Response of ‘Hass’ avocado to temporal stresses: role of irrigation management and root constraint

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Abstract
The performance of ‘Hass’ avocado trees grown in lysimeters under different irrigation regimes obtained by manipulating drip irrigation frequency and root volume was examined. The experimental design comprised six treatments (3x2) with three irrigation frequencies and two container volumes (100- and 200-L). The three irrigation frequencies were: pulsed irrigation (10-20 min every 30 min) throughout the day (Irg1), one daily irrigation event started at night and terminated in the morning every day (Irg2) and one irrigation event every two days (Irg3). Irrigation managements induced significant differences in water availability in the root zone and subsequently, on the diurnal and periodical water uptake. The experimental treatments induced significant differences on fruitlet drops and accordingly, on fruit yield. Black spots initiated from the seed became apparent on some of the fruits at the beginning of June, and about two weeks later an intensive drop of fruitlet begun that ended at the beginning of July. The drop was more intense in the 100-L than the 200-L containers, followings the order Irg3>Irg2>>Irg1 in both cases. Net CO₂ assimilation during periods of fruit growth decreased in trees exposed to moderate or severe water stress (Irg2 and Irg3, respectively) and therefore, it is plausible that fruitlet drop resulted from carbohydrates stress as suggested earlier. In addition, it is logical to assume that improvement of water and nutrient availability, especially in periods where the activity of the root system was weak as a result of low carbohydrates supply played a dominant role in seeds or fruit function.

Keywords: fruit development, June drop, Persea Americana, transpiration, water stress, water uptake,

Introduction
The vegetative growth of avocado trees is generally vigorous, bearing a potential photosynthetic capability for producing more than 30 t ha⁻¹ of fruit containing 17% oil (Wolstenholme, 1986). Unfortunately, high rates of flower and fruit abscission determine the actual yield and consequently, the worldwide average avocado yield is less than 10 t ha⁻¹ (Garner and Lovatt, 2008). Total number of flower, bud and fruitlet abscised is huge (approximately 1.3 million) and only 1% of the fruitlet is finally picked (Lahav and Zamet, 1999). Weekly abscission rate of 140 thousand flowers and 5 thousand fruits per individual avocado tree which annually accumulated to almost 500 thousand flowers and 15 thousand fruits has been reported (Slabbert, 1981). Flower abscission and fruit set problems has been attributed to heat stress (Lomas, 1988, 1992). Nevertheless, severe abscission of ‘Hass’ and ‘Fuerte’ flower and fruit occurred at lower temperatures than the Lomas (1988, 1992) threshold value and the abscission could not be correlated with weather conditions in California (Garner and Lovatt, 2008) and South Africa ( Slabbert, 1981). Wolstenholme (1990) suggested that carbohydrates stress during the period of rapid fruit growth and oil accumulation coinciding with high temperatures and often high evaporative demand may be the most important cause for fruit drop. Under Mediterranean climate the fruit-set occur at the end of the rainfall period in spring while water availability does not limit avocado development. In cases where fruit-set is the dominant determinant of the avocado productivity, irrigation does not affect yield (Michelakis et al., 1993). However, during the early summer, as fruitlet drop limits the productivity, an efficient irrigation management induced higher yield (Lahav and Kalmar, 1983; Lahav and Whiley, 2002).

Despite the large body of research related to avocado productivity, the reasons for low worldwide fruit yields of avocado, especially in ‘Hass’ variety, are yet to be determined. The majority of studies that examined avocado productivity issues were conducted under field conditions, and accordingly, could not control or isolate all the variables affecting plant growth, and measure directly the dynamics of water and nutrient uptake. In order to improve our knowledge, it is essential to monitor at high temporal resolution water uptake throughout different growth periods while trying to isolate the effect of the main factors that may influence tree activity. Therefore, we examined the performance of ‘Hass’ avocado trees grown in lysimeters under different irrigation regimes obtained by manipulating drip irrigation frequency. Because of the interaction between water dosage and salinity, it is difficult to
determine the direct effect of water regime in the root zone on plant performance in lysimeter experiments. However, it is possible to investigate it indirectly, by generating different types of stress. The general objective of this research was to study the impact of the water regime in the root zone, achieved by manipulating irrigation frequency and root volume, on fruit yield of ‘Hass’ avocado grown in relatively hot environment, as a first step towards the definition of the management policy required to increase yields close to the potential ones. The specific objectives were to examine the effect of stress generated by different irrigation frequencies and container volumes on: (i) the dynamics of water regime in the rhizosphere and in the plant; and (ii) plant performance and yield production.

