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# Quick Recovery of Leaf Photosynthesis and Fruit Quality from Soil Water Deficit of Citrus aurantiifolia Growing in a City

Pantana Tor-ngern[1,*], Vijittar Jan-uthai[2], Nisa Leksungnoen[3]

[1] *Department of Environmental Science, Faculty of Science, Chulalongkorn University, Bangkok, Thailand*
[2] *Interdisciplinary Program in Environmental Science, Graduate School, Chulalongkorn University, Bangkok, Thailand*
[3] *Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok, Thailand*

* Corresponding author : pantana.t@chula.ac.th

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## Abstract

Under the projected warming climate, water scarcity will become one of the main challenges for growing crops. Such issue is particularly difficult in urban environments where growing conditions for plants are limited and warming effect is intensified. Here, we showed that infrequent irrigation may be performed when growing lime (*Citrus aurantiifolia*) saplings in Bangkok, Thailand, with quick recovery of photosynthesis and fruit quality. During a two-week water-deficit experiment, stomatal conductance of the lime saplings decreased up to 67% when soil moisture declined by 40% from the control level on day 6, resulting in 27% and 16% reductions of net photosynthesis ($A_{net}$) and transpiration (E), respectively. Accordingly, water-use efficiency decreased by 20%. After that, irrigation was resumed to study the recovery effect on the gas exchange parameters. Results showed full recovery after 3 days with Anet, E and WUE values not statistically different from those in the control group. Lime fruits were harvested for analysis of vitamin C content. We found that, after the water deficit and re-watering, vitamin C content in the lime fruits was not affected, showing similar values across treatments. Our results suggested that discontinuous irrigation (i.e. up to 6 days of withheld irrigation) may be applied to induce moderate soil water deficit (-40% of the control level) when growing the lime saplings in a raised-bed plot in the city, without affecting photosynthesis and fruit quality. This finding offers an approach for sustainable urban agriculture in the future drying environments.

***Keywords:*** Citrus aurantiifolia; net photosynthesis; water-use efficiency; vitamin C; water deficit

## 1. Introduction

With high atmospheric $CO_2$, many parts of the world will likely experience droughts with increases in intensity and frequency (Sheffield and Wood, 2008). One of the major drought impacts is decreasing plant growth and therefore crop yield (Ferrara et al., 2011; Rebey et al., 2012). In urban areas, the drought impacts on plants become intensified compared to those in natural and rural settings because of the warmer atmosphere resulting from the so-called urban heat island effect (Li and Bou-Zeid, 2013). As the world population is expected to reach ~9.7 billion in 2050 (UN, 2015), combined with the predicted increases of drought, decline in crop yield will occur in many areas and thus shortage of food supply. In many developing countries, the consumption of fruits and vegetables by urban residents is less than the daily minimum intake of 400 g per person per day as recommended by the joint WHO-FAO Expert Consultation on Diet, Nutrition and Prevention of Chronic Diseases for the prevention of non-communicable diseases and of micronutrient and vitamin deficiency (WHO, 2003). Also, most fruits and vegetables are grown in rural areas, making it difficult for urban dwellers to access. With these regards, urban agriculture, which includes fruit trees, vegetables and other specialized crops, wood production, small-scale animal farms and aquaculture (Drescher and Iaquinta, 1999; FAO, 2001; Ghosh, 2004; Mougeot, 1994), has been proposed and already implemented in some cities to tackle food insecurity (Agbonlahor et al., 2007). However, growing crops in cities is challenging due to many limiting environmental conditions, including limited space, compact soil, water scarcity and pollution. Therefore, we need to optimize the limited resources for good crop yield in urban agriculture.

Besides providing food security, urban agriculture plays a role in urban greening which involves using plants to remove the high atmospheric $CO_2$ concentration through photosynthesis. Because crop production capacity may be reduced by 19 – 35% by urban tree shading (Richardson and Moskal, 2016), utilization of the limited urban space for urban agriculture needs to be carefully planned. Therefore, if one wants to acquire both climate change mitigation and food security, effective land use in cities should be considered. This may be achieved by selectively planting crop species that possess relatively high and sustained photosynthesis ($CO_2$ mitigation) through extreme events, such as drought, while consuming little water and whose quality is not severely affected by water deficit.

