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Field Performance of 'Hamlin' Orange Trees Grown on Various Rootstocks in Huanglongbing-endemic Conditions

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***Abstract.* Most of the commercially important citrus scion cultivars are susceptible to Huanglongbing (HLB), which is the most devastating disease the citrus industry has ever faced. Because the rootstock can influence the performance of the scion in various ways, including disease and pest tolerance, use of superior rootstocks can assist citrus growers with minimizing the negative effects of HLB. The objective of this study was to assess rootstock effects on the horticultural performance and early production potential of 'Hamlin' sweet orange (*Citrus sinensis*) trees in commercial field settings under HLB-endemic conditions. Two field trials were conducted in different locations in Central and Southeast Florida. The trials were established in 2015 and included 32 diverse diploid and tetraploid rootstock cultivars and advanced selections. One trial was performed in Highlands County, FL, on a poorly drained flatwoods-type site. Another trial was performed in Polk County, FL, on a well-drained sandy Central Florida Ridge site. Horticultural traits including tree height, canopy volume, trunk diameter, canopy health, leaf nutrient content, yield, and fruit quality were assessed during the 2018–19 and 2019–20 production years. Significant differences were found among trees on different rootstocks for most of the measured traits, particularly tree vigor and productivity, but rootstock effects also varied by location. Rootstocks that induced large tree sizes, such as the diploid mandarin × trifoliate orange hybrids 'X-639', 'C-54', 'C-57', and 'C-146', also induced higher yield, but with lower yield efficiency. Most of the tetraploid rootstocks significantly reduced tree size, among which 'Changsha+Benton', 'Green-3', 'Amb+Czo', 'UFR-3', and 'UFR-5' induced high yield efficiency. Therefore, these rootstocks have the potential to be used in high-density plantings. However, trees on some of these small size-inducing rootstocks had a higher mortality rate and were more vulnerable to tropical force winds. This study provides important information for the selection of rootstocks with the greatest production potential in an HLB-endemic environment, especially during the early years of production.**

The success of modern citrus industries relies on the suitable combination of superior scions and rootstocks and their adaptability to diverse soil and environmental conditions (Castle, 2010; Castle and Gmitter, 1998). The importance of rootstocks in the citrus industry has increased since they were recognized to provide tolerance against various pests and diseases. Use of sour orange rootstock to protect previously own-rooted citrus trees from *Phytophthora* disease and the use of trifoliate orange-type rootstocks to protect trees from citrus tristeza virus (CTV) are the major events (Roistacher et al., 2010) that shaped the citrus industry in Florida and other production areas. Furthermore, rootstocks can generate tolerance against various abiotic stresses such as drought, flooding, extreme pH conditions, extreme temperatures, and salinity (Cimen and Yesiloglu, 2016). The influences of rootstocks on the precocity of flowering and fruiting and on other horticultural traits of the scion, such as tree vigor, nutrient uptake, yield, and fruit quality, have also been established (Castle, 2010; Forner-Giner et al., 2003; Nimbolkar et al., 2016; Webster, 1995; Wutscher, 1979). Therefore, rootstock selection is crucial for determining the sustainability, productivity, and long-term profitability of a citrus orchard (Castle, 2010; Nimbolkar et al., 2016; Webster, 1995).

The Florida citrus industry grew from the introduction of seeds and plants of sour orange, sweet orange, lemon, lime, and citron by the Spanish in the 16th century, and the use of grafted trees commenced in the1830s (Castle et al., 1993). Since then, the industry has changed over time to adapt to different pests and diseases and environmental events. The introduction of the destructive disease HLB is the most recent event, and it continues to impact citrus production not only in Florida but also worldwide.

HLB is a disease associated with the phloem-limited bacterium *Candidatus* Liberibacter asiaticus that is transmitted by Asian citrus psyllids (*Diphorina citri*); it was found in Florida in 2005 (Gottwald et al., 2007). Since the confirmation of HLB in Florida, the HLB incidence has rapidly increased from 0.2% in 2006 to essentially 100% at present (Graham et al., 2020). This has resulted in tremendous economic losses of more than 70% in citrus production (year 2018–19) compared with the era before HLB (year 2003–04) (FDACS, 2020a). Different disease management strategies include vector exclusion (Ferrarezi et al., 2019; Schumann and Singerman 2016), vector control (Gottwald et al., 2007; Stansly et al., 2014), nutrient management (Rouse et al., 2017; Stansly et al., 2014; Zambon et al., 2019), and the application of plant defense inducers and antibiotics (Hu and Wang 2016; Hu et al., 2018). However, there are difficulties adopting some of these technologies under large-scale field conditions because of environmental or economic constraints.

Most citrus scion cultivars are HLB-susceptible and decline quickly if not managed properly (Miles et al., 2017). In contrast, several rootstock cultivars are tolerant to HLB and can render grafted trees more productive in the presence of the disease (Albrecht and Bowman, 2012; Bowman and McCollum, 2015; Bowman et al., 2016a, 2016b). The recognition of the importance of rootstocks for sustaining citrus production in an HLB-endemic environment has led to a shift in rootstock use in Florida, such as the preference for US-942 and other rootstocks over Swingle, which for decades has been the most propagated rootstock in Florida (FDACS, 2020b). The demand for other rootstocks bred to combine many of the most desired rootstock traits is increasing and necessitates field evaluation in a commercial production environment.

Bowman and Joubert (2020) identified 21 rootstocks as major world rootstocks; of

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which, 10 are naturally occurring species or hybrids and the rest are hybrids from breeding programs with one of the parents being *Poncirus trifoliata*. Therefore, there are opportunities for developing more sophisticated hybrid rootstocks by using modern breeding tools that allow the incorporation of superior traits from diverse parents (Germanà et al., 2020). Modern technologies such as molecular markers and somatic hybridization have emerged and have been successfully implemented, thus waiving many barriers associated with conventional breeding methods (Grosser et al., 2010; Khan and Kender, 2007).

We compared the field performance of several advanced experimental rootstock selections with other commercially used rootstocks. Many of the rootstocks used are tetraploid hybrids developed from either somatic hybridization of two complementary parents or crosses at the tetraploid level using somatic hybrid parents. The other rootstocks are diploid hybrid cultivars, except for sour orange (*C. aurantium*). The rootstocks included in our study have a wide range of genetic diversity, including combinations of trifoliate orange, mandarin, lime, lemon, pummelo, grapefruit, citrange, and sour orange. The objective of this study was to evaluate the effect of rootstocks on the horticultural performance of ‘Hamlin’ orange and to assess their potential for commercial production in an HLB-endemic environment.

Materials and Methods

Plant material

The rootstocks were developed in Florida (University of Florida), California (University of California, Riverside), and Spain (Valencian Institute of Agricultural Research). They contain sexual and somatic hybrids from a wide range of different germplasms (Table 1). The same rootstocks were used in both trials, except for sour orange, which was only included in one trial. Rootstock liners were grown from seeds and grafted with ‘Hamlin’ orange (*C. sinensis*) scion using standard procedures (Albrecht et al., 2017; Lewis and Alexander, 2008). Trees were produced in a commercial citrus nursery (Lykes Citrus, Basinger, FL) and planted in 2015 in commercial citrus orchards at the locations described.

Trial locations

Two field trials were conducted, with each in a separate location with different environmental conditions but under the same commercial management (Lykes Bros. Inc.). The first trial was established in Apr. 2015 near Fort Basinger (lat. 27.373321°N, long. –81.135209°W) in Highlands County, FL. The second trial was established in June 2015, near Lake Wales (lat. 27.935447°N, long. –81.49927°W) in Polk County, FL. Because HLB has been endemic in Florida since 2013 (Graham et al., 2020), the HLB incidence in both production areas was 100% at the time of planting.

