

Drying half of the root-zone from mid fruit growth to maturity in ‘Hass’ avocado (*Persea americana* Mill.) trees for one season reduced fruit production in two years

A. Neuhaus^{a,c}, D.W. Turner^{a,*}, T.D. Colmer^a, A. Blight^b

^a School of Plant Biology M084, Faculty of Natural and Agricultural Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

^b Avowest, 85 Carabooda Road, Carabooda, WA 6033, Australia

^c CSBP Limited, PO Box 345, Kwinana, WA 6966, Australia

ARTICLE INFO

Article history:

Received 22 May 2008

Received in revised form 4 December 2008

Accepted 10 December 2008

Keywords:

Fruit trees

Irrigation management

Split-root design

Mineral distribution

Fruit quality

Water deficit

ABSTRACT

We tested the effect of extended drying of half the root system on fruit yield and fruit Ca concentration, an indirect measure of fruit quality, in avocado (*Persea americana* Mill. cv Hass). In a field experiment on a sandy soil, withholding irrigation and plastic sheeting was used to dry the root-zone beneath the whole canopy (DD) or half the canopy (WD), compared with well-watered trees (WW). The irrigation water contained added nutrients and was slightly saline. Yield, shoot growth, leaf conductance, leaf and fruit water status and mineral concentrations of leaves and fruit were studied. The responses of treated trees were assessed in the following season during which normal irrigation practices were restored. With respect to yield, the WD treatment behaved the same as the DD treatment. It reduced yield by more than half and proportionately more than the reduction in water supply thus reducing irrigation efficiency. Re-watering did not restore yield of WD or DD-trees in the next season. The WD and DD treatments had no effect on the concentration of Ca in the fruit mesocarp and so are unlikely to affect fruit quality. The main impact of reduced water supply on the trees was fruit abscission and this was linked to dry soil around the roots rather than the water status of the leaves or fruits. We conclude that extended drying of half of the root-zone in one season reduced irrigation efficiency for two seasons by promoting the abscission of developing fruit to the same extent as occurred when the whole root system was exposed to extended drying.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The efficiency of irrigation, defined as economic yield per unit water applied in irrigation, is an important production criterion in dry areas. Partial root-zone drying (PRD) involves withholding irrigation from half of the root system for periods of 2–4 weeks, before re-watering and alternating this treatment. PRD improves the efficiency of irrigation in perennial crops, such as grapevines, because it constrains vegetative growth without influencing yield (Loveys et al., 1997; Stoll et al., 2000). Its use in fruit crops, such as pear, has been investigated (Kang et al., 2002). PRD relies on the capacity of the root system to generate signals that influence leaf conductance and restrict vegetative growth. Such phenomena have been demonstrated in a number of plants using pot experiments involving split-root systems, e.g. apple (Gowing et al., 1990), passionfruit (Turner et al., 1996) and *Ricinus* sp. (Jokhan et al., 1996). In some species, such as *Betula* sp., split-root

experiments do not support the hypothesis of a root-sourced signal (Fort et al., 1998) and this was recently demonstrated for avocado cv Hass (Neuhaus et al., 2007). The absence of signals indicates that PRD may not be an effective strategy for increasing the efficiency of irrigation in avocado.

In a pot experiment, Neuhaus et al. (2007) found that avocado plants exposed to partially dry root systems used a similar amount of water to well-watered controls because they absorbed more water from the well-watered side and maintained plant functions. Nonetheless, PRD may be useful in the field as other factors come into play, such as a restriction in the total amount of water supplied, the possibility of maintaining plant function if half the roots are well-watered and, assessing yield and fruit quality. Drying half the root system may improve the efficiency of irrigation since the reproductive structures (inflorescences) in avocado were better able to withstand drying soil than vegetative structures (Neuhaus et al., 2007). Before PRD can be used as a management technique in irrigation of avocado it is necessary to know the response of the trees to drying part of the root system. Of interest is the sequence in which different processes are affected as the soil dries and how the trees might adjust to a partially dry root

* Corresponding author. Tel.: +61 8 6488 2415; fax: +61 8 6488 1108.

E-mail address: David.Turner@uwa.edu.au (D.W. Turner).

system. To obtain this knowledge, we did not use PRD in the traditional sense, but an extended single cycle of drying half the root system applied during fruit growth to examine its effect on yield and fruit quality. In the Mediterranean environment of south-western Australia the avocado flowers in spring (September–October) and the fruit matures in August/September, 10–11 months later. We evaluated selected plant physiological parameters, mineral nutrients fruit yield and the concentration of Ca in the fruit as this is correlated with fruit quality in avocado (Bower, 1985; Thorp et al., 1997; Hofman et al., 2002). The irrigation treatments were applied to mature, field-grown avocado trees irrigated with slightly saline bore water.

Our objective was to determine the effect of drying half of the root system on fruit yield and quality in mature avocado trees in the field.

