Why Is ‘Honeycrisp’ so Susceptible to Bitter Pit?

Lailiang Cheng[1] and Mario Miranda Sazo[2]
[1]Horticulture Section, School of Integrative Plant Science, Cornell University, Ithaca, NY
[2]Cornell Cooperative Extension, Lake Ontario Fruit Program, Newark, NY

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‘Honeycrisp’ is a major apple variety grown in New York and other northern apple-producing states in the US. Due to the high consumer demand generated by its unique crispy texture, apple growers get a much higher wholesale price on ‘Honeycrisp’ than most other varieties ($600 to $1,000 vs. $125 to $300 per bin). However, ‘Honeycrisp’ fruit is very susceptible to bitter pit, a physiological disorder related to calcium (Ca) deficiency. Based on reports from packing houses, industry representatives, and fruit extension agents in New York, Michigan, Pennsylvania and Washington, it is estimated that growers lose about 15–25% of the ‘Honeycrisp’ crop to bitter pit on average and up to 60–80% in extreme cases, which causes significant economic losses to NY apple growers and the entire US apple industry.

> **“By comparing ‘Honeycrisp’ with ‘Gala’ and ‘Honeycrisp’ fruits with or without bitter pit in terms of tissue nutrient levels, we found that ‘Honeycrisp’ fruit had only half the calcium, but nearly 50% more potassium in the peel than ‘Gala’; and the imbalance of Ca with K and other nutrients in fruit peel is closely associated with bitter pit development.”**

Bitter pit development is related to localized Ca deficiency in fruit, but bitter pit incidence is only loosely correlated with bulk fruit Ca level in a negative manner (Ferguson and Watkins 1989; Rosenberger et al. 2004). Growers have been using foliar Ca sprays to provide supplemental Ca to fruit for mitigating the problem, but the effectiveness of these sprays varies considerably between orchard blocks and between growing seasons. Currently we do not have a good understanding of why ‘Honeycrisp’ is so susceptible to bitter pit, which hampers the development of new strategies to effectively control the problem.

It has been demonstrated that function of the cell membrane is dependent on the amount of Ca bound to the membrane, which is in an equilibrium with Ca in the intercellular space (Hanson 1960). The parenchyma cells of fruit with bitter pit are characterized by leaky membranes and disintegration of the membranes due to low Ca (De Freitas et al. 2010). So, from a physiological standpoint, it is the cell membrane-bound Ca that is closely related to cell membrane function and bitter pit occurrence. There are several steps in Ca uptake and partitioning that affect the cell membrane Ca level in fruit (Figure 1). First, the amount of Ca taken up by the roots is affected by rootstock genotype, soil Ca availability and its balance with other cations such as K and Mg, soil moisture and root growth and function. Second, once Ca is taken up by roots, its partitioning between leaves and fruit is driven by transpiration. As fruit transpires much less water than do leaves, fruit gets only a fraction of the total Ca taken up by roots. Our previous work showed that only 14% of the Ca transported to the aboveground is partitioned into the fruit in ‘Gala’, a bitter pit-resistant variety (Cheng and Raba 2009). Finally, the Ca delivered to fruit is partitioned to subcellular compartments, including cell wall structures, cell membranes, cytosol and vacuoles. This cellular partitioning of Ca and its balance with other cations may affect the level of cell membrane-bound Ca and bitter pit occurrence (De Freitas and Mitcham 2012).

