Aspects of the water economy of avocado trees
(*Persea Americana, cv. Hass*)

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ABSTRACT

Aspects of the water regime of "Hass" avocado trees were studied in a one hectare experimental plot in which the performance of a fully automated irrigation system based on water application in response to the diurnal cycling of leaf thickness was compared with three variations of conventional irrigation regimes. Gas exchange was studied in four series of measurements over a solar day with a Li-Cor 6200 infra-red gas exchange module. Simultaneous variations in leaf (ψl) and stem water potential, leaf thickness (LT), trunk radius (TR), soil water potential (SWP) and vapor density deficit (VPD) were recorded.

Despite significant tissue water losses as evidenced by leaf and trunk contraction, stomates remained open, enabling photosynthesis and transpiration to continue unabated throughout the day. Leaf and stem water potential varied in unison with LT and TR contractions, but never were more negative than -1.05 MPa at midday. It was concluded from these results that there are significant differences in the water economy of the avocado tree as compared with other sub-tropical orchard crops which have been studied more intensely, such as citrus. Consequently, similar tissue was subjected to pressure/volume analysis, and studies of leaf matric potential, saturated water content of lemon and avocado leaves and twigs, optic microscope cross-sections of twigs and leaves, root hydraulic conductivity of avocado and two citrus root stocks, and the diurnal cycling of avocado leaf and twig photosynthates, were carried out.

These studies indicated that avocado trees maintain leaf metabolism in the face of significant water losses as long as soil water remains plentiful, by means of high root hydraulic conductivity and extremely elastic leaf mesophyll cell walls.

Key words: plant water status; leaf water potential; gas exchange.

BACKGROUND

Tree species that have evolved in the understory of tropical rain forests often have difficulty in acclimatising to semi-arid mediterranean climates. They are sensitive to extremes in temperature, humidity and soil salinity, and the adjustments they make to the new venue are never complete, thus requiring special agrotechniques in order to be successfully cultivated. The physiological basis for posited adaptations allowing avocado cultivation in semi-arid zones has been sparingly studied. A limited number of studies have been devoted to establishing correlations between water stress, leaf water potential and gas exchange in avocado, without delving into the underlying anatomical or metabolic basis for the differences noted between avocado and other orchard crops (Sterne *et al*, 1977, Bower *et al*, 1977, Kimmelman, 1979, Scholefield *et al*, 1981, Ramadasan, 1981, Adato & Levinson, 1987). The state of knowledge was recently reviewed by Whiley and Schaffer, 1995. Scholefield and Kreidemann, 1979, examined avocado stomatal development. Whiley *et al*, 1988, discussing water loss by floral structures during flowering, studied anatomical and morphological features of leaves and floral structures as they relate to water losses with a scanning electron microscope (SEM). Edwards, 1990, made SEM studies of the stomatal complexes of four *Lauraceae* species. Blanke, 1992, examined avocado fruit photosynthesis, and Blanke & Lovatt, 1993, examined the anatomy of avocado inflorescence transpiration with a SEM. Kimmelmann, 1979, investigated the physiological parameters of gas exchange involved in avocado responses to light and temperature. These studies have not given a definitive picture of the physiology of the soil, plant, atmosphere continuum of the avocado growing in its adapted venues.

It is the object of this work to investigate the background of some features of the water regime in the avocado, in order to further the understanding of anomalies noted in field studies of avocado gas exchange.

MATERIALS AND METHODS

Avocado trees were studied in a 1.0 hectare experimental plot containing Hass, Fuerte and Ettinger cultivars planted in alternate rows. The plot was divided into sixteen random blocks of 15 trees, each block comprising one of four replicates of each of four irrigation treatments. The treatments compared irrigation with minisprinklers at 100% and 75% of recommended coefficients for Class "A" pan evaporation, drip irrigation at 100% of recommended application and an automated drip irrigation treatment triggered by a leaf thickness sensor developed by the authors. Trees of the Hass cultivar, the central trees in each block, were selected for study. In a central tree in one replicate of each of the irrigation treatments, trunk radius and leaf thickness were continuously and automaticly monitored. Each station also included tensiometers at 30, 60 and 90 cm depth, and instruments measuring air temperature, relative humidity and soil temperature at 10 cm depth.

Table 1 The Irrigation treatments.

Treatment T-1: Daily dripper irrigation at 100% of recommended rate.

Treatment T-2: Daily pulsed dripper irrigation according to leaf sensor.

Treatment M-1: Irrigation with mini-sprinklers every two days at 100% of recommended rate.