2. Materials and methods

2.1. Experimental site

The field experiment was conducted in a commercial orchard at Carabooda, Western Australia (31°S, 115°E), which has a Mediterranean climate with hot dry summers and cool wet winters. The 15-year-old cv 'Hass' avocado trees grew on a deep, siliceous, weakly podsolised sand of the Spearwood dune system (Salama et al., 2005). At this site, the upper 100 mm of soil was enriched with humus, the result of mulching over many years. All trees had been grafted onto Guatemalan seedling rootstocks and the tree spacing in the orchard was 7 m × 7 m. Rainfall and class A_{pan} evaporation were recorded daily at the orchard. A total of 545 mm of rainfall and 785 mm of evaporation were recorded during the experimental period of 8 months in 2000. In the first 4 months (February–May) and in the last month (September) evaporation exceeded rainfall.

Mineral elements were applied in the irrigation water. During the 8 months of treatment each well-watered (control) tree received 255 g N, 170 g K, 19 g Ca, 466 g S, 89 g Zn and 80 g Mn. The trees with the WD treatment (see below) received half these amounts since water was applied only to one side of the trees and the trees of the DD treatment (see below) received nil nutrients from the irrigation water. All trees received a single application of gypsum (2.4 kg Ca and 1.9 kg S/tree) 4 months before treatments began and 1 month after treatments ceased. In February 2000, in the month that treatments began, microfine gypsum was applied through the irrigation system and supplied 19 g Ca per tree. Foliar sprays supplied B (6.4 g/tree) and urea (18 g N/tree) during treatment.

2.2. Treatments

At Carabooda, fruit drop occurs in November, soon after fruit set, and again in January. Treatments began in early February 2000 when the number of fruit on the tree could reasonably be expected to grow through to maturity. They ended 8 months later in September. Four trees per treatment were irrigated daily either beneath the whole tree canopy (WW), beneath half the tree canopy (WD) or were not irrigated (DD). Water deficit was achieved by shutting off sprinklers and by spreading a plastic sheet over the soil area to ensure WD- and DD-trees were subjected to root-zone drying even when rain fell. The plastic sheet covered 12 m² for WD-trees and 24 m² for DD-trees. Irrigation was applied daily using a replacement factor of 1.2 A_{pan} from February to May and 0.9 A_{pan} during winter (June–August) (Paulin, 1988). Irrigation was not applied if rainfall exceeded 5 mm. During winter, 5.5 mm of irrigation was applied each 2–3 days if this amount was not received as rain. The salinity of the bore water used for irrigation

ranged from 0.94 to 1.09 dS/m and contained about 150 mg L⁻¹ Cl. Treatments ceased in September and from October 2000 all trees received the irrigation regime of the WW-trees.

2.3. Soil and plant water status and fruit yield

Volumetric soil water content to 300 mm depth was measured each 2 weeks, from February to September, using Time Domain Reflectometry (TDR, Model Trase System 1, Irricrop Technologies Pty. Ltd., Narrabri, Australia). Measurements ($n=4$) were taken under all experimental trees, on both sides of the root system of WW-, WD- and DD-trees. About 70% of the total root length of the trees was present in the top 300 mm of soil (Neuhaus, 2003).

Beside visual symptoms, plant water status was monitored using direct and indirect approaches. Leaf water content ($n=8$, 2 leaves per WW- and DD-tree, 4 leaves per WD-tree) at midday of the youngest fully expanded leaf was taken as a volumetric measurement to directly indicate the leaf water status after 2 months of treatments. Leaf conductance was measured about every 2 weeks at midday on fully expanded leaves ($n=16$, 4 leaves per WW- and DD-tree, 8 leaves per WD-tree) of non-fruiting branches at about 1.5–2.0 m height above ground using a combined infrared gas analysis system (CIRAS-1, Portable Photosynthesis System, Hitchin, UK). Diurnal readings were taken once on 2 April 2000 in conjunction with the tissue water potential of expanded leaves, a shoot and fruit. Measurements of conductance and water potential were alternated hourly from dawn to dusk. Tissue water potential was measured using a pressure chamber (Scholander et al., 1965). That day, photosynthetically active radiation varied from 50–100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 7 am and 5 pm to 1400–1550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ from 10 am to 2 pm. Air temperatures rose from 15 to 26 °C during the first 3 h of measurements and remained at 25 °C from 2 to 5 pm.

Shoot extension ($n=8$, 2 shoots per WW- and DD-tree, 4 shoots per WD-tree) was monitored on labeled shoots from mid-February to mid-March 2000 using a digital caliper. One non-fruiting branch, 39–43 mm in diameter, was collected from all treatments (WD-tree was sampled on the dry and watered side) in May 2000 to examine the anatomy of xylem vessels. Hand cross-sections were taken, photographed and the outer secondary xylem vessels were examined using a light microscope with a fluorescent attachment (Axioplan Universal Microscope, Carl Zeiss Pty. Ltd., Oberkochen, Germany).

The effect of treatments on flowering in September 2000, 8 months after treatments began, was assessed visually. However, fruit number per tree and fruit fresh weights were recorded that month. Treatments were then stopped and water supply restored to all trees. Fruits per tree were counted during May 2001 and yields of these trees were obtained in September 2001 to assess the impact of the dry treatments in the following season.