Materials and Methods
The experiments were carried out at the Zemach Experimental Station, located in the northern part of the Jordan Valley, in Israel (32° 42' 09" N, 35° 35' 07" E). The climate is Mediterranean, with cool, wet winters followed by dry, hot summers. The elevation is -204 m. ‘Hass’ avocado trees grafted on ‘Degania 117’, a West-Indian avocado rootstock, were planted in September 2006 in 250-L plastic containers (50-cm height x 80 cm diameter). A volume of 50-L of coarse tuff (volcanic material) was placed at the bottom of the container to insure proper drainage and the rest of the volume was filled with 200-L or 100-L perlite of 2-mm grain size. The drainage from the containers was collected using PVC pipes and conducted to a deep ditch for manual drainage measurements. The containers were buried to the rim in local soil to avoid excessive heating. Vegetative growth characterised plant development until 2008 and the first fruit yield was collected on December 2009. The results presented in the following focussed on the reproductive fruit yield and accordingly, only data related to the years 2009 and 2010 will be presented in details. The rainfall season in the region is between November to April, and annual precipitation at Zemach totalled 243 and 111 mm in 2009 and 2010, respectively.

The experimental design comprised six treatments (3x2) with three irrigation frequencies and two container volumes (100- and 200-L) allocated to five randomised blocks. Each block included four plants in 200-L containers and two plants in 100-L containers. Irrigation schedules were set up by a computer and the three irrigation frequencies were: pulsed irrigation (10-20 min every 30 min) throughout the day (Irg1), one daily irrigation event started at night and terminated in the morning every day (Irg2) and one irrigation event every two days (Irg3). Each container was irrigated by 7 pressure-compensated drippers with emitting rate of 3.5-L h⁻¹ (Netafim Inc., Israel). All the horticultural treatments were performed uniformly in all treatments according to the recommendations of the Israeli Extension Service.

Two 200-L containers (representative containers) from each of the three irrigation treatments were selected for monitoring medium moisture content, drainage and container weight changes. These representative containers were placed on a weight-recording scale (B-500-P, Shekel Healthweigh™, Israel). The drainage from each of these six representative containers was connected to a 30-L vessel located outside the experimental field in a deep ditch, equipped with an electronic pressure transducer that recorded every 10 seconds the pressure at the bottom of the vessel. These data were collected in a computer and transformed into water height and finally into drainage volume. This extensive experimental set-up enables the measurements at a high temporal resolution (10 min interval) of three out of the four main components of the water balance equation for each representative container, namely, irrigation input, water content changes in the growing medium, and drainage output (evaporation from the perlite surface was neglected). Consequently, the remaining unknown in the water balance equation, the plant water uptake, could be estimated quite accurately for each treatment in two replicates for the 200-L case.

In order to characterize the impact of the different irrigation frequencies on the dynamic changes in water content, temperature, and electrical conductivity (EC) in the growing medium, two 5TE probes with 5 cm sensor length (Decagon Devices Inc., WA) were installed horizontally, 20 and 40 cm below the top of each of the six representative containers, and data collected every 30 min. A calibration curve for the specific perlite used in the experiment was carried out by Decagon's calibration service, and this curve was used to estimate the volumetric water content at the probe locations.

