

Frequent Irrigation Increases Yield in Huanglongbing-Affected Sweet Orange

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KEYWORDS. citrus greening, HLB, irrigation, water deficit

ABSTRACT. A steady decline in sweet orange (*Citrus sinensis*) tree health is associated with Huanglongbing (HLB). Part of this decline includes root dieback, which limits their capacity to take up water. For this reason, affected trees tend to be more susceptible to drought stress. This raises a significant concern during the dry season (October to May) when trees are largely dependent on supplemental irrigation for water. Unfortunately, most growers continue using irrigation schedules that were optimized for healthy trees. We hypothesized that irrigating more frequently but in smaller amounts would provide more opportunities for uptake and improve water relations in HLB-affected sweet orange trees. The control treatment received the standard practice of irrigating every other day for 2 h (12 gal/h). The experimental treatment received water every day, three times a day, for 20 min (12 gal/h). The two treatments received the same amount of water over the course of a week, but the experimental treatment received water more often. Treatments were initiated before flowering in Jan 2022 and were continued for 2 consecutive years. Upon implementation, tree water status improved in the experimental trees as reflected in higher midday leaf water potentials than in the control. In the second year, flowering was more synchronized in the experimental treatment. The control treatment saw two peaks in bud production with the latter one being consistent with a drought stress-induced flowering event. The experimental trees also saw increases in fruit set in year 1 (41% higher in experimental) and year 2 (18% higher in experimental). Trees receiving the experimental and control treatments dropped a similar proportion of their crop load during June drop and preharvest fruit drop in years 1 and 2. Finally, the experimental treatment resulted in significantly higher yields on average than the control in both year 1 and year 2. Altogether, more frequent irrigation improved sweet orange tree productivity by maintaining a better water status.

The state of Florida has seen a steady decline in citrus production since the arrival of Huanglongbing (HLB) in 2005 (Graham et al. 2020; US Department of Agriculture, National Agricultural Statistics Services 2022). Asian citrus psyllid vector the presumed causal bacteria, *Candidatus Liberibacter asiaticus*, which they transfer to citrus trees while feeding on vegetative flush (Ammar et al. 2020; Bové 2006; Inoue et al. 2009). Once infected, trees slowly

decline in health and productivity before finally succumbing to secondary stressors (Bové 2006).

One of the symptoms associated with HLB is root dieback (Johnson et al. 2014; Kumar et al. 2018). HLB-affected roots have a shorter lifespan than healthy roots (Kumar et al. 2018), leading to a reduction in fibrous roots and resulting in the root dieback commonly associated with HLB (Graham et al. 2013; Fan et al. 2013; Kumar et al. 2018). The smaller root systems of HLB-affected trees are limited in their capacity to take up water compared with healthy trees as evidenced by their lower stem water potentials, sap flow, and daily water usage compared with healthy trees (Graham et al. 2013; Hamido et al. 2017; Kadyampakeni et al. 2014; Tang et al. 2020). This reduced uptake capacity suggests that HLB-affected trees are more susceptible to water deficits. However, this may only be a concern during the dry season, when

trees are reliant on supplemental irrigation. In Florida, the dry season extends from October to May (Fig. 1 and Supplemental Table 1).

In sweet orange (*Citrus sinensis*), flowering, fruit set, and fruit maturation occur during the dry season. Therefore, any water deficits occurring during the dry season could negatively affect these developmental stages. In fact, several of the symptoms associated with HLB are also seen under drought stress (Table 1). Therefore, it is possible any water deficits HLB-affected trees experience will exacerbate some of these symptoms.

Historically, irrigation has been viewed as purely supplemental and only needed during extended dry periods (Parsons and Wheaton 2000). Moreover, FL growers still use irrigation practices that were optimized for healthy trees and have not been modified for HLB-affected trees. Such frugal irrigation practices will not sustain HLB-affected citrus trees with their limited uptake capacity. In fact, it has been previously shown that HLB-affected trees benefit from regular irrigation (Kadyampakeni and Morgan 2017). Nonetheless, simply increasing the amount of water applied during a single irrigation event will not improve tree water relations as the roots of HLB-affected trees will still be limited in their uptake capacity. As a result, additional water added during a single irrigation event would likely run off due to the poor water holding capacity of the fine sands common to Central Florida (Mylavarapu et al. 2019; Obreza and Collins 2002). Rather, applying water frequently but in smaller amounts would provide more opportunities for HLB-affected trees to take up water. Therefore, the objective of the current study was to determine whether frequent, small irrigation events would improve water relations and tree productivity in HLB-affected trees. To do so, an experimental irrigation regime consisting of multiple daily irrigation events was implemented and compared with the standard practice of irrigating every other day. Treatments were evaluated based on volumetric soil water content, leaf water potential, fruit set and retention, yield, juice quality, and canopy volume. The results presented herein will provide a baseline for future recommendations

