Effect of the soil water-to-air ratio on water status, leaf gas exchange and biomass of avocado trees

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ABSTRACT

Avocado (*Persea americana* Mill.) is one of the most sensitive fruit tree species to flooded or poorly drained soil conditions. In Chile, avocado orchards are often planted in poorly drained soils that are low in oxygen resulting in tree stress. Understanding the relationship between the water-to-air ratio of different soils and avocado tree physiology and growth, should be helpful for irrigation management of the crop. The objective of this study was to relate the water-to-air ratios in different soils to water status, leaf gas exchange and biomass of avocado trees. Avocado trees were grown in each of five soils each collected from a different area of the Chilean avocado growing region with different physical properties and hence different water to air ratios. Thus, there were five treatments (T1-T5) corresponding to each of the five soils. The experiment was conducted during the spring and summer of 2005-2006 and 2006-2007 starting with two-year-old 'Hass' avocado trees planted outdoors in containers filled with one of the five soil treatments. At field capacity, the two-season average soil water-to-air ratio (W/A) was 1.7, 1.3, 0.6, 0.4 or 0.3 for treatments T1, T2, T3, T4, or T5, respectively. In addition to determining soil physical characteristics and monitoring W/A, net CO_2 assimilation (A), transpiration (Tr), stomatal conductance (gs), stem water potential (SWP), shoot and root fresh and dry weights, leaf area and leaf retention were evaluated for trees in each treatment. Although aerobic soil conditions were maintained in all treatments, trees in soil with lower W/A had higher A, Tr, gs, and SWP than trees in the treatments with higher W/A. Also, trees in treatments with lower W/A had more biomass and longer leaf retention than trees in treatments with higher W/A. The results of this study indicate that the soil water-to-air ratio significantly affects physiology and growth of 'Hass' avocado trees.

Efecto de la relación agua/ aire del suelo en el estatus hídrico, intercambio gaseosos de la hoja y biomasa de paltos.

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RESUMEN

El palto o aguacate (*Persea americana* Mill.) es una de las especies más sensible al anegamientoo condiciones de pobre drenaje del suelo. En Chile, los huertos de palto son a menudo plantados en suelos de pobre drenaje que son pobres en oxígeno lo que provoca estrés en los árboles. Entendiendo cómo se relaciona una característica del suelo tal como la relación agua/aire en diferentes tipos de suelo, y la fisiología y crecimiento del palto, podría ser una información importante para determinar el manejo de riego de este cultivo. El objetivo de este estudio fue relacionar la relación agua/aire del suelo en diferentes suelos con el estatus hídrico, intercambio gaseoso y biomasa de árboles de palto. Árboles de palto fueron establecidos en uno de cinco tipos de suelo recolectados desde diferentes zonas de la región de cultivo del palto; cada suelo tenía diferentes propiedades físicas y por tanto diferente relación agua/aire. Por tanto, se aplicaron 5 tratamientos, (T1-T5) correspondientes a cada uno de los 5 suelos. El experimento se condujo durante la primavera y verano de las temporadas 2005-2006 y 2006-2007, comenzando con plantas cv. 'Hass' de 2 años, plantados en condiciones de campo en contenedores de 200 L conteniendo cada uno de los suelos. A capacidad de campo, el promedio relación agua/aire (W/A) de ambas temporadas fue de 1.7, 1.3, 0.6, 0.4 o 0.3 para los tratamientos T1, T2, T3, T4, o T5, respectivamente. Además de determinar las características físicas del suelo y monitorear W/A, se determinó la asimilación neta de CO_2 (A), transpiración (Tr), conductancia estomática (gs), potencial hídrico xilemático (SWP), peso seco y fresco de brotes y raíces, área foliar y retención de hojas. Aunque las condiciones del suelo se mantuvieron como aeróbicas en todos los tratamientos, los árboles en suelo con baja relación tuvieron mejores valores de A, Tr, gs, y SWP que árboles en tratamientos con alta relación W/A. También, los árboles en tratamientos con menor W/A tuvieron más biomasa, área foliar y mayor retención de hojas que árboles desarrollados en suelos con mayor W/A. Los resultados de este estudio indican que la relación agua/aire del suelo afectan significativamente la fisiología y crecimiento de paltos cv. 'Hass'.

1. INTRODUCTION

In Chile, commercial avocado production has expanded to slopes of hills, commonly with soils that have a high clay content and bulk density, are poorly drained and are low in oxygen. Avocado trees are very sensitive to waterlogging (Schaffer *et al.*, 1992; Schaffer and Whiley, 2002; Whiley and Schaffer, 1994) and the relatively low productivity of this species may be related to the water status of the crop, which at times is over irrigated resulting in root asphyxiation. Previous studies (Ferreyra *et al.*, 2007a) have shown that the soil air content affects avocado water relations. Ferreyra *et al.* (2007a) reported that low soil air content (5% to 18%) negatively affect stomatal conductance (gs) in avocado trees. The same authors established that soil air content lower than 17% restricts the oxygen diffusion rate to less than 0.2 µg cm^{-2} min^{-1} and that macroporosity values were correlated with soil O_2 and CO_2 contents. Those studies indicated that for proper root and vegetative development of avocado trees, it is necessary to maintain an appropriate water-to-air balance in the soil, especially in clay soils.