One of the major drought impacts on plants is stomatal closure (Damour et al., 2010). As a consequent, transpiration is reduced, together with lower net $CO_2$ uptake. The decrease in net photosynthesis translates into reduced carbohydrate supply to the yield and lessened $CO_2$ mitigation. High sunlight stress associated with drought induces photo-oxidative stress which stimulates the accumulation of antioxidant compounds (Kasote et al., 2015), thus increasing crop quality. In fact, a recent review indicated changes in nutritional value in some crop species in response to many abiotic stresses (Wang and Frei, 2011). Therefore, for effective land and resource management in the warming cities, crop species that require infrequent irrigation, yet can sustain or even increase photosynthesis and quality (i.e. nutritional value) may be desired.

Although several studies demonstrated benefits of water deficit irrigation in agricultural practice in the field or an orchard (e.g. Fereres and Soriano, 2006; García-Tejero et al., 2010a,b), only few studies addressed this aspect in urban agriculture. Here, we examined effects of water deficit and recovery on leaf photosynthesis, water-use efficiency (WUE) and fruit quality of *Citrus aurantiifolia* (lime) growing in a raised-bed plot on a balcony in Bangkok, Thailand. We selected lime because it is one of the most popular ingredients in Thai dishes with significant economic value. Also, because the leaf phenology of lime is evergreen, lime can photosynthesize and may provide higher environmental benefit for atmospheric $CO_2$ mitigation compared to other crops. The objectives of this study are (1) to investigate the responses of photosynthesis and WUE of lime under water deficit with and without recovery of soil water and (2) to determine the effect of water deficit with and without recovery of soil water on fruit quality, represented by vitamin C content in the lime fruits. Findings from these analyses will benefit water management for sustainable urban agriculture, especially in lieu of the future drying environments.

## 2. Materials and Methods

### 2.1 Site and Plant Materials

This study was conducted on the balcony of the 4$^{th}$ floor in the Department of Environmental Science building, Chulalongkorn University in Bangkok, Thailand (13 ˚N 100 ˚E). We purchased 21 lime (*Citrus aurantiifolia*) saplings that were grafted at the same time and were bearing fruits from a local nursery. All 50 cm-tall 21 saplings were planted in a 5 x 1.5 x 0.35 m raised-bed garden plot that was constructed using cement bricks at the site. For planting materials, we used garden soil mixed with dried monkeypod leaves, husk, coconut husks and some manure with the proportion of 2:0.5:0.5:1. We installed a net above the saplings to prevent excessive light reaching the plants, resulting in ~20% reduction of the incident light intensity (averaged 663 ± 190 μmol/m$^2$/s throughout the study period). We planted the saplings in three rows with 50 cm spacing to ensure that none of them was shaded by one another. An automatic drip irrigation system was applied to continuously supply 10 Litre of water per sapling every 24 hours such that soil moisture was maintained at ≥80% of the field capacity. Environmental sensors were installed at 2-Meter height above the saplings to measure air temperature and relative humidity (HMP35C probes, Campbell Scientific, Logan, UT, USA) and photosynthetically active radiation (LI190R-L quantum sensor, Campbell Scientific, Logan, UT, USA) continuously. Additionally, soil moisture was continuously monitored with a TDR probe (CS616-L water content reflectometer, Campbell Scientific, Logan, UT, USA) at 15 cm soil depth to confirm the well-irrigated condition. All environmental data were recorded at 30-minute intervals by a data logger (CR1000, Campbell Scientific, Logan, UT, USA). Field capacity of the soil was determined by collecting three soil samples within 10 cm depth using a 25 mL crucible. The samples were soaked with water in a beaker for 24 hours. Then, they were drained out for 2 hours before being weighed for wet mass. Next, the soil samples were dried in an oven at 110 °C until the mass was stable and obtained dry mass.

$$\theta_{FC} = \frac{V_w}{V_c} \quad (1)$$

$$Vw = \frac{m_{wet} - m_{dry}}{P_w} \quad (2)$$

where: $V_w$ – volume of water in the soil sample after drainage;

$V_c$ – volume of the crucible which equals 25 $cm^3$;

$m_{wet}$ – mass of the wet soil;

$m_{dry}$ – mass of the dry soil;

$P_w$ – specific gravity of water which is 1 $g/cm^3$.