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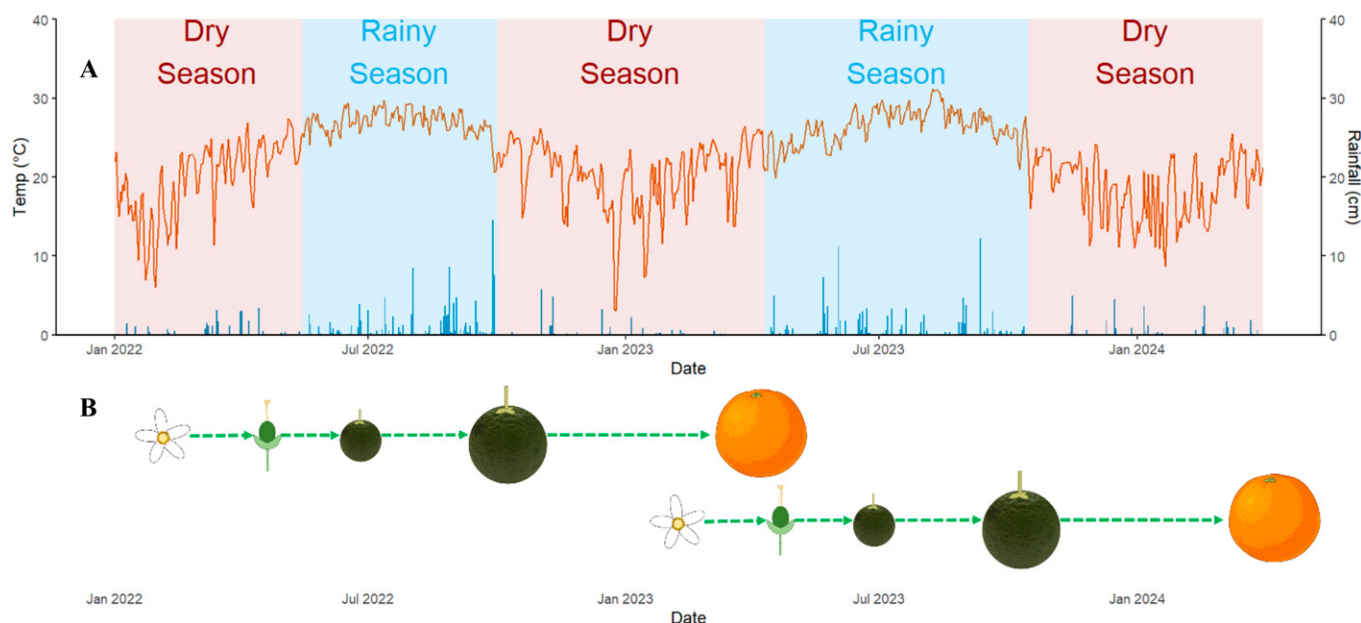


Fig. 1. (A) Weather patterns in Lake Alfred, FL, during the 2-year course of the study ranging from Jan 2022 to Apr 2024. The daily average temperature (Temp, °C) is represented by the orange line. Total daily rainfall (cm/day) is represented by the blue columns. The dry season is highlighted by a red background, and the rainy season is highlighted by a blue background. Weather data were retrieved from the Florida Automated Weather Network (<https://fawn.ifas.ufl.edu/>). **(B)** General fruit growth and development timeline of ‘Valencia’ Sweet Orange. Its 14-month-long season overlaps with the subsequent crop. Flowering, fruit set, early fruit growth, and fruit maturation fall during the dry season in Central Florida.

for Florida citrus growers regarding their irrigation practices.

Materials and methods

PLANT MATERIALS, CULTURAL PRACTICES, AND EXPERIMENTAL DESIGN. Fifteen-year-old ‘Valencia’ on ‘Swingle’ rootstock trees located in Lake Alfred, FL, USA were used for this study. The soil in this orchard is a Candler fine sand (entisol). The orchard was maintained following recommendations made by the University of Florida/Institute of Food and Agricultural Sciences apart from irrigation. Additional irrigation lines were

installed before the start of the study so that multiple irrigation schedules could run in the same orchard on trees side by side. The control treatment consisted of the standard practice of running irrigation every other day at 6:00 AM, for 2 h, at a rate of 12 gallons/hour. The experimental treatment received water every day, three times a day (5:40 AM, 10:00 AM, and 2:00 PM), for 20 min at a time, at a rate of 12 gallons/hour. The two treatments received the same amount of water over time but differ in the frequency and duration in which they receive it.

Treatments were applied to blocks of three trees with the two outer trees acting as buffers. Measurements, observations, and sampling were done on the middle trees ($n = 5$) for the 2 consecutive years of the study (2022–24). Blocks were selected based on the HLB symptom severity of the middle tree. Trees displaying moderate HLB symptoms, tree canopies intercepting more than 85% of photosynthetically active radiation, were selected (Singh et al. 2022). The same trees were used for the entire course of study.