2.4. Analyses of Ca, Mg, K, Na and Cl concentrations in plant tissues

Leaves ($n=8$ per tree) of the experimental trees were sampled in April 2000 and fruits ($n=4$ per tree) were sampled in September 2000 for analyses of inorganic ions. All trees had a late summer flush and the second youngest fully expanded leaf from this flush was taken in April. This leaf would have been 8 weeks old. Growth of the late summer flush was suppressed on DD-trees and so fully expanded leaves were sampled from the previous flush which was a spring 'flush'. These leaves were 5–7 months old and they showed some symptoms of chlorosis or necrosis. Fruit were at commercial maturity when harvested in September and were selected randomly. They were cut longitudinally and only mesocarp tissue was used for the analysis of minerals. Fresh and dry weights were recorded of all sampled tissues.

For leaf and fruit samples from the experimental trees, Cl was extracted from sub-samples of oven-dried and ground tissue that were boiled for 3 h in weak sulphuric acid at pH 3.5 (Chirachint and Turner, 1988). The extracts were then shaken for 2 days (Short and Colmer, 1999) before being analyzed using a Buchler-Cotlove Chloridometer (Buchler Instruments, Model 4-2000, New Jersey, USA). The Cl concentration was expressed in mmol L^{-1} , since Cl is soluble.

For the leaf and fruit samples of the experimental trees, Ca, Mg, Na and K were extracted from sub-samples of 0.8 g oven-dried ground tissue. A dry ashing technique was applied, as described by Brown et al. (1992), before samples were analyzed using Inductively Coupled Plasma–Optical Emission Spectroscopy (ICP–OES). The instrument was checked using standard reference samples and blanks were included among the samples from the experiment. Na and K concentrations were calculated in the units of mmol L^{-1} of ‘tissue water’ because they are soluble elements. The concentrations of Ca and Mg were expressed per unit of dry matter.

Orchard practice was to apply nutrient through the irrigation water and use leaf analysis as part of the strategy for nutrient management. We used the results of this sample to determine whether the trees used in the experiment had a similar nutrient status compared with the trees in the surrounding orchard. The leaf analysis sample of the orchard was taken in May 2000 using leaves of non-fruiting shoots of the late summer flush. The sample was analyzed by the Soil and Plant Analysis Service of CSBP Ltd., Bibra Lake, WA. These analyses were expressed as concentration of element per unit dry weight. Their molar concentrations in tissue water (see Tables 1 and 2) were calculated using the leaf water content of the well-watered (WW) trees in the experiment.

2.5. Statistical analysis

An ANOVA was used to analyze the data and the significance of differences between treatment means was evaluated using LSD at $P < 0.05$.

Table 1

Tissue water content (mL g^{-1} d.wt) and mineral concentrations in leaves ($n = 8$) (concentrations of Na, Cl and K are mmol in leaf water, concentrations of Ca and Mg are $\%$ d.wt) from watered trees (WW), the W and D sides of the WD-trees and the DD-trees.

| Parameter | WW | W side of WD | D side of WD | DD | $P < 0.05$ |
|---------------|---------------|--------------|--------------|--------------|------------|
| Water content | 1.57 (0.38) | 1.77 (0.28) | 1.64 (0.14) | 1.41 (0.05) | ns |
| Na | 1.3aA (0.2) | 4.5b (1.3) | 2.6b (0.4) | 1.1a (0.2) | * |
| Excess Na | 69 | 61 | 66 | 77 | |
| Orchard Na | 3B | | | | |
| Cl | 110aA (23) | 130a (23) | 194ac (48) | 265bc (31) | * |
| Excess Cl | 45–90 | 40–80 | 44–88 | 51–102 | |
| Orchard Cl | 198B | | | | |
| K | 179aA (20) | 105b (14) | 68bd (13) | 59cd (7) | * |
| Adequate K | 147–327 | 130–290 | 141–313 | 164–364 | |
| Orchard K | 245B | | | | |
| Ca | 0.91A (0.13) | 1.48 (0.28) | 1.11 (0.13) | 1.21 (0.18) | ns |
| Adequate Ca | 1.0–3.0 | 1.0–3.0 | 1.0–3.0 | 1.0–3.0 | |
| Orchard Ca | 2.04B | | | | |
| Mg | 0.29aA (0.03) | 0.45b (0.07) | 0.26a (0.04) | 0.26a (0.03) | * |
| Adequate Mg | 0.25–0.80 | 0.25–0.80 | 0.25–0.80 | 0.25–0.80 | |
| Orchard Mg | 0.49B | | | | |

Leaves were sampled in April 2000. Leaves of the DD-trees were 5–7 months old and 8 weeks old for the other treatments. Standard errors are in parentheses. The asterisk indicates significant differences between treatments at $P < 0.05$ and ns is not significant. Within rows, means followed by the same lower case letter are not significantly different. In italics are the excess concentrations for Na and Cl, and the commercial range of K, Ca and Mg following Lahav and Whiley (2002). The ‘Orchard’ values are the concentrations in leaves sampled in May 2000 from the orchard surrounding the experiment. Within the WW column and within an element, values followed by the same upper case letters are not significantly different ($P = 0.05$).