The soil type at the Fort Basinger location is a poorly drained sandy Entisol with Spodosol-like properties, whereas that at the Lake Wales location is a well-drained sandy Entisol (Obreza and Collins, 2008). Both soil types have little organic matter and a low cation exchange capacity. Random soil samples were collected across each trial site to a depth of 25 cm near the drip line of trees and pooled for physicochemical analysis (Waters Agricultural Laboratories, Inc., Camilla, GA). An analysis showed an organic matter content of 0.72%, pH of 5.7, and cation exchange capacity (CEC) of 4.5 meq/100 g for the Basinger location, and an organic matter content of 0.34%, pH of 5.5, and a CEC of 3.2 meq/100 g for the Lake Wales location. Sand, silt, and clay contents were 95.2%, 0.8%, and 4%, respectively at Basinger, and 99.2%, 0.8%, and 0%, respectively, at Lake Wales. Thirty-two (trial 1) and 31 (trial 2) different rootstocks were used.

Experimental design

The experimental design was completely randomized, with six replications arranged in linear plots of eight trees each. Trees at the Basinger location were planted in double-row raised beds separated by furrows at a spacing of 8 ft (2.4 m) along the rows and 25 ft (7.6 m) between the rows. Trees at the Lake Wales location were planted in nonbedded single rows at a spacing of 8 ft (2.4 m) along the rows and 22 ft (6.7 m) between the rows.

Table 1. Rootstock names and their parentage.

Rootstock	Parentage
Tetraploids	
6058 + 2071-02-2*	*Citrus aurantium*+*C. limonia* ‘Rangpur’ × *C. reticulata* ‘Cleopatra’+*Poncirus trifoliata*
Amb+Benton*	*C. amblycarpa*+*Citroncirus* spp. ‘Benton’
Amb+Czo*	*C. amblycarpa*+*Citroncirus* spp. ‘Carrizo’
Changsha+Benton*	*C. reticulata* ‘Changsha’+*Citroncirus* spp. ‘Benton’
Green-3*	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. aurantium*+*Citroncirus* spp. ‘Carrizo’
Green-7*	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. aurantium*+*Citroncirus* spp. ‘Carrizo’
Orange-14*	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. reticulata* ‘Cleopatra’+*P. trifoliata*
White-1*	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. sinensis* ‘Succari’+*P. trifoliata*
Sorp+Sh-991*	*C. aurantium*+*C. limonia* ‘Rangpur’ × *C. reticulata* ‘Cleopatra’+*P. trifoliata*
Wgft+50-7*	*C. paradisi* ‘White’+*P. trifoliata* ‘50–7’
UFR-1	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. reticulata* ‘Cleopatra’+*P. trifoliata*
UFR-2	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. reticulata* ‘Cleopatra’+*P. trifoliata*
UFR-3	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. reticulata* ‘Cleopatra’+*P. trifoliata*
UFR-4	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. reticulata* ‘Cleopatra’+*P. trifoliata*
UFR-5	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. sinensis* ‘Succari’+*P. trifoliata*
UFR-6	*C. reticulata* ‘Changsha’+*P. trifoliata* ‘50-7’
UFR-17	*C. reticulata* ‘Nova’+*C. maxima* ‘Hirado Buntan’ × *C. aurantium*+*Citroncirus* spp. ‘Carrizo’
Diploids	
C-146	*C. reticulata* ‘Sunki’ × *P. trifoliata* ‘Swingle’
C-22 (‘Bitters’)	*C. reticulata* ‘Sunki’ × *P. trifoliata* ‘Swingle’
C-54 (‘Carpenter’)	*C. reticulata* ‘Sunki’ × *P. trifoliata* ‘Swingle’
C-57 (‘Furr’)	*C. reticulata* ‘Sunki’ × *P. trifoliata* ‘Swingle’
ES-1	*C. reticulata* ‘Cleopatra’ × *P. trifoliata*
ES-2	*C. reticulata* ‘Cleopatra’ × *P. trifoliata*
ES-3	*C. reticulata* ‘Cleopatra’ × *P. trifoliata*
ES-5	*C. reticulata* ‘King’ × *P. trifoliata*
ES-4	*C. reticulata* ‘King’ × *P. trifoliata*
ES-6	*C. reticulata* ‘King’ × *P. trifoliata*
US-897	*C. reticulata* ‘Cleopatra’ × *P. trifoliata* ‘Flying dragon’
ES-7	*C. volkameriana* × *P. trifoliata*
Sour orange	*C. aurantium*
Swingle	*C. paradisi* ‘Duncan’ × *P. trifoliata*
X-639	*C. reticulata* ‘Cleopatra’ × *P. trifoliata* ‘Rubidoux’

+ indicates somatic hybridization (allotetraploid). × indicates sexual hybridization (diploid or tetraploid).

*Experimental rootstocks.

Irrigation was automated by under-tree microjets. A controlled-release fertilizer (17N–6P–12K; Harell's LLC, Lakeland, FL) was applied at rates of 1 lb (0.45 kg), 2 lb (0.91 kg), and 3 lb (1.36 kg) per tree in years 1, 2, and 3 after planting, respectively. Starting in year 4, dry fertilizer (12N–0P–13K; Howard Fertilizer, Lake Placid, FL) was applied in the fall, spring, and summer of every year at a rate of 36 lb N per acre (40 kg/ha) per application. Liquid fertilizer (7N–2P–8K; Howard Fertilizer) was applied annually at a rate of 60 lb N per acre (67 kg/ha) during January to June and September to October. Weed management and insecticide applications were performed according to the grower's standards and were similar for both locations.

Plant assessments

Canopy health, tree survival, and leaning. Canopy color, canopy thickness, and foliar HLB disease symptoms were determined during Nov. 2019 by visual assessment of the third and sixth trees of each replicated plot. Canopy color and canopy thickness were rated on a scale of 1 to 5, with 1 representing the worst and 5 representing the best. Foliar disease symptoms (HLB disease index) were rated on a scale of 1 to 5, with 1 representing the best (no foliar disease symptoms) and 5 representing the worst (75% to 100% of the canopy showing foliar disease symptoms); ratings of 2, 3, and 4 represented 1% to 25%, 25% to 50%, and 50% to 75%, respectively, of the affected canopy. HLB symptoms included blotchy mottling of leaves, chlorosis, and other abnormalities associated with HLB (Bove, 2006). Eight ratings per tree were performed by dividing the tree into four quadrants on each side of the row, and the average was calculated for each tree. All assessments were conducted in Sept. 2019.

Dead and missing trees were counted in each plot of eight trees, and the tree survival was expressed as a percent. In 2017, hurricane Irma crossed Florida, which presented the opportunity to assess rootstock resistance to wind-induced leaning. The number of leaning trees in each plot was counted and expressed as a percent. A tree was defined as leaning when the angle between trunk and soil was less than 70°.

Tree size. Tree size measurements included tree height, canopy spread, and scion and rootstock trunk diameters. Measurements were conducted in Nov. 2019 using the third and sixth trees of each replicated tree plot. Tree height was measured using a digital measuring pole (Sokkia, Mississauga, ON, Canada) from the soil surface to the top of the tree excluding any erratic shoots. Canopy spread was measured parallel and perpendicular to the row using a measuring tape, and canopy volume (m^3) was calculated using the formula reported by Wutscher and Hill (1995): canopy volume = ($\text{diameter}^2 \times \text{height}$)/4. Scion and rootstock trunk circumferences were measured at 5 cm above and below the graft union using a measuring tape. Trunk diameters (d) were determined using the circle circumference (C) formula $C = \pi \times d$.

Yield and fruit quality. Fruits were harvested from the third and the sixth trees in each replicated plot in 2018–19 and from all eight trees in 2019–20. Harvest dates were 22 Jan. 2019 and 21 Jan. 2020 (Lake Wales) and 18 Dec. 2018 and 8 Jan. 2020 (Basinger). Fruits were weighed using a digital scale (CW P-150; CAS, East Rutherford, NJ) and the average yield per tree was calculated. Yield efficiency was calculated by dividing the yield per tree (kg) by the canopy volume (m^3). Before harvest, a random fruit sample of 48 fruits per replicated plot was collected and analyzed at the Juice Processing Pilot Plant, Citrus Research and Education Center, University of Florida, Institute of Food and Agricultural Sciences, Lake Alfred, FL. The average fruit weight was determined using a digital scale. Juice was extracted using a pinpoint extractor (JBT, Chalfont, PA), and the fruit juice percentage was calculated. The total soluble solids (TSS) and acid content were determined using standard procedures.