The field capacity ($\theta_{FC}$) was calculated as We used the average $\theta_{FC}$ of the three samples to represent $\theta_{FC}$ of the entire plot and as the reference for the water deficit study. Starting from June 26, 2017, all saplings were allowed to adjust to the site environments for four weeks before we began the water deficit experiment.

## *2.2 Water Deficit Experiment*

In this study, we tested the effect of mild drought rather than the extreme, letting the soil dry to ~50% of $\theta_{FC}$. We divided the saplings into three groups for the water deficit experiment: (1) control group (W) in which the saplings received continuous irrigation throughout the study period (2) water-deficit-treated group (D) in which the saplings were withheld from irrigation throughout the experimental period and (3) water-deficit-recovery group (DR) in which the saplings were re-watered after soil moisture reached ~50% of the control. We used plastic cardboards to partition groups of saplings throughout the soil depth (35 cm) in the plot. Because small sprinklers were used for irrigation, the cardboards were able to prevent irrigated water from percolating to other compartments in the rooting zone (15 cm soil depth). In addition to withholding irrigation, we covered the soil surface of the D and DR groups with black plastic sheet during the treatment to prevent possible water input as rainfall to the soil. We manually measured soil moisture of the three groups in the rooting zone (i.e. within 15 cm depth), using a soil tester (Takemura Japan test instruments), prior to taking measurements to ensure that it reached the desired water deficit and recovery conditions.

### *2.3 Measurements and Analyses*

We measured gas exchange of the leaves using a portable photosynthesis system (LI-COR 6400, LI-COR, Lincoln, NE, USA) at four stages: (1) before the water deficit experiment, denoted by 'Wet' (2) when soil moisture of the D and DR groups was ~70% of $\theta_{FC}$, denoted by 'D1' (3) when soil moisture of the D and DR groups was ~50% of $\theta_{FC}$ , denoted by 'D2' and (4) when soil of the DR group was re-watered with soil moisture reaching ~80% of $\theta_{FC}$ , similar to the control, and soil moisture of the D group reached 40% of $\theta_{FC}$ (denoted by 'Recovery'). We randomly selected one fully expanded leaf per sapling for measurement (total number of sample was n = 7 per group). We set the chamber conditions with flow rate of 500 μmol/$m^2$/s, photosynthetically photon flux density of 1200 μmol/$m^2$/s , $CO_2$ concentration of 400 μmol/mol and block temperature of 25 °C. We were particularly interested in net photosynthesis per unit leaf area ($A_{net}$, μmol/$m^2$/s), stomatal conductance ($g_s$, μmol/$m^2$/s), and transpiration (E, μmol/$m^2$/s). The water-use efficiency (WUE) was calculated as the ratio $A_{net}$/E (Medrano et al. 2015). At the end of the water deficit experiment, we harvested lime fruits and sent to the laboratory for analysis of vitamin C content using the High Performance Liquid Chromatography method based on Compendium of Methods for Food Analysis (2003). The sample size for each group was reduced to n = 4 to meet the minimum requirement of 100 g fresh weight of each sample for the analysis.

The experiment design was a complete randomized design (CRD) with 1 factor, 3 levels, each containing 7 replications. We employed *t*-test to compare group means of the control and treated groups during a certain stage of the water deficit experiment. A one-way ANOVA was performed to test the effect on vitamin C content. All statistical tests were conducted in SPSS (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY, USA) and based on the 5% significance level. Graphical presentations were generated using SigmaPlot 12.0 (Systat Software, Inc., San Jose, California, USA).