Table 1. HLB-affected citrus trees and drought-stressed citrus trees share a number of symptoms.

Symptom	Drought stress	HLB
Off-season flowering	Syvertsen and Hanlon 2008; Agusti et al. 2022	Dewdney 2015
Reduced fruit set	Ginestar and Castel 1996; García-Tejero et al. 2010; Iglesias et al. 2007; Talon et al. 1997	Vashisth and Sutton 2022
Increased rates of fruit abscission	Ginestar and Castel 1996; González-Altozano and Castel 1999	Tang et al. 2019; 2020
Reduced canopy growth	Ginestar and Castel 1996; Romero et al. 2006; Pérez-Pérez et al. 2009	Bové 2006; Neupane et al. 2023
Increased levels of abscisic acid	Gomes et al. 2004	Rosales and Burns 2011; Martinelli et al. 2013; Neupane et al. 2023
Poor fruit quality	Ginestar and Castel 1996; García-Tejero et al. 2010	Bassanezi et al. 2009; Rosales and Burns 2011; Liao and Burns 2012
Lower yields	Ginestar and Castel 1996; Pérez-Pérez et al. 2009; García-Tejero et al. 2010	Bassanezi et al. 2009

The following is a summary of literature describing these similar symptoms in HLB-affected citrus trees and drought-stressed citrus trees. HLB = Huanglongbing.

WATER RELATIONS MEASUREMENTS.

The volumetric water content (VWC) of the soil was determined using a FieldScout TDR150 soil moisture meter with an 8-inch probe (Spectrum Technologies, Inc., Aurora, IL, USA). Measurements were conducted between 1:00 PM and 2:00 PM on clear, sunny days that were also preceded by at least 3 d of similar conditions with no rain.

Leaf water potential was determined using a Scholander pressure chamber (model 615D; PMS Instrument Company, Albany, OR, USA). Two hardened-off leaves per tree were collected from the sun-exposed side of the canopy between 1:00 PM and 2:00 PM on clear, sunny days that were also preceded by at least 3 d of no rain (Tang et al. 2020). The small sample size was to ensure that all measurements could be taken before the experimental irrigation treatment began at 2:00 PM. While all the trees were sampled on each date, sampling dates varied across the 2 years of the study based on conducive weather conditions.

PHYSIOLOGICAL MEASUREMENTS.

The flowering frames method was used to monitor bud, flower, and early fruit production during the spring flush (Tang et al. 2021). The frames used measured 10×10 inches, and counts extended ~ 10 inches into the canopy (~ 1000 inches³). The results were recorded for two frames on the east side and two on the west side of the tree (four frames/tree). The results recorded from the four frames were totaled and are reported herein. In year 1, only fruit production was recorded. In year 2, bud, flower, and fruit production was recorded. In year 2, 10 branches (~ 6 to 8 inches long) were tagged before the start of flowering. Bud, flower, fruit, and leaf production were monitored on these branches through harvest. In year 2, a late flowering event (in the month of May) also occurred. Up to 20 inflorescences (not all trees produced at least 20) with newly set fruit were tagged on each tree to monitor the retention of these late emerging fruit.

In year 1, three small, elevated wire frames were placed beneath each tree to collect immature fruit drop. The frames were constructed out of polyvinylchloride pipes and chicken wire. The frames measured 20×35 inches and

sat ~ 6 inches above the ground. The dropped immature fruit were collected and counted weekly from the start of fruit set through the end of June drop. These collection frames were not used in year 2 due to their proclivity for attracting snails.

Fruit equatorial diameters were obtained using digital calipers regularly throughout the season. In year 1, 50 random fruit were measured at each time point. In year 2, only 30 random fruit were measured at each time point due to the low fruit set in the control trees.

On 20 Sep 2023, root samples were collected to determine root density. A stainless-steel soil core with an internal diameter of 35 mm and length of 25 cm was used to extract soil cores from three places beneath the canopy of each tree. Soil cores were pooled for each tree. Roots were extracted from the pooled core samples by gently washing them over a 2-mm screen. The extracted roots were dried at 65 °C for 3 d and then weighed. Root density is reported as grams roots/L soil.

To monitor preharvest fruit drop, the area beneath each tree was raked, and the dropped fruit were tallied. This was done biweekly from January to harvest. The trees were harvested on 30 Mar 2023 in year 1 and on 16 Feb 2024 in year 2. At the time of harvest, all fruit were removed from the tree, weighed, and counted to obtain the final yield and fruit number. A subsample of 20 fruit was taken back to the laboratory for juice quality assessment. The soluble solids content and percentage of citric acid were determined using a citrus pocket brix-acidity meter (Atago Co., Ltd., Tokyo, Japan).