In well-irrigated soils, there can be different water-to-air ratios which could influence the productivity of avocado trees, because the relationship between crop production potential and soil type is closely related to the water-to-air ratio in the soil (Shein and Mizury, 1998; Zhou and You, 2005; Ferreyra *et al.*, 2007a; Ferreyra *et al.*, 2007b). The soil water-to-air ratio is a result of water management as well as the physical properties of the soil. Factors that most affect soil aeration are soil water content, texture and structure. The higher the soil water content, the lower the air volume and therefore the greater the limitation to aerobic metabolism of the roots (Letey, 1961; Blokhina *et al.*, 2003). Therefore, a slight error in the irrigation rate or frequency, due to a lack of understanding of soil properties, may lead to below optimum oxygen content in the root zone for adequate plant growth and yield (Letey, 1961; Blokhina *et al.*, 2003).

For avocado trees, root hypoxia or anoxia usually results in reductions of leaf gas exchange including gs, transpiration (Tr) and net CO_2 assimilation (A) (Schaffer and Ploetz, 1989; Schaffer *et al.*, 1992; Schaffer, 1998; Schaffer and Whiley, 2002). In a study of avocado trees on Waldin seedling rootstock subjected to soil flooding, trees showed high susceptibility to root hypoxia, with significant reductions in gs, Tr and A eight days after the flooding treatment was initiated for "Beta" avocado and ten days for "Hass" avocado (Gil et al., 2007). Also, low soil oxygen content can result in root tissue damage, inhibition of vegetative and reproductive growth, changes in plant anatomy and morphology, premature senescence and plant mortality (Schaffer *et al.*, 1992; Drew, 1997; Kozlowski, 1997).

Although there are several reports of the effects of flooding on net CO_2 assimilation and water relations of avocado, little is known about the effects of soil water-to-air ratios on physiology and biomass of avocado trees. An understanding of the relationship between the soil water-to-air ratio and avocado physiology should provide valuable information for irrigation management of this crop in different soils, particularly in areas with poor soil aeration. The objective of this study was to evaluate the effects of the water-to-air ratio in five different soils maintained near field capacity, on plant water status and leaf gas exchange (A, gs and Tr) and biomass of avocado trees.

2. MATERIALS AND METHODS

2.1. Plant material

The experiment was conducted from the spring of 2005 to the end of the summer 2007, beginning with two-year-old 'Hass' avocado trees grafted onto Mexícola seedling avocado rootstock. Trees were planted in one of five different soils in approximately 200-L "containers" constructed by mounding field-collected soil and holding mounds in place with a white plastic mesh sustained by a structure of metal wire.

2.2. Climatic conditions

The study site was located outdoors at the Regional Research Center, INIA, in the La Cruz region of Valparaíso, Chile. The region has a humid marine Mediterranean climate with an average annual temperature of 14.5 ºC, a minimum average temperature of 5.2 ºC (July) and a maximum average temperature of 29.3 ºC (January). The nine-month period from September to May is frost-free. The average total annual precipitation in the region is 328.5 mm with 80% of the precipitation occurring from May to August.

2.3. Experimental design

Five different soils were obtained from 5 different fallow fields and hills with soils common to avocado orchards in Chile. The different soil textures and their physical characteristics are shown in Table 1. Soil was steam sterilized and periodically treated with fungicides to prevent root damage from *Phytophthora cinnamomi*. Trees were drip irrigated with well water by 16 drippers (0.5 L h^{-1}) per plant. The irrigation frequency varied from 2 to 6 times per day to maintain relatively constant water content near field capacity (soil tension of -0.33 KPa). The volume of water applied daily was the same for all treatments. Trees were fertilized once each week from October to March with 145 g N applied as Urea, 10 g P applied as phosphoric acid, 63 g K applied as potassium nitrate and 14 g Mg applied as magnesium sulfate per tree.

Treatments. The water content in each of the five soils was kept near field capacity during the experimental period; each of the 5 soils had different physical characteristics resulting in different water and air contents. Thus, there were five soil treatments (T1-T5) each with different average W/A: T1, trees in fine loam clay with an average W/A of 1.7 and an average seasonal soil air content of 17.4%; T2, trees in loam clay soil, with an average W/A of 1.3 and an average seasonal soil air content of 19.5%; T3, trees in loam clay soil with higher silt content, with an average W/A of 0.6 and an average seasonal soil air content of 35.0%; T4, trees in loam sandy soil with an average W/A of 0.4 and an average seasonal soil air content of 32.8%; and T5, trees in sandy soil irrigated with an average W/A of 0.3 and an average seasonal soil air content of 36.8%. Soil textures were determined in a laboratory by the Bouyoucos hydrometer method (Day, 1965). The experimental design was a randomized complete block with 5 single-tree replications per treatment.

2.4. Measurements of soil physical proprieties.

Soil bulk density. Soil bulk density (BD) was determined by the cylinder method of Blake and Hartage (1986). Final BD values were obtained from the average of 3 *in-situ* measurements and one laboratory determination.

Soil porosity. Total soil porosity was calculated as described by Danielson and Sutherland (1986) using a soil real density value of 2.64 g cm^{-1}, which is a typical value in most mineral-originated soils (Blake and Hartage, 1986). Soil macroporosity (air capacity) *in situ* was calculated as described by Ball and Smith (1991). The *in-situ* value was averaged with a laboratory air capacity measurement obtained using the method described by Carrasco (1997).

Field capacity. The soil water content at '*in situ* field capacity' (FC) was determined six times during the each season using the method described by Cassel and Nielsen (1986). The FC was also determined once in a laboratory by subtracting the percentage of macropores from the percentage of total pores; the percentage of pores that remained corresponded to the total microporosity which in saturated soil is the same as the volumetric water content at field capacity (Danielson and Sutherland, 1986). The six *in-situ* and the laboratory measurements were pooled to obtain an average FC value. The volumetric soil water content (θ) at field capacity was determined by multiplying the gravimetric water content (ω) by the BD value as described by Cassel and Nielsen (1986).