All the treatments received the same amount of water and nutrients daily; it was sufficient to ensure that the leaching fraction (ratio of drainage and irrigation amounts) exceeded 0.4, and that the EC of the draining solution did not exceed 1.8 dS m⁻¹. Samples of the fertigation solutions were collected weekly, to monitor their pH, electrical conductivity (EC), and major nutrient concentrations. The pH and EC of the fertigation solution were 7.2 ± 0.2 and 1.5 ± 0.1 dS m⁻¹, respectively. The N, P and K
concentrations in the irrigation solution were 40, 10 and 60 mg L\(^{-1}\), respectively. The nutrient solutions were prepared from commercial fertilizers ((NH\(_4\))\(_2\)SO\(_4\), NH\(_4\)NO\(_3\), KNO\(_3\), KCl and H\(_3\)PO\(_4\)), and tap water containing (mg L\(^{-1}\)): 60 Ca, 35 Mg, 150 Na, 150 CO\(_3\), and 320 Cl\(^{-}\). Micronutrient concentrations (mg L\(^{-1}\)) applied was: 0.3 Zn, 0.6 Mn, 1.0 Fe, 0.04 Cu, 0.4 B, and 0.03 Mo, all EDTA-based. Leachates from the containers were collected and the volume monitored daily.

**Results**

The different irrigation managements and container volumes induced significant differences in the vegetative growth as expressed by trunk diameter (Fig. 1a). The canopy area of the trees was evaluated from an aerial photo taken on June 2008 and a significant linear regression was obtained between the measured trunk diameter at this period and the canopy area (data not presented). Similar to canopy area, the total dry biomass production (including trunk, stems, leaves and fruits) at the end of the experiment (2010) was also closely related to the measured trunk diameter. This indicates that trunk diameter is an efficient, easy-to-measure, proxy to the vegetative status of the trees. An apparent trend indicating trunk growth during the reproductive years (2009 and 2010) in the order: Irg1>Irg2>Irg3 could be observed (Figs. 1b and c). However, the effect of irrigation managements was significant solely for trees in 100-L containers in 2009 (Fig. 1b).

**Figure 1.** Effect of irrigation treatments and container volume on: (a) trunk diameter at the end of 2008; (b) trunk growth during 2009; and (c) trunk growth during 2010.

Relative water content values, computed by dividing the water content at a given time by the measured water content prior to initiation of the irrigation, are depicted to account for gradual changes in the container substrate during trees growth that affected the accuracy of the initial calibration curve for the 5TE probes corresponding to pure perlite Water regime in the root zone was significantly
affected by the irrigation treatments during the experiment, as shown for two representative consecutive days (19 and 20 July 2009) in Fig. 2. Applied daily water amount in these two representative days was 196 L tree\(^{-1}\) and irrigation started at 01:00 for all the treatments and terminated at 17:00 for Irg1, at 09:00 for Irg2, and at 17:00 of the first day for Irg3. Water content rapidly increased as irrigation started and after \(~30\) min a quasi-steady state has been reached between the amount of water added by irrigation, drainage and tree water uptake (Fig. 2a). The lower relative water content of Irg1 treatment resulted from the combination of higher water content prior to the initiation of irrigation, and from the lower mean irrigation rate characterizing the pulsed irrigation (Assouline, 2002; Assouline et al., 2006). Fast drainage decreased the water content at the end of every irrigation event and after that, water content decreased slowly as a result of water uptake by the trees (Fig. 2a). The drainage stopped \(~30\) min after irrigation (Fig. 2a and c) and therefore, the slow decrease of water content during the evening and the night probably indicated water uptake by the trees. Net weight addition (measured container weight - container weight on 19 July at 0:00) exhibited similar trend, i.e., steep increase as irrigation started, steady weight during irrigation, fast decrease as irrigation ended, slower decrease during the rest of the day and very slow decrease at night resulting from uptake. The fluctuations in the container weight and drainage (Figs 2b and c) of Irg1 treatment illustrate the pulsed irrigation events.

![Figure 2](image-url)

**Figure 2.** Effect of irrigation treatments on the dynamic changes in water balance components in the representative containers during two representative days (19 and 20 July 2009). Total daily water amount was 196 L tree\(^{-1}\); Irg1 - pulsed irrigation (15 min every 30 min) throughout the day (terminated at 17:00); Irg2 - one daily irrigation event, terminated at 09:00; Irg3 - one irrigation event every two days, terminated at 17:00 of the first day. (a) relative water content (dividing each water content at a
given constant time by the measured water content prior to initiation the irrigation); (b) net container weight (pertinent container weight-container weight at 19 July, 0:00); and (c) drainage.

