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Enhancing the Natural Resistance of Plant Tissues to Postharvest Diseases through Calcium Applications

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Elucidating and enhancing natural mechanisms of resistance to postharvest diseases currently is of paramount importance, especially concerning storage organs. Consumers are concerned about residues left on produce by postharvest fungicide treatments, and the use of such chemicals is becoming more restricted because of their increasing association, either real or imagined, with human maladies. Since Ca has often been associated with disease resistance, increasing the amount of Ca in plant storage organs by various methods is a means of enhancing natural resistance.

Early research into the effects of Ca on fruit and vegetable quality was concerned mainly with Ca's association with physiological disorders (DeLong, 1936). Subsequently, more than 30 Ca-related disorders in various crops have been identified (Shear, 1975). Disorders of storage organs of fruits and vegetables appear closely related to low Ca content in tissues. Storage disorders of apples *(Malus domestics* Borkh.), such as water core, bitter pit, internal breakdown, and softening, have been reduced by postharvest Ca treatment (Bangerth et al., 1972; Mason et al., 1975; Reid and Padfield, 1975). Similarly, with certain potato *(Solarium tuberosum* L.) cultivars, disorders such as internal brown spot in tubers (Tzeng et al., 1986) and subapical necrosis in sprouts (Dyson and Digby, 1975; Tzeng et al., 1986) were reduced by treatments that increased tissue Ca content.

With certain storage organs, increases in tissue Ca content led to reductions in decay caused by fungi and bacteria (Huber, 1981). In England, preharvest Ca sprays reduced storage losses caused by *Gloeosporium* spp. in apple (Sharples and Johnson, 1977). In the United States, postharvest treatments that increased tissue Cain apples reduced postharvest decay caused by *Penicillium expansum* Link ex. Thorn (Conway, 1982; Conway and Sams, 1983). Likewise, with potatoes, bacterial soft rot caused by *Erwinia carotovora* pv. *atroseptica* (van Hall) Dye decreased as tissue Ca increased (McGuire and Kelman, 1984, 1986).

Research concerning the effects of Ca on apple tissue resistance to postharvest decay has progressed similarly, but independently, of that with potato. The results and conclusions have been similar, and each supported and strengthened the other. Below, we discuss factors and mechanisms in treating apples and potatoes with Ca to reduce the potential for postharvest decay.

CALCIUM TREATMENT METHODS

Many disorders that result from inadequate Ca in storage organs may arise from poor Ca distribution rather than low Ca uptake, because, in the same plant, leaves are often higher in Ca concentration than storage organs and concentrations vary widely in specific tissues for a given organ (Bangerth, 1979). Various methods of increasing the

Ca concentration of storage organs have been investigated. Fertilizer and liming practices would seem to be the most efficient way of increasing Ca in storage tissues. However, many complex environmental and physiological interactions affect Ca uptake and distribution; thus, these practices may not result in sufficient increases in Ca concentration (Bangerth, 1979). Calcium fertilization has proven successful in increasing the Ca content of potato tubers (McGuire and Kelman, 1984). Foliar and tuber Ca concentrations of potato were increased following $Ca(NO_3)_2$ and $CaSO_4$ applications, with the highest Ca concentrations deposited in the foliage (0.19% to 1.2% dry weight). Tuber Ca also increased in the peel (0.06% to 0.28% dry weight) and medullar tissues (0.011% to 0.062% dry weight) as soil Ca was increased. Thus, Ca in the peel and medullar tissue of the tubers increased 5× over the range of fertilizer regimes. As tuber Ca increased, percent surface area of tuber decay caused by *E. carotovora* pv. *atroseptica* decreased. Tubers with the highest tissue Ca concentrations had 50% less decay than those with the lowest.