Soil air content. Volumetric air content of the soil was calculated as described by Benavides (1994). Volumetric water content was subtracted from total porosity and the remaining value was the percentage of air in the soil.

Soil water content. Soil water content was measured daily at a soil depth of 30 cm by frequency domain reflectometry (FDR) using a Diviner probe (Diviner 2000, Sentek Sensor Technologies, Stepney, Australia). Soil water content was also determined gravimetrically (ω) and volumetrically (θ) at a soil depth of 30 cm. The ω was determined with the formula:

$$\omega = ((\text{wet soil weight - dry soil weight}) / \text{dry soil weight})*100$$

The θ was determined by multiplying ω by the BD value. The θ from saturation to the permanent wilting point was used to calibrate the FDR probe and for FC determination.

Soil oxygen diffusion rate and CO_2 and O_2 contents. The oxygen diffusion rate (ODR) in the soil was measured on 2 dates during the first season and on 3 dates during the second season with a Pt-electrode and oxygen diffusion meter (Eijkelkamp, Netherlands) as described by Letey and Stolzy (1964). Measurements were made during the morning with 2 irrigation pulses applied during the measurement period; the Pt-electrode was inserted at 15-cm depth. Air in the soil was sampled at a 30-cm depth through "point-source soil atmospheric sampler" described by Staley (1980). Air samples were collected on two dates each season, during the morning before irrigation started. Samples were analyzed for O_2 and CO_2 concentrations by injecting a 1 mL headspace sample into an AutoSystem XL gas chromatograph (Perkin-Elmer, Waltham, Massachusetts, USA) equipped with a TCD detector and a CTR-1 column.

2.5. Leaf gas exchange and water relations measurements.

Stomatal conductance (gs) and transpiration (Tr): Stomatal conductance and Tr were measured with a Li-1600 steady state porometer (Li-Cor, Inc., Lincoln, Nebraska, USA) as described by Prive and Janes (2003) and Raviv *et al.* (2001). Both gs and Tr were measured at two-week intervals in the morning (900 - 1100 hr) and at noon (1300 - 1600 hr). Measurements were made on 3 mature, sun-exposed leaves per plant.

Stem (xylem) water potential: Stem water potential (SWP) was measured at the same frequency as gs and Tr. For SWP determinations, 3 sun-exposed leaves per tree were covered with plastic and aluminum foil and then excised 30 minutes after covering (Meyer and Reickosky, 1985). The SWP of the excised leaves was immediately measured with a pressure chamber as described by Scholander *et al.* (1965). Leaves were excised and SWP was measured during the morning (9:00 - 11:00 hr) and after noon (13:00 -16:00 hr).

Net CO_2 assimilation: Net CO_2 assimilation (A) was measured once each month during the second season with an open system portable gas analyzer Li-6400 (Li-COR Inc., Lincoln, Nebraska, USA). Measurements were made from 1000 to 1300 hr on 3 mature leaves, of similar size with similar light exposure located in the middle of a spring shoot, for each plant. Measurements were made at a photosynthetic photon flux (PPF) > 1300 µmol m^{-2} s^{-1}, a reference CO_2 concentration in the leaf cuvette between 375 to 400 ppm, and an air flow rate into the cuvette of 200 µmol s^{-1}.

2.6. Leaf retention and tree biomass

Ten similar shoots from the autumn vegetative flush were labeled and the total number of leaves per shoot was determined from January to March of the second season to determine leaf retention.

At the end of the study period, all plants were harvested, aerial parts were separated from the roots and the fresh weight of leaves, shoots and wood was determined with a digital balance (Shanghai SP-300, Shanghai Huade Weighing Apparatus Co., Shanghai, China). A "shoot" refers to the current season's branches and "wood" refers to the older trunk and branches. Tissues were then oven-dried at 70ºC for 3 days (to a constant weight) and leaves, shoots and wood dry weights were determined with an electronic balance (Transcell ESW-5M, Transcell Technology, Inc. Buffalo Grove, IL, USA). Root density was determined for 3 replications per treatment by subsampling roots with a 9-mm diameter, 1-m long tube sampler (Split tube sampler, Eijkelkamp, Netherlands) inserted into the soil as described by Ferreyra *et al.* (1984, 1989). The depth of soil sampled for root density ranged between 40 and 45 cm, depending on the depth of the soil in the sampled pot. Root samples were rinsed twice with tap water and once with deionized water, separated from the soil and fresh weights were determined. Roots were then oven-dried at 70ºC for 3 days and root dry weight and root density (g cm^{-3}) were determined for each plant. Total root dry weight was estimated by multiplying the root density by the total soil volume in each pot.

After detaching and weighing all the leaves of each tree, approximately 300 leaves from each tree were randomly sampled and leaf area was measured with a portable leaf area meter (model LI-3000C, Li-Cor, Lincoln, Nebraska, USA). Leaf samples were also weighed with an electronic balance

(Transcell ESW-5M, Transcell Technology, Inc. Buffalo Grove, Illinois, USA) and the total leaf area per tree was estimated by multiplying the area/weight ratio of the 300 sub-sampled leaves per plant by the total leaf weight per plant.

2.7. Climatic variables

Throughout the experiment, air temperature and relative humidity were continuously monitored with a Hobo datalogger (Onset Computer Corporation, Pocasset, Massachusetts, USA) and vapor pressure deficit was calculated from these variables.

2.8. Statistical analyses

Data are expressed as means. The effects of treatments on ODR, soil CO_2 and O_2 concentrations, gs, Tr, SWP, A, autumn leaf retention and dry weights were analyzed by a one-way ANOVA and mean differences were determined with a Waller-Duncan K-Ratio Test. All statistical analyses were performed using the SAS statistical software package (SAS Institute, Cary, North Carolina, USA).

