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Supplemental Nutrition Mitigates Huanglongbing Symptoms, and Improves Fruit Quality and Shelf-life of 'LB8-9' (Sugar Belle®) and 'Tango' Mandarins

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Abstract. **Huanglongbing (HLB)-affected mandarin trees produce HLB-symptomatic fruit with poor quality (e.g., small; lopsided; persistent, blotchy peel color; acidic; bitter), posing a major challenge to their marketability. Diminished feeder root biomass results in low nutrient and water uptake, contributing to poor fruit development. We investigate the effects of supplemental foliar-applied mineral nutrients [potassium (K), boron (B), and calcium (Ca)] on tree health (leaf antioxidants and phytohormones), as well as fruit quality at harvest and during ambient storage (24 ± 1 °C with 80% to 85% relative humidity for 14 d), for HLB-affected 'LB8-9' (Sugar Belle®) and 'Tango' mandarins. In both cultivars, K and B treatments resulted in larger fruit, less HLB-symptomatic fruit development, and better peel color compared with the untreated control and Ca treatments. Ca treatment resulted in greater fruit firmness and less storage decay, but fruit were small, greener, and difficult to peel, resembling immature fruit. No major differences were found in the juice sugar or the organic acids profile among treatments, suggesting the supplemental K and B treatments improve fruit size without compromising internal fruit quality in these HLB-affected mandarin cultivars. No differences were found in measured leaf enzyme activities among 'LB8-9' treatments. However, in 'Tango', the K treatment resulted in greater superoxide dismutase, ascorbate peroxidase, and catalase activities compared with the untreated control, indicating enhanced scavenging of reactive oxygen species. Phytohormone analysis showed that the abscisic acid concentration was greatest in spring, but less than the detection threshold in summer, indicating a water deficit and osmotic stress in spring, during the early stages of fruit growth. Furthermore, K and B treatments resulted in greater cytokinin and gibberellin concentrations than the untreated control, suggesting enhanced cell division, growth, and development as a result of those treatments. Taken together, K and B foliar nutritional treatments possibly reduced oxidative stress and improved hormonal balance, resulting in better tree health and fruit quality in HLB-affected mandarins.**

Huanglongbing (HLB), also known as citrus greening disease, is a severe threat to citrus-producing regions worldwide (European and Mediterranean Plant Protection Organization 2021; Jagoueix et al. 1994). To combat HLB progression in citrus orchards, mitigation strategies including tree replacement, thermotherapy, biological control, plant growth regulators, trunk injection, nutritional treatments, and more are practiced to improve tree health and fruit productivity (Li et al. 2020; Shahzad et al. 2024). Citrus production in Florida, USA, has declined by more than 90% as a result of the effects of HLB (US Department of Agriculture 2023). HLB-affected trees exhibit leaf nutrient deficiency symptoms, feeder root loss, increased fruit drop, and low yields. HLB-symptomatic fruit have poor quality and flavor; are small, lopsided, acidic, and bitter; and they also exhibit a greener and tougher peel (Bové 2006; Plotto et al. 2017). As HLB symptoms become more severe within a canopy, increasing numbers of symptomatic fruit and preharvest fruit drop can be observed (Sutton et al. 2024; Tang et al. 2020). Unfortunately, HLB-symptomatic fruit do not respond well to degreening treatment and exhibit a decreased shelf life, including increased decay resulting from organisms such as *Penicillium digitatum* and *Lasiodiplodia theobromae* (Shahzad et al. 2023).

Reduced feeder root biomass in HLB-affected trees results in less nutrient and water uptake and accumulation (Shahzad et al. 2020). Because developing fruit are strong sinks for nutrients and photoassimilates, many growers have adopted enhanced

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nutrition programs (including foliar application, which makes nutrients more readily available to the plants) to overcome the impaired feeder root system and satisfy the nutrient requirements of HLB-affected trees (Giles 2011; Morgan et al. 2016; Stansly et al. 2014; Vashisth 2020). Many nutrients are known to improve fruit growth and quality in healthy (HLB-free) citrus trees. Potassium (K) increases fruit size, peel thickness, and acid content (Obreza and Morgan 2008). Calcium (Ca) is involved in cell division and enlargement, maintaining membrane stability and cell integrity, which prolong fruit resistance to decay (Marschner 1995; McGuire and Kelman 1986). Boron (B) acts as a sugar transporter and improves fruit peel color, juice content, and yield (Graham and Webb 1991; Marschner 1995; Srivastava and Singh 2005). Although nutrient management strategies have been well studied in healthy citrus trees in the pre-HLB era, there is an urgent need to investigate the nutrient requirements of HLB-affected trees, especially K, Ca, and B, based on fruit productivity and quality improvement as well as tree health (antioxidant and phytohormone levels) in HLB-affected trees.

Unfortunately, all commercial citrus germplasm is susceptible to HLB. However, some mandarins such as the cultivars LB8-9 and Tango exhibit greater HLB tolerance compared with grapefruit and sweet orange cultivars (Stover et al. 2016). However, mandarin production is challenging in Florida, USA, because weather conditions inhibit the breakdown of peel chlorophyll, and the additional HLB presence further exacerbates poor peel color development. Nonetheless, Florida citrus growers are opting to grow mandarins; therefore, visual and physical characteristics such as size, color, peel removal force, and defect-free peel must meet consumer purchase expectations (US Department of Agriculture Agricultural Marketing Service 1997). Moreover, to meet the requirements of the domestic citrus supply chain, fresh citrus fruit from harvest to consumption must accommodate a sometimes lengthy period of distribution and marketing; therefore, a postharvest shelf life of ~2 weeks is critical.

We aimed to achieve a better understanding of the nutritional requirements of HLB-affected mandarins and to explore the underlying mechanism behind any resulting benefits in improved tree health and fruit quality in HLB-affected 'LB8-9' and 'Tango' mandarins. The specific objectives were 1) to determine the effect of supplemental, foliar-applied K, Ca, and B on changes in leaf metabolites and productivity of HLB-affected mandarin; and 2) to determine the effect of supplemental, foliar-applied K, Ca, and B on fruit quality at harvest and during storage of HLB-affected mandarin.

Materials and Methods

Plant material

Ten-year-old 'LB8-9' and 'Tango' mandarin trees grafted on trifoliate citrus hybrid 'US-897' and 'Swingle' rootstocks, respectively, and exhibiting mild HLB symptoms (including blotchy leaf and twig dieback) growing in Felda, FL, USA (lat. 26°25′16″N, long. 81°25′22″W), were used for this study for 2 years: 2018 and 2019. All mandarin trees were further confirmed for the presence of *Candidatus Liberibacter asiaticus* (*C*Las) using quantitative real-time polymerase chain reaction following the methods described by Vashisth and Livingston (2019). The same soil-applied fertilization program was followed each year, with seven split applications (January, April, May, June, July, August, and October): nitrogen (N) at 205 $kg \cdot ha^{-1}$, phosphorus at 7.2 $kg \cdot ha^{-1}$), K at 257 $kg \cdot ha^{-1}$, Ca at 82 $kg \cdot ha^{-1}$, magnesium (Mg) at 64 $kg \cdot ha^{-1}$), sulfur at 166 $kg \cdot ha^{-1}$, manganese at 0.35 $kg \cdot ha^{-1}$, zinc (Zn) at 0.62 $kg \cdot ha^{-1}$, iron at 0.94 $kg \cdot ha^{-1}$, and B at 0.44 $kg \cdot ha^{-1}$. In addition, the following supplemental foliar-applied nutrition treatments were applied: 1) control (untreated); 2) K, as potassium nitrate (0.11 kg/tree; 34 $kg \cdot ha^{-1}$); 3) Ca, as calcium nitrate (0.18 kg/tree; 56 $kg \cdot ha^{-1}$); and 4) B, as sodium borate (0.003 kg/tree; 0.94 $kg \cdot ha^{-1}$). The foliar-applied treatments were applied at 45-d intervals during the fruit development period (Jul, Sep, and Oct 2018; and Apr, May, Jun, Sep, Oct, and Nov 2019). Although the 2018 production season received fewer spray applications than those in 2019, the total amount of nutrients applied per tree per year was kept the same in both years. All the foliar-applied nutrient treatments included a surfactant (Induce, 0.15%; Helena Chemical, Collierville, TN, USA) to enhance nutrient retention and absorption on leaf and fruit peel surfaces. This study was set up using a completely randomized design, with four replicates per treatment. A group of three trees was considered one replicate, with the data collected from the middle tree.