Foliar sprays can increase the Ca content of apple fruit slightly (Drake et al., 1979), but these increases can vary from year to year depending on growing conditions (Glenn et al., 1985). Calcium analyses of tissue taken from 'York' or 'Rome' fruit sprayed with up to 50 kg $CaCl_2$/ha were compared to nontreated fruit during the 1990 growing season in southern Pennsylvania. Little significant difference in tissue Ca resulted with Ca concentrations ranging from= 150 to 250 $\mu g \cdot g^{-1}$ (Conway and Sams, unpublished data).

Applying Ca directly to a storage organ may be the best method of increasing flesh Ca content. Dipping apples in $CaCl_2$ solutions can increase tissue Ca (Bangerth et al., 1972). Adding food thickeners such as Keltrol to Ca dip solutions can further increase Ca uptake in apples (Mason et al., 1974). Active infiltration procedures, such as vacuum or pressure, that force solutions into fruit were more effective than dipping for controlling bitter pit (Scott and Wills, 1979). 'Golden Delicious' apples were treated with 0 to 12% CaCl, solutions by dipping (2 rein), vacuum infiltration (2 rein; 33.33 kpa), or pressure infiltration (2 rein; 68.95 kpa) (Conway and Sams, 1983). Over the range of $CaCl_2$ treatment solutions, dipping (250 to 700 µg Ca/g dry weight) was the least effective in increasing the Ca concentration of the tissue. Vacuum infiltration (250 to 1500 µg Ca/g dry weight) was superior to dipping, but pressure infiltration (250 to 3250 µg Ca/g dry weight) was most successful in increasing apple tissue Ca. As the Ca concentration of the fruit tissue increased, there was a corresponding decrease in decay following inoculation with *P. expansum.* The highest Ca concentrations reduced the decay area by >50%. There was some superficial peel injury at the higher CaCl, concentrations.

Vacuum infiltration (1 h; 13.33 kPa) of $Ca(NO_3)_2$ solutions at various concentrations (McGuire and Kelman, 1984) also increased potato tuber Ca. Peel Ca increased from 0.10% to 0.51% dry weight and medullar Ca from 0.022% to 0.075% dry weight. In tubers inoculated with *E. carotovora* pv. *atroseptica,* the percentage of decayed surface area-was reduced from 93% to 15% over the range of infiltrated Ca concentrations. The Ca treatments caused no noticeable injury to the tuber surface (McGuire and Kelman, 1984). Some practical considerations would limit the effectiveness of this procedure's commercial use; in particular, the logistics of handling large volumes of tubers and the need for adequate drying. However, vacuum infiltration in these trials was designed to test the role of Ca in reducing tissue decay by soft rot bacteria and to evaluate possible commercial applications.

FACTORS INVOLVED IN CALCIUM UPTAKE

Apples

Differences in growing conditions, environmental factors, and fruit development can influence the amount of Ca taken up by fruit and other fleshy organs during treatment. The amount of Ca taken into apple fruit from preharvest sprays or postharvest treatments can vary from year to year and by fruit maturity and cultivar. Calcium probably enters primarily through the lenticels (Betts and Bramlage, 1977), but cracks in the cuticle and epidermis may also provide an entrance, especially with fruit picked late in the season (Clements, 1935). 'Golden Delicious' fruit, compared with other cultivars, are prone to an especially high degree of cuticle and skin cracking early in the growing season (Meyer, 1944); the width and number of cracks increase during fruit development (Faust and Shear, 1972). Growing season conditions can also influence the number of cracks. Cuticles isolated from 'Golden Delicious' apples harvested in Sept. 1982 had far more cracks than fruit that were harvested in Sept. 1981 (Glenn et al., 1985). Crack development during the latter part of the growing season may play a significant role in Ca uptake by apple fruit. Thus, variations in cuticular cracking may be associated with variations in the effectiveness of Ca sprays and postharvest Ca treatments among sources or fruit lots. Such cracks appear to be an important mode of entry for Ca uptake.