3. RESULTS

3.1. Physical soil proprieties

The physical soil characteristics measured are summarized in Table 1. The W/A for seasons 2005/2006 and 2006/2007 were obtained from total porosity and the average volumetric soil water content (θ) during each season (Table 1).

Soil water content. Volumetric soil water content tended to fluctuate more in the T2, T3 and T4 treatments than in the T1 and T5 treatments (data non showed).

Soil oxygen diffusion rate (ODR) and CO_2 and O_2 content. The mean ODR, CO_2 and O_2 contents throughout the experiment are shown in Table 2. In 2005/2006, T4 had the highest ODR, followed by the T5 and T3, and the lowest ODR in the T2 and T1. In 2006/2007, T5 had the highest ODR, followed by the T4, and finally T3, T2 and T1 which did not show statistical differences among them. During both seasons, T2 had the highest CO_2 content and T4 and T5 had the lowest CO_2 contents. No significant differences were observed in soil O_2 content among treatments during the first measurement season, but there was a significant difference in O_2 content between the T4 and T3 during the second season.

Non-linear regression analysis showed an inverse exponential relationship between the average W/A of each soil per season and soil ODR (R^2=0.75) (Figure 1). There was a direct exponential relationship between the average soil air content and ODR (R^2 = 0.61, data not shown), but this relationship was not as strong as the relationship between the W/A and ODR.

Percentage of days with soil air content below a critical (17%) level for avocado trees. The percentage of days with soil air content below 17% was determined for each soil treatment during each season because soil air content below that level restricts ODR to less than 0.2 μg cm^{-2} min^{-1} (Ferreyra *et al.,* 2007a) and can restrict root growth and cause root damage to avocado (Valoras *et al.,* 1964, Stolzy *et al.,* 1967). Taking into account the water content measured each day during both seasons, the percentage of days with the soil oxygen content below the critical 17% level during 2005/2006 was 40.78%, 18.78%, 0.96%, 0% and 0% for T1, T2, T3, T4 and T5, respectively. During 2006/2007 the percentage of days with the soil air content below the critical level was 54.89%, 68.90%, 15.16%, 0% and 0% for T1, T2, T3, T4 and T5, respectively (Table 3).

3.2. Leaf gas exchange and water relations

Stomatal conductance, transpiration and stem water potential: The effect of treatment on gs, Tr and SWP during 2005/2006 and 2006/2007 are shown in Tables 4 and 5, respectively. There were no significant differences among treatments for any plant water relation variable measured during the morning in 2005/2006. During 2005/2006, gs and Tr measured in the afternoon were higher for trees in the T4 and T5 treatments than for trees in the other treatments, with exception of gs of T2 which was not significantly different from that of T4 or T5. In the afternoon, SWP was higher for trees in T5 and T3 than the other treatments (Table 4).

During 2006/2007, there were no significant differences among treatments in gs or SWP measured during the afternoon, possibly due to the very high vapor pressure deficits observed during

December and January, which reached a maximum of 4.5 KPa compared to a maximum VPD of 3.9 KPa during the summer of 2005/2006 (data non showed). However transpiration measured during the afternoon was higher for trees in T5, T4 and T2 than in the other treatments. In the mornings of 2006/2007 there was a clearer effect of treatment on water relations. Trees in T5, T4 and T1 had significantly higher gs and Tr than the T2 and T3 and trees in the T3 and T5 had significantly higher SWP than trees in T2 (Table 5).

Net CO_2 assimilation: Net CO_2 assimilation (A) is shown in Table 6. Trees in T5 had significantly higher A than trees in T3 or T2, during the second season of measurements.

3.3. Leaf retention and tree biomass

Leaf retention was consistently longer on trees in the T5 or T4 than in the other treatments throughout the entire season; in these treatments a higher number of leaves developed from autumn 2006 sprouts remained on the tree until February 2007 (Figure 2).

Total wood, shoot, root and total plant dry weights were significantly lower for trees in T1 than in trees in all other treatments (Table 7). Trees in T4 had the highest total dry weight as a result of higher wood, shoot, leaf and root dry weights compared with the other treatments. Trees in T3 had the lowest leaf dry weight. There was no significant difference in dry weights between trees in T2 and T4, with the exception of root dry weight which was higher for T4 than T2 (Table 7). Biomass partitioning ranged from 20.2% to 25.2% for wood, 12.5% to 16.8% for shoots, 26.3% to 33.8% for leaves and 29.8% to 35.2% for roots. The proportion of biomass partitioned to the roots was higher in T4 and T5 than in the other treatments (Table 7).

3.4. Climatic variables

Vapor pressure were recorded during 2005/2006 and 2006/2007. The maximum VPD (4.5 KPa) was much higher in December and January 2006/2007 than during the same period in 2005/2006. The average VPD during 2005/2006 in the morning and afternoon were 1.7 and 2.7 KPa, respectively, while the VPD during 2006/2007 averaged 1.6 and 3.03 KPa during the morning and afternoon, respectively (data non showed).

4. DISCUSSION

In soils irrigated to maintain water content near field capacity, ODR of the soil was more closely related to the W/A than to the soil air content. Also, differences in W/A due to different soil physical properties had a significant effect on leaf gas exchange, water relations and biomass of avocado trees. In general, the lower the W/A, the higher the gs, Tr, A, SWP and biomass. Avocado roots are highly sensitive to lack of oxygen in the soil caused by flooding or excessive water in the root zone (Schaffer *et al.*, 1992; Whiley and Schaffer, 1994; Schaffer and Whiley, 2002). This sensitivity may, in part, be due to avocado´s root system which is extensively suberized with inefficient water absorption due to low hydraulic conductivity and few root hairs (Whiley and Schaffer 1994; Du Plessis, 1991).