Table 2

Tissue water content (mL g^{-1} d.wt) and mineral concentrations (concentrations of Na, Cl and K are mmol in fruit water, concentrations of Ca and Mg are mg kg^{-1} d.wt) in fruit ($n = 4$) from watered trees (WW), the W and D sides of the WD-trees and the DD-trees.

| Parameter | WW | W side of WD | D side of WD | DD | $P < 0.05$ |
|---------------|--------------|--------------|--------------|--------------|------------|
| Water content | 2.95a (0.10) | 2.84a (0.08) | 2.70a (0.11) | 2.32b (0.03) | * |
| Na | 10.8a (1.1) | 17.5b (2.7) | 12.4a (1.1) | 16.8b (1.5) | * |
| Cl | 17a (3) | 54b (14) | 37abc (11) | 42bc (3) | * |
| K | 162 (16) | 155 (25) | 199 (20) | 210 (28) | ns |
| Ca | 238 (38) | 209 (43) | 267 (70) | 334 (55) | ns |
| Mg | 488 (109) | 394 (64) | 663 (82) | 569 (69) | ns |

Fruit were sampled at commercial harvest in September 2000. Standard errors are in parentheses. The asterisk indicates significant differences between treatments at $P < 0.05$ and ns is not significant. Within rows, means followed by the same letter are not significantly different at $P = 0.05$.

3. Results

In February A_{pan} evaporation was high at 250 mm per month (Fig. 1) and there was 0.5 mm of rain. From March until May, there was about 50 mm of rain per month and A_{pan} evaporation decreased from 200 to 100 mm per month. Rain from June to August ranged from 100 to 150 mm per month.

The 300 mm upper soil layer of the dry (D) side of the WD-trees and both sides of the DD-trees dried from 17% to 6% volumetric soil water content within 14 days of applying the treatments. From then onwards there was no net change in the water content of this layer beneath these trees. Daily irrigation maintained the volumetric soil water content between 16% and 24% in root-zones of WW- and the wet-side of the WD-trees.

The number of fruit at commercial harvest on the control trees was 600 in 2000 and fell to 100 in 2001, thus treatments were applied in an ‘on’ year and the following year, 2001, was an ‘off’ year for this set of trees. Despite this difference between seasons, complete (DD) and partial root-zone drying (WD) reduced yield proportionately to a similar extent in both years, even though the treatments were applied only in 2000. In 2000 the DD treatment reduced the number of large fruits (0.36–0.29 kg fresh weight) by 53%, medium sized fruits (0.25–0.21 kg fresh weight) by 60% and small fruits (0.18–0.14 kg fresh weight) by 75%, compared with WW-trees. The WD treatment reduced the number of large fruits by 71%, medium sized fruits by 75% and small fruits by 89% compared with WW-trees (Fig. 2). Apart from yield reduction, DD-

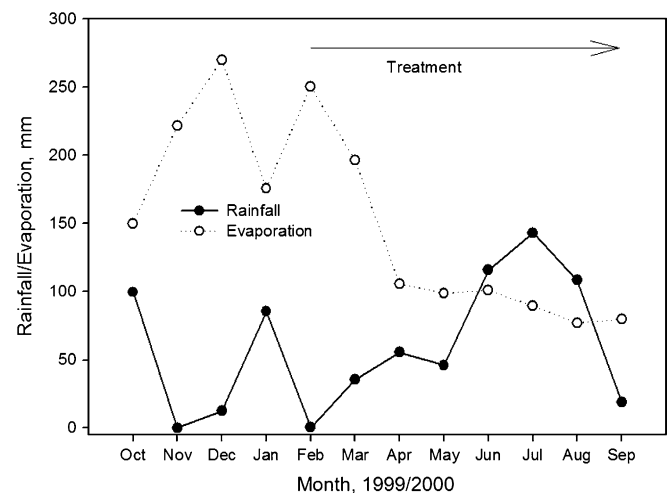


Fig. 1. Rainfall (●) and evaporation (○) (class A_{pan} evaporimeter) during fruit growth at the experimental site. From fruit set in October 1999 until January 2000 all trees received irrigation at the rate of 1.2 A_{pan} evaporation. Water deficit treatments began in February 2000 and ended at harvest in September 2000.

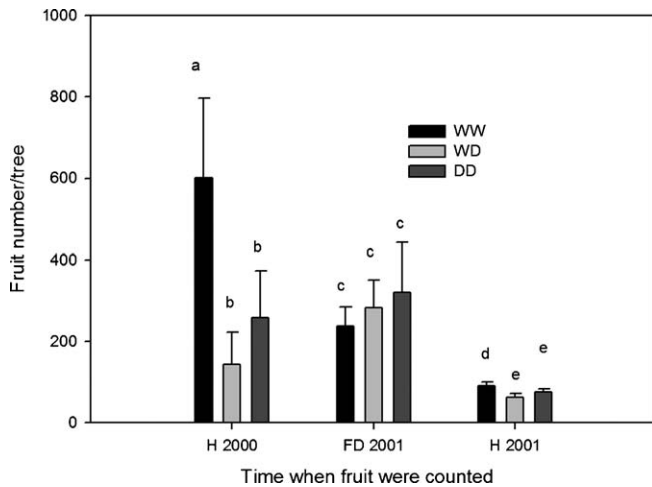


Fig. 2. Number of fruit per tree on WW-, WD- and DD-trees at commercial harvest in September 2000 (H 2000), after the second fruit drop in May 2001 (FD 2001), and at commercial harvest in September 2001 (H 2001). Treatments were applied from February to September in 2000. Significant differences between treatment means ($P < 0.05$), within each time of counting, are indicated by different letters. Vertical bars are standard errors ($n = 4$).

trees suffered some defoliation and necrosis appeared on the leaf margins in winter. However, these trees showed enhanced flowering in spring (September/October 2000). The strong flowering response did not occur on WD- or WW-trees. Re-watering caused the DD-trees to retain the same number of fruits per tree in May 2001, 8 months after treatments had ceased, as did the WD- and WW-trees. However, at harvest in September 2001, DD- and WD-trees had again the lowest fruit number per tree, compared with the WW-trees, even though the DD- and WD-trees had been irrigated normally for 12 months.