Treatment M-2: Irrigation with mini-sprinklers every two days at 75% of recommended rate.

Dripper treatments were irrigated with two parallel lines of
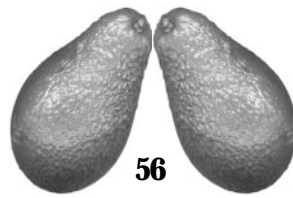
integral, volume regulated drippers, 3.6 l/hr ("Netafim", Israel) spaced one meter apart; hourly application rate per tree: 42 l/hr. Mini-sprinkler treatments were irrigated with a single volume regulated mini-sprinkler per tree, either 105 l\hr (Treatment M-1), or 78 l/hr (Treatment M-2).

RESULTS AND DISCUSSION
1) Gas exchange
On 21 September 1995, four rounds of measurements of gas exchange were carried out with a Li-Cor 6200 infra-red gas analyzer. Concurrently, stem water potential was determined with a pressure bomb (ARI, Kfar Charuv, Israel). Four "sun" leaves on the station tree of each treatment were marked for mechanical leaf thickness readings and gas exchange measurements. Each leaf gas exchange measurement comprised 3 X 30 second integrations. Vapor density gradient was calculated from Li-Cor leaf to air temperature differential data, and independent readings of ambient air temperature and relative humidity. Boundary layer resistance to gaseous flow was estimated at 0.2 sec/cm for calculation of transpiration rates. Resistance to CO_2 assimilation not attributable to stomatal influences, Rm, was calculated from the relationship of intercellular CO_2 concentration and net photosynthesis. At the conclusion of each round of gas exchange measurements, four leaves similar to those selected for gas exchange study were detached from each station tree for water potential determination. Sixteen leaves from the station tree of the 100% dripper treatment were previously prepared for parallel determination of stem water potential. At each round, four were detached and similarly measured in the pressure bomb.

Table 2 demonstrates that there were small (statisticly non-significant) differences between the treatments. Photosynthesis (Pn) and transpiration (Tr) were slightly higher in the sensor treatment. Notwithstanding significant losses in plant water content (see columns Rlt (relative leaf thickness) and Dtk (trunk shrinkage), (Table 2), leaf water potential never fell below -1.05 MPa (see column Ψl, Table 2). This conservatism in avocado leaf water potential has been discerned in the past (Sterne *et al*, 1977, Ramadasan, 1981, Scholefield *et al*, 1981), and would appear to be a strategy calculated to prevent movement of water from fruits, which store photosynthate as lipids, and therefore don't develop highly negative osmotic potentials as do fruits which store sugars.

2) Pressure/volume analysis
Mature, sun leaves were detached from two minisprinkler treatments (M-1: 100% of recommended irrigation quantity and M-2: 75% of recommended quantity) at sunrise and immediately sealed in humidified, clear polyethylene bags. They were extracted singly and subjected to pressure/volume (p/v) analysis employing an ARI (Kfar Charuv, Israel) pressure bomb. Leaf weight and area was measured prior to insertion and subsequent to extraction from the pressure bomb. Extracted leaves were oven-dried at 80 degrees C. for 24 hours and then reweighed. Leaf potential parameters were calculated according to the method of Robichaux, 1984. Results are summarized in Table 3.

It can be seen that avocado leaves don't develop osmotic potentials as negative as most species (compare average citrus vs. avocado values in columns Ψsmx and Ψso, Table 3). This result was verified by osmometer readings (four replicates) of leaf sap extracted from similar wilted, frozen and thawed leaves from treatment M-2. Average osmotic potential was -1.2 MPa. In consequence, avocado leaves develop relatively low values of turgor potential, which is nevertheless maintained in the face of significant losses of water content. Avocado leaves are much more elastic (column *e*) than citrus leaves, allowing avocado leaves to lose considerably more water without losing turgor. The calculated values of *e* are among the lowest recorded in the literature.

3) The water content of avocado and lemon twigs, 21/1/96
In pursuance of the possibility that avocado trees maintain vital functions in the face of excessive transpiration losses by supplying the shortfall with tissue water reserves, the water contents of saturated avocado and lemon twigs were measured and compared. Round, symmetrical, 3 cm long sections of twigs with a diameter of 6-7 mm were cut from the current year's spring flush of

Table 2 Results of 4 rounds of measurements taken on 21/9/95.