In the *Phytophthora*-free soils examined in this study, the different W/A were primarily due to differences in soil texture and bulk density as well as the ODR and CO_2 concentration in the soil. Soil ODR values of 0.2 µg cm^{-2} min^{-1} (Valoras *et al.*, 1964) and 0.17 µg cm^{-2} min^{-1} (Stolzy *et al.*, 1967) have been reported as limiting to avocado development. Menge and Marais (2000) reported that soil CO_2 concentrations of 16% inhibited avocado root growth and survival. Although none of the soils tested in the present study had limiting ODR values or CO_2 concentrations when those variables were directly measured, the percentage of days that the soil air content was below 17% and thus reaching a critical ODR (Ferreyra *et al.*, 2007a) for normal avocado root functioning in T1 and T2 was 40.8% and 18.9%, respectively during 2005/2006, and 54.9% and 68.9%, respectively during 2006/2007. The soil air content in T4 or T5 never reached below the critical level was below the critical soil air content 0.9% of the time in T3 during season 2005/2006 and 15.2% during 2006/2007. In general, the results of this study showed that the lower the W/A, the higher the ODR and the lower the CO_2 concentration. Oxygen concentrations were not significantly different among soils. However, O_2 content diminished considerably from the first to the second season, probably because the water content was kept closer to field capacity during the second season.

In avocado trees, root hypoxia or anoxia usually results in reductions in gs and Tr (Schaffer and Ploetz, 1989; Schaffer *et al.*, 1992; Schaffer, 1998; Schaffer and Whiley, 2002). During the first season of this study, gs, Tr and SWP were higher for trees in the T4 and T5 than for trees in the other treatments. However during the second season, trees in had similar gs, Tr and SWP as plants in T4 or

T5. Ferreyra *et al.* (2007a) reported that low soil air content (5% to 18%) negatively affected gs, but not the SWP. In the present study, net CO_2 assimilation (A) was also affected by the soil treatments. Trees in soils with a low W/A had higher A which was highly correlated with gs (R^2=0.88, data not shown). For avocado trees, root hypoxia or anoxia usually results in reductions in gs, Tr and A (Schaffer and Ploetz, 1989; Schaffer *et al.*, 1992; Schaffer, 1998; Schaffer and Whiley, 2002). In other species including *Citrus sinensis*, continuous soil flooding reduced A by 94% after 24 days (Vu and Yelenosky, 1991).

Avocado trees in soils with lower W/A (T4: sandy loam and T5: sandy) had greater biomass and longer leaf retention than trees in a heavy loam clay soil (T1) with a higher W/A. Considering that all soils were kept at field capacity and were fertilized with the same amount of nutrients, differences in tree growth and development were presumably due to soil physical features which affected root oxygenation and nutrient availability or absorption. Avocado trees grown in soils with high W/A, particularly heavy loam clay soils (T1), had significantly less leaf, shoot and root biomass than trees in soils with lower W/A such as sandy or sandy loam soils. Previous work has shown that the lack of oxygen in the root zone can adversely affect shoot growth of many woody plant species by suppressing formation and expansion of leaves and internodes, or causing premature leaf senescence and abscission (Kozlowski *et al.* 1991; Kozlowski and Pallardy 1997; Schaffer *et al.* 1992). Also, soil hypoxia reduces root growth of most plants by inhibiting root formation and branching and growth of existing roots and mycorrhizae and by inducing root decay (Kozlowski 1984; Kozlowski and Pallardy 1997). Leaf abscission is a common response of avocado trees to root hypoxia (Schaffer *et al.* 1992; Gil et al. 2007, 2009). In many plants, root hypoxia stimulates ethylene production (Kozlowski 1997; Jackson 2002) because under hypoxic conditions (when partial pressures of O_2 in the root zone are between 0 and that of air) the conversion of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene is actually stimulated (Jackson 2002). In recent studies, root hypoxia resulted in increased ethylene concentration in leaves (Gil *et al.* 2009). In the current study, soils never reached hypoxic conditions, but tree biomass and leaf retention were reduced when soil W/A were high, indicating that not only root hypoxia but high W/A may halt ethylene production and thus increase organ abscission such as leaves.

In conclusion, the W/A ratio in non-*Phytophthora*-infested soils irrigated to near field capacity is an important factor that affects avocado physiology and biomass. When W/A is low, gs, Tr, SWP, A, leaf retention and tree biomass of avocado are higher than in soils with high water-to-air ratios. Taking into account that avocado production in Chile and other places in the world is expanding to areas with marginal soils that are often poorly drained and low in oxygen, W/A should be an important consideration when assessing the potential productivity of an avocado orchard.

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REFERENCES

Ball, B., Smith, K. 1991. Gas movement. In: Smith KK and Mullins Ch (eds) Soil Analysis. Marcel Dekker, inc. 511-550.

Benavides, C. 1994. El suelo como un sistema físico. p. 121-152. In: Suelos, una visión actualizada del recurso. Universidad de Chile, Facultad de Ciencias Agrarias y Forestales, Departamento de Ingeniería y Suelos, Santiago, Chile.

Blake, G.R., Hartage, K.H. 1986. Bulk density. p. 363-375. In: Klute A (ed) Methods of Soil Analysis. Physical and Mineralogical Methods. Amer. Soc. Agron., Madison, Wisconsin, USA.

Blokhina, O., Virolainen, E., Fagerstedt, K.V. 2003. Antioxidants, oxidative damage and oxygen deprivation stress: a review. Annals Bot. 91:179-194.