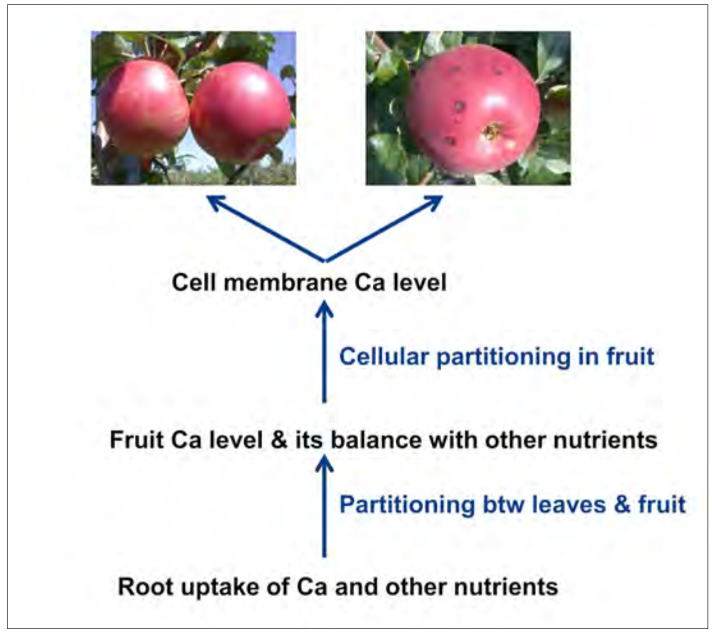

Figure 1. Bitter pit susceptibility in relation to uptake and partitioning of Ca and other nutrients.

As the first step towards understanding the susceptibility of ‘Honeycrisp’ to bitter pit, we determined Ca level and its balance with other nutrients in leaves and fruit of ‘Honeycrisp’ and ‘Gala’, and also compared ‘Honeycrisp’ fruits with or without bitter pit in terms of fruit nutrient levels.

Materials and Methods

Orchard site

Mature ‘Honeycrisp’/M.9 trees with moderate levels of bitter pit and adjacent mature 'Gala'/M.9 trees (no bitter pit at all) were selected for this experiment at a site 3.6 miles from the Lake Ontario shoreline in Alton, NY (lat. 43˚13'N, long. 76˚58'W, elevation 365 ft). The orchard is located on a Williamson silt loam soil with a silt loam profile from 0 to 8 inches and a very fine sandy loam from 8 to 20 inches depth (Natural Resource Conservation Service, NRCS 2013). There was adequate rainfall, and trees grew normally without experiencing water stress during the 2015 fruit growing season. In the first four months (April–July), there was a total of 13.61" of rainfall, and 1.20", 5.68", and 0.38" of rainfall in the months of July, August, and September, respectively. There were only seven days with temperatures above 85˚F in July and August and only two days above 85˚F in the first 15 days of September. All trees received standard disease and insect control. Both cultivars received the same foliar and ground nutrient applications throughout the growing season. Yields averaged 800 and 1,000 bushels/acre for 'Honeycrisp' and 'Gala', respectively.

Tissue sampling, preparation, and nutrient analysis

Five replicate samples of leaves (50 leaves per sample) and fruits (50 to 150 fruits per sample) of each fruit type (with and without bitter pit) were taken at harvest on 15 Sept 2015. After being brought to the lab, two types of tissue were sampled for fruits with bitter pit: pitted tissue, and apparently healthy tissue at the calyx end. Peel and outer cortex tissues were taken separately. For fruits without bitter pit, both peel and outer cortex tissues at the calyx end were taken. These samples were frozen in liquid nitrogen, and then freeze-dried with a freeze-dryer (Labconco Corporation, Kansas City, MO) for nutrient analysis. Nitrogen was analyzed via combustion analysis with a Leco C/N analyzer (LECO, St. Joseph, MO) and all the other nutrients were wet digested and analyzed using a Spectro Arcos inductively coupled plasma atomic emission spectrometer (Spectro Analytical Instruments Inc., Kleve, Germany).

Results

Leaf nutrient concentrations of 'Honeycrisp' and 'Gala'

No difference in leaf N or S levels was detected between 'Honeycrisp' and 'Gala'. However, compared with 'Gala', 'Honeycrisp' had a higher Ca level, but lower levels of P, K and Mg in the leaves (Figure 2).

Fruit nutrient concentrations and nutrient ratios of 'Honeycrisp' and 'Gala'

In the flesh tissue, 'Honeycrisp' and 'Gala' had comparable levels of K, Mg and P, but 'Honeycrisp' had much lower concentrations of Ca compared with Gala (Figure 3). The ratios of K/Ca, Mg/Ca, (K+Mg)/Ca and P/Ca in 'Honeycrisp' were significantly higher than in 'Gala' (Figure 4).

In the peel, 'Honeycrisp' had a much lower concentration of Ca and much higher concentrations of K and P than 'Gala', with comparable Mg concentrations (Figure 3), resulting in higher values of K/Ca, Mg/Ca, (K+Mg)/Ca and P/Ca (Figure 4).