Trt	Hr.	qn	ΔT	Vdg	Rs	Tr	Pn	P/T	Cint	Rm	Rlt	Swt	Δtk	Ψl
T-1	7:56	893	0.68	6.12	1.4	4.08	13.2	14.2	241	3.2	0.99	5.0	-1	-0.15
	10:39	1403	1.79	23.4	2.9	8.05	7.96	4.34	202	4.3	0.95	8.0	15	-0.42
	11:53	1724	1.91	24.9	4.7	5.29	4.34	3.60	240	9.9	0.93	8.0	26	-0.57
	14:29	1696	2.55	23.0	15.0	1.49	1.44	4.26	209	25.0	0.87	11.0	48	-0.82
	AVG	1429	1.73	19.4	6.1	4.73	6.75	6.62	223	10.3	0.94	8.0	22	-0.49
T-2	8:13	1192	0.51	8.23	1.1	6.97	13.6	8.59	221	2.8	0.99	9.7	-.0.5	-0.46
	10:48	1475	1.62	23.9	3.0	7.97	9.42	5.20	224	4.2	0.98	6.5	4	-0.56
	12:02	1803	2.56	26.2	5.1	5.06	4.18	3.62	221	10.1	0.96	6.5	5	-0.61
	15:00	1652	2.24	22.1	4.7	4.62	3.25	3.09	207	11.3	0.93	8.0	8	-0.73
	AVG	1530	1.73	20.1	3.5	6,16	7.61	5.13	218	8.6	0.97	7.6	4.1	-0.59
M-2	8:21	1080	0.29	7.43	1.4	5.14	14.8	12.6	248	3.0	0.97	33.0	-1.5	-0.21
	10:57	1614	2.15	24.9	4.0	6.15	5.99	4.28	207	5.9	0.91	36.0	8.5	-0.47
	12:16	1748	2.35	25.9	5.6	4.61	1.80	1.72	237	23.6	0.91	37.0	10	-0.51
	15:08	695	2.07	20.6	4.4	4.64	4.01	3.80	202	8.6	0.90	38.0	13	-0.69
	AVG	1284	1.72	19.7	3.8	5.14	6.66	5.62	223	10.3	0.92	36.0	7.5	-0.47
M-1	8:31	981	1.02	9.16	3.0	2.99	9.80	14.4	223	4.0	0.96	13.0	0	-0.34
	11:05	1799	0.51	21.6	2.1	9.92	9.07	4.02	199	3.7	0.94	17.0	8	-0.63
	12:29	1340	1.60	23.8	17.2	1.39	-0.6	-2.1	324	∞	0.89	23.0	13	-0.81
	15:17	1516	1.74	18.7	3.1	5.91	8.13	6.05	174	3.4	0.88	25.0	17	-1.05
	AVG	1409	1.22	18.3	6.3	5.05	6.57	5.57	230	?	0.92	19.5	9.5	-0.71

Legend: qn=quantum sensor reading (µE/m²/sec); ΔT= leaf to air temperasture differential (degrees C.); Vdg=vapor density gradient (gr/m³);Rs=stomatal resistance (sec/cm); Tr=transpiration (µgr/cm²/sec); Pn=net photosynthesis (µmol/m²/sec); P/T=ratio of CO_2 assimilation to water losses; Cint=intercellular CO_2 concentration (ppm); Rm=mesophyll resistance (sec/cm); Rlt=relative leaf thickness; Swt=soil water tension (-KPa); Δtk=accumulated trunk contraction (µ); Ψl=leaf water potential (MPa).
1. Data in colums 3-11 (qn to Rm) represent average of four readings of 3X30 second integrations.

Table 3 Pressure/ volume analysis, avocado, 11/11/95.

Treat.	Ψsmx	Ψso	Ψtmx	RLTo	DW/FWo	A	FWo/Vo	e
M-1a	-0.90	-1.10	0.11	0.94	0.30	-	-	1.70
M-1b	-0.66	-1.00	0.19	0.86	0.36	69.34	1.40	1.49
M-1c	-0.84	-1.08	0.09	0.85	0.34	48.17	1.41	1.17
M-1d	-0.72	-0.94	0.28	0.92	0.34	83.96	1.16	2.86
M-2a	-0.70	-1.02	0.19	0.89	0.36	67.63	1.41	1.12
M-2b	-0.73	-0.96	0.08	0.91	0.35	73.35	1.30	0.95
M-2c	-0.87	-1.09	0.20	0.90	0.34	66.85	1.23	-
AVG	-0.77	-1.03	0.16	0.90	0.34	68.22	1.32	1.55
Citrus	-1.40	-1.70	1.00	0.92	0.45	~30.0	1.08	13.5

Notes: 1) Potentials and elasticity values are given in MPa.

