapper leaves. When root pressure was favoured by minimizing transpiration, calcium moved readily into the inner leaves to lower the incidence of tipburn (Palzkill et al., 1976).

4. Cultivars. Different cultivars of the same crop clearly differ in their susceptibility to Ca-related physiological disorders. In a local tomato cultivar trial (University of Stellenbosch, 2001), cultivars with bigger or oval shaped fruit seemed to be more sensitive to BER than cultivars with round shapes and smaller fruit sizes. This may be due to insufficient xylem development (Ho and Adams, 1993) or more Ca-adsorption to fruit tissue when moving from the stem to the blossom end. High yielding tomato cultivars are often more susceptible to BER, probably due to more assimilates accumulating in the fruit via the phloem, increasing the demand for Ca. In lettuce, there are also clear cultivar differences in susceptibility to tipburn (www.dpi.vic.gov.au).

CONTROL MEASURES

Due to the immobility of Ca, foliar sprays to add Ca are inefficient. However, Ho and Adams (1993) showed that the incidence of BER on tomatoes might decrease when $CaCl_2$ sprays are directed at young developing fruit. Blom and Marcelis (2000) lowered the incidence of BER on peppers with two Ca fruit sprays in the 2nd and 3rd weeks after anthesis. They did not report the Ca concentration or source of Ca used, but did mention that leaf damage occurred. Benoit and Ceustermans (2001) reduced the incidence of BER on peppers with $CaCl_2$ sprays but only where the sprays were directed at young fruit (<1.5 cm diameter). The optimum concentration was about 4.0% $CaCl_2 \cdot 2H_2O$ but leaves that were accidentally exposed to the sprays were damaged. Due to the risk of foliar damage with Ca-sprays, procedures should rather be followed to prevent the development of BER. In the case of tipburn on lettuce, foliar Ca spays are totally inefficient (www.dpi.vic.gov.au).

Since interacting factors affect the development of Ca-deficiency disorders, all of these factors should be taken into account when sensitive crops are grown. These factors were discussed above, as part of the three scenarios associated with the development of Ca-related disorders.

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