Fruit nutrient concentrations and nutrient ratios of 'Honeycrisp' with and without bitter pit

In the flesh, the pitted tissue (BP) of 'Honeycrisp' fruit with bitter pit had significantly higher concentrations of K, Mg and P than the apparently healthy tissue (BPH) of fruit with bitter pit

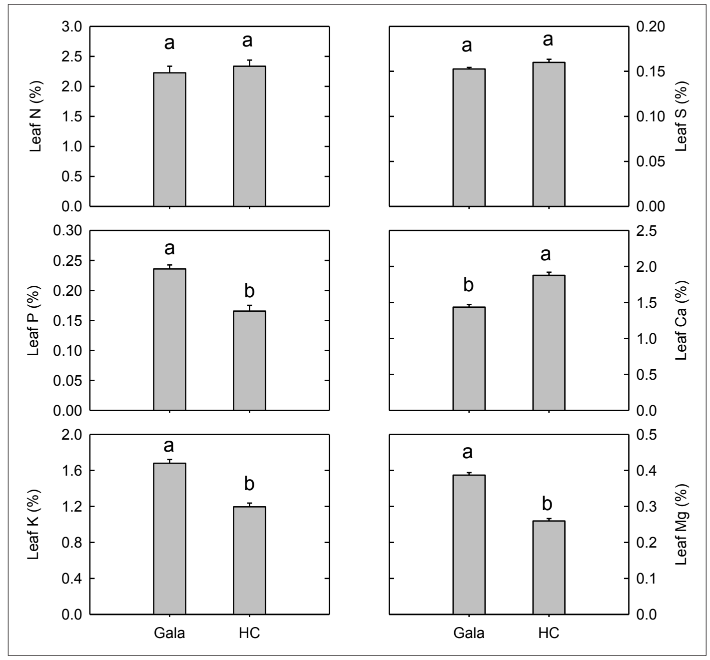

Figure 2. Leaf nutrient levels in samples taken from mature Honeycrisp/M.9 and Gala/M.9 trees at fruit harvest. Different letters indicate significant difference at P<0.05 via t-test.

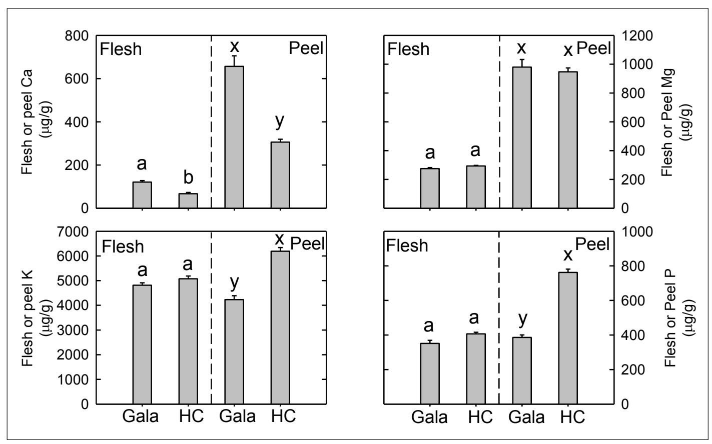

Figure 3. Flesh and peel nutrient levels of Honeycrisp and Gala at fruit harvest. Different letters indicate significant difference at *P*<0.05 via t-test.

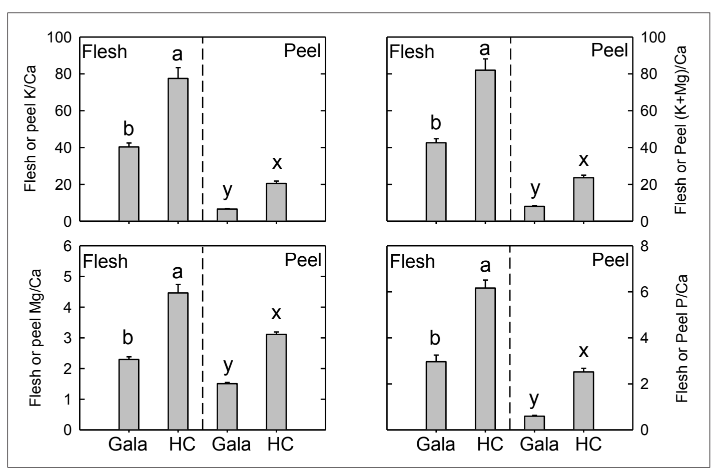

Figure 4. Flesh and peel nutrient ratios of Honeycrisp and Gala at fruit harvest. Different letters indicate significant difference at *P*<0.05 via t-test.