Fruit maturity also has a profound effect on Ca absorption (Conway and Sams, 1985). 'Golden Delicious' apples were harvested on three separate occasions at 2-week intervals: 1) 2 weeks before the predicted prime harvest period, 2) at the prime harvest period, and 3) 2 weeks thereafter. Fruit picked 2 weeks after prime harvest and treated with an 8% $CaCl_2$ solution contained three times as much flesh Ca as fruit treated similarly but harvested 2 weeks before prime harvest. This study shows that fruit injury is one of the major problems associated with postharvest Ca treatment of apples. Little to no injury occurred on the fruit picked 2 weeks before prime harvest. Surface injury occurred on the fruit picked at prime harvest and treated with the higher $CaCl_2$ concentrations, but the injury was superficial and limited mainly to the peel; thus, even the injured fruit would be acceptable for processing. Fruit picked and treated 2 weeks after prime harvest absorbed an excessive amount of Ca, especially from the 8% solution, and injury was severe, extending into the cortex. These fruit would be unsuitable for the fresh market or processing. The fruit in the maturity study were not rinsed. By using an active infiltration procedure, such as vacuum or pressure, the Ca can be forced into the fruit and the surface residue can be removed by rinsing to reduce the possibility of injury. In the fruit picked 2 weeks before prime harvest, there was little reduction in decay caused by *P. expansum* because the fruit did not absorb enough Ca to affect the decay process. In the fruit picked 2 weeks after prime harvest, the decay area was reduced by 67% in the fruit treated with the higher $CaCl_2$ concentrations compared to nontreated fruit, but Ca injury was severe. The optimum Ca treatment at prime harvest reduced decay by 40% with no injury. The obvious concern with fruit maturity is that if fruit are harvested and treated too early, little Ca is taken into the fruit and decay is not inhibited. In contrast, if fruit are harvested too late, too much Ca is taken into the fruit and severe injury results.

Potatoes

Reducing decay of potatoes also depends on the amount of Ca taken into the tubers. One factor influencing the amount of Ca taken into the tuber is the Ca source with which the potato plants are fertilized (Simmons et al., 1988). Pelleted $CaSO_4$, granulated $CaSO_4$, or sieved $CaSO_4$ was superior to dolomitic lime, triple superphosphate, or $CaCl_2$ for increasing tuber Ca. The high-Ca tubers were also less susceptible to decay caused by *E. carotovora* pv. *atroseptica* (McGuire and Kelman, 1984, 1986).

Calcium uptake also was affectedly fertilizer placement (Simmons et al., 1988). Preplant strip, broadcast, or sidedress application was studied. The preplant strip method concentrated more material in the central portion of the potato hill where the tubers formed. This method, compared to the sidedress and broadcast treatments, increased Ca uptake in both periderm and medullar tissue.

Soil type also is an extremely important factor in determining the amount of Ca deposited in the potato tuber (Simmons and Kelling, 1987). Research on the effect of soil type on Ca uptake was conducted in Wisconsin at four sites. The soil types were: 1) low cation exchange capacity (CEC), low exchangeable Ca, and loamy sand; 2) medium CEC, high exchangeable Ca, and silt loam; and 3) intermediate CEC with medium to high soil exchangeable Ca levels and sandy loam. The preplant application method was used to apply five rates of sieved $CaSO_4$. Tubers grown at sites containing the low-Ca loamy sand had the greatest increase in Ca concentration; however, results obtained in

the high-Ca sandy loam soil were inconsistent. Finally, the potato cultivar, field location, and growing conditions are important as well. For 'Russet Burbank' and 'Superior' potatoes grown in Wisconsin, Ca fertilization greatly enhanced tuber Ca concentration and significantly reduced bacterial decay caused by *E. carotovora* pv. *atroseptica.* For 'Superior' potatoes grown in Florida, Ca fertilization increased tuber Ca concentration, but not to the extent of 'Superior' potatoes grown in Wisconsin; however, bacterial decay was still significantly reduced. 'Atlantic' potatoes grown in Florida showed inconsistent results with respect to Ca uptake or decay resistance (Bartz et al., 1992). Other studies have shown that cultivars vary greatly in Ca content of tubers (Tzeng et al., 1990).