After 10 days of complete root-zone drying the stomata began to close. Leaf conductance at midday (g_L) fell by 50% compared with g_L of irrigated trees (Fig. 3). During the summer and autumn months (10–50 days after treatments began), g_L of DD-trees remained at 100–150 $\text{mmol m}^{-2} \text{s}^{-1}$ at midday, whereas g_L of watered trees fluctuated between 200 and 300 $\text{mmol m}^{-2} \text{s}^{-1}$. Two months after treatments began, g_L of DD-trees recovered to control levels (200 $\text{mmol m}^{-2} \text{s}^{-1}$) although the top 300 mm of the soil profile remained dry. The WD treatment reduced g_L on the unwatered side after 10 days of treatments. The g_L on the unwatered side then recovered and followed the pattern of the watered side, and of fully watered trees. The g_L of all trees varied

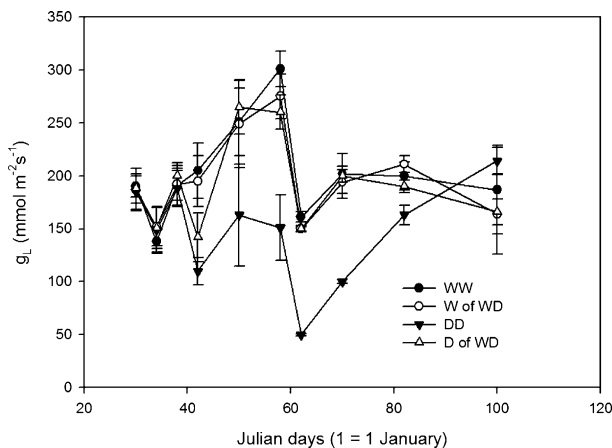


Fig. 3. Leaf conductance (g_L), measured at midday, of WW-, W of WD-, D of WD- and DD-trees. W is the watered side of the tree and D is the side from which water was withheld. Vertical bars are standard errors ($n = 16$). Day 20 is 20 January 2000.

diurnally. The g_L of WW-trees was 25 $\text{mmol m}^{-2} \text{s}^{-1}$ at 7 am and 5 pm on 2 April 2000, but increased to 200–250 $\text{mmol m}^{-2} \text{s}^{-1}$ from 10 am until 2 pm. The g_L of leaves of the WD-trees followed the same pattern as those of the WW-trees, but the maximum midday opening was less at 150–200 $\text{mmol m}^{-2} \text{s}^{-1}$. The g_L of the DD-trees behaved quite differently. The conductance gradually increased from 25 $\text{mmol m}^{-2} \text{s}^{-1}$ at 7 am to 120 $\text{mmol m}^{-2} \text{s}^{-1}$ at 2 pm and fell to 80 $\text{mmol m}^{-2} \text{s}^{-1}$ at 5 pm.

At dawn on 2 April 2000, 2 months after treatments began, the water potential of the leaves, shoots and fruits was the same in all treatments (-0.09 ± 0.01 MPa). Throughout the day there were no differences between treatments in their total water potential but the organs behaved differently. The water potential in all organs fell to -0.88 ± 0.01 MPa by 1 pm. After this the leaves and shoots recovered and by 6 pm had risen to -0.29 ± 0.02 MPa. Fruit, on the other hand remained drier and at 6 pm had a total water potential of -0.65 ± 0.03 MPa.

Buds present when treatments began (1 February) commenced growth in the WW- and WD-trees in early March. After this they grew rapidly and increased from 10 to 65 mm in 15 days. The shoots of the W and D sides of the WD-trees followed the same pattern. However, complete soil drying almost stopped shoot growth during the first 2 months of treatment and these shoots were only 10 mm long while the shoots on the WD- and WW-trees had reached 65 mm in length. Shoots of the DD-trees contained tyloses in their vascular tissues, while those of the WW- and WD-trees did not.

Soil drying had no significant effect on leaf water content in April 2000 (Table 1) but the DD treatment reduced fruit water content by about 20% at maturity in September (Table 2). The concentrations of K, Ca and Mg in the leaves of the WW-trees were within the adequate range for avocado (Table 1) but the concentration of Cl was excessive, as it was in the orchard.