and the control (CK) (Figure 5). The apparently healthy tissue of fruit with bitter pit had a slightly lower Ca level, but the pitted tissue had a slightly higher Ca level than that of the control. The level of Mg was similar between the apparently healthy tissue of fruit with bitter pit and the control, but their levels of P and K were significantly different. These changes led to higher values of K/Ca, Mg/Ca, (K+Mg)/Ca and P/Ca in the apparently healthy tissue and pitted tissue than in the control (Figure 6).

In the peel, the pitted tissue (BP) of 'Honeycrisp' fruit with bitter pit had significantly lower concentrations of Ca and significantly higher concentrations of K, Mg and P than the apparently healthy tissue (BPH) of fruit with bitter pit and the control (CK) (Figure 5). The apparently healthy peel of fruit with bitter pit had significantly higher K and P levels than the control (CK), but the Mg levels were similar between the apparently healthy peel and the control. As a result, the apparently healthy peel and the pitted peel had significant higher values of K/Ca, Mg/Ca, (K+Mg)/Ca and P/Ca than the control (Figure 6).

Discussion

Comparison of fruit nutrient levels between 'Honeycrisp' and 'Gala' clearly show that high susceptibility of 'Honeycrisp' to bitter pit is closely linked to its imbalance of Ca with other nutrients such as K and P. In fruit flesh, the nutrient imbalance is solely caused by lower Ca level in 'Honeycrisp', as there was no difference in other nutrients between 'Honeycrisp' and 'Gala' (Figure 3 and 4). However, in fruit peel tissues, the nutrient imbalance in 'Honeycrisp' results from both a lower Ca level and higher K and P levels (Figures 3 and 4). Comparison of 'Honeycrisp' fruits with and without bitter pit indicates that the imbalance of Ca with K and P in peel tissues is more closely associated with bitter pit development than in flesh tissues (Figures 5 and 6). So, it is most likely that both a lower level of Ca levels and higher levels of K and P contribute to higher susceptibility of 'Honeycrisp' to bitter pit.

In 'Gala', about 14% of the total Ca supplied to the new growth (shoots, leaves and fruit) from roots is partitioned to fruit (Cheng and Raba 2009). Compared with 'Gala', a higher leaf Ca level and a lower fruit Ca level detected in 'Honeycrisp' (Figures 2 and 3) clearly indicate that much less Ca is partitioned to fruit in this variety (almost 50% less). This more acute partitioning of Ca between fruit and leaves in 'Honeycrisp' predisposes this variety to Ca deficiency and development of bitter pit. As the partitioning of Ca between fruit and leaves is entirely driven by their transpiration rates, our data suggest that either 'Honeycrisp' fruit have a significantly lower transpiration rate than 'Gala', or 'Honeycrisp' leaves have a significantly higher transpiration rate than 'Gala'.

Increasing fruit Ca level has been the main approach growers have taken to mitigate bitter pit incidence. This includes 1) adjusting soil pH to 6.5–7.0 to make sure there is enough Ca in the soil (Stiles and Reid 1991; Cheng and Stiles 2004; Cheng 2015; Miranda Sazo and Cheng 2017), which is particularly important for acid soils in the eastern US; 2) promoting root growth and