2) Citrus values are a composite average of measurements made over several years and reported elsewhere.

$\Psi smax$=fully turgid osmotic potential; Ψso=osmotic potential at the turgor loss point; Ψtmx=saturated turgor potential; RLTo=relative leaf thickness at turgor loss point; DW/Fwo=fraction of dry weight to turgid fresh weight; A= leaf area (cm^2); FWo/Vo=fraction of fresh leaf weight to fresh volume (g/cm^3); e=modulus of elasticity.

Table 4 Comparison of water content of avocado and lemon twigs.

Replicate	V	FW	DW	DW/FW	FW/V	Vw/V
L-1	0.871	1.046	0.427	0.408	1.2014	0.711
L-2	0.941	1.118	0.400	0.358	1.1881	0.763
L-3	0.905	1.120	0.460	0.411	1.238	0.729
L-4	0.865	1.045	0.410	0.392	1.208	0.734
L-5	1.019	1.279	0.483	0.378	1.255	0.781
A-1	1.212	1.305	0.635	0.4866	1.0765	0.553
A-2	0.922	1.125	0.618	0.5493	1.2205	0.550
A-3	1.165	1..367	0.625	0.4572	1.1744	0.637
A-4	1.155	1.230	0.550	0.4472	1.065	0.589
A-5	1.122	1.245	0.700	0.5622	1.110	0.486
Lemon Twig Average				0.389	1.2181	0.781
Avocado Twig Average				0.5005	1.1293	0.563
Pomelit Leaf Average				0.45	1.08	0.594
Avocado Leaf Average				0.34	1.32	0.845

Notes: Pomelit leaf data from Bravdo & Sharon, 1993.

L-1,2...=lemon; A-1,2..=avocado; V=volume (cm^3); FW=fresh weight (gr.); DW=dry weight (gr.); Vw/V=fraction of volume of water to total volume

Treatment T-1 and a Eureka lemon tree, in the early morning hours, and after a 24 hour period of rain. The length, diameter and weight of each section were determined. The sections were oven dried at 80 degrees C. for 24 hours., and then reweighed.

The pertinent figures are the proportions of water volume to tissue volume in the two species. Avocado twigs contain less water than lemon twigs, while avocado leaves have a higher proportion of water than citrus (pomelit) leaves. Leaf matric potential (Boyer, 1965) was studied and was always more negative than water potential at equivalent RWC's.

4) Avocado leaf and twig anatomy

Cross-sections of the same twigs were prepared and examined under a light microscope (X100, X200, X400). The delineation and proportions of different tissues were similar in both species. Lemon twigs of the same age and diameter had more new xylem than avocado twigs. Tyree and Jarvis, 1985, claimed that new xylem contains a major share of total stem water content.

An experiment was conducted to ascertain the percentage of leaf volume occupied by intercellular air space (IAS). It has been claimed by Kikuta & Richter, 1988, that intercellular space can be infiltrated in saturated leaves, increasing leaf capacitance for transpiration. Four sun leaves from treatment T-1 and four from treatment T-2 were brought to full turgidity and fresh weight determined. The 8 leaves were then subjected to four stages of vacuum evacuation and subsequent release of vacuum while the leaves were submerged under distilled water. The infiltrated leaves were then reweighed and IAS computed (Levitt and Ben Zaken, 1979). Treatment T-1 leaves had an average of 5.186% IAS and treatment T-2 leaves an average of 5.68%, indicating that avocado leaves have a tightly packed internal cell configuration. This result was verified by microscopic examinations of transverse sections of avocado sun leaves (treatments T-1 and M-2). Two layers of elongated palisade mesophyll made up approximately two-thirds of total leaf thickness. There was also little IAS between spongy mesophyll cells, which were concentrated around small sub-stomatal cavities above the abaxial surface. The tightly packed internal structure with less than 6% IAS dovetails well with the results of tissue and p/v analysis.