Leaf nutrient analysis. Leaves were collected from the third and the sixth trees of each replicated plot in Sept. 2019. A random sample of 16 mature leaves per tree were collected from nonfruiting spring flush, resulting in 32 leaves per replicated plot. The leaf samples were sent to Waters Agricultural Laboratories (Camilla, GA) for macronutrient and micronutrient concentration analyses. Total nitrogen (N) concentration was determined using the Dumas combustion method modified by Sweeney (1989). For phosphorus (P), sulfur (S), potassium (K), zinc (Zn), magnesium (Mg), calcium (Ca), iron (Fe), manganese (Mn), copper (Cu), and boron (B), the leaves were digested using nitric acid and hydrogen peroxide solution and analyzed by an inductively coupled argon plasma (ICAP) analysis (Huang and Schulte, 1985).

Statistical analysis

A one-way analysis of variance was conducted for all variables measured, and the comparison of means was performed by Tukey's honestly significant difference test. Pearson correlation coefficients were calculated among selected response variables to test their associations. Differences were defined as statistically significant when $P < 0.05$. Data were analyzed using Rstudio version 1.3.1093 (R Core Team, 2020).

Results

Canopy health, tree survival, and leaning

The rootstock effect was significant for foliar disease symptoms and canopy thickness in both locations (Supplemental Table 1). In general, most trees looked healthy, with average disease indices not exceeding 1.6. At the Basinger location, trees on 'Amb+Benton' had a significant lower HLB disease index (1.2) than trees on 'ES-3' (1.6). At the Lake Wales location, trees on 'UFR-5' had a significant lower disease index (1.1) than trees on 'ES-7' (1.5). Most rootstocks induced thick canopies at either location. At the Basinger location, 'C-54' induced a significantly thicker canopy (4.8) than 'Changsha+Benton' (4.3). At the Lake Wales location, most rootstocks induced significantly thicker canopies (4.6–4.8) than 'Green-3' (3.8). Canopy color ratings ranged from 4.7 to 4.9, but there were no significant differences among rootstocks.

The rootstock significantly affected tree survival and leaning (Table 2). The survival rate was 98%, on average, in both locations, and significant rootstock effects were only found for the Basinger location, where trees on 'Green-3' had a significantly lower survival rate (85.4%) compared with most of the other rootstocks. At the Basinger location, the percentage of leaning trees was highest for trees on 'Amb+Benton' (41.7%), followed by 'C-22' (33.3%) and 'Changsha+Benton' (31.3%), and no leaning was observed for trees on 'Green-7', 'UFR-2', 'Wgft+50-7', and 'UFR-5'. At the Lake Wales location, trees on 'Amb+Benton', 'Changsha+Benton', and 'C-22' had the highest percentage of leaning (52.1% to 66.7%), whereas less than 10% of trees leaned on most other rootstocks.

Across both locations, the lowest percentage of survival was found for trees on 'Green-3' (90.6%). The percentage of leaning trees was highest for trees on 'Amb+Benton' (54.2%), followed by trees on 'Changsha+Benton' and 'C-22' (42.7%). The leaning of trees at the Basinger location and the Lake Wales location was significantly and inversely correlated with tree height (R = –0.24 and R = –0.35) and canopy volume (R = –0.27 and R = –0.30). A significant but weak correlation was also found between tree survival and canopy volume (R = 0.15 and R = 0.24).

Tree size

Tree height, canopy volume, scion trunk diameter, and scion-to-rootstock trunk diameter ratio (SRR) were significantly influenced by rootstock in both locations (Table 3). 'X-639', 'C-54', 'C-57', and 'C-146' induced the tallest trees (2.3 m) at the Basinger location and were among the rootstocks producing the tallest trees (2.2–2.3 m) at the Lake Wales location. 'Green-3', 'Changsha+Benton', and 'Amb+Benton' produced the smallest trees (1.5–1.6 m) at the Basinger location and were among the rootstocks producing the smallest trees (1.4–1.6 m) at the Lake Wales location.

Similar results were found for the canopy volume, which was largest for trees on 'X-639' and 'C-54' (2.8–3.1 m^3) at the Basinger location and for trees on 'X-639', 'C-54', and 'C-57' (3.0–3.3 m^3) at the Lake Wales location. Trees on 'UFR-3', 'Green-3', and 'Changsha+Benton' produced the smallest canopy volume (1.0–1.1 m^3) at the Basinger location, and together with 'Sorp+Sh-991' at the Lake Wales location (0.8–1.0 m^3).

Scion trunk diameters were largest in trees on 'C-54' and 'C-57' (8.5 cm) at the Basinger location and on 'C-57' (8.5 cm) at

Table 2. Tree survival and leaning of 'Hamlin' orange trees on different rootstocks.

	Trial 1 (Basinger)		Trial 2 (Lake Wales)		Avg	
Rootstock	Survival (%)	Leaning (%)	Survival (%)	Leaning (%)	Survival (%)	Leaning (%)
Amb+Benton	93.8 ab	41.7 a	100	66.7 a	96.9 a-c	54.2 a
Changsha+Benton	97.9 a	31.3 a-c	95.8	54.2 ab	96.9 a-c	42.7 ab
C-22	97.9 a	33.3 ab	100	52.1 a-c	99.0 ab	42.7 ab
6058+2071-02-2	100 a	20.8 a-d	100	29.2 b-d	100 a	25.0 bc
UFR-4	100 a	20.8 a-d	100	27.1 b-d	100 a	24.0 bc
UFR-6	97.9 a	18.8 a-d	100	27.1 b-d	99.0 ab	22.9 bc
Sorp+Sh-991	100 a	16.7 a-d	97.9	27.1 b-d	99.0 ab	21.9 bc
UFR-17	93.8 ab	12.5 a-d	97.9	25.0 b-d	95.8 a-c	18.8 bc
Green-3	85.4 b	16.7 a-d	95.8	16.7 cd	90.6 c	16.7 c
ES-7	97.9 a	10.4 b-d	100	16.7 cd	99.0 ab	13.5 c
UFR-3	91.7 ab	16.7 a-d	95.8	8.3 d	93.8 a-c	12.5 c
US-897	100 a	12.5 a-d	100	12.5 d	100 a	12.5 c
UFR-1	100 a	8.3 b-d	100	12.5 d	100 a	10.4 c
White-1	89.6 ab	6.3 b-d	95.8	14.6 d	92.7 bc	10.4 c
ES-4	100 a	8.3 b-d	100	12.5 d	100 a	10.4 c
Amb+Czo	100 a	8.3 b-d	100	10.4 d	100 a	9.4 c
ES-2	100 a	12.5 a-d	100	4.2 d	100 a	8.3 c
C-54	100 a	2.1 cd	100	12.5 d	100 a	7.3 c
C-57	100 a	10.4 b-d	100	4.2 d	100 a	7.3 c
Green-7	100 a	0 d	97.9	12.5 d	99.0 ab	6.3 c
ES-6	100 a	2.1 cd	100	7.5 d	100 a	4.6 c
UFR-5	97.9 a	0 d	100	8.3 d	99.0 ab	4.2 c
C-146	100 a	6.3 b-d	100	2.1 d	100 a	4.2 c
ES-3	97.9 a	2.1 cd	100	6.3 d	99.0 ab	4.2 c
ES-5	100 a	6.3 b-d	100	2.1 d	100 a	4.2 c
Orange-14	100 a	2.1 cd	100	4.2 d	100 a	3.1 c
UFR-2	97.9 a	0 d	95.8	4.2 d	96.9 a-c	2.1 c
Wgft+50-7	100 a	0 d	97.9	4.2 d	99.0 ab	2.1 c
ES-1	97.9 a	2.1 cd	100	2.1 d	99.0 ab	2.1 c
X-639	97.9 a	4.2 b-d	100	0 d	99.0 ab	2.1 c
Swingle	97.5 a	2.5 b-d	100	0 d	98.8 ab	1.3 c
Sour orange	97.9 a	2.1 cd	—	—	—	—
F value	3.14***	3.35***	1.497	6.03***	3.78***	8.76***

Different letters within columns indicate significant differences according to Tukey's honestly significant difference test. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

the Lake Wales location. The smallest scion trunk diameters were found in trees on 'Green-3' (5.3 cm) at the Basinger location and in trees on 'UFR-3' (5.1 cm) at the Lake Wales location. The SRR was highest (0.86) for trees on rootstocks 'ES-5' and sour orange at the Basinger location and for trees on 'Changsha+Benton' (0.88) and 'Amb+Czo' (0.87) at the Lake Wales location. The lowest SRR (0.63) was found for the trees on 'Swingle' at both locations along with trees on 'Wgft+50-7' (0.63) at the Basinger location and 'UFR-3' (0.65) at the Lake Wales location.