Lastly, canopy density and volume were determined yearly to monitor growth. Canopy density was determined as described by Singh et al. (2022), and canopy volume was determined by measuring the height of the canopy and two diameters (perpendicular to the row and parallel to the row). Canopy volume was calculated as follows: $\text{Volume} = \frac{4}{3} \pi \times \frac{1}{2} \text{Height} \times \frac{1}{2} \text{Width} \times \frac{1}{2} \text{Length}$. The height, width (perpendicular diameter), and length (parallel diameter) are divided by 2 to calculate their respective radii. Canopy volume measurements were taken at harvest each

year. Canopy density measurements were taken in Jan 2022, Feb 2023, and Feb 2024.

STATISTICAL ANALYSIS. All statistical analyses were performed in R (version 4.1.0; R Core Team, Vienna, Austria) (R Core Team 2021). Repeated-measures analyses of variance were used to determine differences in bud, flower, fruit, and leaf production and in fruit diameter between the two treatments over time. Where appropriate, two sample *t* tests were used to determine differences between the two treatments. An α -value of 0.1 was used for all analyses due to the high degree of HLB symptom variability seen both within and across affected trees (Nehela and Killiny 2020).

Results

WATER RELATIONS. Mid-afternoon soil VWC was significantly higher in the experimental treatment (10.5%) compared with the control treatment (5.6%) on days when only the experimental irrigation treatment ran ($P = 0.0006$). This difference in soil water availability was reflected in the above-ground water status of the tree. Mid-afternoon leaf water potentials were consistently lower in the control treatment compared with the experimental treatment during the dry season in both years 1 and 2 (Table 2). This trend was observed on days when only the experimental treatment was run and on days when both the experimental and control treatments were run.

FLOWERING AND FRUIT SET. In year 1, the experimental treatment consistently had numerically more fruit than the control treatment (Supplemental Fig. 1A). By the end of June drop (6 Jun 2022), the experimental trees had significantly higher fruit numbers than the control trees. Interestingly, the experimental trees also dropped significantly more immature fruitlets during immature fruit drop and June drop compared with the control (Supplemental Fig. 1B).

In year 2, the experimental treatment saw a single peak in bud production (23 Feb 2023), whereas the control treatment saw two [23 Feb 2023 and 11 May 2023 (Fig. 2A)]. The experimental treatment produced significantly more buds at its peak compared with the control during its first peak (Fig. 2A). The control treatment

Table 2. Average leaf water potential of ‘Valencia’ trees receiving the current standard irrigation (control) and those receiving small, frequent irrigation applications (experimental).

Treatment	Year 1		Year 2		
	March		February	May	
	Both Run	Only Exp Run	Only Exp Run	Both Run	Only Exp Run
Control	−1.56 b	−1.87 b	−1.60 b	−2.44 b	−2.37 b
Experimental	−1.327 a	−1.41 a	−1.51 a	−2.01 a	−1.95 a
<i>P</i> value	0.0398	0.0366	0.0644	0.0037	0.0004

The values are reported in MPa. The values are the average of two leaves taken from the sun-exposed side of each tree ($n = 5$). The samples were taken between 1:00 PM and 2:00 PM on clear, sunny days that were preceded by at least 3 d of clear, sunny conditions and no rain. To meet these conditions, the sampling dates were different during the 2 years. Measurements were taken on days when the experimental and control treatments were run so that both treatments received water that day (Both Run). Measurements were also conducted on the days when only the experimental treatment was run (Only Exp Run). The herein reported *P* values are the results of a *t* test between the control and experimental treatment. Trees either received the standard practice of running irrigation every other day, for 2 h, at a rate of 12 gallons/hour (the control treatment) or received water every day, 3 times a day, for 20 min at a time, at a rate of 12 gallons/hour (the experimental treatment). Exp = experimental treatment.

had significantly more buds at its second peak (11 May 2023) compared with the experimental treatment (Fig. 2A). This trend was reflected in flower production as well (Fig. 2B). The experimental treatment consistently had higher fruitlet production during initial fruit set. Despite having a second peak in reproductive growth, the control trees still had numerically fewer fruit at the end of June drop (significantly so on 15 Jun 2023) compared with the experimental trees (Fig. 2C). The retention of the late emerging fruit was also low, regardless of irrigation treatment; on average, only 3.5% of the late emerging fruit was retained through June drop, and only 0.84% was retained through harvest.

Monitoring bud, flower, and fruitlet production on individual branches rather than at the canopy scale revealed that the branches on the experimental trees were generally more productive than those on the control trees (Fig. 3A–3C). Generally, at their peak, bud (Fig. 3A), flower (Fig. 3B), and fruitlet (Fig. 3C) numbers were higher in the experimental treatment. Notably, following June drop, fruit numbers were relatively consistent between the two treatments (Fig. 3C).