The WD treatment increased the concentration of Na in the leaf water by 2 to 4 times, compared with the control (WW) (Table 1). The values ranged from 1.3 to 4.5 mmol and were well below the concentration regarded as excessive. A feature of the concentrations of Cl in the leaf water of all treatments was that they all exceeded the range associated with excess Cl for avocado (Table 1). The WD treatment had no significant effect on the concentration of Cl in the leaf water but the DD treatment increased Cl by 2.5 times compared with the WW treatment (Table 1). However, the leaves of the DD-trees were much older than those of the WD-trees. Soil drying almost halved the concentration of K in the leaf water of the W side of the WD trees and more than halved it on the D side (Table 1). The concentration of K in the leaf water of the DD-trees was similar to that on the D side of the WD-trees. Soil drying had no effect on the concentration of Ca in the leaves. Soil drying affected the concentration of Mg in leaves (Table 1). The leaves on the W side of the WD-trees accumulated more Mg than the leaves of the control (WW) or the DD-trees. Soil drying increased the concentrations of Na and Cl in the water of the fruit mesocarp, but only in fruit from the D side of the WD-trees and the fruit from the DD-trees (Table 2). There was no effect of soil drying on the concentrations of K, Ca or Mg in the fruit mesocarp (Table 2).

4. Discussion

Drying half the root system of mature avocado trees, after their normal fruit drop, reduced their yield further, compared with well-watered trees. The number of fruit on the WD trees was reduced proportionately more than the reduced amount of irrigation applied so that irrigation efficiency was reduced. In the season following treatment, the WD- and DD-trees were well watered but yielded much less than the WW-trees and so the irrigation efficiency of these trees was reduced by the treatments applied in

the previous season. The treatments caused the soil under the trees to dry out from mid-February until September. Despite 7 months of dry soil, the effect of the treatments on leaf water status, as reflected in stomatal conductance, lasted less than 2 months. The top 300 mm of soil in this orchard contained about 70% of the avocado roots (Neuhaus, 2003). The trees in the DD treatment obtained water presumably from deeper in the soil and possibly by extending roots laterally beyond the protective plastic cover. This is consistent with a flush of root growth that would normally be expected in avocado trees in this environment at this time of year (Whiley, 2002). The new root growth was sufficient for the trees to access water and replenish the water status of the leaves, in addition to the effect of reduced evaporative demand. The WD treatment did not affect leaf conductance to a large degree on either side of the trees and so the reduced amount of water supplied to these trees maintained leaf function, but did not prevent fruit abscission.

The reduction in yield in the WD- and DD-trees was mainly the result of fruit abscission (Fig. 2) caused by drying the root system either partially or completely. These treatments indicate that leaves attract water and retain their function compared with fruit. This is supported by the water potentials of the leaves, shoots and fruit in April, 2 months after the treatments began. In the middle of the day the total water potential of the leaves, shoots and fruit was the same across treatments and so each organ within each treatment had the same capacity to attract water from the stems. However, at the end of the day the water potential of the fruit had not risen, as it had in the leaves. This was the case in the WW-trees with roots in moist soil as well as when the roots were extensively exposed to dry soil in the WD- and DD-trees. Thus it was not the extent of the dryness of the root system that maintained low water potentials in the fruit, compared with the leaves. It is more likely that the low water potentials in the fruit at the end of the day reflect osmotic solutes, such as sugars, that are used for fruit growth because the water potential is restored by the next morning. A reduction in carbon supply is believed to contribute to fruit drop in avocado (Schaffer and Whiley, 2002), and while this may be true for the DD-trees where leaf conductance was reduced, our results show that other factors are important since the WD-trees had functioning leaves but lost as many fruit as the DD-trees. Thus, in avocado, soil water deficit applied to half of the root system did not close the stomata, but contributed significantly to fruit abscission (Fig. 2).

In this experiment, where commercial practices were used, nutrients were applied in the irrigation water and so some of the effects caused by the differential supply of water could be attributed to a differential supply of nutrients. Leaf analysis indicated that K supply was the most affected since it was reduced in the WD- and the DD-trees. The data for the DD-trees are not strictly comparable since older spring flush leaves made up the sample for this treatment. However, there is a clear indication that drying half of the root system reduced K concentrations in the fully expanded leaves of the late summer flush (Table 1). Despite the effect of drying on the K concentration in the leaves of the trees sampled 2 months after treatments began, there was no effect of treatment on the K concentration in the fruit at commercial harvest. Nonetheless, K supply could still be involved since the reduced K uptake in February and March, when fruit were growing rapidly (Whiley et al., 1995; Neuhaus, 2003) could limit the capacity for fruit growth, resulting in abscission, then the limited amount of K within the trees could be allocated to remaining fruit. However, this mechanism is unlikely to explain the impact of the WD and DD treatments in the following season, since K supply to the trees was restored when they were returned to the standard orchard practice in September 2000.

Since the irrigation water supply available to this orchard was slightly saline, the results need to be interpreted with this in mind. Chloride concentrations in the leaves of the control and treated trees, 2 months after treatments began, and in the leaves of the orchard trees 1 month later, were above those concentrations considered excessive (Table 1) (Reuter and Robinson, 1986; Lahav and Whiley, 2002). This applied to all treatments and one explanation for the impact of the treatments in 2000 on the crop in the following year might be the increased accumulation of Cl caused by the treatments. Our data were too variable to determine whether this was the case. While there was a tendency for Cl concentrations in the leaves to increase as more of the root system was exposed to drying (Table 1), the differences between the WW- and WD-trees were not significant and the sample for the DD-trees contained leaves that were much older than those in the samples from the WW- and WD-trees. Chloride concentration, per unit dry matter, increases in avocado leaves as they age (Lahav et al., 1990).