Tree health assessment: Changes in leaf metabolites

For mineral nutrient analysis, 30 mature and fully expanded leaves from nonfruiting branches of each replicate tree per treatment were collected on 15 Jun 2018 and 15 Jul 2019. After washing and drying, the leaves were sent to Waters Agricultural Laboratories (Camilla, GA, USA) for standard nutrient analyses following the protocols described by Shahzad et al. (2020). Another set of 60 mature and fully expanded leaves from nonfruiting branches was collected from all four quadrants of the tree, pooled together to make a homogenous group at two time points [15 Mar 2019 (spring) and 15 Aug 2019 (summer)], and transported immediately in an ice-cooled cooler from Felda, FL, USA, to the Tree Fruit Production Laboratory located at the Citrus Research and Education Center, Institute of Food and Agricultural Sciences (IFAS), University of Florida, Lake Alfred, USA. Upon arrival, leaves were processed for *C*Las and carbohydrate quantification, whereas leaves used for antioxidants and phytohormones levels were flash-frozen immediately in liquid N and stored at –80 °C until further analysis. In both cultivars, *C*Las was quantified using leaf midribs following the protocols described by Vashisth and Livingston (2019). Leaf carbohydrates (glucose, fructose, sucrose, and inositol) were quantified for 'LB8-9' only using the protocols described by Tang et al. (2020). To assess the oxidative stress, enzyme activities for superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR). The content of proline, hydrogen peroxide (H_2O_2), malondialdehyde (MDA), and total soluble proteins were determined using the methods described by Khalid et al. (2020). For phytohormone quantification, the ground leaf samples were sent to the Proteomics and Metabolomics Facility, Nebraska Center for Biotechnology, University of Nebraska at Lincoln, NE, USA, to ascertain the phytohormonal profile. Hormones and their derivatives, including cytokinins [trans-zeatin riboside (tZR), cis-zeatin riboside (cZR), trans-zeatin (tZ), and cis-zeatin (cZ)], auxins [indole-3-acetic acid (IAA), methyl-indole-3-acetic acid (methyl-IAA), indole-3-acetyl-L-alanine (IAA-Ala), indole-3-acetic acid-aspartic acid (IAA-Asp), and indole-3-acetic acid conjugated with tryptophan (IAA-Trp)], gibberellins (GA_1, GA_3, GA_4, GA_8, GA_9, GA_{12}, GA_{19}, GA_{20}, GA_{24}, GA_{29}, and GA_{53}), strigolactones (orobanchol, 5-deoxystrigol, and strigol), abscisic acid (ABA), jasmonates [jasmonoyl-isoleucine (JA-Ile), jasmonic acid (JA), oxo-phytodienoic acid (OPDA)], and salicylic acid (SA) were extracted and analyzed using liquid chromatography–mass spectrometry-targeted assays as described by Hung et al. (2016). The Ca treatment was excluded for phytohormone quantification based on observations of undesirable fruit quality traits (small size and greener peel) in HLB-affected 'LB8-9' and 'Tango' in the first year (2018).

Fruit harvesting and postharvest storage

Fruit were harvested at commercial maturity in 2018 (12 Dec) and 2019 (9 Dec), and a subsample of ~60 fruit per replicate was transported immediately from Felda, FL, USA, to the postharvest laboratory located in the Department of Horticultural Sciences, IFAS, University of Florida, Gainesville, FL, USA (transport time, ~4.5 h). Upon arrival, fruit were stored overnight at 4 °C, the recommended cold storage temperature for mandarins (Ritenour et al. 2019), before being subjected to ambient storage. Fruit that were free of any damage or defects were stored at 24 ± 1 °C, with 80% to 85% relative humidity, for 14 d. Four replicates (consisting of 10 fruit each) were used for measurements of postharvest physical and compositional attributes that were sampled at three time points: 1) at harvest/prestorage (after transport to Gainesville + overnight storage at 4 °C, designated as D0), 2) after 7 d of storage (D7), and 3) after 14 d of storage (D14). The following variables were evaluated at harvest and during shelf life storage at each time point.

Variables evaluated only at harvest. All the trees were harvested manually when the fruit reached the commercial maturity standard: total soluble solids (TSS) and titratable acidity (TA) ratio ≥ 9 measured using a handheld refractometer (Pocket PAL-BX1 ACID1; Atago USA, Bellevue, WA, USA). Fruit yield is expressed as kilograms per tree. At harvest, fruit were categorized as HLB symptomatic or HLB asymptomatic based on size and shape (lopsided and small fruit with a threshold cutoff of < 60 mm were categorized as symptomatic). Fruit diameter was measured at the fruit equator using a fruit sizing loop (Cranston Machinery Co., Inc., Oak Grove, OR, USA). The sizing loop determines fruit circumference and converts it to the average diameter of the associated circle. The symptomatic and asymptomatic fruit were categorized further based on different diameter ranges: < 60 mm, 61 to 65 mm, 66 to 70 mm, 71 to 75 mm, and > 75 mm. Peel removal force, an indicator of ease or difficulty of fruit peeling, was determined using a texture analyzer (model TMS-Pro; Food Technology Corporation, Sterling, VA, USA) following the protocols described by Shao et al. (2021), with slight modifications. Briefly, using the machine's cutting system, a 17.5-mm-wide strip of peel was cut around the equator of the fruit and a crosscut was then made where ~6.4 mm of the end of the strip was pulled away to attach a clamp. The peel was then pulled, allowing the fruit to rotate freely as needed. A computer macro was set at a maximum of an 80-mm pull distance. The area under the force–distance curve was used for calculating the peel removal force (expressed in Newtons). For juice content, fruit were cut in half and juiced using a press juicer (model 2702; Brown International Crop, Covina, CA, USA). Then, the fruit juice was weighed and expressed as a percentage (w/w) of the total fruit weight. A fruit sensory attributes evaluation for 'LB8-9' mandarin was done using the generalized labeled magnitude scale (gLMS) on three different days (one replication per day; only three replicates were used) after fruit harvest, as described by Sung et al. (2019). The gLMS scale has a range from 0 to 100 points, with 0 point representing no sensation and 100 points representing the strongest imaginable sensation for the attribute being evaluated. Sixty panelists on each day were given two quarter-fruit pieces randomly from each nutritional treatment. Panelists rated the fruit for overall liking, sweetness, sourness, bitterness, and flavor intensity.

Variables evaluated both at harvest and during postharvest storage. Individual fruit weight (measured in grams) was recorded using a digital weighing balance at each time point. Fruit compression and peel puncture resistance forces (expressed in Newtons) were determined at the fruit equator using a computer-controlled texture analyzer machine (TA.HD Plus; Texture Technologies Corp., Surrey, UK) following the method described in Shahzad et al. (2023). The area under the force–distance curve was used for calculating the fruit compression forces, and positive bioyield was used to determine the peel puncture resistance forces. Peel and pulp color were measured using a colorimeter (CR-300; Minolta, Tokyo, Japan), following the protocols described in Shahzad et al. (2022), and were expressed as hue and chroma. Fruit peel thickness was measured at the fruit equator using a digital caliper (carbon fiber composite, Fisher Scientific, USA) to the nearest 0.01 mm. For fruit compositional analysis, fruit juice was hand-squeezed and stored at –30 °C. An aliquot of the composited juice was used for the following analyses. TSS (expressed as a percentage) was measured by placing a few drops of juice on the prism of an ultraprecision digital refractometer (model r2i300 Benchtop Refractometer; Reichert Technologies Inc., Depew, NY, USA). The TA percentage (based on citric acid content) was determined using a computer-controlled titremeter platter (814 USB sample processor; Metrohm, Herisau, Switzerland) following the protocols described by Shahzad et al. (2023). The TSS-to-TA ratio was determined and represented the fruit maturity index. Sugars (fructose, glucose, and sucrose) and organic acids (malic acid and citric acid) in fruit juice were determined and quantified using an Ultimate 3000 HPLC (Thermo Fisher Scientific, Waltham, MA, USA) following the protocols described by Shahzad et al. (2022). For storage decay incidence, decayed fruit were counted and removed at 2-d intervals during 14 d of storage and the incidence was expressed as a percentage cumulative decay, indicating the total percentage of infected fruit from postharvest diseases during storage.

Statistical analysis

All the data were analyzed using an analysis of variance (ANOVA) or correlation analysis in Sigma Plot v. 12 (Systat Software, San Jose, CA, USA). One-way ANOVA was used for leaf mineral nutrient analysis, fruit sensory quality evaluation, storage decay incidence, and fruit physical and biochemical attributes at D0, D7, and D14 during postharvest storage. Pearson's correlation test was used to assess correlations between leaf nutrient concentrations and fruit diameter. For tree health assessment, two-way repeated-measures ANOVA was used for leaf antioxidants and phytohormones levels to determine the differences among treatments. Because seasonal changes affect the measured variables, significant differences in nutrition treatment effects or seasons (spring or summer) were shown regardless of interaction effect (mineral nutrition × seasons).

Results of fruit physical and chemical quality attributes were similar at both harvest and during storage (2018 and 2019). Tree