Tree height was significantly correlated with both canopy volume and scion trunk diameter at the Basinger location (R = 0.92 and R = 0.88, respectively) and the Lake Wales location (R = 0.89 and R = 0.85, respectively).

Fruit yield

Fruit yield was measured in production years 2018–19 and 2019–20, and the cumulative yield was calculated. Rootstock effects on yield were significant for both years and at both locations (Table 4). At the Basinger location, the average yield was nearly threefold lower in 2018–19 (5.6 kg/tree) than in 2019–20 (15.4 kg/tree). Yield per tree ranged from 2.8 kg/tree for trees on 'ES-5' to 8.5 kg/tree for trees on 'US-897' in 2018–19, and from 9.6 kg/tree for trees on 'UFR-3' to 20.2 kg/tree for trees on 'ES-1' in year 2019–20; however, separation of means was not significant in either production year.

The average yield at the Lake Wales location was similar in both production years (Table 4). 'UFR-5' and 'ES-1' induced the highest yields per tree in 2018–19 (20.2 and 18.0 kg), and 'X-639' and 'C-54' induced the highest yields per tree (19.9 and 18.3 kg) in 2019–20. The lowest yields per tree were induced by 'Sorp+Sh-991', 'Wgft+50-7', 'UFR-3', and 'Amb+Benton' (4.6–6.8 kg) in year 2018–19, and by 'Changsha+Benton' and 'Sorp+Sh-991' (4.6 and 4.9 kg) in 2019–20.

Across both locations, the most productive rootstocks in terms of average cumulative yield were 'ES-1' (29.5 kg/tree), followed by 'UFR-5', 'C-54', and 'X-639' (27.8–28.0 kg/tree). The least productive rootstocks were 'UFR-3' (13.1 kg), followed by 'Sorp+Sh-991' (14.1 kg), 'Changsha+Benton' (15.3 kg), and 'Amb+Benton' (15.6 kg/tree). Fruit yield per tree was significantly correlated with canopy volume at the Basinger location (R = 0.39) and at the Lake Wales location (R = 0.66).

Yield efficiency

The rootstock effect was significant for yield efficiency in both locations and both production years (Table 5). In 2018–19, yield efficiency at the Basinger location ranged from 2.1 kg/m^3 for trees on 'X-639' to 9.9 kg/m^3 for trees on 'Amb+Benton', but the mean separation was not significant. In 2019–20, the average yield efficiency was highest for trees on 'Green-3' (14.3 kg/m^3) and lowest for trees on 'C-146', 'C-54', and 'C-22' (4.3–5.4 kg/m^3).

At the Lake Wales location, 'UFR-5', 'Green-3', and 'Changsha+Benton' induced the highest yield efficiency (15.7–17.3 kg/m^3) and 'ES-2', 'ES-3', 'C-57', and 'UFR-2' induced the lowest (6.1–6.2 kg/m^3) in 2018–19. In 2019–20, 'Green-3' induced the highest yield efficiency (10.5 kg/m^3) and 'UFR-6', 'UFR-17', 'ES-6', 'UFR-4', 'UFR-2', 'ES-3', and 'ES-2' induced the lowest yield efficiency (4.2–5.1 kg/m^3).

Across both locations and years, the highest average yield efficiency was induced by 'Green-3' (11.9 kg/m^3), followed by 'Amb+Benton' (10.5 kg/m^3), 'Changsha+Benton' (10.2 kg/m^3), and 'ES-4' (10.0 kg/m^3), whereas the lowest yield efficiency was induced by 'ES-2' (4.8 kg/m^3), followed by 'C-146', 'ES-3', and 'X-639' (5.2–5.4 kg/m^3). Yield efficiency was significantly and inversely correlated with canopy volume at the Basinger location (R = –0.59) and the Lake Wales location (R = –0.30).

Fruit quality

Fruit quality variables were measured in the production year 2019–20. The rootstock effect was significant for most variables in both locations. In the Basinger trial, 'Green-3' induced the highest weight fruit (174 g) and 'ES-2' induced the lowest fruit weight (140 g) (Table 6). The juice percentage was

Table 3. Tree size of ‘Hamlin’ trees on different rootstocks.

	Trial 1 (Basinger)				Trial 2 (Lake Wales)			
Rootstock	Ht (m)	Scion trunk diam (cm)	Canopy vol (m^3)	SRR	Ht (m)	Scion trunk diam (cm)	Canopy vol (m^3)	SRR
X-639	2.3 a	7.9 a-e	2.8 ab	0.77 b-h	2.3 ab	8.3 ab	3.3 a	0.75 g-l
C-54	2.3 a	8.5 a	3.1 a	0.79 a-g	2.3 a-c	8.1 a-c	3.0 a-c	0.81 a-h
C-57	2.3 a	8.5 a	2.6 a-d	0.80 a-e	2.3 a	8.5 a	3.1 ab	0.79 c-j
C-146	2.3 a	8.2 ab	2.8 a-c	0.75 c-h	2.2 a-d	7.9 a-d	2.6 a-e	0.77 d-k
ES-1	2.2 ab	7.8 a-e	2.6 a-d	0.76 b-h	2.2 a-d	7.7 a-e	2.5 a-f	0.76 f-k
ES-3	2.2 a-c	7.4 a-f	2.4 a-e	0.75 d-h	2.1 a-e	7.3 a-g	2.5 a-f	0.76 f-l
ES-2	2.0 a-e	7.0 a-g	2.1 a-g	0.79 a-f	2.1 a-e	7.5 a-f	2.7 a-d	0.80 b-i
C-22	2.2 a-c	8.0 a-d	2.5 a-d	0.84 ab	2.1 a-f	7.7 a-f	2.3 b-g	0.82 a-g
ES-6	2.1 a-e	7.6 a-f	2.4 a-e	0.84 ab	2.1 a-e	7.6 a-f	2.3 b-g	0.86 ab
Orange-14	2.1 a-e	7.4 a-f	2.2 a-f	0.78 b-h	2.1 a-e	7.4 a-f	2.2 b-g	0.79 c-j
UFR-4	2.1 a-d	8.0 a-c	2.5 a-d	0.80 a-e	1.9 b-h	6.8 c-i	1.9 d-i	0.83 a-f
UFR-5	2.1 a-e	7.5 a-f	2.2 a-g	0.76 b-h	2.0 a-g	7.0 b-h	2.1 b-g	0.75 g-l
US-897	2.0 a-e	7.2 a-f	2.1 a-g	0.75 d-h	2.0 a-g	7.1 b-h	2.1 b-g	0.78 d-k
ES-7	2.0 a-e	7.8 a-e	2.0 a-g	0.79 a-g	2.1 a-e	7.4 a-f	2.0 c-h	0.80 b-i
ES-5	2.0 a-e	7.4 a-f	1.8 a-g	0.86 a	2.2 a-d	7.2 a-h	2.1 c-g	0.83 a-e
Swingle	1.9 a-e	6.6 b-g	1.8 b-g	0.63 j	1.9 a-h	6.6 d-k	2.0 c-h	0.63 n
UFR-17	2.0 a-e	7.0 a-g	1.9 a-g	0.70 h-j	1.9 a-h	6.7 d-i	1.8 d-k	0.73 h-l
UFR-2	1.9 a-e	6.6 b-g	1.9 a-g	0.75 d-h	1.9 c-i	6.4 e-l	1.6 f-k	0.78 d-k
Green-7	2.1 a-e	7.3 a-f	2.1 a-g	0.71 g-i	1.9 b-h	6.3 f-l	1.4 g-k	0.71 k-m
ES-4	1.8 a-e	6.9 a-g	1.6 c-g	0.84 ab	2.0 a-g	7.1 b-h	1.9 d-j	0.85 a-c
UFR-1	1.8 a-e	6.5 b-g	1.6 c-g	0.75 d-h	1.9 a-h	6.5 d-l	1.8 d-k	0.78 c-k
White-1	1.7 a-e	6.3 d-g	1.6 c-g	0.73 e-h	1.8 d-j	6.6 d-k	1.7 d-k	0.76 e-k
Wgft+50-7	2.0 a-e	6.9 a-g	1.8 b-g	0.63 ij	1.9 c-i	6.0 g-l	1.3 g-k	0.69 l-n
UFR-6	1.8 a-e	6.3 c-g	1.5 d-g	0.81 a-d	1.8 d-j	6.8 c-i	1.6 e-k	0.84 a-d
Amb+Czo	1.8 a-e	6.9 a-g	1.5 d-g	0.84 ab	1.8 d-j	6.4 e-l	1.5 g-k	0.87 a
6058+2071-02-2	1.8 a-e	6.6 b-g	1.5 d-g	0.74 d-h	1.7 e-j	6.6 d-k	1.4 g-k	0.73 i-l
Sorp+Sh-991	1.8 a-e	6.5 c-g	1.5 d-g	0.71 f-i	1.4 ij	5.2 kl	0.9 jk	0.72 j-m
Amb+Benton	1.6 c-e	5.9 fg	1.2 e-g	0.82 a-d	1.6 g-j	5.8 h-l	1.0 h-k	0.82 a-g
UFR-3	1.6 b-e	5.9 fg	1.1 fg	0.71 h-j	1.6 f-j	5.1 l	0.9 i-k	0.65 mn
Green-3	1.5 e	5.3 g	1.0 g	0.72 e-h	1.5 h-j	5.4 j-l	1.0 i-k	0.73 i-l
Changsha+Benton	1.5 de	6.2 e-g	1.1 fg	0.83 a-c	1.4 j	5.5 i-l	0.8 k	0.88 a
Sour orange	2.0 a-e	8.0 a-d	2.0 a-g	0.86 a	—	—	—	—
F value	3.9***	6.19***	5.75***	15.38***	9.32***	12.17***	12.88***	19.95***