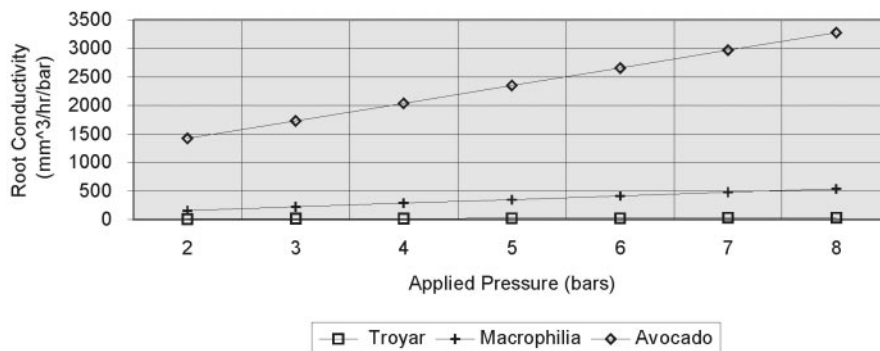### 5) Root hydraulic conductivity, 1996-1997

A study of root conductivity was conducted over an extended period with avocado and citrus root stocks grown in eight litre plastic containers. When the saplings reached a trunk diameter of at least one cm, 5 cm above the root throat, and if the root system extended throughout the 8 litre container and total leaf area was at least 1500 cm^2, the saplings, were thoroughly hydrated and decapitated 5 cm above the root throat. The sapling, still in its container, was then placed in an especially constructed stainless steel pressure tank. The trunk stump protruded from an adjustable seal in the tank cover capable of hermetically sealing diameters between 0.8 to 1.2 cm. A section of flexible clear plastic tubing was then fitted over the trunk stump, and into it was pressed a 1 cm diameter graduated glass cylinder open at both ends, so that the open bottom end of the cylinder was contiguous to the stump of the sapling. Air pressure was introduced into the tank and held at the desired pressure by a regulator. Initial pressure was 0.2 MPa and held for 24 hours, at which time the accumulated xylem sap was measured and the pressure increased an additional ~ 0.1 MPa. The process was repeated until tank pressure was 0.8 MPa. Occasionally, the process was then reversed and pressure reduced in steps for 24 hour periods,
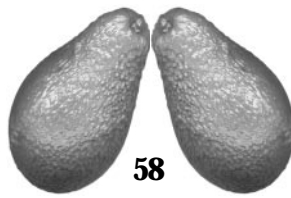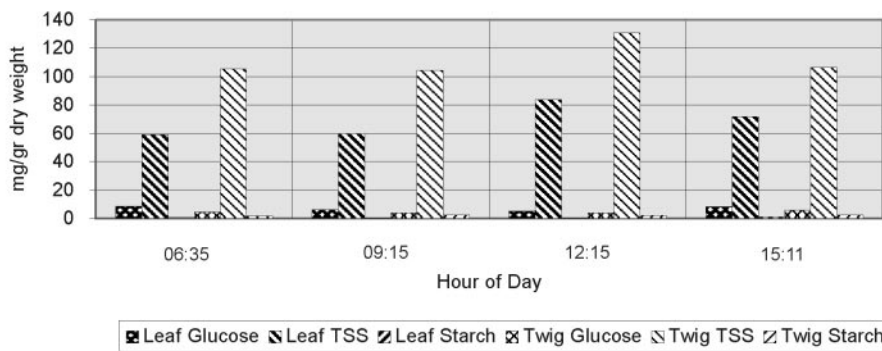
while similarly recording the volume of extruded sap.
The initial series was conducted in five replicates on Troyar citrus rootstocks. The results showed considerable variability. Linear regression analysis of all data (n= 27, V² = 0.37) indicate a slight increase in root conductivity with pressure (Figure 1). However, the average value of all measurements, 21.3 mm³/hr./MPa, compares well with measurements made on citrus root stocks by Graham & Syvertsen, 1984, and Ramos & Kaufmann, 1979. When pressure was reduced in steps, there was no noticeable hysteresis in the results beyond that due to the expected reduced conductivity of a drier soil volume.
A second series was performed with Macrophilia citrange saplings. A similar trend of increased conductivity as the pressure differential was increased was noted. Finally, a series of tests were carried out with avocado (Degania 3) root stocks. The difference in average measured root conductivity was dramatic, being an order of magnitude greater (2600 mm³/hr/MPa) than the conductivity found in citrus rootstocks (Figure 1).

and twigs were taken at 09:15, 12:15 and at 15:11. The 32 samples were freeze-dried in a Lyophilizer for 48 hours, and then reduced to a powder in a blender. 100 mg of each sample was measured into envelopes constructed from filter paper and closed with staples, and placed in 50 ml tubes, 6 ml of 70% ethanol added and the tubes immersed in a 60 degree C stirring bath. After one hour, the ethanol solution was replaced and the process repeated five times. The replaced solutions for each sample were collected separately for subsequent sugar analysis.