Water uptake was affected by both irrigation treatments and climatic conditions, as shown for two representative days (19 and 20 July 2009) in Fig. 3. Water uptake of trees exposed to Irg1 treatment closely followed the instant changes in the VPD while that corresponding to Irg2 and Irg3 was depressed by intermediate and severe water stress, respectively (Fig 3). Daily water uptake during 2009 and 2010 correlated best with “Class-A” pan evaporation daily rate, and increased in the order: Irg1>Irg2>Irg3 (Figs. 4a and b). The highest value of daily water uptake during 2009 occurred at the beginning of July. Severe climatic conditions at the beginning of August 2010 (week 32) with maximum air temperature of 41.4°C, maximum VPD of 5.0 kPa, and pan evaporation rate of 10.6 mmd⁻¹ induced a second peak in water uptake during 2010 (Fig. 4b) that decreased as the weather became more moderate.

Figure 3. Water uptake during two representative irrigation events (19 and 20 July 2009). Total daily water amount was 196 L tree⁻¹; Irg1- pulsed irrigation (15 min every 30 min) throughout the day (terminated at 17:00); Irg2 - one daily irrigation event, terminated at 09:00; Irg3 - one irrigation event every two days, terminated at 17:00 of the first day. The diurnal VPD values are presented for comparison.
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Figure 4. Effect of irrigation treatments on daily means (over a week) of water uptake during 2009 and 2010. The diurnal “Class-A” pan evaporation values are presented for comparison.

Intensive flowering process started at the middle of March (both years), without any clear effect of either irrigation treatments or container volumes on flowering intensity or fruit-set. At the beginning of June, black spots became apparent on some of the fruits (Plate 1). Based on several fruit dissections in the field, the black spots apparently initiated from the seeds, in agreement with Adato and Gazit (1977). About two weeks after appearance of the black spots, an intensive drop of fruitlet begun, that ended at the beginning of July. The majority of dropped fruitlets presented the observed black spots, and the drop was more intense in the 100-L than the 200-L containers, followings the order Irg3>Irg2>>Irg1 in both cases. For year 2010, the rate of fruit growth could be separated into two different stages (Fig. 5): (i) stage I – from the beginning of the measurements (23 June) until ~10 July, characterised by high diameter growth rate (0.25, 0.33 and 0.37 mm d	extsuperscript{-1} for Irg1, Irg2 and Irg3, respectively); and (ii) stage II – from second week of July until the harvest, characterised by moderate diameter growth rate (0.061, 0.0.066 and 0.074 mm d	extsuperscript{-1} for Irg1, Irg2 and Irg3, respectively). Fruit measurement in 2009 began only on 1 August and therefore only stage II could be identified (0.11 mm d	extsuperscript{-1} for all the irrigation treatments).

Fruit harvest in 2009 was conducted on 21 December and fruit yield was significantly affected by both irrigation treatment and container volume. Number of fruits per tree was 75, 30 and 27 for Irg1, Irg2 and Irg3 in 200-L container, respectively (Prob>F=<0.0001), and 53, 6 and 6 for Irg1, Irg2 and
Irg3 in 100-L container, respectively (Prob>F=<0.0001). In accord with Fig. 5, the averaged fruit weight was not affected by irrigation treatments (154 g). Harvest in 2010 was conducted on 8 December and fruit yield was that year too significantly affected by irrigation treatment and container volume (Fig. 6). The averaged fruit weight of trees in the 200-L container was not affected by irrigation treatments (148 g), while that of 100-L was significantly affected (Prob>F=0.0233) and increased from 129, to 143 and 152 g for Irg1, Irg2 and Irg3, respectively. Note that yield of trees in 100-L container exposed to Irg1 (least water stress) was only slightly reduced relative to 200-L container (Figs 6). However, the combination of severe water stress and small container volume considerably declined the yield of Irg3 trees (Fig. 6), indicating that the effect of multiple stresses amplify its effect.