SRR, scion-to-rootstock trunk ratio. Different letters within columns indicate significant differences according to Tukey’s honestly significant difference test. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

highest for trees on ‘ES-4’ (59.1%) and lowest for trees on ‘ES-7’ (48.6%). ‘Green-3’, ‘White-1’, and sour orange induced the largest amount of TSS (9.40% to 9.80%), and ‘C-22’, ‘C-146’, and ‘ES-2’ induced the smallest amount of TSS (7.95% to 8.10%). The acid percentage was highest for trees on ‘Green-3’ (0.565%) and lowest for trees on ‘ES-2’ (0.443%). The TSS-to-acid ratio ranged from 16.2 to 18.4, but the mean separation was not significant.

At the Lake Wales location, the average fruit weight was 147 to 168 g, but there was no significant rootstock effect (Table 7). Juice percentage was highest for trees on ‘Swingle’ (58.3%) and lowest for trees on ‘ES-7’ (49.9%). ‘UFR-5’, ‘Amb+Czo’, and ‘Changsha+Benton’ induced the largest TSS % in the fruit (9.63% to 9.84%), whereas ‘ES-2’ and ‘ES-3’ induced the smallest TSS% (8.38% and 8.42%, respectively). ‘UFR-5’ induced the highest percentage of acid in the fruit (0.557%), and ‘ES-4’ and ‘ES-6’ induced the lowest (0.322% and 0.348%, respectively). The highest TSS-to-acid ratio was induced by ‘ES-4’ (28.4), and the lowest was induced by ‘Swingle’ (17.4). TSS was significantly and inversely correlated with canopy volume at the Basinger location (R = –0.68) and at the Lake Wales location (R = –0.53).

Leaf nutrient concentration

Leaf macronutrient (N, P, K, Ca, Mg, and S) and micronutrient (B, Zn, Mn, Fe, and Cu) concentrations were analyzed in production year 2019–20. The rootstock effect was significant for Mg and Mn at the Basinger location and for K, Mg, B, and Mn at the Lake Wales location (Supplemental Table 2).

At the Basinger location, the leaf Mg contents were highest for trees on ‘ES-4’ (0.40%) and lowest for trees on many of the other rootstocks (0.30% to 0.33%). Leaf Mn concentrations were significantly higher in trees on ‘ES-3’ (54 ppm) compared with trees on ‘ES-6’, ‘Green-7’, ‘C-22’, ‘C-54’, ‘Changsha+Benton’, and sour orange (38–40 ppm).

At the Lake Wales location, K concentrations ranged from 1.7% to 2.0%, but separation of means was not significant. Leaf Mg concentrations were highest for trees on ‘X-639’ (0.36%) and lowest for trees on ‘ES-2’ (0.29%). Leaf B concentrations were highest for trees on ‘ES-7’ (124 ppm) and lowest for trees on ‘Amb+Benton’ (101 ppm). The highest leaf Mn concentrations were induced by ‘UFR-2’ (69 ppm) and the lowest by ‘UFR-17’ and ‘UFR-6’ (49 and 50 ppm).

The average concentrations for other leaf nutrients were 3.1% (N), 0.19% (P), 1.9% (K), 2.5% (Ca), 0.32% (S), 98 ppm (B), 23 ppm (Zn), 71 ppm (Fe), and 178 ppm (Cu) at the Basinger location (data not shown). At the Lake Wales location, the average leaf nutrient concentrations were 2.9% (N), 0.17% (P), 2.7% (Ca), 0.33% (S), 35 ppm (Zn), 114 ppm (Fe), and 310 ppm (Cu) (data not shown).

Discussion

Considering the devastation caused by HLB, precocity may be one important criterion for rootstock selection to cope with economic losses due to tree decline when the disease reaches an advanced stage of progression. Our results showed significant variations among rootstocks in their effects on most of the horticultural traits measured. The identification of rootstock traits at an early stage of production is valuable for determining rootstock impacts on the economic viability of the mature orchard in the long term.

Although significant rootstock effects were measured, most trees had a healthy canopy with moderate foliar disease expression. The total percentage of dead trees was less than 2% in both locations, which is normal for young commercial citrus plantings. Trees on the small tree size-inducing rootstock ‘Green-3’ had the highest mortality rate among all rootstocks at the Basinger location. The low foliar disease expression of trees on this rootstock suggests that factors other than HLB may have been responsible.

The average percentages of wind-induced leaning of trees at both locations were 15.8% and 10.6% at Lake Wales and Basinger, respectively. The higher percentage of leaning trees at the Lake Wales location may be attributable to this location being part of the Central Florida Ridge, an ancient sand dune

Table 4. Fruit yield of ‘Hamlin’ orange trees on different rootstocks.