Carrasco, J. 1997. Influencia de diferentes sistemas de laboreo en las propiedades físicas y químicas de un Luvisol cálcico de la meseta central de España. Ph D Thesis, Esc. Tec. Superior de Ingenieros Agrónomos, Universidad Politécnica de Madrid.
Cassel, D.K., Nielsen, D.R. 1986. Field capacity and available water capacity. pp 901-924. In: Klute A (ed). Methods of Soil Analysis. Physical and Mineralogical Methods. Amer. Soc. Agron., Madison, Wisconsin, USA.
Danielson, R.E., Sutherland, P.L. 1986. Porosity. pp 443-461. In: Klute A (ed). Methods of Soil Analysis. Physical and Mineralogical Methods. Amer. Soc. Agron., Madison, Wisconsin, USA.
Day, P.R. 1965. Particle fractionation and particle-size analysis. In C. A. Black (ed) Methods of Soil Analysis. Part I. Soil Sci Soc Amer.
Drew, M.C. 1997. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Ann. Rev. Plant Physiol Plant Mol Biol 48:223-250.
Du Plessis, S.F. 1991. Factors important for optimal irrigation scheduling of avocado orchards. S. African Avocado Growers' Assn. Yrbk.14:91-93.
Ferreyra R, Sellés G, Tosso J (1984). Efecto de diferentes alturas de aguas sobre el cultivo del pimiento 1: Influencia de los excesos de humedad. Agric Tec (Chile) 45:47-51.
Ferreyra R, Tosso J, Ruiz R (1989). Efecto de diferentes alturas de agua sobre el cultivo de tomate (*Lycopersicum esculentum* Mill) 2: Relación evotranspiración-crecimiento-nutrición. Agric Tec (Chile) 48:268-272.
Ferreyra R, Sellés G, Celedón J, Maldonado P, Torres A, Gil P (2007a). Effect of the soil air content in the water status and development of avocado. Proc. Sixth World Avocado Congress, Viña del Mar, Chile.
Ferreyra, R., Sellés, G., Maldonado, P., Celedón, J., Gil, P. 2007b. Efecto del clima, de las características de la hoja y de la metodología de medición en el potencial hídrico xilemático en palto (*Persea americana* MILL.). Chilean J. Agric. Res. 67:182-188.
Gil, P.M., Schaffer, B., Gutiérrez, S.M., Li, C.. 2007. Effect of waterlogging on plant water status, leaf gas exchange and biomass of avocado. Proc. VIth World Avocado Congress, Viña del Mar, Chile, 12-16 Nov. 2007.
Gil PM, Gurovich L, Schaffer L, García N, Iturriaga R. 2009. Electrical signaling, stomatal conductance, ABA and Ethylene content in avocado trees in response to root hypoxia. Plant Signaling and Behavior 4:100-108.
Jackson M. 2002. Long-distance signaling from roots to shoots assessed: the flooding story. J. Exp. Bot. 53:175-181
Kozlowski TT. 1997. Response of woody plants to flooding and salinity. Tree Physiol Monograph 1:1-29.
Kozlowski TT, Pallardy SG. 1984. Effects of flooding on water, carbohydrate and mineral relations. In: Flooding and plant growth. Kozlowski TT (ed). Academic Press, Orlando, Fl, pp 165-193.
Kozlowski TT, Pallardy SG. 1997. Physiology of woody plants. Acadençmic Press, San Diego.
Kozlowski TT, Kramer, PJ, Pallardy SG. 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA.
Letey, J. 1961. Aeration, compaction and drainage. Calif Turfgrass Cult 11:17-21.
Letey, J., Stolzy, L.H. 1964. Measurement of oxygen diffusion rates with the platinum microelectrode. I. Theory and equipment. Hilgardia 35:545-554.
Menge, J.A., Marais, L.J. 2000. Soil Environmental factors and their relationship of avocado root rot. Subtropical Fruit News 8: 1-11.
Meyer, W., Reicosky, D. 1985. Enclosing leaves for water potential measurement and its effect on interpreting soil induced water stress. Agric Meteorol 35:187-192.
Raviv, M., Lieth, J., Wallach, R. 2001. The effect of root-zone physical properties of coir and UC mix on performance of cut rose (cv Kardinal). Acta Hort. 554: 231-238.
Schaffer, B. 1998. Flooding responses and water-use efficiency of subtropical and tropical fruit trees in an environmentally-sensitive wetland. Ann Bot 81:475-481.
Schaffer, B., Ploetz, R.C. 1989. Net gas exchange as damage indicator for Phytophthora root rot of flooded and non-flooded avocado. HortScience 24:653-655.
Schaffer, B., Whiley, A.W. 2002. Environmental physiology. In: Whiley AW, Schaffer B, Wolstenholme BN (eds) Avocado: Botany, Production and Uses, CABI Publishing, Wallingford, UK, pp 135-160.
Schaffer, B., Anderson, P.C., Ploetz, R.C. 1992. Responses of fruit trees to flooding. Hort. Reviews 13:257-313.

Scholander, P., Hammel, H.Tr., Bradstreet, E.D., Hemmingsen, E.A. 1965. Sap pressures in vascular plants. Science 148:339-346.
Shein, E.V., Mizury, M. 1998. Agrophysical assessment of black shrinking soils of Tunisia. Soil Tillage Res 47:97-102.
Staley, Tr. 1980. A point-source method for sampling soil atmospheres. Trans. Amer. Soc. Ag. Eng. 23:580-584.
Stolzy, L.H., Zentmyer, G.A., Klotz, L.J., Labanauskas, C.K. 1967. Oxygen diffusion, water, and *Phytophthora cinnamomi* in root decay and nutrition of avocados. Proc. Amer. Soc. Hort. Sci. 90:67-76.
Valoras, N., Letey, J., Stolzy, l., Frolich, F. 1964. The oxygen requirements for root growth of three avocado varieties. Amer. Soc. for Hort. Sci. 85:172-178.
Vu, J., Yelenosky, G. 1991. Photosynthetic responses of citrus trees to soil flooding. Physiol Plant 81: 1-14.
Whiley, A.W., Schaffer, B. 1994. Avocado. In: Schaffer B, Anderson P (eds) Handbook of Environmental Physiology of Fruit Crops, Vol 2, Subtropical and Tropical Crops. CRC Press, Boca Raton Florida, pp 3-35.
Zhou, J., Yu, J. 2005. Influences affecting the soil-water characteristic curve. J Zhejiang Univ SCI 2005 6A:797-804.