RELATIONSHIP OF CALCIUM AND CONTROLLED-ATMOSPHERE STORAGE TO DECAY DEVELOPMENT

Controlled-atmosphere (CA) storage of apples, like postharvest Ca treatment, can prevent or delay the onset of storage disorders (Smock, 1979). The effect of CA on decay of stored fruit seems to vary depending on the particular fungus involved. *Penicillium expansum* lesion development was retarded when 'Golden Delicious' apples were stored at 2.5% O_2 and 5% CO_2 at 0C (Sommer et al., 1977). In subsequent tests with 'Delicious' apples that were wound-inoculated with *P. expansum,* CA storage (3% O_2 and 2% CO_2 or 1% O_2) or pressure infiltration with $CaCl_2$ solutions before inoculation led to an ≈ 50% reduction of decay compared with control fruit (Sams and Conway, 1985). When these treatments were combined, disease control was greater than that from either treatment alone (Sams and Conway, 1987). Calcium-induced changes in the cell wall of the fruit renders the fruit more resistant to enzymes produced by the fungus and delays senescence; Ca also may reduce pathogen germination, sporulation, and growth. Thus, factors related to the host and pathogen lead to reduced storage decay. The combination of CA storage with Ca infiltration treatments, then, is additive, and either treatment improves the effectiveness of the other in reducing postharvestlosses caused by fungal decay.

ROLE OF CALCIUM IN REDUCING DECAY

The Ca-induced resistance of storage organs to postharvest pathogens has been attributed to an interaction between certain cell wall components and Ca ions. Postharvest pathogens macerate host tissues primarily through the action of pectolytic enzymes. Calcium ions bind to the pectins present in the cell wall (Demarty et al., 1984). Pectins are chains of polygalacturonic acid residues into which rhamnose is inserted (Preston, 1979). These rhamnose insertions cause kinks in the chain, which allows cation attachment. Cations form bonds between adjacent pectic acids or between pectic acids and other polysaccharides. Such cross bridges make the cell walls less accessible to the action of pectolytic enzymes. Soluble polyuronide levels were reduced in apple fruit treated with Ca before storage (Sams and Conway, 1984). When apple fruit were infiltrated with Ca, or potato tubers were fertilized with high Ca or infiltrated with Ca, the quantity of Ca bound to the cell walls increased (Conway et al., 1987; McGuire and Kelman, 1984).

In studies with polygalacturonase extracted from lesions caused by *P. expansum* and cell walls from apple fruit, significantly less product was formed when high-Ca cell walls were used as a substrate compared to low-Ca cell walls (Conway et al., 1988). Similarly, with potato, a purified pectate lyase from *E. carotovora* pv. *atroseptica* had less effect on cell walls high in Ca than those low in Ca (Maher et al., 1986). Here, too, as with apples, less product was formed when high-Ca cell walls were used as a substrate. Because Ca improves the structural integrity of the cell wall, the mechanism of resistance associated with tissues high in Ca probably involves a reduced rate of cell wall maceration as a result of the enhanced structural integrity. Calcium may also affect pectolytic enzymes directly. Calcium inhibits polygalacturonase activity at low concentrations (Buescher et al., 1979). However, such concentrations stimulate pectate lyase activity, but higher Ca concentrations reduced the reaction rate of pectate lyase (Pratt and McIntyre, 1972).

PRATICAL CONSIDERATIONS

Enhancing endogenous Ca levels in apple and potato tissues has been effective in reducing decay. The major problem involves finding the optimum method for sufficiently elevating the tissue Ca level to reduce decay without injuring the organ being treated.

Fertilizer regimes, which are unsuccessful for apples, have elevated potato Ca levels sufficiently to reduce decay without injuring the tubers. However, some soil types are more amenable than others in producing tubers high in Ca. Fertilization with $CaSO_4$ on sandy soils low in CEC and Ca has been effective in raising Ca concentrations in tubers.

The geographic area in which potatoes are grown can affect Ca uptake as well. Plants grown on a certain soil type in one part of the country may respond positively to high Ca fertilization, whereas plants grown under a similar regime in another area may not.