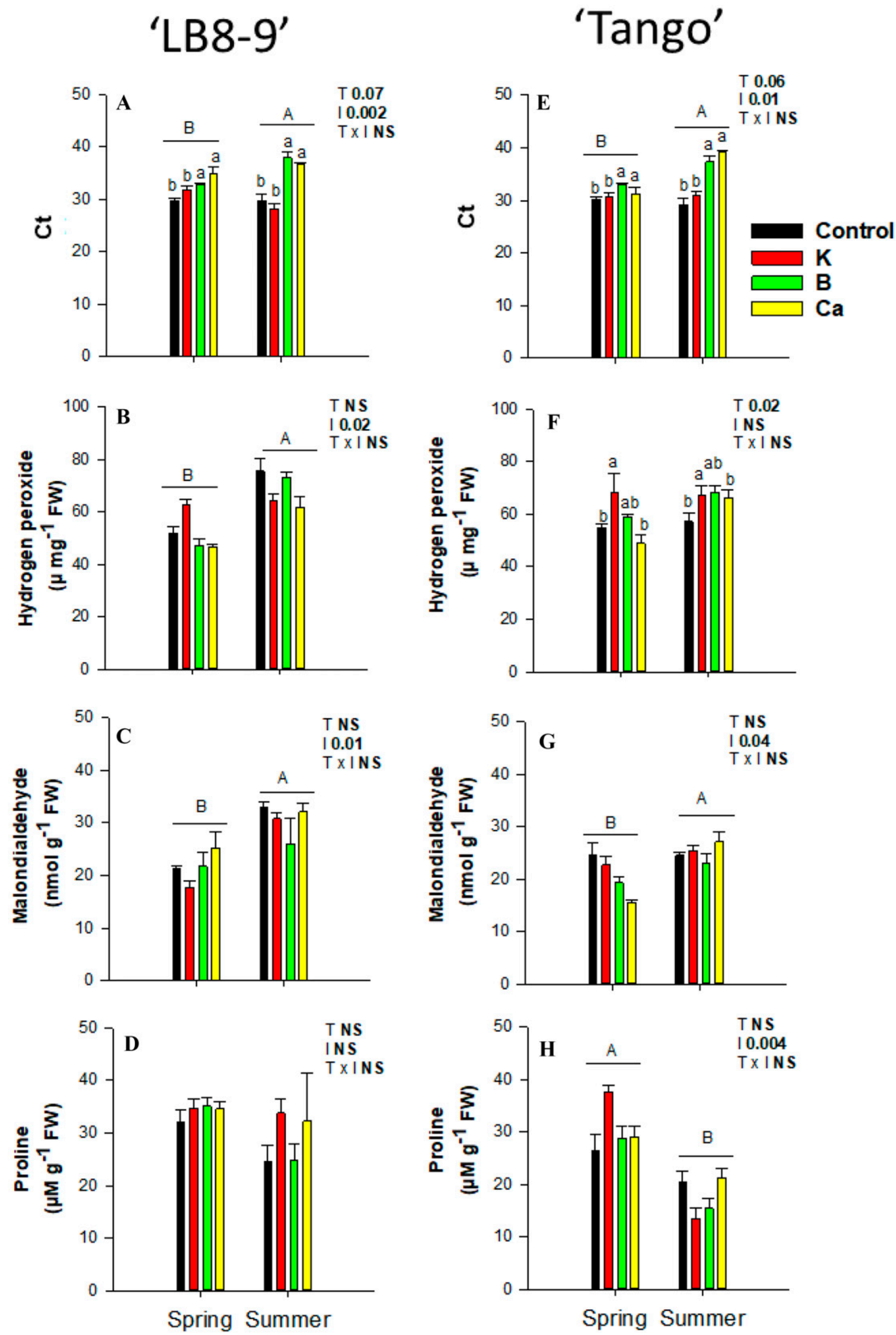


Fig. 1. Means with standard deviation for cycle threshold (Ct) value (a marker for *Candidatus Liberibacter asiaticus* presence) and hydrogen peroxide, malondialdehyde, and proline content in the leaves of Huanglongbing-affected trees of 'LB8-9' (**A–D**) and 'Tango' (**E–H**) as affected by foliar-applied mineral nutrient treatments [control, potassium (K), boron (B), and calcium (Ca)] in spring and summer. Different letters indicate significant differences among treatments ($P \leq 0.1$). Lower- and uppercase letters correspond to the nutrition treatments and seasons, respectively. FW = fresh weight; I = seasons; T = nutrition treatments; T × I = interaction between nutrition treatments and seasons. NS = nonsignificant.

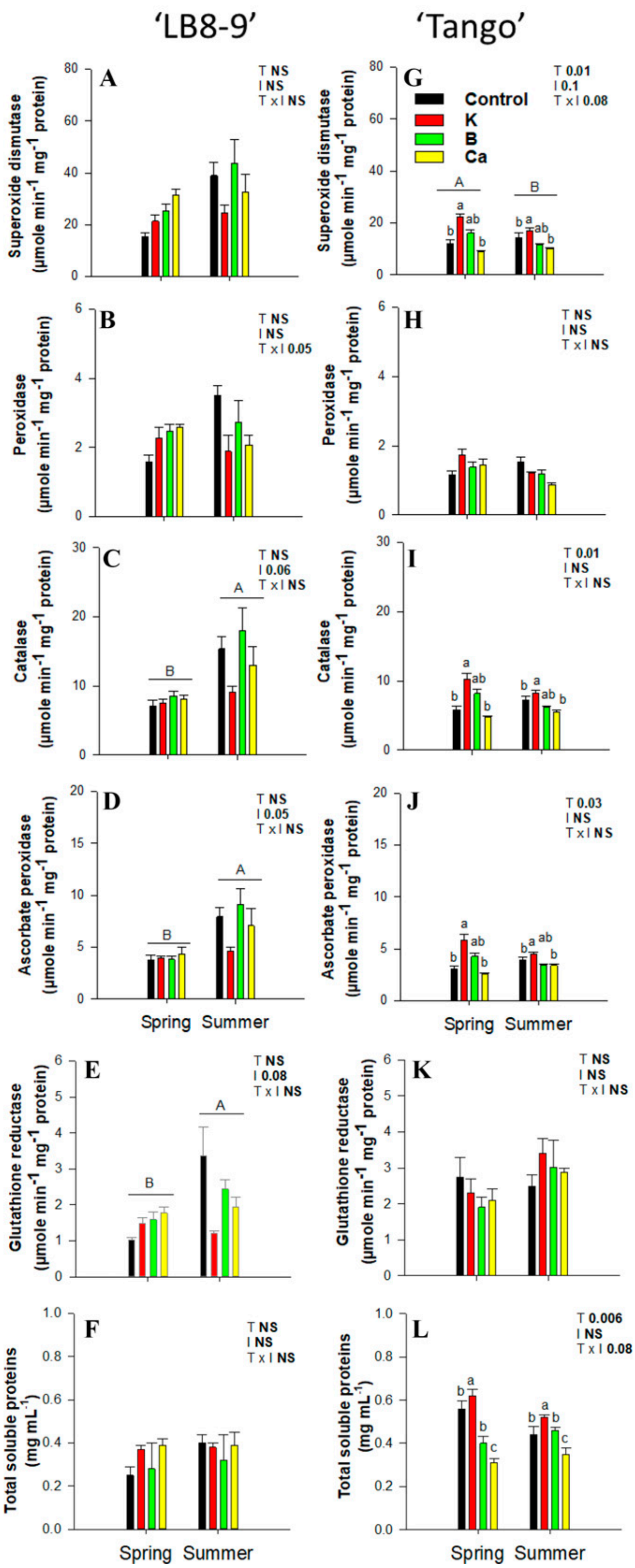


Fig. 2. Means with standard deviation for superoxide dismutase, peroxidase, catalase, ascorbate peroxidase, glutathione reductase, and total soluble protein content in the leaves of Huanglongbing-affected trees of 'LB8-9' (**A–F**) and 'Tango' (**G–L**) as affected by foliar-applied mineral nutrient [control, potassium (K), boron (B), and calcium (Ca)] in spring and summer. Different letters indicate significant differences among treatments ($P \leq 0.1$). Lower- and uppercase letters correspond to the nutrition treatments and seasons, respectively. I = seasons; T = nutrition treatments; T × I = interaction between nutrition treatments and seasons. NS = nonsignificant.

health assessment was conducted the second year of the study; therefore, the results from fruit physical and biochemical quality attributes presented herein are from 2019.

An α value of 0.1 was used for all analyses because of the high degree of HLB symptom variability seen both within and across affected trees (Nehela and Killiny 2020).

Results

Tree health assessment: Changes in leaf metabolites

Leaf mineral nutrient analyses conducted in Summer 2019 revealed that for 'LB8-9', the Ca treatment resulted in a ∼10% greater Ca concentration than the control (Supplemental Table 1). For 'Tango', the K and B concentrations were numerically highest in those respective treatments but were not found to be statistically different than the control (Supplemental Table 1). All the leaf nutrient concentrations were in the optimum range as recommended for healthy citrus by the IFAS, University of Florida, Lake Alfred, FL, USA.

In both cultivars, the B and Ca treatments had ∼16% higher cycle threshold (Ct) values (Fig. 1A and E) compared with the control and K treatments (higher Ct values suggest lower *C*Las bacterial titers, suggesting a lower HLB disease index). For 'LB8-9', leaf carbohydrate results showed an ∼32% lower sucrose content in the B treatment among all treatments (Supplemental Fig. 1). No differences in leaf glucose, fructose, and inositol contents were found in the nutrient treatments compared with the control. Regarding oxidative stress, no differences were found in MDA contents among the treatments in both cultivars (Fig. 1). For 'Tango', a 1.2-fold higher H_2O_2 content and ∼1.5-fold higher SOD, CAT, and APX activities were found in the K treatment compared with the control and Ca treatments (Figs. 1 and 2). For 'LB8-9', no differences were found in enzyme activities (SOD, POD, CAT, APX, GR) in all nutrient treatments (Fig. 2A–F). Regarding phytohormones, for 'LB8-9', GA_{24} (1.8-fold) and ABA (1.4-fold) contents were higher in the K and B treatments than in the control (Figs. 3 and 4). The B treatment had a higher OPDA content (2.0-fold) in comparison with the control (Fig. 4). For 'Tango', the control had a ∼1.3-fold higher IAA and lower cZR among the treatments (Fig. 3). The B treatment also had a higher JA content (1.4-fold) than all the other treatments (Fig. 4). No differences were found in other isoforms of phytohormones among treatments at any time points. Overall, ABA, IAA, cZR, tZR, JA, and JA-Ile concentrations were greater in spring than in summer.