LEAF PRODUCTION. Average leaf production was monitored on 10 tagged branches over the course of the season. During the spring flush,

branches on trees receiving the experimental treatment produced significantly more leaves than those on control trees (8 vs. 3.6 leaves/branch, respectively; $P = 0.0003$). This resulted in the branches from experimental trees having significantly higher leaf numbers during the early spring (overlapping with early fruit development) compared with the control (Fig. 3D). Interestingly, the opposite was observed during the summer flush; branches from control trees produced significantly more leaves than those from the experimental trees (7.4 vs. 2.75 leaves/branch; $P = 0.0146$). Notably, this summer flush occurred after the start of the rainy season. Following

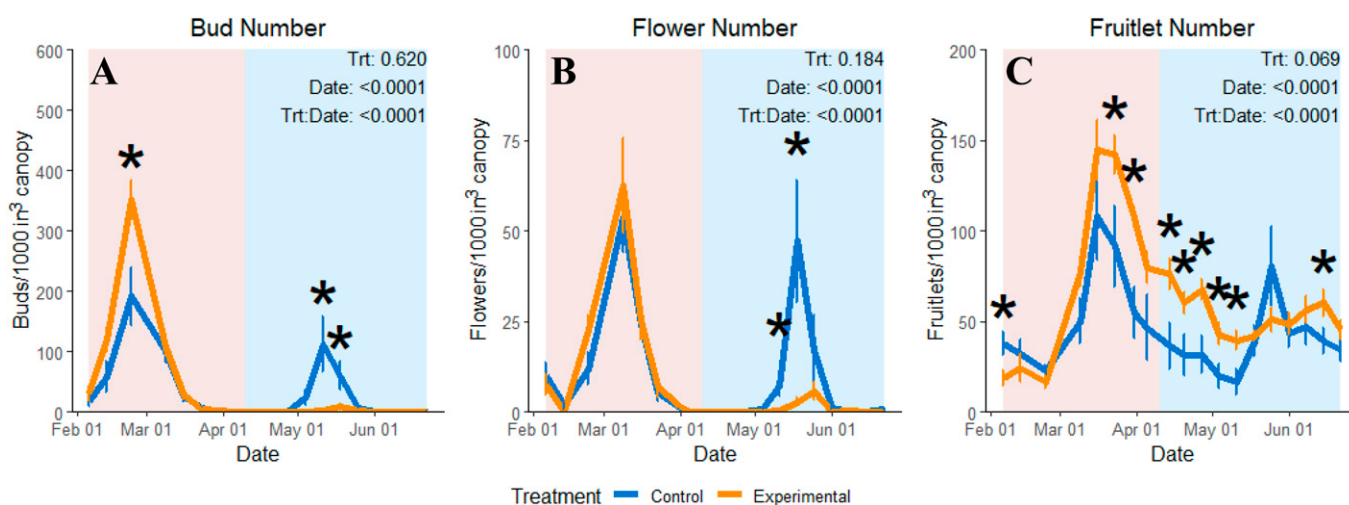


Fig. 2. Year 2 (2023) flowering trends. Bud (A), flower (B), and fruitlet (C) numbers were counted in ‘Valencia’ trees using the frame method: a 10 × 10-inch PVC frame was held to the canopy, and buds, flowers, fruit that fell within the confines of the frame were counted. Counts extended ~10 inches into the canopy. The reported values are an average of four frames per tree ($n = 5$). The values in the upper right-hand corner are *P* values resulting from a repeated-measures analysis of variance looking at irrigation treatment (Trt), time (Date), and the interaction between treatment and time. Asterisks indicate dates when the control and experimental treatments significantly differed in their counts as evidenced by individual *t* tests at each time point. Red and blue backgrounds indicate the dates falling within the dry and rainy season, respectively. Trees either received the standard practice of running irrigation every other day, for 2 h, at a rate of 12 gallons/hour (the control treatment) or received water every day, three times a day, for 20 min at a time, at a rate of 12 gallons/hour (the experimental treatment).