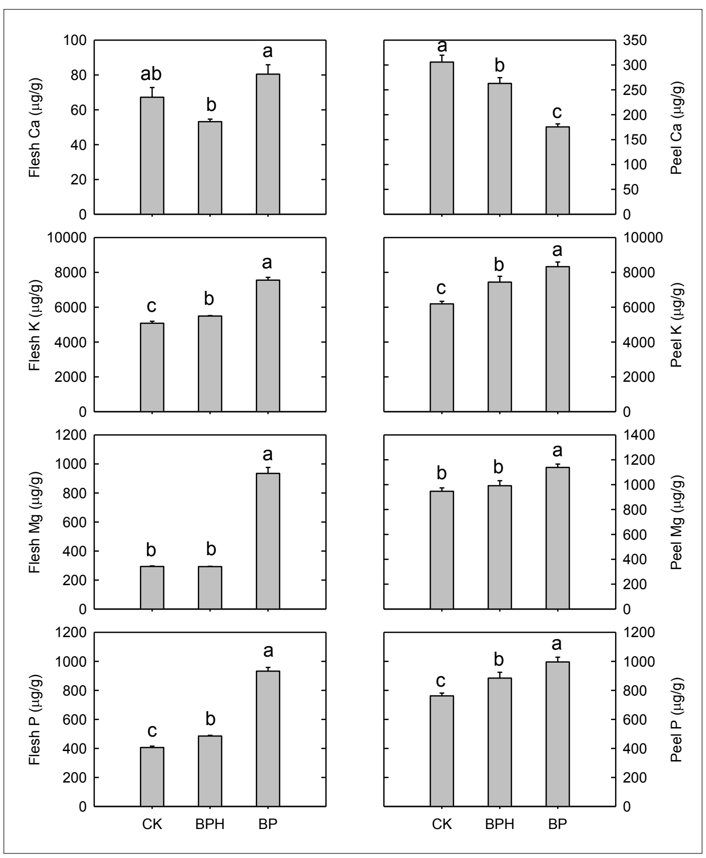

Figure 5. Flesh and peel nutrient levels of Honeycrisp fruits with or without bitter pit at fruit harvest. CK: fruit without bitter pit; BPH: healthy tissue of fruit with bitter pit; BP: bitted tissue of fruit with bitter pit. Different letters indicate significant difference at *P*<0.05 via Duncan's multiple range test.

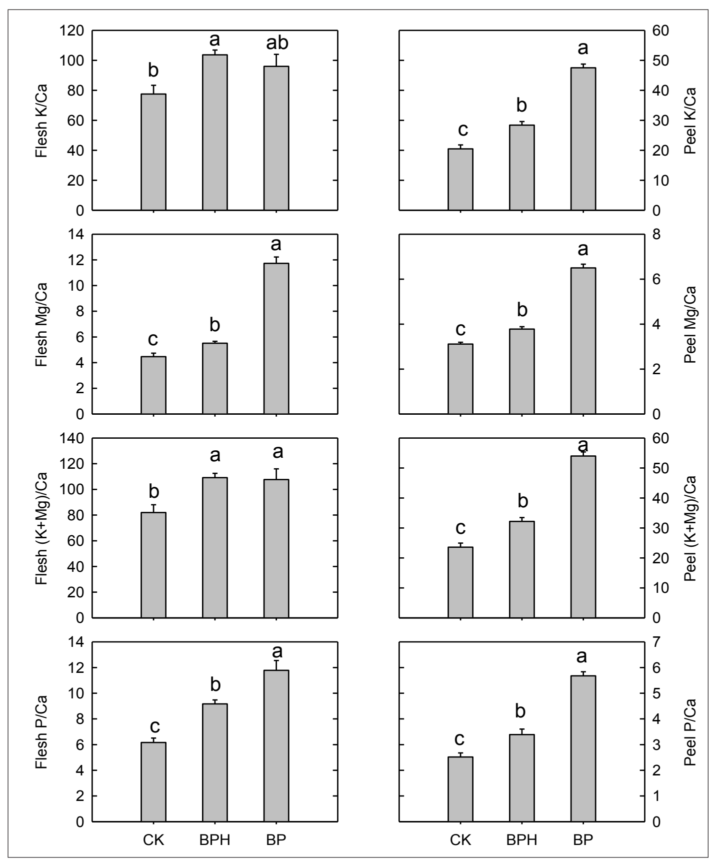

Figure 6. Flesh and peel nutrient ratios of Honeycrisp fruits with or without bitter pit at fruit harvest. CK: fruit without bitter pit; BPH: healthy tissue of fruit with bitter pit; BP: bitted tissue of fruit with bitter pit. Different letters indicate significant difference at *P*<0.05 via Duncan's multiple range test.