	Trial 1 (Basinger)		Trial 2 (Lake Wales)		
Rootstock	2018–19 (kg/tree)	2019–20 (kg/tree)	2018–19 (kg/tree)	2019–20 (kg/tree)	Avg cumulative (kg/tree)
ES-1	4.4 a	20.2 a	18.0 ab	16.3 a-e	29.5 a
UFR-5	6.7 a	17.4 a	20.2 a	11.8 a-h	28.0 ab
C-54	4.4 a	16.0 a	17.2 a-c	18.3 ab	28.0 ab
X-639	3.7 a	17.6 a	14.4 a-d	19.9 a	27.8 ab
C-57	7.3 a	14.7 a	13.4 a-d	17.7 a-c	26.6 a-c
ES-4	7.7 a	14.5 a	17.1 a-c	13.7 a-f	26.5 a-c
US-897	8.5 a	13.8 a	13.6 a-d	13.3 a-g	24.6 a-d
Swingle	7.2 a	15.6 a	13.9 a-d	12.1 a-h	24.4 a-e
ES-7	4.5 a	16.7 a	10.3 a-d	17.1 a-d	24.3 a-e
ES-6	5.1 a	18.9 a	11.4 a-d	11.9 a-h	23.6 a-e
ES-5	2.8 a	17.1 a	14.4 a-d	12.4 a-h	23.4 a-e
Green-7	7.3 a	19.9 a	10.5 a-d	9.0 d-h	23.2 a-e
C-22	6.0 a	13.3 a	13.2 a-d	13.7 a-f	23.1 a-e
Orange-14	7.6 a	13.2 a	12.0 a-d	13.2 a-h	22.9 a-e
ES-3	4.0 a	18.7 a	11.8 a-d	10.4 b-h	22.5 a-e
Amb+Czo	6.1 a	18.2 a	12.5 a-d	7.6 f-h	22.2 a-e
6058+2071-02-2	6.3 a	18.3 a	9.3 b-d	10.3 b-h	22.1 a-e
UFR-4	4.9 a	17.4 a	11.7 a-d	9.6 c-h	21.8 a-e
C-146	4.9 a	11.4 a	13.5 a-d	13.8 a-f	21.8 a-e
White-1	5.0 a	15.2 a	10.8 a-d	11.2 b-h	21.1 a-e
UFR-1	4.8 a	16.3 a	9.2 b-d	9.6 c-h	20.0 a-e
Wgft+50-7	6.1 a	18.2 a	6.0 d	9.5 c-h	19.9 a-e
UFR-17	4.5 a	15.6 a	10.9 a-d	8.4 e-h	19.7 a-e
UFR-6	6.8 a	13.8 a	10.1 a-d	7.1 f-h	18.9 a-e
UFR-2	6.3 a	16.4 a	7.7 cd	7.3 f-h	18.8 a-e
ES-2	3.9 a	11.2 a	11.1 a-d	10.8 b-h	18.5 a-e
Green-3	4.2 a	12.6 a	8.3 b-d	9.0 d-h	17.0 b-e
Amb+Benton	5.4 a	11.7 a	6.8 d	7.3 f-h	15.6 c-e
Changsha+Benton	6.5 a	10.5 a	9.0 b-d	4.6 h	15.3 c-e
Sorp+Sh-991	4.3 a	14.4 a	4.6 d	4.9 gh	14.1 de
UFR-3	4.9 a	9.6 a	6.2 d	5.7 f-h	13.1 e
Sour orange	7.4 a	13.3 a	—	—	—
F value	1.62*	1.78*	3.79***	6.19***	3.95***

Different letters within columns indicate significant differences according to Tukey’s honestly significant difference test. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 5. Yield efficiency of ‘Hamlin’ orange trees on different rootstocks.

	Trial 1 (Basinger)		Trial 2 (Lake Wales)		
Rootstock	2018–19 (kg/m^3)	2019–20 (kg/m^3)	2018–19 (kg/m^3)	2019–20 (kg/m^3)	Avg (kg/m^3)
Green-3	7.2 a	14.3 a	15.7 ab	10.5 a	11.9 a
Amb+Benton	9.9 a	12.5 a-c	11.5 a-d	7.9 ab	10.5 ab
Changsha+Benton	9.4 a	9.7 a-d	15.7 ab	6.0 ab	10.2 a-c
ES-4	7.9 a	9.7 a-d	15.0 a-c	7.6 ab	10.0 a-c
Amb+Czo	6.1 a	12.9 ab	13.4 a-d	5.8 ab	9.5 a-d
6058+2071-02-2	8.2 a	12.8 ab	7.6 b-d	7.4 ab	9.0 a-e
UFR-5	4.6 a	7.9 a-d	17.3 a	5.8 ab	8.9 a-e
Swingle	8.1 a	8.9 a-d	9.8 a-d	6.3 ab	8.3 a-f
UFR-3	6.5 a	8.4 a-d	11.3 a-d	6.5 ab	8.2 a-f
Green-7	6.1 a	9.5 a-d	10.7 a-d	6.4 ab	8.2 a-f
White-1	6.3 a	9.9 a-d	9.7 a-d	6.9 ab	8.2 a-f
UFR-6	8.0 a	9.9 a-d	9.8 a-d	4.7 b	8.1 a-f
Wgft+50-7	6.4 a	11.2 a-d	7.6 b-d	7.1 ab	8.0 a-f
Sorp+Sh-991	6.6 a	10.1 a-d	9.3 a-d	5.6 ab	7.9 a-f
UFR-1	5.8 a	10.5 a-d	7.9 b-d	5.6 ab	7.4 b-f
ES-1	3.6 a	8.3 a-d	11.1 a-d	6.5 ab	7.4 b-f
ES-7	4.2 a	8.2 a-d	7.9 b-d	9.0 ab	7.3 b-f
UFR-17	5.1 a	9.2 a-d	10.1 a-d	4.8 b	7.3 b-f
ES-5	2.8 a	10.5 a-d	9.7 a-d	6.2 ab	7.3 b-f
US-897	6.5 a	7.0 b-d	9.3 a-d	6.2 ab	7.3 b-f
Orange-14	7.1 a	6.0 b-d	7.5 b-d	6.0 ab	6.6 b-f
ES-6	4.1 a	8.2 a-d	9.1 a-d	5.1 b	6.6 b-f
UFR-4	3.0 a	7.3 a-d	10.3 a-d	5.1 b	6.4 b-f
C-22	4.5 a	5.4 d	9.0 a-d	6.3 ab	6.3 c-f
UFR-2	5.9 a	8.4 a-d	6.2 d	4.6 b	6.3 c-f
C-54	2.6 a	5.3 d	8.6 a-d	6.3 ab	5.7 d-f
C-57	4.3 a	5.8 b-d	6.1 d	5.8 ab	5.5 d-f
X-639	2.1 a	6.7 b-d	6.7 cd	6.0 ab	5.4 ef
ES-3	3.2 a	7.9 a-d	6.1 d	4.3 b	5.4 ef
C-146	3.3 a	4.3 d	8.0 b-d	5.3 ab	5.2 ef
ES-2	3.4 a	5.6 cd	6.1 d	4.2 b	4.8 f
Sour orange	7.2 a	6.7 b-d	—	—	—
F value	2.04**	3.54***	3.47***	1.87**	5.00***

Different letters within columns indicate significant differences according to Tukey’s honestly significant difference test. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 6. Fruit quality of 'Hamlin' orange trees on different rootstocks in trial 1 (Basinger).

Rootstock	Fruit wt (g)	Juice (%)	TSS (%)	Acid (%)	TSS-to-acid ratio
Green-3	174 a	57.2 a-d	9.80 a	0.565 a	17.4 a
White-1	162 a-f	56.6 a-d	9.53 ab	0.547 a-e	17.5 a
Sour orange	153 a-g	56.5 a-d	9.40 a-c	0.518 a-f	18.2 a
Changsha+Benton	169 ab	57.4 a-c	9.28 a-d	0.558 a-c	16.7 a
Wgft+50-7	171 ab	58.1 ab	9.27 a-d	0.562 ab	16.6 a
UFR-6	165 a-f	57.6 a-c	9.25 a-d	0.563 ab	16.5 a
Amb+Benton	167 a-d	57.0 a-d	9.23 a-e	0.547 a-e	16.9 a
UFR-1	158 a-g	57.1 a-d	9.18 a-f	0.543 a-e	16.9 a
Amb+Czo	164 a-f	57.1 a-d	9.14 a-g	0.548 a-d	16.7 a
Sorp+Sh-991	158 a-g	55.2 a-d	9.12 a-h	0.515 a-g	17.7 a
ES-4	161 a-g	59.1 a	9.11 a-h	0.520 a-f	17.5 a
Swingle	149 b-g	57.2 a-d	9.06 a-i	0.522 a-f	17.3 a
UFR-5	157 a-g	57.1 a-d	8.90 a-i	0.542 a-e	16.5 a
UFR-3	165 a-f	55.0 a-e	8.81 a-i	0.518 a-f	17.0 a
6058+2071-02-2	166 a-e	53.4 a-e	8.72 b-i	0.507 a-g	17.3 a
US-897	145 e-g	57.8 a-c	8.72 b-i	0.487 c-g	18.0 a
ES-5	161 a-g	52.8 a-e	8.69 b-i	0.473 e-g	18.4 a
Green-7	164 a-f	51.2 c-e	8.55 b-i	0.492 a-g	17.4 a
UFR-2	158 a-g	55.0 a-e	8.53 b-i	0.487 c-g	17.6 a
UFR-17	169 ab	53.7 a-e	8.49 b-i	0.515 a-g	16.5 a
ES-1	153 a-g	53.8 a-e	8.42 c-i	0.465 fg	18.1 a
C-54	146 c-g	52.4 b-e	8.35 c-i	0.458 fg	18.3 a
UFR-4	164 a-f	53.4 a-e	8.31 d-i	0.487 c-g	17.2 a
C-57	147 c-g	51.5 b-e	8.28 d-i	0.462 fg	18.0 a
ES-3	154 a-g	50.7 de	8.28 d-i	0.458 fg	18.1 a
ES-7	143 fg	48.6 e	8.28 d-i	0.457 fg	18.2 a
ES-6	168 a-c	51.7 b-e	8.27 d-i	0.463 fg	17.9 a
Orange-14	167 a-e	51.6 b-e	8.17 e-i	0.503 a-g	16.2 a
X-639	146 d-g	52.8 a-e	8.15 f-i	0.475 d-g	17.2 a
ES-2	140 g	51.5 b-e	8.10 g-i	0.443 g	18.3 a
C-146	149 b-g	51.7 b-e	8.08 hi	0.490 b-g	16.6 a
C-22	144 fg	50.5 de	7.95 i	0.465 fg	17.3 a
F value	5.59***	5.39***	6.50***	7.53***	2.01**