The extended nature of the soil water deficit (7 months) may have killed roots beneath the trees in the WD and DD treatments and this may have contributed to the impact of the treatments on the crop in the following season. There are two factors of importance here. One is whether there was a significant amount of root death under the DD-trees and the D side of the WD-trees and the other is whether this had any effect, given the capacity of the DD-trees to adjust within 2 months of the treatments being applied (Fig. 3). Neuhaus (2003) investigated the root systems of several trees in this orchard during 1998 and 1999. Irrigation had been withheld from one tree for 6 months from late spring until late autumn. At the end of the period of root-zone drying there was no effect on the root length density down to 1.3 m soil depth. The proportion of root tips that were either white or brown was similar to trees that had been irrigated throughout the season. However, the extended root-zone drying significantly reduced the length of roots adjacent to the soil surface from $2.1 \pm 1.5 \text{ m m}^{-2}$ to $0.8 \pm 0.4 \text{ m m}^{-2}$. If there had been extensive root death beneath the WD- and DD-trees, then we would expect this to reduce the capacity of the trees to retain their fruit during the normal periods of fruit drop in spring and summer, in this environment. This did not occur (Fig. 2) as the WW-, WD- and DD-trees had a similar number of fruit in May 2001, well after the summer fruit drop. We conclude that the treatments did not significantly damage the root system in terms of its capacity to supply water to the tree canopy. However, immediate and long term changes in the root system were instigated by the WD and DD treatments that prevented the trees from retaining all the fruit present at the end of the period of summer fruit drop.

Shoots of the DD-trees contained tyloses in the vascular tissue that can significantly reduce axial hydraulic conductivity (Neuhaus et al., 2007). This may have contributed to loss of fruit in the second season but it does not explain the loss in the WD-trees where no tyloses could be detected in this field experiment or in the pot experiment conducted by Neuhaus et al. (2007).

We assessed fruit quality indirectly by assuming that the Ca concentration in the fruit mesocarp was correlated with fruit quality. Hofman et al. (2002) established correlations between the Ca concentration in the fruit mesocarp and days to eating ripe, mesocarp discoloration and the severity of anthracnose (*Colletotrichum gloeosporioides*). Since the drying treatments did not significantly affect Ca concentration in the fruit (Table 2) we conclude that drying part of the root system reduced yield but was unlikely to have affected fruit quality. Hofman et al. (2002) attributed the associations between Ca concentration and fruit quality to variations in the rootstocks (seedling Guatemalan, unknown origin) of the trees or the root stock-scion interaction. Willingham et al. (2001) found that rootstocks of known origin influenced anthracnose development in the fruit of Hass trees, but there was no significant effect on the concentration of Ca in the fruit flesh. So, it is possible in our

experiment that the association between Ca concentration in the fruit and fruit quality established by Hofman et al. (2002) may not apply. This needs further investigation.

The knowledge gained from this study increases the options for irrigation management of avocado trees where water supply is limiting. Under reduced supply, water may be withheld either from part of an orchard (a combination of DD and WW treatments) or may be withheld from part of the root system in each tree in the orchard (WD treatment). Withholding water from the whole root system will reduce yield and tree growth and this effect is likely to carry over to the second season (longer term effects were not assessed). Withholding water from part of the root system will also reduce yield, and for (at least) two years, but the growth and functioning of the vegetative component of the trees is maintained. Whether partial root-zone drying (PRD), in the traditional sense, where the drying would be shorter term and switched from one side to another, would be effective in avocado needs to be evaluated. Our data suggest PRD would not reduce vegetative growth and may cause some fruit to drop.

We conclude that extended drying of half of the root-zone in one season reduced irrigation efficiency by promoting the abscission of developing fruit to the same extent as occurred when the whole root-zone was exposed to extended drying. The abscission of fruit was promoted by exposure of the roots to dry soil and was not necessarily related to the water status of the fruit or canopy. Drying half of the root system does not appear to affect fruit quality.

Acknowledgements

Technical assistance for the analysis of Ca, K, Na and Mg concentrations using ICP–OES was given from Murdoch University (WA, Australia). Horticulture Australia Ltd and Avocados Australia Limited funded this project (AV96005). We are grateful to colleagues with whom we discussed issues raised in this work.