Fruit at Harvest and During Postharvest Storage

Variables evaluated only at harvest. For 'LB8-9', fruit yield was ∼40% greater in the K and B treatments compared with the control and Ca treatments, whereas for 'Tango', the B treatment had a higher yield (30%) compared with the control (Table 1). Fruit external and internal aspects at harvest for both 'LB8-9' and 'Tango' are shown in Fig. 5A and B. At harvest, for 'LB8-9', the K and B treatments had an average of 14% symptomatic fruit compared with 50% in the control (Supplemental Table 2). For 'Tango', the K and B treatments had 7% symptomatic fruit compared with 12% in the control (Supplemental Table 2). In 'LB8-9', the control had the highest

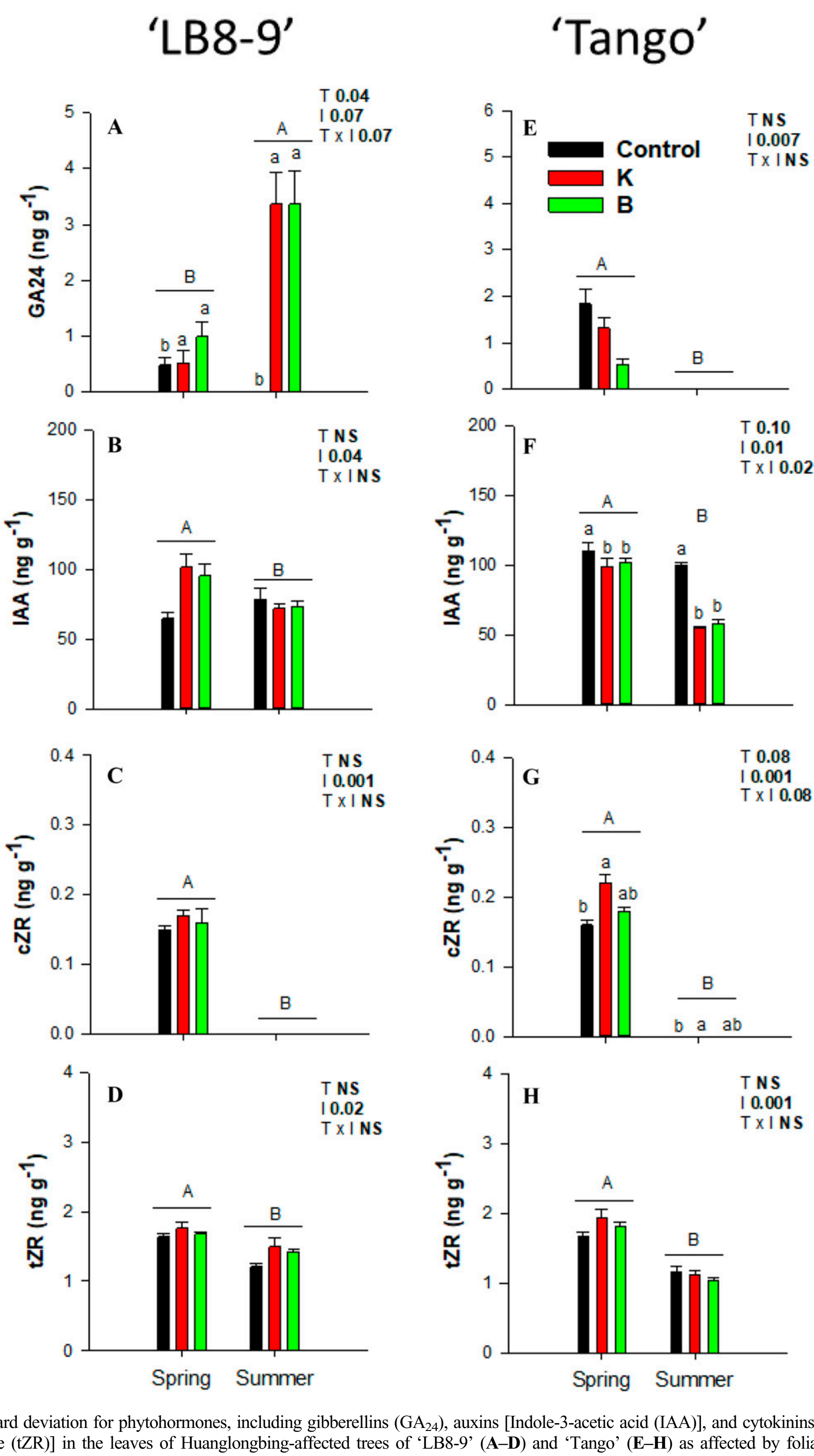


Fig. 3. Means with standard deviation for phytohormones, including gibberellins (GA_{24}), auxins [Indole-3-acetic acid (IAA)], and cytokinins [cis-zeatin riboside (cZR) and trans-zeatin riboside (tZR)] in the leaves of Huanglongbing-affected trees of 'LB8-9' (**A–D**) and 'Tango' (**E–H**) as affected by foliar-applied mineral nutrient treatments [control, potassium (K), and boron (B)] in spring and summer. Different letters indicate significant differences among treatments ($P \leq 0.1$). Lower- and uppercase letters correspond to the nutrition treatments and seasons, respectively. I = seasons; T = nutrition treatments; T × I = interaction between nutrition treatments and seasons. NS = nonsignificant.

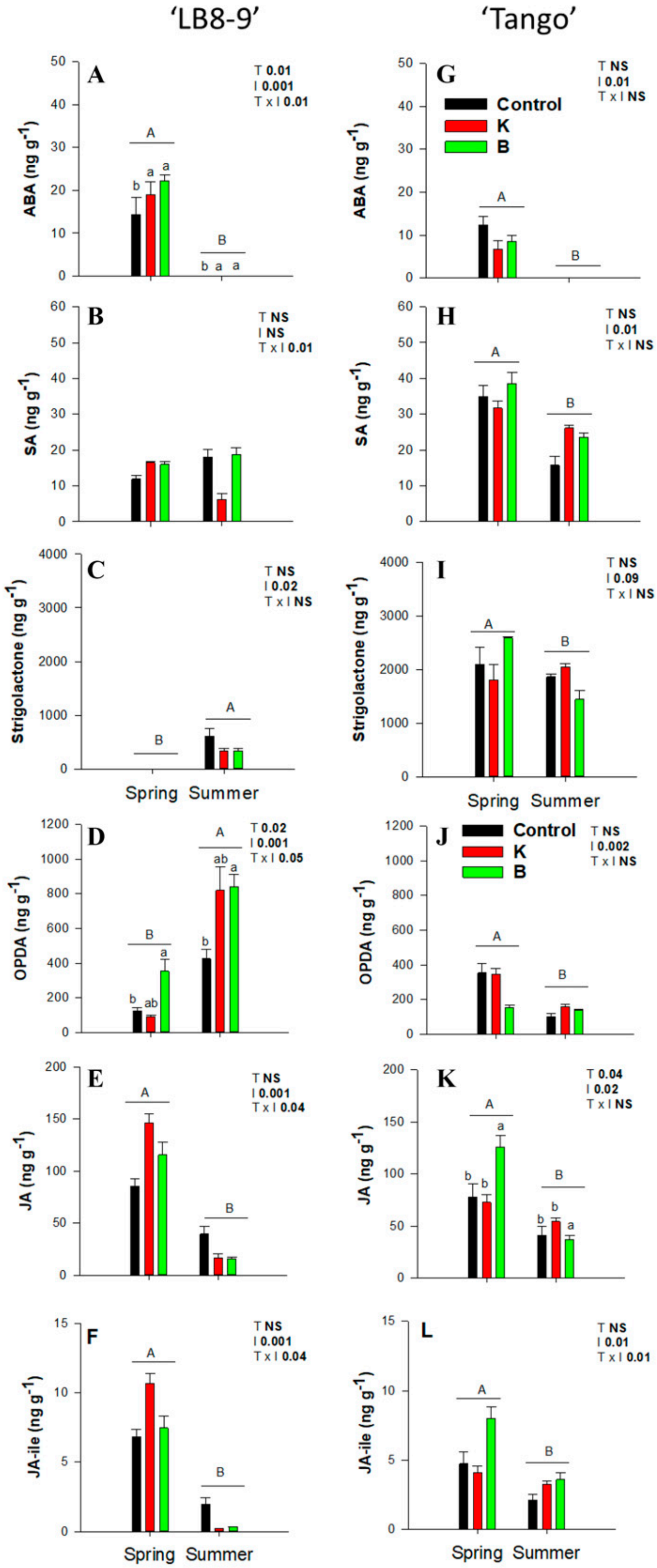


Fig. 4. Means with standard deviation for phytohormones including abscisic acid (ABA), salicylic acid (SA), strigolactone, oxo-phytodienoic acid (OPDA), jasmonic acid (JA), and jasmonoyl-isoleucine (JA-Ile), in the leaves of Huanglongbing-affected trees of 'LB8-9' (**A–F**) and 'Tango' (**G–L**) as affected by foliar-applied mineral nutrient treatments [control, potassium (K), and boron (B)] in spring and summer. Different letters indicate significant differences among treatments ($P \leq 0.1$). Lower- and uppercase letters correspond to the nutrition treatments and seasons, respectively. I = seasons; T = nutrition treatments; T × I = interaction between nutrition treatments and seasons. NS = nonsignificant.

percentage of small fruit (Supplemental Table 2). For 'Tango', the control and Ca treatments had an average of 37% of fruit in the < 60- to 65-mm class compared with 12% in the B treatment (Supplemental Table 2). Overall, the K and B treatments had 74% of the fruit in the > 66-mm class compared with 32% of the control fruit for both cultivars. For 'LB8-9', fruit diameter correlated positively with leaf K ($r = 0.40$, $P < 0.1$), whereas for 'Tango', leaf K and B concentrations correlated positively with fruit diameter (Supplemental Fig. 2). Also, there existed a positive trend of leaf K concentration with applied K, and leaf B concentration with applied B, suggesting effective uptake and mobilization of these nutrients. Peel removal force was unaffected by the treatments in both cultivars (Fig. 5C and D). For 'LB8-9', juice content was higher (21%) in the K treatment than in the Ca treatment, but was not different from the control, whereas no differences were found in juice content across all treatments in 'Tango' (Fig. 5E and F). The flavor sensory quality evaluation of 'LB8-9' showed that the K treatment was preferred for most of the traits (high overall liking, sweetness, and mandarin flavor intensity, and lower sourness) but differences between the K and control treatments were not as distinct (Fig. 5G–K).