TABLES

Table 1. Physical characteristics, water content and water-to-air ratios of five different soil types (treatments; Tmt). Percentages of soil particles represent means obtained from laboratory measurements; other physical feature values represent means obtained from *in situ* and laboratory measurements. LC = Loam Clay, LS = Loam sandy, S = Sandy, FC = field capacity, BD = bulk density, P = porosity, MP = microporosity, AC= Air capacity

Tmt	Texture Class (% Sand-% Silt-% Clay)	BD g cm^{-3}	FC θ	P %	MP %	AC %	Average water content (%θ) 2005-2007	Average soil air content (%θ) 2005-2007	Average soil water/air ratio (W/A) 2005-2007
T1	LC (39.5-25.1-35.4)	1.43	20.0	46.0	28.6	17.5	28.8	17.4	1.7
T2	LC (39.2-22.6-38.2)	1.49	19.6	43.8	29.2	14.6	24.4	19.5	1.3
T3	LC (34.1-37.9-28)	1.14	20.9	57.0	23.8	33.2	22.0	35.0	0.6
T4	LS (84.4-5.5-10.1)	1.45	7.3	45.3	10.5	34.7	12.5	32.8	0.4
T5	S (92-0.5-7.5)	1.38	12	47.9	16.5	31.4	11.2	36.8	0.3

Table 2. Effect of treatment (Tmt) on soil oxygen diffusion (ODR) and CO_2 and O_2 concentrations. Values correspond to means. Different letters (a, b, c) within columns indicate significant difference among treatments (Waller-Duncan Test, P ≤ 0.1).

Tmt	2005/2006				2006/2007			
	W/A	ODR (μg cm^{-2} min^{-1})	CO_2 (%)	O_2 (%)	W/A	ODR (μg cm^{-2} min^{-1})	CO_2 (%)	O_2 (%)
T1	1.5	0.51 c	0.83 ab	16.60 a	1.9	0.34 c	0.44 b	5.02 ab
T2	0.9	0.51 c	0.94 a	18.46 a	1.7	0.38 c	0.74 a	4.63 ab
T3	0.5	0.70 b	0.74 abc	16.60 a	0.8	0.50 c	0.41 b	3.35 b
T4	0.4	1.05 a	0.55 c	18.90 a	0.4	1.05 b	0.32 bc	5.32 a
T5	0.2	0.83 b	0.66 bc	17.36 a	0.4	1.36 a	0.16 c	4.47 ab

Table 3. Percentage of days with soil air content below the critical level (<17%) for each treatment (Tmt), which has been shown to limit oxygen diffusion in soil and availability to avocado roots (Ferreyra *et al.* 2007a). Values correspond to means ± standard error (SE).

	% of Days with soil Ea < 17% (mean ± SE)	
Tmt	**2005/2006**	**2006/2007**
T1	40.78 ± 19.18	54.89 ± 21.45
T2	18.78 ± 7.59	68.90 ± 8.41
T3	0.96 ± 0.96	15.16 ± 7.76
T4	0.00 ± 0.00	0.00 ± 0.00
T5	0.00 ± 0.00	0.00 ± 0.00

Table 4. Effect of treatments (Tmt) on water relations of avocado plants during 2005/2006. Values represent means. AM = 9:30 to 11:00 hr (gs and Tr); 5:30 to 6:30 hr (SWP), PM = 13:00 to 15:00 hr, gs = stomatal conductance, Tr = transpiration, SWP = soil water potential. Different letters (a, b) within columns indicate significant difference among treatments (Waller-Duncan Test, P ≤ 0.1).

		AM			PM		
Tmt	**W/A 2005/2006**	**gs ($cm\ s^{-1}$)**	**Tr ($\mu g\ cm^{-2}\ s^{-1}$)**	**SWP (MPa)**	**gs ($cm\ s^{-1}$)**	**Tr ($\mu g\ cm^{-2}\ s^{-1}$)**	**SWP (MPa)**
T1	1.5	0.30 a	2.88 a	-0.11 a	0.31 c	4.98 c	-0.77 b
T2	0.9	0.37 a	2.84 a	-0.10 a	0.38 ab	6.48 b	-0.75 b
T3	0.5	0.30 a	2.42 a	-0.10 a	0.34 bc	6.08 b	-0.71 ab
T4	0.4	0.46 a	3.46 a	-0.10 a	0.42 a	7.24 a	-0.72 b
T5	0.2	0.42 a	3.23 a	-0.11 a	0.43 a	7.22 a	-0.61 a

Table 5. Effect of treatments (Tmt) on water relations of avocado plants during 2006/2007. Values represent means. AM = 9:30 to 11:00 hr, PM = 13:00 to 15:00 hr, gs = stomatal conductance, Tr = transpiration, SWP = soil water potential. Different letters (a, b) within columns indicate significant difference among treatments (Waller-Duncan Test, P ≤ 0.1) during the AM or PM measurement time.