References

- Bower, J.P., 1985. The calcium accumulation pattern in avocado fruit as influenced by long term irrigation regime. *South African Avocado Growers Association Yearbook* 8, 97–99.
- Brown, P.H., Picchioni, G., Jenkin, M., Mu, H., 1992. Use of ICP-MS and ¹⁰B to trace the movement of boron in plants and soil. *Communications in Soil Science and Plant Analysis* 23, 2781–2807.
- Chirachint, W., Turner, D.W., 1988. Shade reduces the foliar symptoms of 'Fuerte' avocado affected by salt, without significantly changing the concentration of Na, K, or Cl in the leaves. *Scientia Horticulturae* 36, 1–15.
- Fort, C., Muller, F., Label, P., Granier, A., Dreyer, E., 1998. Stomatal conductance, growth and root signaling in *Betula pendula* seedlings subjected to partial soil drying. *Tree Physiology* 18, 769–776.
- Gowing, D.J.G., Davies, W.J., Jones, H.G., 1990. A positive root-sourced signal as an indicator of soil drying in apple, *Malus x domestica* Borkh. *Journal of Experimental Botany* 41, 1535–1540.
- Hofman, P.J., Vuthapanich, S., Whiley, A.W., Klieber, A., Simons, D.H., 2002. Tree yield and fruit mineral concentrations influence 'Hass' avocado fruit quality. *Scientia Horticulturae* 92, 113–123.
- Jokhan, A.D., Else, M.A., Jackson, M.B., 1996. Delivery rates of abscisic acid in xylem sap of *Ricinus communis* L. plants subjected to part-drying of the soil. *Journal of Experimental Botany* 47, 1595–1599.
- Kang, S., Hu, X., Goodwin, I., Jerie, P., 2002. Soil water distribution, water use, and yield response to partial root zone drying under a shallow groundwater table condition in a pear orchard. *Scientia Horticulturae* 92, 277–291.
- Lahav, E., Bar, Y., Kalmar, D., 1990. Effect of nitrogenous fertilization on the annual variations in nutrients in avocado leaves. *Communications in Soil Science and Plant Analysis* 21, 1353–1365.
- Lahav, E., Whiley, A.W., 2002. Irrigation and mineral nutrition. In: Whiley, A.W. (Ed.), Wolstenholme, B.N. (Eds.), *The Avocado: Botany, Production and Uses*. CABI Publishing, Wallingford, pp. 259–297.
- Loveys, B.R., Grant, W.J.R., Dry, P.R., McCarthy, M.R., 1997. Progress in the development of partial root-zone drying. *Australian Grapegrower and Winemaker* 403, 18–20.
- Neuhaus, A., 2003. Managing irrigation for yield and quality in avocado. Ph.D. Thesis. The University of Western Australia, Crawley, Western Australia.
- Neuhaus, A., Turner, D.W., Colmer, T.D., Kuo, J., Eastham, J., 2007. Drying half the root-zone of potted avocado (*Persea americana* Mill., cv Hass) trees avoids the symptoms of water deficit that occur under complete root-zone drying. *Journal of Horticultural Science and Biotechnology* 82, 679–689.
- Paulin, R., 1988. Irrigation requirements of avocado. Western Australian Department of Agriculture. Farmnote No. 42/88.
- Reuter, D.J., Robinson, J.B., 1986. *Plant Analysis—An Interpretation Manual*. Inkata Press, Melbourne.
- Salama, R.B., Silberstein, R., Pollock, D., 2005. Soils characteristics of the Bassendean and Spearwood sands of the Gnangara mound (Western Australia) and their controls of recharge, water level patterns and solutes of the superficial aquifer. *Water, Air and Soil Pollution* 5, 3–26.
- Schaffer, B., Whiley, A.W., 2002. Environmental physiology. Whiley, A.W., Schaffer, B., Wolstenholme, B.N. (Eds.), In: *The Avocado: Botany, Production and Uses*. CABI Publishing, Wallingford, pp. 135–160.
- Scholander, P.F., Hammel, H.T., Bradstreet, E.D., Hemmingsen, E.A., 1965. Sap pressure in vascular plants. *Science* 148, 339–346.
- Short, D.C., Colmer, T.D., 1999. Salt tolerance in the halophyte *Halosarcia pergranulata* subsp. *pergranulata*. *Annals of Botany* 83, 207–213.
- Stoll, M., Loveys, B., Dry, P., 2000. Hormonal changes induced by partial rootzone drying of irrigated grapevine. *Journal of Experimental Botany* 51, 1627–1634.
- Thorp, T.G., Hutching, D., Lowe, T., Marsh, K.B., 1997. Survey of fruit mineral concentrations and postharvest quality of New Zealand-grown 'Hass' avocado (*Persea americana* Mill.). *New Zealand Journal of Crop and Horticultural Science* 25, 251–260.
- Turner, D.W., Menzel, C.M., Simpson, D.R., 1996. Short term drying of half the root system reduces growth but not water status or photosynthesis in leaves of passionfruit (*Passiflora* sp.). *Scientia Horticulturae* 65, 25–36.
- Whiley, A.W., 2002. Crop management. In: Whiley, A.W., Schaffer, B., Wolstenholme, B.N. (Eds.), *The Avocado: Botany, Production and Uses*. CABI Publishing, Wallingford, pp. 231–258.
- Whiley, A.W., Hargreaves, P.A., Pegg, K.G., Doogan, V.J., Ruddle, L.J., Saranah, J.B., Langdon, P.W., 1995. Changing sink strengths influence translocation of phosphate in avocado (*Persea americana* Mull.) trees. *Australian Journal of Agricultural Research* 46, 1079–1090.
- Willingham, S.L., Pegg, K.G., Cooke, A.W., Coates, L.M., Langdon, P.W.B., Dean, J.R., 2001. Rootstock influences postharvest anthracnose development in 'Hass' avocado. *Australian Journal of Agricultural Research* 52, 1017–1022.