Variables evaluated both at harvest and during postharvest storage. For both cultivars, individual fruit weight was ∼12% greater in the K and B treatments than in the control and Ca treatments (Table 1). At harvest and during storage, 'LB8-9' fruit compression forces were greater (18%) in the Ca treatment compared with the B treatment and the control, although not different from the K treatment (Table 1). In 'Tango', the Ca treatment had greater fruit compression forces (14%) than the control. For both cultivars, peel puncture resistance forces were greater (15%) in the Ca treatment compared with the control at harvest and on D7, and no differences were found on D14 of postharvest storage (Table 1). Peel thickness was ∼14% greater in all nutrient treatments than in the control for 'LB8-9', whereas no differences were found for 'Tango' (Table 1). For both cultivars, the peels of the control, K, and B treatments had lower hues (lower values indicating more orange) and higher chroma (higher values indicating more pure color) than the Ca treatment (Fig. 6A–C). On D7, the K and B treatments for 'LB8-9', and the B treatment for 'Tango' had lower peel hues (more orange) and higher peel chroma (more pure color) compared with the control and Ca treatments (Fig. 6C). On D14, the fruit peel from the K and B treatments had lower (more orange) hues than the Ca treatment for both cultivars (Fig. 6C). There were visual differences in the appearance (peel and pulp color) of the fruit from different treatments at harvest, and those were retained during storage (Figs. 5 and 6). The K treatment for 'LB8-9' had a lower (more orange) pulp hue in comparison with the rest of the treatments, whereas for 'Tango' the control had a lower hue compared with the Ca and B treatments, but it was not different from the K treatment (Supplemental Table 3). The K treatment had higher chroma compared with the control (Supplemental Table 3). On D7, for 'LB8-9', the control and K treatments had a lower pulp hue than the Ca and B treatments, whereas, for 'Tango', the control had a lower pulp hue (more orange) than the K and Ca treatments, but it was not different from the B treatment

Table 1. Fruit yield and fruit physical quality attributes at harvest and during postharvest storage for Huanglongbing-affected trees of 'LB8-9' and 'Tango' as affected by foliar-applied mineral nutrient treatments [control, potassium (K), calcium (Ca), and boron (B)].[i]

		LB8-9					Tango				
Parameter	Day	Control	K	Ca	B	P value	Control	K	Ca	B	P value
Fruit yield (kg/tree)	—	69 ± 17 b	98 ± 16 a	27 ± 14 b	105 ± 25 a	0.001[ii]	47 ± 9 b	54 ± 6 ab	61 ± 7 ab	70 ± 10 a	0.09
Fruit weight (g)	D0	135 ± 6 b	158 ± 12 a	135 ± 8 b	149 ± 4 a	0.01	128 ± 5 b	137 ± 5 a	123 ± 4 b	138 ± 6 a	0.001
Fruit weight (g)	D7	122 ± 7 b	157 ± 14 a	128 ± 6 b	141 ± 7 a	0.01	128 ± 4 b	131 ± 4 a	120 ± 8 b	137 ± 5 a	0.001
Fruit weight (g)	D14	117 ± 9 b	128 ± 9 a	113 ± 13 b	137 ± 9 a	0.02	122 ± 2 b	128 ± 3 a	119 ± 8 b	138 ± 4 a	0.002
Compression force (N)	D0	66 ± 3 b	66 ± 2 ab	78 ± 9 a	62 ± 4 b	0.003	61 ± 4 b	68 ± 2 ab	71 ± 4 a	64 ± 6 ab	0.04
Compression force (N)	D7	60 ± 2 b	63 ± 2 ab	65 ± 2 a	59 ± 3 b	0.05	42 ± 1 b	44 ± 2 ab	46 ± 2 a	44 ± 2 ab	0.02
Compression force (N)	D14	49 ± 2 b	53 ± 2 ab	57 ± 2a	50 ± 2 b	0.002	29 ± 1 b	30 ± 2 ab	32 ± 1 a	31 ± 1 ab	0.02
Peel puncture resistance (N)	D0	17.6 ± 1.5 b	18.4 ± 0.8 ab	20.7 ± 1.2 a	18.2 ± 1.3 ab	0.01	16.5 ± 1.5 b	19.0 ± 2.1 ab	19.5 ± 1.3 a	17.9 ± 1.3 ab	0.03
Peel puncture resistance (N)	D7	15.4 ± 0.6 b	16.2 ± 0.9 ab	18.4 ± 1.0 a	15.4 ± 0.8 b	0.002	15.6 ± 0.3b	16.7 ± 0.6 ab	17.6 ± 0.8 a	16.5 ± 1.3ab	0.02
Peel puncture resistance (N)	D14	14.7 ± 0.6	16.4 ± 0.8	17.7 ± 1.0	16.5 ± 0.9	NS	13.7 ± 1.3	14.1 ± 0.8	14.5 ± 0.8	15.0 ± 0.1	NS
Peel thickness (mm)	D0	2.4 ± 0.1 b	3.0 ± 0.1 a	2.8 ± 0.1 a	3.1 ± 0.1 a	0.001	2.6 ± 0.2	2.7 ± 0.2	2.5 ± 0.1	2.6 ± 0.2	NS
Peel thickness (mm)	D7	2.3 ± 0.1 b	2.9 ± 0.1 a	2.8 ± 0.1 a	2.9 ± 0.1 a	0.01	2.4 ± 0.7	2.5 ± 0.7	2.4 ± 0.6	2.5 ± 0.7	NS
Peel thickness (mm)	D14	2.0 ± 0.1 b	2.4 ± 0.1 a	2.2 ± 0.1 a	2.2 ± 0.1 a	0.003	1.8 ± 0.6	1.8 ± 0.5	1.9 ± 0.5	2.1 ± 0.6	NS
Storage decay incidence (%)	D14	13 ± 7 a	17 ± 6 a	11 ± 3 b	13 ± 5 a	0.09	17 ± 4 a	18 ± 3 a	10 ± 3 b	18 ± 3 a	0.05

[i] Means with standard deviation within rows followed by different letters are significantly different ($P \leq 0.1$).
[ii] Values in bold type are significant.
D0 = at harvest; D7 = 7 d after harvest; D14 = 14 d after harvest.
NS = nonsignificant.

(Supplemental Table 3). On D14, for 'LB8-9', the Ca treatment had the highest hues in all treatments; for 'Tango', the K treatment pulp had higher pulp hues than the control (Supplemental Table 3).

At harvest, the juice of 'LB8-9' fruit from the B treatment had an ~25% lower TA and a higher TSS-to-TA ratio compared with the control, but no differences were found among treatments for 'Tango' (Table 2). For both cultivars, no other differences were found in TSS, glucose, and fructose in all treatments at harvest and during storage (Table 2; Supplemental Table 4). No differences were found in sucrose among treatments for 'LB8-9' at any time point, whereas for 'Tango' the Ca treatment had lower sucrose (12%) than all the other treatments on D7, and the control and Ca treatments had lower sucrose (9%) compared with the K and B treatments on D14 (Table 2). For 'LB8-9', the B treatment had less citric acid (22%) compared with the control at harvest and on D7, and the B treatment had more malic acid (12%) at harvest compared with the control. No other differences were found in acid concentrations during storage for both cultivars (Table 2).

Decay incidence was ~30% less in the Ca treatment compared with the other treatments for both cultivars (Table 1). In our study, green mold (*P. digitatum*) and stem end rot (*L. theobromae*) were the most prominent causal organisms for decay during storage.

Discussion

Because of widespread *C*Las infection in citrus orchards, the Florida, USA, citrus industry relies on findings of sustainable solutions to help decelerate HLB symptom severity development through easy-to-apply, efficient, and cost-effective methods. Our 2-year-long field trials show the positive effects of supplemental foliar nutrient treatments (K and B) to mitigate HLB symptoms and improve fruit quality both at harvest and during storage in the HLB-affected mandarins 'LB8-9' and 'Tango'. Our results indicate that foliar K and B treatments resulted in larger fruit size compared with the control for both 'LB8-9' and 'Tango', thus increasing productivity as seen by greater fruit yield. Reports in the literature suggest that K-related improvements in fruit size could be ascribed to improved solute transport through the phloem (White and Karley 2010), enzyme activation in energy production [adenosine triphosphate (ATP)] (Brunt and Sultenfuss 1998), and a potential role in osmoregulation (as HLB-affected trees have reduced water and nutrient uptake capacity). On the other hand, B has been found to be involved in sugar and acid translocation (Graham and Webb 1991), and maintenance of normal leaf transpiration and hydraulic conductivity of xylem and vascular tissues (Wimmer and Eichert 2013). Therefore, it is reasonable to speculate that in our research, K and B determined the final fruit growth and final size via stimulation of ATP, osmoregulation, and carbohydrate transport. Most mandarin growers in Florida, USA, harvest fruit when they meet minimum maturity standards to escape excessive preharvest fruit drop; however, the fruit may still show a green peel color (Whitney and Harrell 1989, Wardowski et al. 2006). Moreover, Florida's subtropical weather hinders the breakdown of peel chlorophyll and peel color development. Our results show that, in both cultivars, the K and B treatments attained the desired peel color attributes (higher chroma and lower hues, indicating more pure and more orange color), thus eliminating the need for degreening. In addition, the peel removal force was less in fruit from the K