function by optimizing soil moisture level and micronutrient supply such as boron and zinc to ensure adequate Ca uptake; 3) strictly controlling vegetative growth (shoots and leaves) to promote Ca partitioning into fruit; and 4) making direct sprays of Ca to fruit. When Ca sprays are used to prevent bitter pit, it is important to apply enough Ca (at least 3 lbs of elemental Ca per acre per season), and frequent sprays are more important than making sprays at a particular time during the growing season (Rosenberger et al. 2004; Watkins et al. 2004). Recent work done by Baugher et al. (2017) confirms that both tree N status and shoot growth are important factors contributing to bitter pit incidence in 'Honeycrisp'. Field experiments with multiple applications of foliar abscisic acid sprays have shown that inhibiting leaf transpiration enhances Ca partitioning into fruit and reduces bitter pit incidence (Francescatto et al. 2017, unpublished data).

Considering that 1) 'Honeycrisp' fruit have lower Ca levels in both flesh and peel tissues and higher K levels in peel than 'Gala' (Figure 3); and 2) there is 20–50 (peel) to 80–100 (flesh) times more K than Ca in 'Honeycrisp' fruit (Figures 4 and 6), we think that decreasing fruit K level would be as important as increasing fruit Ca level to bringing Ca into balance with K for the purpose of mitigating the bitter pit problem. This includes 1) reducing the input of K during pre-plant soil preparations to maintain a ratio of K to Ca at 6–7.5% instead of 9.5–10% for most varieties; and 2) keeping leaf K level at the lower end (1.2–1.3%) of the optimal range (1.3–1.8%); and 3) for maintenance application of K, reducing the rate by 25–30% that was recommended for 'Gala', 'Empire' and 'McIntosh' at the same yield level (Cheng et al. 2014). If your soil analysis indicates that there is over 400 lbs of K in the top 6" of soil per acre, we suggest skipping K fertilization for one to two years to draw down the soil K reserves and then make a decision based on leaf analysis. Preliminary field experiments using this approach have shown that decreasing K supply improves the balance of Ca with K, lowering bitter pit incidence in 'Honeycrisp'. We expect that the effectiveness of this approach on bitter pit control will be dependent on the background tree K status and its balance with Ca.

A high K level decreases Ca uptake into apple fruit due to the competition between the two. It has been demonstrated in 'Cox Orange Pippin', another bitter pit-susceptible variety, that low cropload elevates fruit K level, leading to lower fruit Ca level, higher fruit K/Ca ratio, and higher bitter pit incidence (Ferguson and Watkins 1992). The same mechanism operates in 'Honeycrisp' under a low cropload situation (Telias et al. 2006). So, strictly controlling cropload to 4 fruits/cm^2 trunk cross-sectional area (TCA) for young trees (year 2 to year 4) and 5–7 fruits/cm^2 TCA for older trees (Robinson and Watkins 2003; Robinson 2008; Robinson et al. 2009) is important not only for minimizing biennial bearing, but also for balancing Ca and K and mitigating bitter pit incidence in 'Honeycrisp'.

Bitter pit incidence is often higher in a dry year, especially when drought stress occurs early in the growing season during fruit cell division, because Ca uptake is compromised by the lack of soil moisture. However, we have observed that bitter pit also occurs under excessive irrigation conditions or in a wet year for a different set of reasons: 1) excess water supply promotes K uptake to a degree that significantly inhibits Ca uptake into fruit; 2) overly vigorous shoot growth stimulated by excess water competes with fruit for Ca; and 3) excessive fruit growth resulting from excess water and K further dilutes Ca concentration in fruit. All these upset the balance between Ca and K.

When adjusting K level for mitigating bitter pit, it should be kept in mind that K is a critical nutrient for fruit growth, sugar accumulation and tree cold hardiness development. Lowering K to a threshold level would negatively affect fruit size and quality and tree cold hardiness. The optimal range for K levels in leaves and fruit of 'Honeycrisp' needs to be experimentally developed for 'Honeycrisp' to balance fruit growth, sugar accumulation, tree cold hardiness, Ca levels and bitter pit incidence.

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Acknowledgements

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Lailiang Cheng is a research and extension professor in the School of Integrative Plant Science, specializing in apple nutrition physiology and nutrient management. **Mario Miranda Sazo** is an Extension Associate who specializes in orchard management and orchard mechanization with the Lake Ontario Fruit Program, Cornell Cooperative Extension.