## 3. Results and Discussion

The experiment was conducted during June 26 – August 8, 2017 with the water deficit experiment performed since July 26. During the water deficit experimental period, weather conditions varied (Figure 1), except air temperature which seemed to be stable at 31.02 ± 1.1 °C throughout the study period. Relative humidity ranged from 56 to 72 % and was high in the beginning and towards the end, but was lower in the middle of the experiment. The profile of light intensity, represented by daytime-average photosynthetically active radiation (PAR), indicated four cloudy days with some rainfall (not measured). With continuous irrigation, soil moisture of the control (W) group was relatively high, averaging 85 ± 3% of the field capacity ($\theta_{FC}$ = 0.64 ± 0.15) (Figure 2). We performed gas exchange measurements on 4 days: (1) before the water deficit experiment (DOY 209, "Wet" arrow in Figure 2) (2) when soil moisture declined by 10 ± 1% (DOY 212, "D1") (3) when soil moisture reached 51 ± 0.7 % of $\theta_{FC}$ (DOY 215, "D2") and (4) when the DR group was re-watered and soil moisture returned to similar level to that of the W group (DOY 219, "Recovery"). On "Recovery" day, irrigation was still withheld in the D group, resulting in soil moisture reaching 40 % of $\theta_{FC}$. The soil moisture values for DR and D groups were expressed as the average fractions of $\theta_{FC}$ for three random measurements within each group.

To understand plant response to water deficit, we analysed the physiological parameters related to photosynthesis and water transport. With increasing water deficit, stomatal conductance ($g_s$) of the lime saplings in both DR and D groups decreased by 6-67% relative to the control (Figure 3A, $p \leq 0.032$, Table 1), indicating stomatal closure. The closure of stomata in response to soil drying reduced gas exchange in the lime leaves. As a result, net photosynthesis ($A_{net}$) decreased by 13-15% ($p \leq 0.007$, Table 1) with mild water deficit (D1) in DR and D groups and by 22-27% ($p = 0.0001$, Table 1) as the soil was dried further on D2 (Figure 3B). To the less extent, leaf transpiration (E) did not decline with mild water deficit on D1 ($p \geq 0.074$) but reduced by 4-16% when the soil moisture was decreased further ($p \leq 0.034$) (Figure 3C, Table 1). The combined effects of water deficit on Anet and E resulted in 13-20% declines of WUE ($p \leq 0.003$, Figure 3D), largely due to the less effects on E. However, the similar decreases in WUE between D1 and D2 indicated that the effect on WUE was not affected by the degree of water deficit. It is well-known that drought stress reduces plant photosynthesis per unit leaf area through stomatal closure or metabolic impairment (Tezara et al., 1999). While it may be expected that stomatal closure will also limit transpiration, our results showed less decrease in E with water deficit, compared to $A_{net}$. This indicated plants' adjustment under mild drought

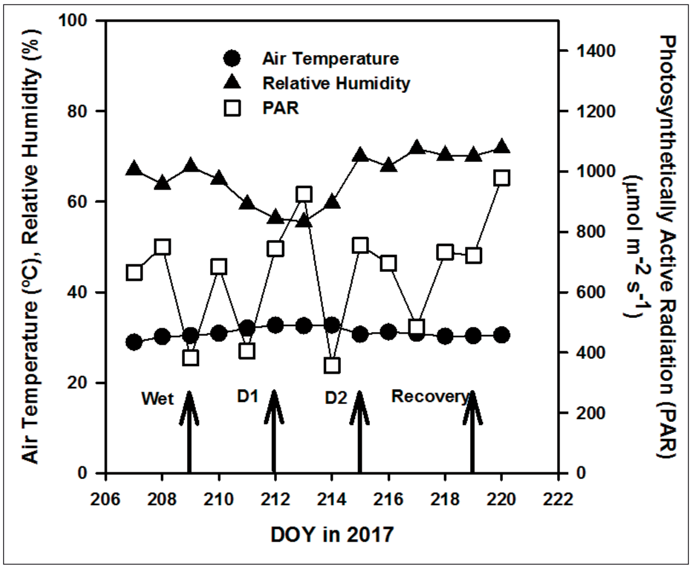


**Figure 1.** Weather conditions during the water deficit experiment (DOY 207 - 220). Circles, triangles and squares represent air temperature (°C), relative humidity (%) and photosynthetically active radiation (PAR; μmol/m$^2$/s), respectively. Values are averages of those during 6.00 – 18.00 hr. Arrows indicate measurement days following soil drying and recovery.