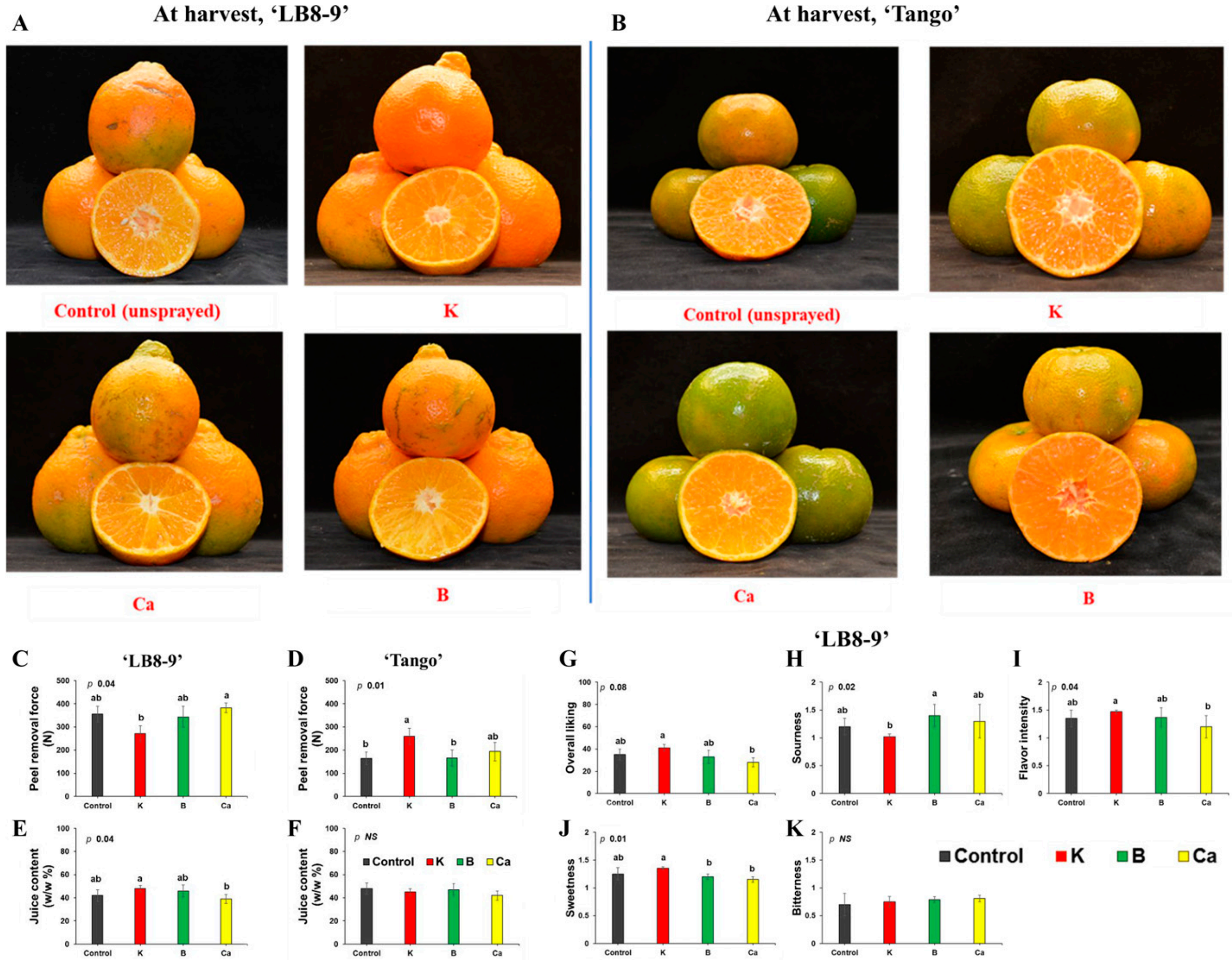
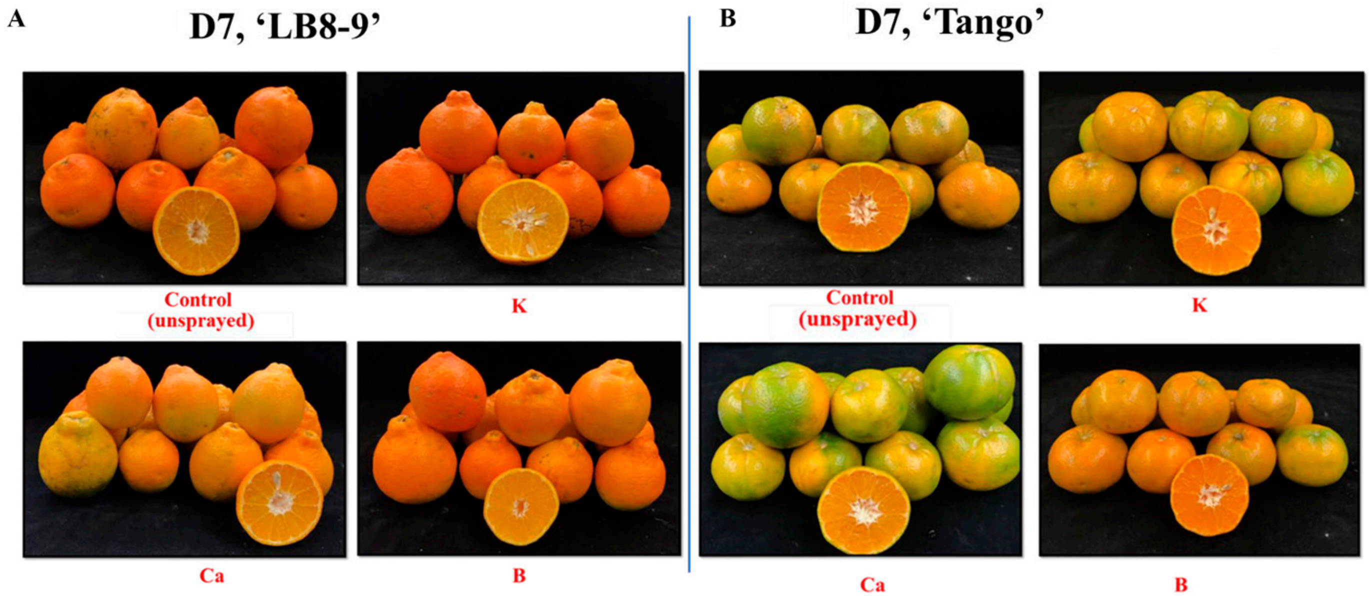


Fig. 5. At harvest (D0), external and internal fruit aspect (**A** and **B**), and means with standard deviation for fruit peelability force (**C** and **D**) and fruit juice content (**E** and **F**) at harvest for Huanglongbing (HLB)-affected trees of 'LB8-9' and 'Tango' as affected by foliar-applied mineral nutrient treatments [control, potassium (K), calcium (Ca), and boron (B)]. Postharvest, sensory characteristics—overall liking (**G**), sourness (**H**), flavor intensity (**I**), sweetness (**J**), and bitterness (**K**)—were assessed by consumer test using the generalized labeled magnitude scale for the fruit of HLB-affected 'LB8-9' trees as affected by foliar-applied nutrient treatments (control, K, Ca, and B). Different letters indicate significant differences among treatments ($P \leq 0.1$). NS = nonsignificant.

treatment for 'LB8-9' and from the B treatment for 'Tango', adding another desirable attribute for these fresh-market fruit. Results from fruit sensory quality testing indicate higher scores for sweetness and mandarin flavor intensity in the K treatment of 'LB8-9' fruit compared with the other treatments. Potassium is known to contribute to the development of better fruit taste and aroma in different fruit (Adams 1978; Cronje et al. 2009). Mandarin juice quality depends on the percentage of juice per fruit, TSS, sugars, and organic acids profile, and no major differences were found in these variables among treatments. This result suggests the successful use of K and B treatments in improving fruit size without altering internal fruit quality. Mandarin fruit firmness is essential during storage to maintain a good postharvest shelf life. Our results showed that in both cultivars, the Ca treatment resulted in greater fruit firmness and less storage decay compared with the control. Improved fruit firmness from the Ca treatment has been reported in many fruit crops to be the result of improved cell wall stability related to the cross-binding of polygalacturonate chains with Ca ions, along with decreased respiration and ethylene production rates, thus delaying ripening and senescence (Huang et al. 2023; Lara 2013; Madani and Forney 2015). However, in both cultivars, the foliar-applied Ca treatment did not improve fruit size. Similarly, foliar-applied Ca did not improve fruit size and yield in highbush blueberries (Arrington and DeVetter 2017). Taken together, these results suggest there exists an interaction between mineral nutrients and citrus genotypes. Additional research is needed to revisit and standardize fertilization strategies for commercial citrus cultivars of sweet oranges, grapefruits, limes, and lemons under HLB-prevalent conditions.

Ma et al. (2022) reported that HLB symptoms are triggered by reactive oxygen species production and accumulation, resulting in oxidative stress. Our results indicated higher SOD, CAT, and APX activities (1.5-fold) in the 'Tango' K treatment compared with the control. Neupane et al. (2023) reported that HLB-affected trees had greater resources used in defense (SA and ABA) than



C

Table. Fruit peel color attribute at harvest and during postharvest storage.