Different letters within columns indicate significant differences according to Tukey's honestly significant difference test. **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

Table 7. Fruit quality of 'Hamlin' orange trees on different rootstocks in trial 2 (Lake Wales).

Rootstock	Fruit wt (g)	Juice (%)	TSS (%)	Acid (%)	TSS-to-acid ratio
UFR-5	153	57.2 a-e	9.84 a	0.557 a	17.7 ef
Amb+Czo	149	57.8 a-c	9.65 ab	0.505 a-g	19.1 c-f
Changsha+Benton	162	57.9 ab	9.63 ab	0.522 a-c	18.6 d-f
White-1	155	57.2 a-f	9.57 a-c	0.507 a-f	18.9 c-f
Green-3	157	55.0 a-g	9.47 a-d	0.510 a-e	18.6 d-f
UFR-1	149	57.4 a-d	9.47 a-d	0.515 a-d	18.4 d-f
Wgft+50-7	159	57.9 ab	9.46 a-d	0.537 ab	17.6 ef
Sorp+Sh-991	150	55.8 a-g	9.43 a-e	0.503 a-h	18.8 c-f
Amb+Benton	168	57.2 a-e	9.42 a-e	0.497 b-i	19.0 c-f
UFR-6	159	56.6 a-g	9.38 a-f	0.508 a-e	18.5 d-f
UFR-17	161	54.3 a-g	9.36 a-f	0.493 b-i	19.0 c-f
UFR-3	153	53.8 c-i	9.30 a-g	0.498 a-h	18.8 c-f
ES-5	151	54.2 b-g	9.29 a-g	0.477 c-j	19.5 c-f
Green-7	157	54.9 a-g	9.17 b-h	0.510 a-e	18.0 d-f
Swingle	150	58.3 a	9.16 b-h	0.526 a-c	17.4 f
Orange-14	157	55.9 a-g	9.09 b-h	0.500 a-h	18.2 d-f
US-897	148	58.0 ab	9.06 b-i	0.458 d-k	19.8 c-f
UFR-4	152	55.4 a-g	9.06 b-i	0.445 h-k	20.4 c-e
ES-4	156	54.9 a-g	9.05 b-i	0.322 l	28.4 a
C-22	154	53.1 g-i	8.97 c-j	0.432 jk	20.8 cd
UFR-2	157	55.2 a-g	8.88 d-j	0.478 b-j	18.6 d-f
C-54	149	55.7 a-g	8.83 d-j	0.460 d-k	19.3 c-f
ES-7	156	49.9 i	8.78 e-j	0.408 k	21.5 c
6058+2071-02-2	161	53.2 f-i	8.77 e-j	0.502 a-h	17.6 ef
C-146	159	53.6 d-i	8.74 f-j	0.438 i-k	20.0 c-f
X-639	155	54.0 b-h	8.68 g-j	0.452 e-k	19.2 c-f
ES-1	158	52.8 g-i	8.67 g-j	0.447 g-k	19.5 c-f
C-57	158	52.7 g-i	8.61 h-j	0.432 jk	20.0 c-f
ES-6	159	53.6 d-i	8.51 h-j	0.348 l	24.6 b
ES-3	151	50.0 hi	8.42 ij	0.448 f-k	18.8 c-f
ES-2	147	53.3 e-i	8.38 j	0.438 i-k	19.2 c-f
F value	1.15	8.97***	10.29***	21.65***	16.08***

Different letters within columns indicate significant differences according to Tukey's honestly significant difference test. **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

representing the highest elevation in Florida, and its characteristic sandy soils. Trees on some of the dwarfing rootstocks leaned more than trees on some of the larger size-inducing rootstocks, but the (inverse) correlation between tree size and leaning was weak. One of the exceptions was 'C-22', which induced a high percentage of leaning while producing larger than average trees. The leaning of trees did not appear to have a negative influence on tree health and productivity at the time of evaluation; however, it is expected that growers will prefer wind-tolerant rather than wind-susceptible cultivars. To our knowledge, this is the first report of citrus that compared rootstock cultivar effects on the ability of citrus trees to withstand tropical force winds. A study of apple rootstocks also found that trees on dwarfing rootstocks leaned more than trees on vigorous rootstocks (Schupp, 1992); this was attributed to the heavy crop load of dwarfing trees and weak anchorage. Differences in wind resistance among rootstocks observed in our study are likely associated with different root architectures because trees were bearing few fruit at the time of the hurricane. A study following the aftermath of hurricane Andrew, which destroyed much of the tropical fruit acreage in South Florida in 1992, found that the percentage of toppled and surviving trees was correlated with tree height and age and depended on the crop species and other factors (Crane et al., 1993).

The rootstocks induced a wide range of vigor in the 'Hamlin' scion. The diploid rootstocks produced mostly medium to large trees, with 'X-639', 'C-54', 'C-57', 'C-146', and 'ES-1' producing the largest trees in the trials. Surprisingly, 'US-897' and 'C-22', which are generally regarded as small tree size-inducing rootstocks (Bowman et al., 2008; Siebert et al., 2010), produced medium trees in both locations when compared with the rootstock standards 'Swingle' and sour orange which are known to produce medium trees. Other studies that included the rootstocks 'C-22', 'C-54', 'C-57', 'C-146', and 'X-639' showed similar results (Castle et al., 2011; Louzada et al., 2008; Roose, 2008). It is anticipated that the size-limiting effect of 'US-897' and 'C-22' will manifest during later production years. The delayed effect of 'US-897' on tree size has also been observed by commercial citrus growers (personal communications). It must be noted that some hybrids of *C. reticulata* and *P. trifoliata* (citrandarins) are regarded as HLB-tolerant (Albrecht and Bowman, 2012; Boava et al., 2014). A higher level of tolerance may have contributed to the vigorous growth of trees on the citrandarin rootstocks 'X-639', 'C-54', 'C-57', 'C-146', 'ES-1', 'US-897', and 'C-22' observed in our study.

Among the tetraploid rootstocks, 'Orange-14', 'UFR-4', and 'UFR-5' induced the largest tree size, which was average when compared across all rootstocks. Most of the other tetraploid rootstocks induced below-average size trees, which is in accordance with the results from other field trials conducted on both flatwood and Central Ridge sites in Florida (Grosser et al., 2011). During those trials, many of the tetraploid rootstocks induced a tree size smaller than 9 ft (2.7 m) after 10 years of growth. The dwarfing capacity of tetraploid rootstocks was suggested to be a graft union response because diploid and tetraploid cells differ morphologically, with the latter being larger and containing thicker cell walls (Grosser et al., 2011). However, the reduced growth of tetraploid rootstocks in comparison with diploid rootstocks was also observed at the seedling stage (Allario et al., 2011; Guerra et al., 2014). It is generally recognized that the reduced capacity of the dwarfing rootstocks to transport water from the soil to the aboveground part of the plant contributes to the vigor-inducing potential of a rootstock. Lower hydraulic conductivity was reported for apple trees on the dwarfing rootstock M.27 compared to those on the invigorating rootstock MM.106 (Atkinson et al., 2003). Forner-Giner et al. (2014) reported a reduced hydraulic conductance of 'Navelina' orange trees on dwarfing rootstocks 'FA-517' and 'FA-418' compared with trees on Carrizo rootstock. Factors such as soil and environmental conditions, management practices, pest and disease pressure, and rootstock compatibility with the scion may further affect the rootstock influence on tree size (Bowman and Joubert, 2020). The observed variations in the tree size induced at different locations for some of the rootstocks in our study were likely due to the differences in the soil and other environmental conditions because both sites had similar management practices, the same scion, and similar HLB disease pressure.