Plate 1. Typical black spots on avocado fruits, photographed at the beginning of June drop (14 June 2010).
Figure 5. Fruit growth during 2010. Measurement began on 23 June 2010 and terminated before harvest. DOY is the day of year.

Figure 6. Fruit yield in 2010. (a) number of fruit per tree; and (b) fruit weight per tree. Prob>F of irrigation treatments on fruit number and weight for both, 200-L and 100-L were <0.0001. Vertical lines indicate the standard errors.
Discussion

The appearance of black spots on the fruits (Plate 1) and the consecutive intensity of fruit drop associated with the different experimental conditions clearly indicate that fruitlet drop is the finale of a multifaceted process starting some weeks before it begun, rather than a sudden and abrupt event as could be imagined from the visible phenomenon. The black spots depicted in Plate 1 closely resembled those described by Adato and Gazit (1977), and seem to initiate from the seeds, leading to the hypothesis that the fruitlet drop is caused by a malfunction of the embryo or the seed (Adato and Gazit, 1977). Seeds have the highest priority for carbohydrates (Wolstenholme, 1987) and it is likely that the very fast fruit growth during June (stage I, Fig. 5) has created a huge demand for carbohydrates. Hence, it is plausible that fruitlet drop resulted from carbohydrates stress as suggested earlier (Whiley and Wolstenholme, 1990; Wolstenholme, 1986).

Although the favourable irrigation management in the present study (Irg1) increased the net CO₂ assimilation during periods of fruit growth (data not presented), the difference is much less significant than that characterising fruit yield (Fig. 10). Therefore, additional factors on top of carbohydrates production or reserves can be considered that would have affected fruitlet drop intensity: the considerable differences in fruit yield may also result from differences in water or nutrient availability and uptake efficiency. During fruit development, and especially during seed development, the carbohydrates quantities allocated to the roots are diminutive (Whiley and Wolstenholme, 1990). Consequently, roots ability to supply plant demand for water and nutrients is reduced. The growth of the root system was found to be the lowest in periods of fruit development (Whiley and Wolstenholme, 1990) and paradoxically, the activity of root system is at its lowest level precisely in periods of high demand for water and nutrients. In this experiment, manipulating the irrigation frequency allowed to affect water and nutrients availability and uptake efficiency. Earlier studies demonstrated that high irrigation frequency induced an improvement of water and nutrient uptakes, especially those characterised by low water mobility or availability such as phosphorus and micronutrients (Silber, 2005; Assouline, 2006). Also, it was found that blossom-end rot incidence in bell pepper fruits was related to Mn deficiency induced by irrigation frequency (Silber et al., 2005). The strong differentiation in plant response to the different treatments of this study allow us to suggest the possible effect of water and nutrient availability and uptake efficiency on the malfunction of embryo or seeds. Thus, it is logical to assume that improving water and nutrient availability, especially in periods where the activity of the root system is weak as a result of low carbohydrates supply, could play a dominant positive role in seeds or fruit function.

Relative to trunk diameter of pulse-irrigated trees (Irg1), temporal water stress in the 200-L container induced smaller trunks by 12% for the moderate stress (Irg2) and 18% for the more severe one (Irg3). Yet, the relative number of fruits declined by 45 and 82%, respectively, while that of average fruit weight even slightly increased (not significant statistical differences). Similar trend was observed when the effect of container volume was considered. Relative to the 200-L container condition, trunk diameters of trees in 100-L containers decreased by 11, 16 and 17% for Irg1, Irg2 and Irg3 treatments (respectively), while the effect on the number of fruits per tree was 11, 21 and 63% (Irg1, Irg2, Irg3, respectively), the averaged fruit weight being statistically not different. The stronger impact of the treatments on the reproductive stage compared to the vegetative one indicates that the irrigation managements and container volumes considerably affected the number of fruitlet with black spots (Plate 1), the extent of fruitlet drop in June, and finally, the number of harvested fruits (Fig. 6).

References