Potato cultivar may be important as well. 'Russet Burbank' and 'Superior' respond well to Ca fertilizer, but 'Atlantic' is inconsistent in its response.

Postharvest pressure or vacuum infiltration of Ca solutions has worked well with apples, with pressure infiltration being especially effective. The major problem with Ca infiltration of apple fruit is maturity at time of harvest and subsequent infiltration of Ca solutions. If fruit are picked too early, little to no Ca enters the apple and decay is not reduced. If fruit are harvested and infiltrated when too mature, too much Ca may enter the fruit and injury may result. Maturity at time of treatment is probably the single most important factor to consider when treating fruit with Ca on a commercial scale. During a recent test in southern Pennsylvania in cooperation with a processing corporation, three lots of 'Golden Delicious' apples were harvested from three orchards within 1 day of one another. Yet, each lot was of a distinctly different maturity, and the amount of Ca taken up from pressure infiltration was significantly different between fruit lots. Beginning with a tissue Ca concentration of ≈ 200 $\mu g \cdot g^{-1}$, tissue Ca concentration of apples in one orchard increased to just >700 $\mu g \cdot g^{-1}$, to 1300 $\mu g \cdot g^{-1}$ in a second orchard, and to just >1800 $\mu g \cdot g^{-1}$ in a third orchard (Conway and Sams, unpublished data).

Sanitation is another problem that maybe encountered. If the apple surface or Ca solutions become contaminated with large populations of fungal spores, the spores maybe forced into the fruit, or the pressure itself may produce minute injuries that serve as infection courts for the pathogen. Sanitation on both the fruit surface and in the Ca solution with which the fruit is treated is necessary for beneficial Ca treatment.

Calcium also can be combined with postharvest fungicide or biological control treatments, thus allowing a lower concentration of either while maintaining optimum effectiveness in the presence of Ca. Enhancing the Ca concentration of storage organs can be an effective means of reducing postharvest losses. Additional research is necessary to improve our ability to use current procedures, and to increase our understanding of those factors that reduce the effectiveness of Ca enrichment under certain environmental conditions and for certain cultivars.

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Global Regulation of Pectinases and Other Degradative Enzymes in *Erwinia carotovora* subsp. *carotovora,* The Incitant of Postharvest Decay in Vegetables

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Among the myriad bacteria present in our environment, only a small minority can cause diseases in plants, animals, or humans. It seems plausible that such bacteria have co-evolved with their hosts, acquiring traits that allow them to colonize host tissues and produce symptoms by triggering deleterious physiological responses or by destroying preformed structural components. An example of the latter is the elicitation of soft rot in a variety of plant tissues by a microbial consortium containing several *Erwinia* species as the primary component (Perombelon, 1987; Perombelon and Kelman, 1980). These bacteria produce an array of degradative enzymes that act on middle lamella and plant cell wall polysaccharides and proteins, weakening or solubilizing them, and ultimately causing cell separation and death.

Most commonly found enzymes in cultures of soft-rot bacteria or in rotted (i.e., macerated) tissues are pectinases, cellulases, proteases, and phospholipases (Bateman and Millar, 1966; Chatterjee and Vidaver, 1986; Collmer and Keen, 1986). Theoretical considerations alone imply that these enzymes, by acting on such structural components as pectin, cellulose, wall proteins (including hydroxyproline-rich glycoproteins), and membrane phospholipids, could inflict physiological and physical stress to which host tissues may ultimately succumb. Indeed, genetic and biochemical evidence indicates a crucial role for some of the pectinases in the elicitation of soft rot (Barras et al., 1987; Boccara et al., 1988; Collmer and Keen, 1986; Payne et al., 1987; Ried and Collmer, 1988; Roberts et al., 1986; Thum et al., 1987). In contrast, there is no convincing evidence for cellulase, protease, or phospholipase activities in the elicitation of tissue maceration by *Erwinia* spp., with the possible exception of *E. carotovora* subsp.

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