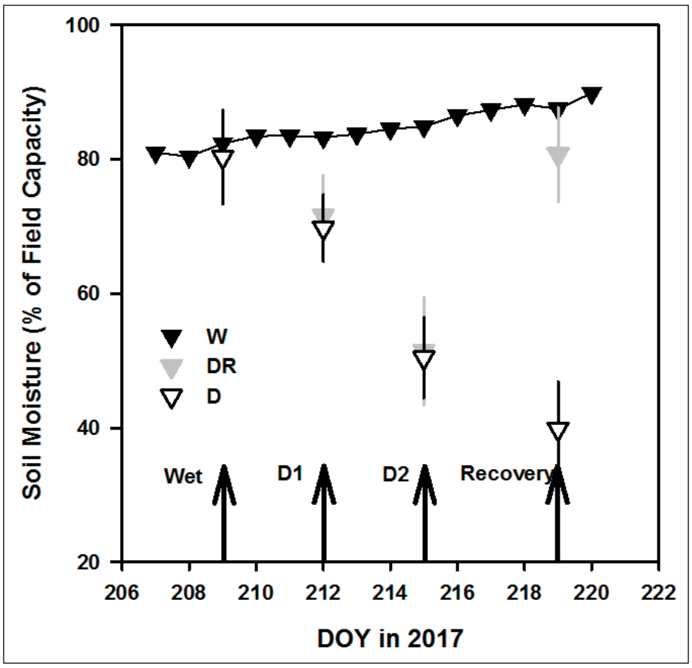


**Figure 2.** Soil moisture conditions during the water deficit experiment. Values are expressed in fraction (%) of the field capacity. Black, grey and white symbols represent soil moisture in the control (W), water deficit & recovery (DR) and water deficit (D) groups, respectively. Error bars show one standard deviation (n = 3).

stress by increasing stomatal density as shown in some previous studies (Xu & Zhou, 2008). Also, the atmospheric demand seems to effect transpiration more than soil moisture content. Transpiration rate can decline at high vapor pressure deficit at a high soil water content (Tuzet et al., 2003). This evidence was observed in this study with the similar E between control and drought-treated groups at D1 stage (Figure 3C). It was due to the high vapor pressure deficit on D1 with low relative humidity and high PAR (Figure 2). Generally, plant adaptations in response to drought stress include a positive impact on WUE, resulting in high yield (Blum, 2005). However, our results showed reduced WUE with moderate soil drying which may correspond to the immediate response of the plants under mild stress with reduced photosynthesis but unaffected transpiration, rather than the well-adapted response that would be observed under severe drought.

When the saplings in DR group were re-watered, $A_{net}$, E and WUE showed full recovery, reaching the levels similar to the control group ($p \geq 0.066$, Figure 3 black bars in "Recovery", Table 1). Such recovery effects were widely observed in *Citrus*, as well as other plants, that experienced a period of drought followed by re-watering. (Izanloo et al., 2008; Lovatt et al., 1988; Southwick and Davenport, 1986; Xu et al.2009). In contrast, lime saplings in the D group closed their stomata due to the continued soil drying, resulting in further decreases of $A_{net}$ and E. However, WUE of the D group was still maintained at similar level to those observed on D1 and D2, suggesting that there

**Table 1.** P values of the statistical tests for the effects of soil drying on stomatal conductance ($g_s$), net photosynthesis ($A_{net}$), transpiration (E) and water-use efficiency (WUE) ($n$ = 7). The comparisons were made between the ratios (Figure 3) of treated to control group and one. DR and D represent the sample groups under water deficit & recovery and water deficit only treatment. Measurements were made on 4 days: 'Wet' = before the water deficit experiment, 'D1' = when soil moisture was at 70% of $\theta_{FC}$, 'D2' = soil moisture was at 50% of $\theta_{FC}$, and 'Recovery' = soil moisture in DR group was returned to similar level as 'Wet' but that in D group was continued to dry out. Bolded numbers indicate significant effects at significance level of 0.05.