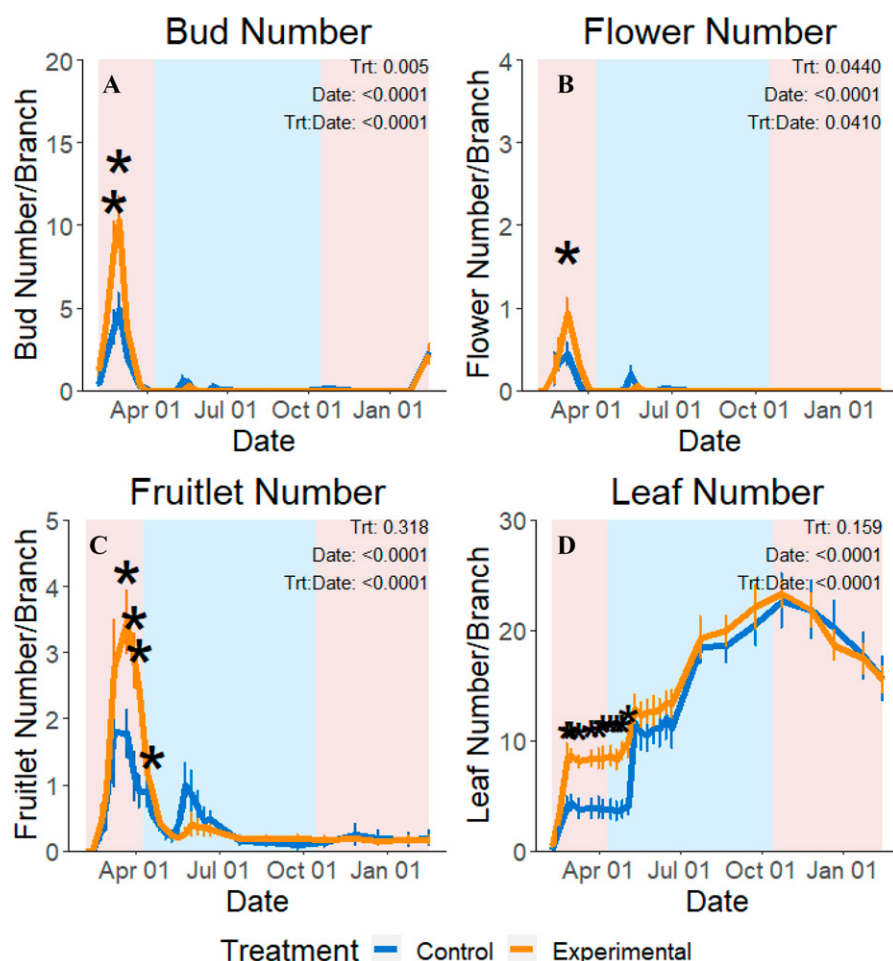


Fig. 3. Average bud (A), flower (B), fruitlet (C), and leaf (D) number per branch in ‘Valencia’ trees. For each tree ($n = 5$), the average number of buds, flowers, fruitlets, or leaves were calculated from the counts of ten ~6- to 8-inch tagged branches. The same ten branches were counted at each time point. The values in the upper right-hand corner are P values resulting from a repeated-measures analysis of variance looking at irrigation treatment (Trt), time (Date), and the interaction between treatment and time. Asterisks indicate dates when the control and experimental treatments significantly differed in their counts as evidenced by individual t tests at each time point. Red and blue backgrounds indicate the dates falling within the dry and rainy season, respectively. Trees ($n = 5$) either received the standard practice of running irrigation every other day, for 2 h, at a rate of 12 gallons/hour (the control treatment) or received water every day, three times a day, for 20 min at a time, at a rate of 12 gallons/hour (the experimental treatment).

the summer flush, the two treatments had similar leaf numbers for the remainder of the season (Fig. 3D). Leaves that emerged during this observation window began to senescence and abscise after the onset of the dry season in October (Fig. 3D) in both sets of trees.

FRUIT GROWTH. Throughout year 1, fruit sizes did not differ between the two treatments except on 20 Jul 2022, when the experimental fruit were larger on average (Supplemental Fig. 2A). By harvest, there were no differences in fruit size between the two treatments. Similarly,

at harvest, fruit size did not differ between control and experimental trees in year 2 (Supplemental Fig. 2B). However, fruit on the experimental trees were initially larger at the start of the season and at three timepoints during rapid fruit growth (Supplemental Fig. 2B). Nonetheless, fruit size was not significantly affected by the experimental irrigation treatment.

PREHARVEST FRUIT DROP. Harvest was later in the calendar year in year 1 (20 Mar 2023) compared with year 2 (19 Feb 2024). For this reason, the preharvest fruit drop window was

longer in year 1 compared with year 2. Nonetheless, in both years, the two treatments dropped a similar proportion of their crop load during preharvest fruit drop (Table 3).

HARVEST AND FRUIT QUALITY. The trees receiving the experimental treatment yielded significantly more fruit than the trees receiving the control treatment in both year 1 (4 kg/tree more) and year 2 [18 kg/tree more (Table 3)]. This difference in yield was largely the result of differences in fruit number (Table 3) rather than differences in fruit size (Supplemental Fig. 2). The juice quality was also similar between the two treatments (Table 3).

CANOPY GROWTH. The trees selected for the present study had comparable canopy densities (measured as the percentage of light interception) before treatment implementation (Jan 2022). The average light interception of the control and experimental trees was 85.5% and 82.7%, respectively ($P = 0.432$). The control and experimental trees had similar canopy densities in Feb 2023 as well; the light interception of the control and experimental trees had dropped to 67.1% and 67.0%, respectively ($P = 0.9896$). However, in Feb 2024, the experimental trees (83.5% light interception) had a significantly denser canopy than the control trees (74.7% light interception). The experimental trees also had significantly higher canopy volumes at harvest compared with the control trees in both year 1 [23.9 m³ vs. 20.0 m³, respectively ($P = 0.0723$)] and year 2 [27.4 m³ vs. 21.6 m³, respectively ($P = 0.0290$)].