Parameter	Day		'LB8-9'				*p* value	'Tango'				*p* value
			Control	K	Ca	B		Control	K	Ca	B	
Peel color attributes	D0	hue	75±4 b	72±4 b	80±5 a	72±4 b	**0.001**	91±9 b	93±13 b	97±7 a	91±10 b	**0.001**
		chroma	65±1 b	67±1 ab	64±1 c	68±1 a	**0.01**	43±2 ab	44±2 a	40±1 b	45±1 a	**0.01**
	D7	hue	74±2 b	68±1 d	80±2 a	71±1 c	**0.001**	87±4 b	85±2 b	93±2 a	83±2 c	**0.01**
		chroma	67.1±1 b	68.7±1 a	64.9±1 c	68.6±1 a	**0.001**	49±2 b	51±2 b	45±2 c	53±2 a	**0.01**
	D14	hue	70±6 b	67±5 c	75±8 a	70±5 b	**0.001**	81±8 ab	81±5 ab	83±9 a	79±7 b	**0.02**
		chroma	70±1 a	68±1 b	68±1 b	70±1 a	**0.01**	57±2	58±2	54±2	54±2	NS

Fig. 6. External and internal fruit aspect on day 7 (D7) during postharvest storage (**A** and **B**), means with standard deviation for fruit peel color attribute at harvest and during postharvest storage (**C**) for Huanglongbing-affected trees of 'LB8-9' and 'Tango' as affected by foliar-applied mineral nutrient treatments [control, potassium (K), calcium (Ca), and boron (B)]. Means with standard deviation within rows followed by different letters are significantly different ($P \leq 0.1$).

on growth (reduction in growth-promoting hormones), contributing to poor leaf and shoot growth, resulting in thinner canopies. Supplemental GA_3 can ameliorate HLB severity symptoms and improve vegetative growth and fruit productivity in HLB-affected sweet oranges (Ma et al. 2022; Shahzad et al. 2024; Singh et al. 2022). A similar trend of a greater concentration of growth-promoting hormones (gibberellins and cytokinins) was seen in K and B treatments in our study. Stansly et al. (2014) also reported that foliar-applied nutrients (a combination of N, K, Mg, Zn) produce new foliage with more leaves, better color, and larger size compared with the standard fertilization strategies. Potassium improves carbon assimilation and vegetative growth by increasing water use efficiency and by maintaining stomatal conductance via stomatal oscillations as documented by Hasanuzzaman et al. (2018). So, it is reasonable to speculate that better growth in HLB-affected trees following nutrient treatments may coincide with a high accumulation of growth-promoting hormones.

Altogether, our results suggest that desirable mandarin fruit quality may be achieved using supplemental foliar K and B treatments (20% higher rate than the recommended dose of nutrients) that possibly reduce oxidative stress and improve hormonal balance. These effects alleviated HLB symptoms and increased fruit yield, with improved fruit quality in HLB-affected mandarin cvs. LB8-9 and Tango.

Conclusion

Foliar K and B treatments improved tree productivity and fruit size, resulted in fewer HLB-symptomatic fruit, and produced fruit with a more attractive peel color. The K and B treatments marginally affected juice quality during storage. The Ca treatment increased fruit firmness and reduced storage decay incidence, but Ca-treated fruit were small, had a greener peel, and were more difficult to peel, all of which are undesirable quality traits for fresh-market fruit. The K and B treatments improved hormonal balance (growth-promoting hormones) and antioxidant activities, which possibly reduced oxidative stress, promoted better vegetative growth, and improved fruit yield in HLB-affected mandarin cvs. LB8-9 and Tango. Altogether, supplemental K and B treatments show efficacy for improving fruit productivity and achieving all the desired fruit quality traits in HLB-affected mandarins grown under subtropical climates such as that found in Florida, USA.

Table 2. Fruit juice total soluble solids (TSS), titratable acidity (TA), TSS-to-TA ratio, sucrose, citric acid, and malic acid concentrations at harvest and during postharvest storage for Huanglongbing-affected trees of 'LB8-9' and 'Tango' as affected by foliar-applied mineral nutrient treatments [control, potassium (K), calcium (Ca), and boron (B)].[i]

		LB8-9					Tango				
Parameter	Day	Control	K	Ca	B	*P* value	Control	K	Ca	B	*P* value
TSS (%)	D0	9.9 ± 0.7	11.2 ± 0.9	11.4 ± 0.9	9.90 ± 1.7	NS	8.6 ± 0.6	8.5 ± 0.3	8.9 ± 0.3	8.9 ± 0.1	NS
TSS (%)	D7	12.4 ± 0.9	11.9 ± 0.7	10.5 ± 0.8	10.6 ± 0.5	NS	9.3 ± 0.4 a	8.9 ± 0.2 a	8.4 ± 0.1 b	9.2 ± 0.2 a	**0.002**[ii]
TSS (%)	D14	11.2 ± 1.2	11.5 ± 0.6	10.9 ± 0.9	10.9 ± 0.8	NS	9.2 ± 0.6	9.2 ± 0.1	8.8 ± 0.2	9.6 ± 0.2	NS
TA (%)	D0	0.98 ± 0.1 a	0.88 ± 0.04 ab	0.97 ± 0.01 a	0.72 ± 0.2 b	**0.03**	0.52 ± 0.03	0.59 ± 0.1	0.53 ± 0.04	0.53 ± 0.02	NS
TA (%)	D7	0.80 ± 0.04	0.85 ± 0.1	0.78 ± 0.1	0.71 ± 0.04	NS	0.49 ± 0.04	0.48 ± 0.04	0.44 ± 0.01	0.47 ± 0.03	NS
TA (%)	D14	0.87 ± 0.1	0.79 ± 0.1	0.81 ± 0.1	0.74 ± 0.1	NS	0.52 ± 0.05	0.49 ± 0.01	0.47 ± 0.02	0.50 ± 0.03	NS
TSS-to-TA ratio	D0	10.3 ± 1.7 b	12.7 ± 0.7 ab	11.7 ± 0.7 ab	13.7 ± 1.6 a	**0.01**	16.5 ± 0.9	14.8 ± 2.6	16.7 ± 0.9	16.9 ± 0.6	NS
TSS-to-TA ratio	D7	15.4 ± 0.2	14.0 ± 0.9	13.5 ± 0.6	14.8 ± 0.5	NS	19.0 ± 1.3	18.5 ± 1.5	19.3 ± 0.8	19.6 ± 1.3	NS
TSS-to-TA ratio	D14	13.0 ± 1.5	14.6 ± 1.4	13.6 ± 1.5	14.8 ± 1.6	NS	17.7 ± 1.1	18.5 ± 0.5	18.9 ± 0.4	19.3 ± 2.7	NS
Sucrose ($g·L^{-1}$)	D0	116 ± 16	147 ± 8	148 ± 9	138 ± 24	NS	99 ± 9	100 ± 1	101 ± 12	103 ± 6	NS
Sucrose ($g·L^{-1}$)	D7	149 ± 33	160 ± 11	128 ± 15	128 ± 17	NS	111 ± 7 a	105 ± 5 a	95 ± 2 b	109 ± 3 a	**0.002**
Sucrose ($g·L^{-1}$)	D14	145 ± 24	152 ± 18	139 ± 14	146 ± 15	NS	106 ± 3 b	109 ± 4 a	102 ± 2 b	114 ± 3 a	**0.05**
Citric acid ($g·L^{-1}$)	D0	11.5 ± 1.3 a	10.8 ± 0.5 ab	11.5 ± 0.2 a	8.4 ± 1.8 b	**0.02**	6.5 ± 0.3	6.5 ± 1.3	6.1 ± 0.4	6.4 ± 0.4	NS
Citric acid ($g·L^{-1}$)	D7	11.1 ± 0.9 a	10.9 ± 1.1 ab	10.2 ± 0.7 ab	9.1 ± 0.5 b	**0.05**	6.2 ± 0.6	6.2 ± 0.4	5.6 ± 0.1	6.1 ± 0.4	NS
Citric acid ($g·L^{-1}$)	D14	12.5 ± 2.7	11.5 ± 2.9	11.5 ± 2.4	10.0 ± 1.8	NS	6.4 ± 0.6	6.2 ± 0.2	5.8 ± 0.2	6.2 ± 0.5	NS
Malic acid ($g·L^{-1}$)	D0	3.0 ± 0.1 b	3.3 ± 0.1 ab	3.2 ± 0.1 ab	3.4 ± 0.1 a	**0.01**	3.8 ± 0.2	3.9 ± 0.2	3.8 ± 0.2	3.6 ± 0.2	NS
Malic acid ($g·L^{-1}$)	D7	3.1 ± 0.2	3.3 ± 0.1	3.2 ± 0.1	3.1 ± 0.2	NS	3.9 ± 0.1	3.9 ± 0.1	3.9 ± 0.1	4.1 ± 0.2	NS
Malic acid ($g·L^{-1}$)	D14	2.3 ± 1.3	2.3 ± 1.2	2.3 ± 1.2	2.7 ± 0.9	NS	4.1 ± 0.1	4.1 ± 0.2	4.1 ± 0.1	4.1 ± 0.2	NS

[i] Means with standard deviation within rows followed by different letters are significantly different ($P \leq 0.1$).
[ii] Values in bold type are significant.
D0 = at harvest; D7 = 7 d after harvest; D14 = 14 d after harvest.
NS = nonsignificant.

References Cited

Adams P. 1978. Tomatoes in peat: Part 1: How feed variation affect yield. Grower. 89:1093–1094.

Arrington M, DeVetter LW. 2017. Foliar applications of calcium and boron do not increase fruit set or yield in northern highbush blueberry (*Vaccinium corymbosum*). HortScience. 52(9):1259–1264. https://doi.org/10.21273/HORTSCI12207-17.

Bové JM. 2006. Huanglongbing: A destructive, newly-emerging, century-old disease of citrus. J Plant Pathol. 88(1):7–37.

Brunt V, Sultenfuss JH. 1998. Better crops with plant food. Potassium: Functions of Potassium. 82:4–5.

Cronje RB, Sivakumar D, Mostert PG, Korsten L. 2009. Effect of different preharvest treatment regimes on fruit quality of litchi cultivar 'Maritius'. J Plant Nutr. 32(1):19–29. https://doi.org/10.1080/01904160802530987.

European and Mediterranean Plant Protection Organization. 2025. EPPO Global data base [Candidatus Liberibacter asiaticus' (LIBEAS)]. https://gd.eppo.int/taxon/LIBEAS/distribution. [accessed 10 Feb 2025].

Giles F. 2011. Daring to be different. Florida Grower. 104(6):8–10.