| | $g_s$ | | $A_{net}$ | | E | | WUE | |
|---|---|---|---|---|---|---|---|---|
| | **DR** | **D** | **DR** | **D** | **DR** | **D** | **DR** | **D** |
| Wet | 0.651 | 0.759 | 0.082 | 0.810 | 0.154 | 0.292 | 0.139 | 0.307 |
| D1 | 0.032 | 0.001 | 0.007 | 0.003 | 0.074 | 0.134 | 0.002 | 0.003 |
| D2 | 0.0001 | 0.0001 | 0.001 | 0.001 | 0.034 | 0.002 | 0.001 | 0.001 |
| Recovery | 0.379 | 0.0001 | 0.128 | 0.0001 | 0.105 | 0.001 | 0.066 | 0.001 |

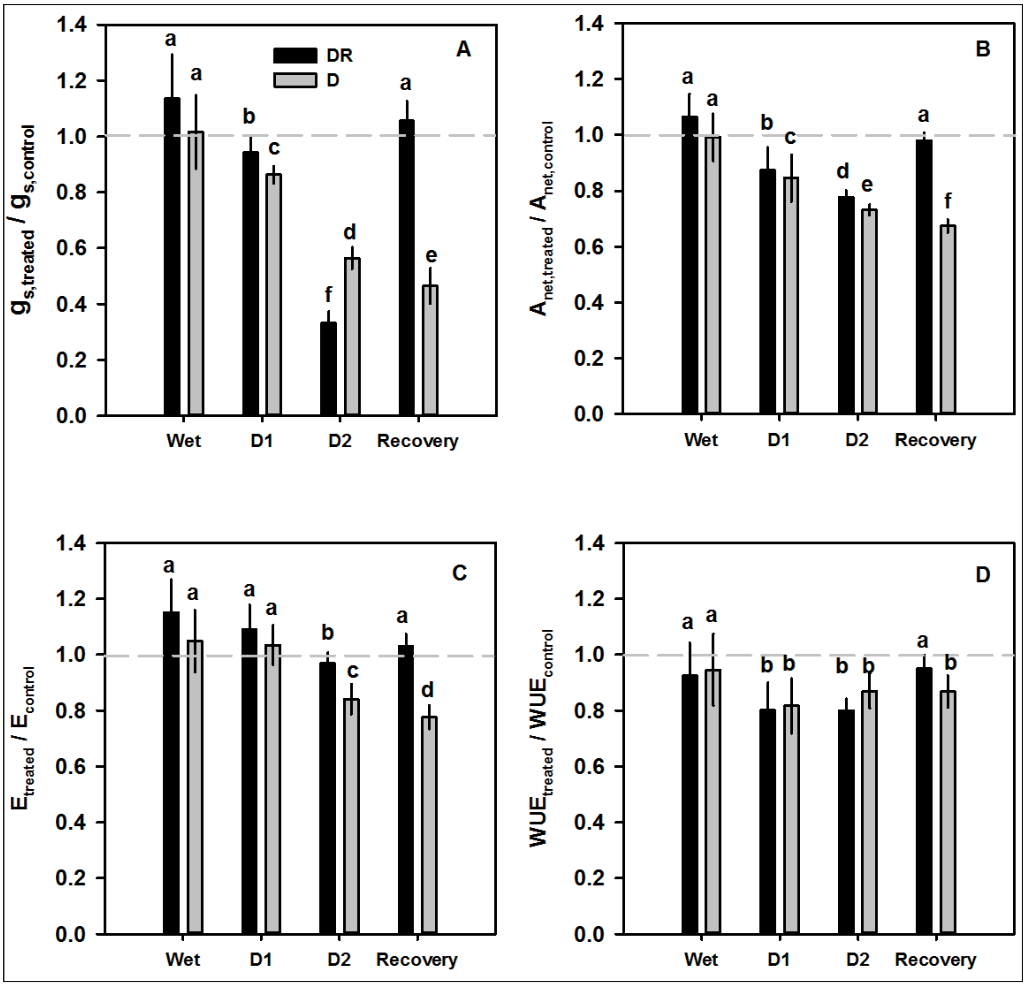


**Figure 3.** Comparisons of the gas exchange measurements. Bars represent ratios of (A) stomatal conductance, gs (B) net photosynthesis, $A_{net}$ (C) transpiration, E and (D) water-use efficiency, WUE of treated groups (either DR or D) and the control (W) group. Error bars show one standard error of the mean (*n* = 7). Dashed lines indicate 'no-effect' of the soil drying treatment at which the ratios of the treated to the control group equal one. Different letters indicate significant difference.

was insensitivity of WUE to soil drying under this stress level. These results demonstrated that net photosynthesis and WUE of the lime saplings can be fully recovered from moderate drought rapidly.

Finally, we considered the effects on lime's nutritional value by analysing vitamin C content in the fruits harvested at the end of the experiment. Results showed that the vitamin C content was not statistically different among the groups, despite different soil water conditions, ranging from 550.76 ± 38.33 to 597.43 ± 75.62 mg/kg ($p$ = 0.419, Figure 4).

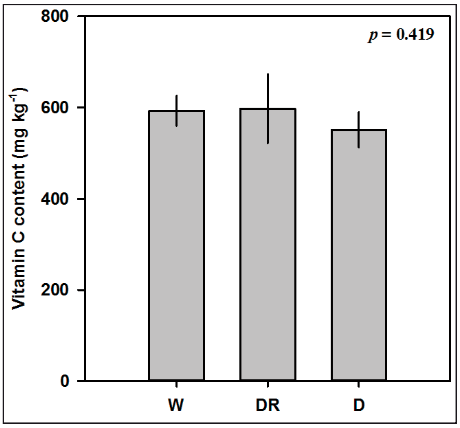


**Figure 4.** Vitamin C content of the lime fruits harvested at the end of the water deficit experiment. Error bars show one standard deviation of the means (n = 4). Values were not different across treatment groups (p = 0.419).