ROOT DENSITY. Trees receiving the control treatment had similar root densities to the trees receiving the experimental treatment [0.40 g root/L soil vs. 0.34 g root/L soil, respectively ($P = 0.6584$)].

Discussion

Florida soils are predominantly sandy (Mylavarapu et al. 2019). The orchard used in the present study was established on Candler fine sand, a sandy entisol. While citrus can be grown on a variety of soil types, citrus production in Central Florida is largely conducted on entisols (Mylavarapu et al. 2019; Obreza and Collins 2002). Candler fine sands generally have a low water-holding capacity and are

Table 3. Average fruit drop, yield, fruit number and brix:acid ratio of ‘Valencia’ trees receiving the current standard irrigation (control) and those receiving small, frequent irrigation applications (experimental) in year 1 (2022) and year 2 (2023).

Treatment	Fruit drop (%)	Year 1			Year 2			
		Yield (kg)	Fruit (no.)	Brix:acid ratio	Fruit drop (%)	Yield (kg)	Fruit (no.)	Brix:acid ratio
Control	77.2	6.0 b	53 b	12.8	25.5	8.9 b	89 b	7.29
Experimental	72.6	10.4 a	87 a	10.6	25.1	27.2 a	249 a	7.46
P value	0.4624	0.0908	0.0800	0.1252	0.9299	0.0408	0.0406	0.7675

Fruit drop is the percentage of the crop load dropped during the preharvest fruit drop period. Yield is the total amount of fruit remaining on the tree at harvest. Brix:acid ratio refers to the ratio of total soluble solids to the percent citric acid of the juice (a common measure of juice quality). Values with different letters indicate they are significantly different as determined by a *t* test between the control and experimental treatments. Trees either received the standard practice of running irrigation every other day, for 2 h, at a rate of 12 gallons/hour (the control treatment) or received water every day, three times a day, for 20 min at a time, at a rate of 12 gallons/hour (the experimental treatment).

well drained (Mylavarapu et al. 2019; Obreza and Collins 2002). For this reason, this soil type can reach field capacity ~1 d after being wetted (Zekri and Parsons 1999). Due to the poor water retention of these soils, providing more water at a single irrigation event does not increase soil water availability throughout the day as the excess water runs off quickly. Rather, providing water in smaller amounts but at multiple times throughout the day would increase soil water availability throughout the day. The higher midafternoon soil VWC under the experimental treatment compared with the control reported herein suggests the experimental treatment did in fact increase soil water availability to the tree throughout the day. The soil VWC under the control treatment was depleted below field capacity before its next irrigation event, whereas the soil under the experimental treatment was maintained at or above field capacity (Zekri and Parsons 1999; Zotarelli et al. 2019). As a result, the experimental treatment trees were able to use the increased soil water availability compared with the control treatment as indicated by higher midafternoon leaf water potentials in the experimental compared with the control. Generally, a leaf water potential of -2.0 MPa serves as a threshold below which negative effects of water deficits begin arising (Chica and Albrigo 2013; Gasque et al. 2016; Syvertsen and Albrigo 1980; Syvertsen et al. 1981). However, this cutoff was established in healthy citrus. It has been previously reported that HLB-affected trees differ from healthy trees in their optimal nutrient levels, suggesting that HLB-affected trees have different requirements compared with healthy trees (Atta et al. 2020; Morgan et al. 2016;

Rouse et al. 2017). As it has already been established that HLB-affected trees differ in their water consumption compared with healthy trees consumption (Hamido et al. 2017), it is therefore possible that the minimum leaf water potential needed to maintain a well-watered status may also differ. Nonetheless, while leaf water potentials only dropped below the -2.0 MPa threshold in year 2, leaf water potentials were consistently lower in the control treatment compared with the experimental treatment. This suggests that under the standard irrigation practice, HLB-affected trees are more likely to be exposed to water-deficit conditions compared with the experimental irrigation schedule despite still receiving supplemental irrigation. Further evidence of this was seen in the late flowering event in the control trees in year 2. Flowering can be induced by both low temperatures ($<20^{\circ}\text{C}$) and rehydration after a water deficit (Iglesias et al. 2007; Moss 1976; Southwick and Davenport 1986). The duration and severity of the water deficit will determine the extent of flowering, with consistent, long-term deficits more likely to induce flowering (Chaikiattiyos et al. 1994; Chica and Albrigo 2013; Southwick and Davenport 1986). There was no rainfall from 16 Mar 2023 to 11 Apr 2023 (27 d), and the daily rainfall was less than 0.1 inches from 6 Mar 2023 to 14 Apr 2023 (40 d) (Florida Automated Weather Network 2024). This was followed by 1.95 inches of rain on 17 Apr 2023 (Florida Automated Weather Network 2024). Average daily temperatures were $\sim 22^{\circ}\text{C}$ during this period (Florida Automated Weather Network 2024), which is above the 20°C temperature threshold for floral