Graham RD, Webb MJ. 1991. Micronutrients and disease resistance and tolerance in plants, p 329–370. In: Mortvedt JJ, Cox FR, Shuman LM, Welch RM (eds). Micronutrients in agriculture (2nd ed). Soil Science Society of America, Madison, WI, USA. https://doi.org/10.2136/sssabookser4.2ed.c10.

Hasanuzzaman M, Oku H, Nahar K, Bhuyan MB, Mahmud JA, Baluska F, Fujita M. 2018. Nitric oxide-induced salt stress tolerance in plants: ROS metabolism, signaling, and molecular interactions. Plant Biotechnol Rep. 12(2):77–92. https://doi.org/10.1007/s11816-018-0480-0.

Huang W, Shi Y, Yan H, Wang H, Wu D, Grierson D, Chen K. 2023. The calcium-mediated homogalacturonan pectin complexation in cell walls contributes the firmness increase in loquat fruit during postharvest storage. J Adv Res. 49:47–62.

Hung CY, Qiu J, Sun YH, Chen J, Kittur FS, Henny RJ, Jin G, Fan L, Xie J. 2016. Gibberellin deficiency is responsible for shy-flowering nature *of Epipremnum aureum*. Sci Rep. 6(1):28598. https://doi.org/10.1038/srep28598.

Jagoueix S, Bove JM, Garnier M. 1994. The phloem-limited bacterium of greening disease of citrus is a member of the α subdivision of the Proteobacteria. Int J Syst Evol Microbiol. 44(3):379–386. https://doi.org/10.1099/00207713-44-3-379.

Khalid MF, Hussain S, Anjum MA, Ahmad S, Ali MA, Ejaz S, Morillon R. 2020. Better salinity tolerance in tetraploid vs diploid volkamer lemon seedlings is associated with robust antioxidant and osmotic adjustment mechanisms. J Plant Physiol. 244:153071. https://doi.org/10.1016/j.jplph.2019.153071.

Lara I. 2013. Preharvest sprays and their effects on the postharvest quality of fruit. Stewart Postharvest Rev. 9(3):1–12.

Li S, Wu F, Duan Y, Singerman A, Guan Z. 2020. Citrus greening: Management strategies and their economic impact. HortScience. 55(5):604–612. https://doi.org/10.21273/HORTSCI14696-19.

Ma W, Pang Z, Huang X, Xu J, Pandey SS, Li J, Achor DS, Vasconcelos FNC, Hendrich C, Huang Y, Wang W, Lee D, Stanton D, Wang N. 2022. Citrus Huanglongbing is a pathogen-triggered immune disease that can be mitigated with antioxidants and gibberellin. Nat Commun. 13(1):529. https://doi.org/10.1038/s41467-022-28189-9.

Madani B, Forney CF. 2015. Recent research on calcium and postharvest behavior, p 19–38. In: Wills RBH, Golding J (eds). Advances in postharvest fruit and vegetable technology. CRC Press, Boca Raton, FL, USA.

Marschner H. 1995. Mineral nutrition of higher plants (2nd ed). Institute of Plant Nutrition University of Hohenheim, Hohenheim, Germany.

McGuire RG, Kelman A. 1986. Calcium in potato tuber cell walls in relation to tissue maceration by *Erwinia carotovora* pv. *atroseptica*. Phytopathology. 76(4):401–406. https://doi.org/10.5555/19861318066.

Morgan KT, Rouse RE, Ebel RC. 2016. Foliar applications of essential nutrients on growth and yield of 'Valencia' sweet orange infected with Huanglongbing. HortScience. 51(12):1482–1493. https://doi.org/10.21273/HORTSCI11026-16.

Nehela Y, Killiny N. 2020. Revisiting the complex pathosystem of Huanglongbing: Deciphering the role of citrus metabolites in symptom development. Metabolites. 10(10):409.

Neupane A, Shahzad F, Bernardini C, Levy A, Vashisth T. 2023. Poor shoot and leaf growth in Huanglongbing-affected sweet orange is associated with increased investment in defenses. Front Plant Sci. 14:1305815. https://doi.org/10.3389/fpls.2023.1305815.

Obreza TA, Morgan KT. 2008. Nutrition of Florida citrus trees (2nd ed). University of Florida Coop. Ext. Publ. SL-253.

Plotto A, Baldwin E, Bai J, Manthey J, Raithore S, Deterre S, Zhao W, do Nascimento Nunes C, Stansly PA, Tansey JA. 2017. Effect of vector control and foliar nutrition on the quality of orange juice affected by Huanglongbing: Sensory evaluation. HortScience. 52(8):1092–1099. https://doi.org/10.21273/HORTSCI12002-17.

Ritenour MA, Miller WM, Wardowski WW. 2019. Recommendations for degreening Florida fresh citrus fruits. https://edis.ifas.ufl.edu/pdffiles/HS/HS19500.pdf. [accessed 9 Aug 2024].

Shahzad F, Chun C, Schumann A, Vashisth T. 2020. Nutrient uptake in Huanglongbing-affected sweet orange: Transcriptomic and physiological analysis. J Am Soc Hortic Sci. 145(6):349–362. https://doi.org/10.21273/JASHS04929-20.

Shahzad F, Livingston T, Vashisth T. 2024. Gibberellic acid mitigates Huanglongbing symptoms by reducing osmotic and oxidative stress in sweet orange. Sci Hortic. 329:112976. https://doi.org/10.1016/j.scienta.2024.112976.

Shahzad F, Vashisth T, Ritenour MA, Brecht JK. 2022. Quest for desirable quality of Tango mandarin in the citrus greening era: The promise of integrated approaches. LWT. 161:113321. https://doi.org/10.1016/j.lwt.2022.113321.

Shahzad F, Vashisth T, Ritenour MA, Brecht JK. 2023. Huanglongbing disease symptoms and the postharvest quality of 'LB8-9' (Sugar Belle®) and 'Tango' mandarins as affected by ethylene treatment. Sci Hortic. 310:111766. https://doi.org/10.1016/j.scienta.2022.111766.

Shao X, Chen H, Pan H, Ritenour MA, Hu C, Xu Q, Bao X. 2021. Effect of steam blanching on peelability and quality of *Citrus reticulata* Blanco. J Food Sci Technol. 58(10):3790–3797. https://doi.org/10.1007/s13197-020-04839-y.

Singh S, Livingston T, Tang L, Vashisth T. 2022. Effects of exogenous gibberellic acid in Huanglongbing-affected sweet orange trees under Florida conditions: II. Fruit production and tree health. HortScience. 57(3):353–359. https://doi.org/10.21273/HORTSCI16277-21.

Srivastava AK, Singh S. 2005. Boron nutrition in citrus: Current status and future strategies: A Review. Agric Rev. 26:173–186.

Stansly PA, Arevalo HA, Qureshi JA, Jones MM, Hendricks K, Roberts PD, Roka FM. 2014. Vector control and foliar nutrition to maintain economic sustainability of bearing citrus in Florida groves affected by huanglongbing. Pest Manag Sci. 70(3):415–426. https://doi.org/10.1002/ps.3577.

Stover E, Inch S, Richardson ML, Hall DG. 2016. Conventional citrus of some scion/rootstock combinations show field tolerance under high Huanglongbing disease pressure. HortScience. 51(2):127–132. https://doi.org/10.21273/HORTSCI.51.2.127.

Sung J, Suh JH, Chambers AH, Crane J, Wang Y. 2019. Relationship between sensory attributes and chemical composition of different mango cultivars. J Agric Food Chem. 67(18):5177–5188. https://doi.org/10.1021/acs.jafc.9b01018.

Sutton M, Stanton D, Vashisth T. 2024. Fruit size as an indicator of fruit drop in Huanglongbing-affected 'Valencia'. HortScience. 59(6):849–857. https://doi.org/10.21273/HORTSCI17722-24.

Tang L, Singh S, Vashisth T. 2020. Association between fruit development and mature fruit drop in Huanglongbing-affected sweet orange. HortScience. 55(6):851–857. https://doi.org/10.21273/HORTSCI14931-20.

US Department of Agriculture Agricultural Marketing Service. 1997. Florida tangerine grades and standards. https://www.ams.usda.gov/

grades-standards/florida-tangerine-grades-and-standards. [accessed 22 Jul 2024].
US Department of Agriculture. 2023. Florida citrus statistics 2022–23 report. US Department of Agriculture, Washington, DC, USA.
Vashisth T. 2020. Nutrition: No one ze fits all. http://citrusindustry.net/2020/03/05/nutrition-no-one-size-fits-all. [accessed 21 Mar 2024].
Vashisth T, Livingston T. 2019. Assessment of pruning and controlled-release fertilizer to rejuvenate Huanglongbing-affected sweet orange. HortTechnology. 29(6):933–940. https://doi.org/10.21273/HORTTECH04382-19.
Wardowski WF, Miller WM, Grierson W. 2006. Degreening, p 277–297. In: Wardowski WF, Miller WM, Hall DJ, Grierson G (eds). Fresh citrus fruits (2nd ed). Florida Science Source, Inc., Longboat Key, FL, USA.
White PJ, Karley AJ. 2010. Potassium, p 199–224. In: Hell R, Mendel R-R (eds). Cell biology of metals and nutrients. Springer, Berlin, Germany.
Whitney JD, Harrell RC. 1989. Status of citrus harvesting in Florida. J Agric Eng Rev. 42(4):285–299. https://doi.org/10.1016/0021-8634(89)90031-0.
Wimmer MA, Eichert T. 2013. Mechanisms for boron deficiency-mediated changes in plant water relations. Plant Sci. 203–204:25–32. https://doi.org/10.1016/j.plantsci.2012.12.012.