Previous studies reported variable effects depending on genetics, seasons or the intensity and duration of the water deficit treatment. García-Tejero et al., (2010a) applied four strategies of deficit irrigation in each phenological stage of 11-year-old *Citrus* trees (*Citrus sinensis* L. Osb. Cv. *Navelina*) grafted onto carrizo citrange (*C. sinensis* L. Osb. × *Poncirus trifoliata* L. Osb.). They found that the titrable acidity (TA) was mainly affected under high water stresses during fruit-growth and maturity periods, with up to 10% higher TA than the control when 45% less water was irrigated compared to the control. However, another study of the postharvest fruit quality of oranges (*Citrus sinensis* L. Osbeck, cv. Salustiano) in commercial orchards reported increases in the fruit quality parameters, including TA, in all stressed treatments with the severe irrigation of 50% of evapotranspiration (García-Tejero et al. 2010b). Nevertheless, Romero et al. (2006) showed unaffected fruit quality of Clemenules mandarin under slight water stress with soil moisture reduced to 59-78% of that of the control (whereas our results showed unaffected vitamin C even when soil moisture was decreased to ~50% of the control). Despite the mixed findings, our results demonstrated that *C. aurantiifolia* growing in a raised-bed plot in urban environments may not need frequent irrigation. In fact, the lime may be withheld from water for as long as 6 days and can be quickly recovered within 3 days with unaffected fruit quality which is the vitamin C content in the fruits. This information will benefit sustainable urban agriculture as it can save water and time for maintenance.

## 4. Conclusion

Overall, the capacity for carbon sequestration through photosynthesis of the lime saplings decreased with increasing water deficit, but could be fully recovered rather rapidly when the irrigation was resumed. Additionally, fruit quality, represented by vitamin C content in the fruits, was unaffected by the changing soil water availability with up to 50% decrease from the well-irrigated level. These findings suggested that less frequent irrigation can be employed in growing lime in the city with quick recovery of net photosynthesis and fruit quality, thus saving time for maintenance and water which may become limited in the projected drying environment.

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