induction (Moss 1976). In ‘Tahiti’ lime (*Citrus latifolia*), water deficits maintained for as little as 14 d were able to induce flowering upon rewetting (Southwick and Davenport 1986). In sweet orange, water deficits implemented under greenhouse conditions for 40 to 60 d were also able to induce flowering (Chica and Albrigo 2013). Altogether, this suggests the control treatment was unable to maintain trees at a well-watered status during the extended dry period seen in Mar to Apr 2023. Such water deficits can also reduce fruit set (García-Tejero et al. 2010; Iglesias et al. 2007; Talon et al. 1997), which may contribute to the reduced peak in fruit set observed in years 1 and 2.

Following rewetting, sweet orange trees subjected to a 60-d water deficit produced more leafy inflorescences and vegetative shoots than trees receiving normal irrigation (Chica and Albrigo 2013). This may account for the initial low leaf production during the spring flush in the dry season and the significant increase in leaf number seen in the control following the start of the rainy season in year 2. A similar trend was not seen in year 1. However, temperatures were lower and daily rainfall higher on average during the dry season in year 1 compared with year 2 (Supplemental Table 1).

Generally, an increase in fruit number like the one observed in the experimental treatment would correspond with a decrease in fruit size as competition for available resources increases (Goldschmidt 1999), but this was not the case in the present study. Despite the increased fruit set, fruit on experimental trees were generally larger than the fruit on the control tree during the season in year 2 and had a comparable fruit size at harvest

in both year 1 and year 2. This may suggest that factors other than crop load were limiting fruit size in the control treatment during the season in year 2. Water deficits during fruit growth will generally reduce fruit size (García-Tejero et al. 2010; Ginestar and Castel 1996). A water deficit during fruit set and early fruit growth may have initially limited the growth of fruit in the control, and rewatering (the start of the rainy season) alleviated this limitation. The reduced crop load in the control may have then reduced competition and allowed for rapid fruit growth, resulting in fruit of a similar size to the experimental treatment. Despite their different crop loads, the two treatments dropped a similar proportion of their crop load during the preharvest fruit drop period, suggesting that the experimental irrigation regime was not able to reduce preharvest fruit drop rates. Nonetheless, the experimental treatment had significantly higher yields than the control treatment, suggesting that the differences in crop load seen as early as fruit set were maintained until harvest. However, yields across both treatments were low. HLB-affected trees typically have lower yields than healthy trees, and yields continue to decline as the disease progresses (Bové 2006). Their continued decline in health and the occurrence of a hurricane in Sep 2022 likely contributed to the lower yields observed in the present study.

Tree water status can likewise influence juice quality (García-Tejero et al. 2010; Ginestar and Castel 1996). Poorly maintained tree water status, as seen under water deficits, results in increased juice total soluble solids and titratable acidity (García-Tejero et al. 2010). However, no difference in juice quality was observed in the present study, suggesting that the frequency of irrigation does not negatively affect juice quality by diluting the sugar and acid content of the juice.

Lastly, at the end of the study, the experimental trees had significantly higher canopy volume and density compared with the control trees. Hurricane Ian made landfall in late Sep 2022, causing significant damage across the state of Florida (Court et al. 2023; Florida Automated Weather Network 2024; National Hurricane Center 2023). Hurricane Ian's path crossed through Central Florida, where the present

study was conducted. The damage done to the canopy was still apparent in the lower canopy densities seen in Feb 2023. The similar decline in canopy density from Jan 2022 to Feb 2023 in both treatments is likely due to damage from the hurricane. However, the significantly higher canopy density and volumes seen in the experimental treatment at harvest in 2024 suggest that the trees receiving the experimental irrigation recovered a larger proportion of their canopy compared with the control trees. Interestingly, no differences were seen between the control and experimental treatments in root density after ~1.5 years, further research is needed to evaluate the long-term effects of this experimental irrigation regime on root growth and health.

Conclusions

Frequent, small irrigation events improved tree water relations, resulting in increased bud, flower, fruitlet, and leaf production during the spring flush. The increased crop load was maintained throughout the year, resulting in higher yields at harvest compared with the control treatment. Altogether, frequent, small doses of irrigation are imperative for maintaining a well-watered status in HLB-affected trees, especially during the dry season when trees are reliant on supplemental irrigation. Further research is needed to evaluate the long-term effects of such an irrigation regime on general tree health and productivity.

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