The SRR represents the smoothness of the graft union, and it has often been considered an indicator of the compatibility of scion and rootstocks (Kallsen and Parfitt, 2011). However, different vigor of the grafting partners can also result in overgrowth of one of the partners without posing any hazard to trunk health and tree physiology (Bowman and Joubert, 2020), as demonstrated by the long-time dominance of 'Swingle'. Together with 'Wgft+50-7', 'Swingle' induced the lowest SRR value in both trials.

The average yield at the Basinger location in 2018–19 was considerably lower than that at the Lake Wales location. One reason for this was an unusually high incidence of *Xanthomonas citri*, the causal organism of citrus canker, at the Basinger location, possibly as aftermath of hurricane Irma. Most of the high vigor-inducing rootstocks, such as 'X-639', 'ES-1', 'C-54', and 'C-57', were among the rootstocks that induced the highest cumulative yields across both production years and both locations, amounting to 149 to 158 boxes of fruit per acre (1 box = 90 lb or 40.8 kg of fruit). Although this amount is not yet considered commercially significant, many of the low vigor-inducing tetraploid rootstocks induced less than half this amount (70–83 boxes/acre), which, if this trend continues, mayprevent their commercial acceptance. Similar to our findings, in a rootstock trial with 'Marsh' grapefruit, 'X-639' and 'C-54' induced high cumulative yields and large tree sizes (Castle et al., 2011). In that trial, 'C-146' also produced high cumulative yields; however, our yield on this rootstock was average to low.

It is generally recognized that the size of the canopy is positively related to fruit yield (Anderson, 1987). An association between tree size and yield was also observed during rootstock trials with 'Valencia' and 'Hamlin' scion in Florida and with 'Pera' scion in Brazil (Albrecht et al., 2012; Bowman et al., 2016a; Quaggio et al., 2004). Despite the general relationship between canopy size and yield, in the present study, the medium vigor-inducing rootstock 'UFR-5' and the lower vigor-inducing 'ES-4' were among the rootstocks that induced higher than average cumulative yields. In contrast, the high vigor-inducing 'ES-2' rootstock induced a lower-than-average cumulative yield. The correlation between canopy size and yield in our trials was moderate (0.39) to high (0.66), depending on the location, suggesting that the canopy size of a citrus tree may not always be a good predictor of yield.

High yield-inducing rootstocks do not necessarily increase the productivity of a citrus orchard if the planting density is not optimized for the size of the mature productive tree (Bowman and Joubert, 2020). Hence, yield efficiency (yield per unit canopy volume) is a more suitable variable for determining productivity of a mature orchard. In two recent studies of 'Ray Ruby' grapefruit, high-density planting resulted in increased yield per hectare, increased fruit TSS contents, and decreased canopy volume (Phuyal et al., 2020). This demonstrates that the use of high-yield efficient rootstocks and optimized planting density can increase productivity and minimize cost per unit production.

Most of the high vigor-inducing rootstocks, such as 'X-639', 'C-54', 'C-57', and 'C-146', and some of the medium vigor-inducing rootstocks, such as 'ES-2' and 'ES-3', were not as yield-efficient in our study as the lower vigor-inducing rootstocks. Among the rootstocks that induced the highest yield efficiency were the tetraploid rootstocks 'Green-3', 'Amb+Benton', 'Changsha+Benton', 'Amb+Czo', and '6058+2071-02-2', which produced some of the smallest trees in the trials. However, despite having high yield efficiency, the overall yield potential of these rootstocks may not be sufficient, in the longer-term, to compete with the more vigorous rootstocks. Moreover, some of these small size-inducing rootstocks were leaning because of the strong winds imposed by the hurricane in 2017; the long-term impact remains to be investigated. 'ES-4', 'UFR-5', and 'Swingle' were among the rootstocks inducing higher-than-average yield efficiency across both locations and production years while producing medium-sized trees.

The priority for different fruit quality traits varies in different production areas based on the scion used and purpose (fresh fruit or juice production). For sweet oranges like 'Hamlin' that are grown for juice processing, TSS (Brix) is the most important fruit quality variable, followed by the acid content and the ratio of the two. Similar to other citrus studies, rootstocks in this study induced significant differences in all measured fruit quality variables in both trials (Bowman et al., 2016b; Grosser et al., 2011; McCollum and Bowman, 2017).

Most rootstocks induced more than 50% juice, except for 'ES-7', which is a lemon-type hybrid. Despite differences among locations for some of the rootstocks, there was a tendency for dwarfing and semi-dwarfing rootstocks to induce larger amounts of TSS than vigorous rootstocks. The inverse correlation between tree size and TSS was more evident at the Basinger location (R = –0.78) than at the Lake Wales location (R = –0.53). Among the highest TSS-inducing rootstocks in both locations were the smallest size-inducing tetraploid rootstocks 'Green-3', 'White-1', 'Changsha+Benton', 'Amb+Benton', 'Amb+Czo', 'Wgft+50-7', 'UFR-1', and 'UFR-6'. These rootstocks were also found to induce excellent fruit quality during a previous field trial with 'Valquarius' scion (Grosser et al., 2011). The low vigor-inducing rootstock 'US-897' and the high vigor-inducing rootstock 'X-639' induced the highest and lowest TSS contents, respectively, during a study of 'Ray Ruby' grapefruit trees (McCollum and Bowman, 2017).

The influence of rootstocks on fruit quality is assumed to be due to the different roles of rootstocks in the translocation of photoassimilates to the fruits (Gardner, 1969) and the movement of water and sucrose to the juice sacs (Castle, 1995). Because these factors also affect the vegetative growth of a tree, the inverse correlation found between TSS and the vigor-inducing capacity of rootstock is expected. In addition to rootstock cultivar, climatic factors (Davies, 1997) and diseases such as HLB can affect the citrus fruit quality (Baldwin et al., 2018; Liao and Burns, 2012) and interact with the rootstock (Dala-Paula et al., 2019). Two of the rootstocks ('ES-4' and 'ES-6') at the Lake Wales location induced a very low acid content, thereby increasing the TSS-to-acid ratio to more than 24. In general, acid ratios were very low in the 2019–20 production season. Unusually high temperatures and excessive rainfall throughout the year, particularly during the preharvest period, may have been responsible for this. The negative influence of warm temperatures on TSS and acid content was previously highlighted (Reuther, 1980; Zekri, 2011).

It is accepted that rootstocks differ in their capacity to uptake nutrients from the soil and distribute them through the scion (Brown et al., 1994; Toplu et al., 2012; Wutscher, 1973). In our study, the rootstock effect was not significant for most of the leaf nutrients and not consistent across both trials. Overall, most of the nutrients were in the range deemed optimal or high for citrus (Kadyampakeni and Morgan, 2020). The high Cu concentration measured in trees at both locations are the result of frequent Cu applications to control citrus canker, which is widespread in Florida (Dewdney et al., 2001; Zambon et al., 2019).

Conclusions

The diploid and tetraploid rootstocks investigated during this study differed in their effects on the 'Hamlin' scion. Among the most prominent effects were those on tree size and productivity. The early production of high-quality fruits and high productivity comprise one strategy that can result in growing citrus profitably under HLB-endemic conditions. Many of the tetraploid rootstocks reduced tree size significantly and consequently reduced yield; however, they increased yield efficiency. Therefore, these rootstocks may be suitable for high-density plantings to increase orchard productivity during the early production years. However, many of the small size-inducing rootstocks rendered the trees more vulnerable to tropical force winds than the large size-inducing rootstocks. Although this study was conducted during the early production years, the results are valuable for predicting rootstock resilience and their economic potential in the longer term.

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