The paste remaining in the envelopes was dried overnight at 60 degree C. The dried powder was emptied from the envelopes into 25 ml bottles and 5 ml of distilled water added. Glucose and starch content were determined by phosphorylization of D-glucose with hexokinase in the presence of ATP and the subsequent oxidation by NADP+ to D-gluconate-6-phosphate and NADPH. The amount of NADPH formed is stoichemetric to the amount of D-glucose and is determined in a photospectrometer at 340 nm. Starch in the autoclaved mixture was determined by enzymatic starch hydrolysis with amyloglucosidase. The resultant glucose was analysed as above and the equivalent starch concentration was computed. Total soluble solids was measured by the Anthrone method.

Leaf soluble sugar content was similar to the results reported by Blumenfeld *et al*, 1989, averaging ~ 70 mg/g dry weight (equivalent to 25.2 mg/g fresh turgid weight). However, in contrast to Blumenfeld *et al*, 1989, who found no significant change in leaf sugar concentrations as measured at 07:00 and 19:00, we found a 25% increase from early morning to midday, gradually falling to predawn levels by evening. The osmotic value of this increase in soluble sugars is difficult to assess, since it is not known whether the increase was in mono or disaccharides. However, since glucose concentrations fell from morning to noon, we made the tentative assumption that the relative proportion of sucrose rose

Figure 1 Root hydraulic conductivity (1996-7) comparison of root stocks

Figure 2 Carbohydrate balance experiment avocado, July 1996

6) Diurnal trends in leaf and twig sugar and starch content
On June 26, 1996, samples were taken for carbohydrate analysis. Sixteen similar, fully expanded shade leaves from the spring flush were selected from a tree of the Hass cultivar bearing an "on" crop (> 150 kg). At 06:20 four leaves were detached in sequence, weighed, leaf thickness remeasured, and water potential determined in a pressure bomb. After extraction from the pressure bomb each leaf was wrapped in gauze, then in aluminum foil and inserted into a sealed container containing liquid air. A 4 cm section (diameter ~ 5mm) of the twig upon which each leaf grew was cut and similarly wrapped and frozen. Additional sets of four leaves

during this time segment. On a sucrose basis, a 25% increase in TSS represented a decrease of 0.11 MPa in leaf mesophyll osmotic potential, which could be entirely explained by concentration of existing solutes by transpiration losses. In any case, while the decrease in osmotic potential is significant, it is hardly pertinent to the maintenance of turgor in avocado leaves, since stem water potential was never more negative than -0.97 MPa. Goldschmidt *et al*, 1991, found that TSS in Shamouti orange leaves increased from 60.1 to 97.4 mg/g dry weight from early morning to evening. Assuming that all leaf water is part of the osmotic volume and that the proportion of dry to fresh weight was as reported by
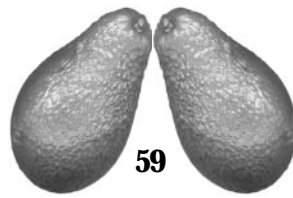
Goldschmidt *et al*, this represents a decrease in osmotic potential in the same time segment from -0.23 MPa to -0.50 MPa. Leaf water potential was highest in the early morning hours (-0.32 MPa), fell precipitously to -0.83 MPa at 09:15, remained essentially the same until midday, then continued to fall slowly in the afternoon, reaching -0.97 MPa by 15:11. Leaf turgor pressure as calculated from relative leaf thickness elicited the same trend, falling to slightly less than 0.4 MPa in the afternoon from a morning maximum of 0.6 MPa.

CONCLUSIONS

The diurnal trends of sugar and starch content of avocado leaves and twigs indicate that osmoregulation of turgor by leaf sugar buildup is not a strategy utilized by avocados. Similarly, an examination of avocado and lemon tissue water content and the finding that leaf matric potential (the binding force of apoplastic water) remains more negative than leaf water potential at comcomitant leaf relative water contents, shows that apoplastic water does not constitute a major reserve for supplying the transpiration stream.

This work determined that the modulus of elasticity *(e)* of avocado leaves is among the lowest recorded in the literature, suggesting that avocado leaves lose a considerably greater proportion of water content without losing turgor. However, the most significant finding explaining the maintenance of avocado leaf metabolism in the face of transpiration losses, is that avocado root hydraulic conductivity was an order of magnitude greater than two citrus root stocks. This allows the root system to supply the canopy with water at a rate approaching or equaling transpiration losses, as long as soil water remains close to field capacity.

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