		AM			PM		
Tmt	**W/A 2006/2007**	**gs ($cm\ s^{-1}$)**	**Tr ($\mu g\ cm^{-2}\ s^{-1}$)**	**SWP (MPa)**	**gs ($cm\ s^{-1}$)**	**Tr ($\mu g\ cm^{-2}\ s^{-1}$)**	**SWP (MPa)**
T1	1.9	0.47 a	4.45 a	-0.62 ab	0.28 a	5.10 b	-0.91 a
T2	1.7	0.41 b	3.83 b	-0.65 b	0.28 a	5.24 ab	-0.88 a
T3	0.8	0.40 b	3.84 b	-0.55 a	0.26 a	4.91 b	-0.91 a
T4	0.4	0.44 ab	4.55 a	-0.59 ab	0.28 a	5.36 ab	-0.90 a
T5	0.4	0.47 a	4.74 a	-0.54 a	0.30 a	5.95 a	-0.83 a

Table 6. Effect of treatments (Tmt) on CO_2 assimilation (A). Values represent means. Different letters (a, b) within columns indicate significant difference among treatments (Waller-Duncan Test, P ≤ 0.1).

Tmt	**W/A 2006/2007**	**A ($\mu mol\ s^{-1}\ m^{-2}$)**
T1	1.9	4.71 ab
T2	1.7	4.44 b
T3	0.8	4.35 b
T4	0.4	5.40 ab
T5	0.4	6.07 a

Table 7. Effect of treatments (Tmt) on avocado dry weight and biomass partitioning. Values represent means (n=4). Different letters within columns indicate significant difference among treatments (Waller-Duncan Test, P ≤ 0.1).

	Dry weight (g/tree)					Biomass partitioning (%)			
	Wood	**Shoots**	**Leaves**	**Roots**	**Total**	**Wood**	**Shoots**	**Leaves**	**Roots**
T1	533.2 c	365.4 c	891.6 bc	848.1 c	2638.3 c	20.2	13.8	33.8	32.1
T2	994.0 ab	587.6 ab	1182.4 ab	1174.8 b	3938.7 ab	25.2	14.9	30.0	29.8
T3	766.9 bc	557.1 abc	883.5 c	1100.3 bc	3307.9 bc	23.2	16.8	26.7	33.3
T4	1061.5 a	691.2 a	1192.5 a	1592.4 a	4537.7 a	23.4	15.2	26.3	35.1
T5	801.8 b	491.9 bc	1255.0 a	1383.0 ab	3931.8 ab	20.4	12.5	31.9	35.2

FIGURES

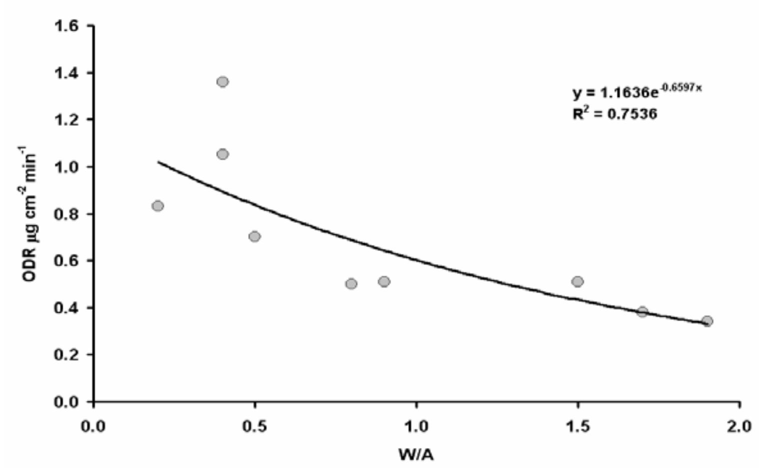

Figure 1. Relationship between the soil water-to-air ratio and the oxygen diffusion rate (ODR) in the soil. Mean W/A and ODR values of each of the five soils during each season (2005/2006 and 2006/2007, Table 5) were used in the regression analysis. W/A = 0.4 (T4) had a mean ODR of 1.05 µg cm^{-2} min^{-1} for both season, thus graphic appear to have 9 point instead of 10.

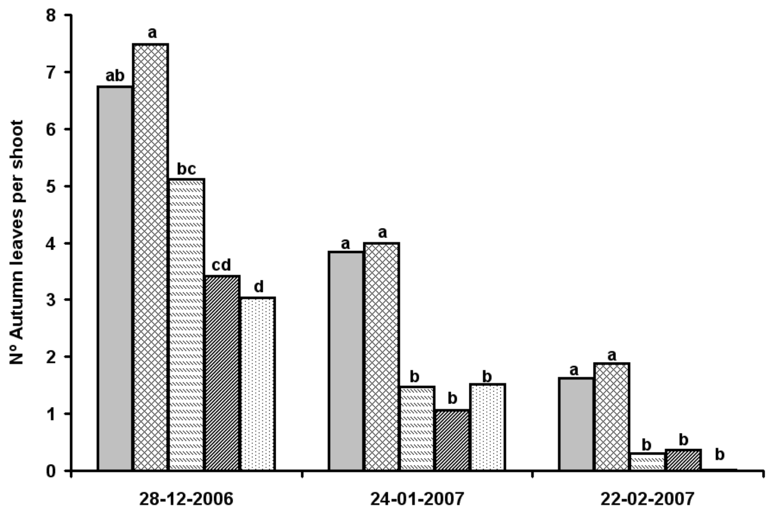

Figure 2. Number of leaves remaining on autumn shoots by December, January and February of 2006/2007. Bars indicate means (n=5). Different letters indicate significant differences (Waller-Duncan Test, $P \leq 0.1$). T5, T4, T3, T2, T1.