

# Chapter 1

## Introduction

Avocado (*Persea americana* Mill.) production is one of the fastest growing agricultural industries in Chile; its area has increased 22.256 hectares during the past 10 years. Currently, 39.303 hectares in Chile are planted with 'Hass' avocado trees, making Chile third among nations in the amount of land area planted with this crop (INE-ODEPA, 2007; Waissbluth and Valenzuela, 2007). After Mexico, Chile today is currently the second largest exporter of avocado fruit in the world, accounting for 18.8 percent of the total world's exports (Schwartz *et al.*, 2007).

Commercial avocado production in Chile has expanded to areas with poorly drained soils presenting low oxygen partial pressure conditions over significant periods of time throughout the year. In many of these areas, irrigation management is difficult because new plantations are often placed on slopes of hills. Poorly aerated soils combined with irrigation design and management problems can limit avocado fruit production and quality due to an excess of water in the root zone. It is well known that 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. An excess or lack of water

during growth limits avocado fruit production and quality, particularly if stress occurs between spring and the beginning of summer (Whiley *et al.*, 1988a; 1988b). Therefore, in order to get adequate yield and fruit quality, proper irrigation management in avocado orchards is necessary (Lahav and Whiley, 2002).

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 greater limitations to aerobic metabolism of the roots can be expected (Letey, 1961; Blokhina *et al.*, 2003). Fine textured soils have a greater capacity for water retention than coarser textured soils. Therefore, a slight error in the irrigation rate or frequency, due to a lack of understanding of soil properties, may lead to continuous anaerobic conditions in the root zone (Letey, 1961; Blokhina *et al.*, 2003). Previous studies (Ferreyra *et al.*, 2007) have shown that the air content is a soil property that affects avocado water relations. Ferreyra *et al.* (2007) reported that low soil air contents (5% to 18%) affected negatively stomatal conductance (gs). The same authors established that soil air content lower than 17% restricts the oxygen diffusion rate to less than  $0.2 \mu\text{g cm}^{-2} \text{min}^{-1}$  and that macroporosity values were highly correlated with soil  $\text{O}_2$  and  $\text{CO}_2$  content. However soil water-to-air ratio is another way to integrate the soil physical and water management. An understanding of the relationship between the soil water-to-air ratio and avocado physiology, growth and yield should provide valuable insight for irrigation management of this crop in different soils, particularly in areas with poor soil aeration.

There has been a considerable amount of research on the effects of flooding on leaf gas exchange of West Indian avocado cultivars, mainly in porous limestone soils native to southern Florida. In these soils, the presence of *Phytophthora* root rot greatly exacerbated reductions of net photosynthesis, stomatal conductance, and transpiration caused by flooding (Ploetz and Schaffer, 1987, 1992; Schaffer and Ploetz, 1989; Schaffer *et al.*, 1992; Schaffer, 1998). However, studies of the effects of poor soil aeration on 'Hass' avocado trees have focused primarily on tree growth and leaf and root mineral nutrition (Stolzy *et al.*, 1967; Labanauskas *et al.*, 1968) and there is little information on the effects of flooding or poor soil aeration on leaf gas exchange of 'Hass' avocado trees. Also, little is known also about techniques for enhancing oxygen content in the soil. In Chile, to reduce problems caused by root asphyxia in avocado orchards, trees are often planted on raised beds to increase the volume of soil occupied by roots and to improve drainage of irrigation and rain water. However, the use of raised beds can result in significant soil erosion of steep hillside orchards, and also can cause serious problems of water obstruction when heavy rains wash soil from raised beds into canals and streams. Increasing soil gas concentrations, especially the oxygen content of the rhizosphere to improve root metabolism has been poorly studied. An alternative technique for injecting oxygen into the soil is the use of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), which has been successfully utilized as an oxygen source for *in situ* remediation in a saturated aquifer (Zappi *et al.*, 2000).

Flooding or root hypoxia is an abiotic stress that causes several responses in plants, which range from stomatal closure and a reduction in CO<sub>2</sub> assimilation, to

leaf abscission and plant death (Schaffer *et al.*, 1992; Drew, 1997; Kozlowski, 1997). Drought is also a limitation to productivity, and plant responses to this stress condition include reductions in xylem turgor, inhibition of leaf expansion, leaf abscission, and stomatal closure, which results in reductions of stomatal conductance ( $g_s$ ). Many studies have suggested that abscisic acid (ABA) is the major chemical root-to-shoot stress signal that is associated with stomatal closure in drought-stressed plants (Davies and Zhang, 1991; Davies *et al.*, 2005). In avocado, in response to drought,  $g_s$  begins to decline when stem water potential (SWP) reaches -0.4 MPa and continues to decline until stomatal closure occurs at SWP of -1.0 to -1.2 MPa (Sterne *et al.*, 1977; Bower, 1978; Scholefield *et al.*, 1980; Whiley *et al.*, 1988a). However, the effect of flooding on stomatal closure and the relationship among stomatal closure, xylem water potential, and stomatal conductance in response to flooding have not been reported.

Plants can adjust to drought or root hypoxia without detectable changes in leaf water status due to osmotic and/or stomatal adjustment (Davies and Zhang, 1991). Thus, the stomata may receive a signal indicating soil water status independently from leaf water status. It has been postulated that changes in the concentrations of abscisic acid (ABA) generated in the roots and transported to the leaves induces stomatal closure (Hartung *et al.*, 2002; Sauter *et al.*, 2001; Düring *et al.*, 1997; Zhang *et al.*, 1987). However, Düring *et al.* (1997) found that a decrease of  $g_s$  was correlated with an accumulation of the ABA synthesized in leaves and not in the roots. Furthermore, much higher (100x) ABA concentrations than those found in the roots are necessary to decrease stomatal conductance (Munns and King,

1988). In *Pinus sylvestris* L. subjected to gradual soil desiccation, closing of stomata was observed before the arrival of ABA from the roots; thus, ABA translocation from root to leaves could be too slow to account for the stomatal closure in response to water stress, and closing of stomata was apparently not mediated by increases of ABA concentration in roots (Perks *et al.*, 2002). Thus, it is likely that in response to soil water deficit, ABA is neither the only nor the principal signal from the roots to the stomata (Munns and King, 1988).

The presence of fast conducting signals generated in the roots and conducted through the vascular system to the leaf has been identified in several plant species. These signals can either be in the form of action potentials or variation potentials. An action potential elicits an all or nothing response when the stimulus reaches a critical threshold, whereas a variation potential varies in amplitude and range depending on the intensity of the stimulus (Dziubinska *et al.*, 2003; Fromm and Lautner, 2007; Davies and Stankovic, 2007). It has been postulated that electric signals could be a communication pathway between roots and shoots when plants are water stressed (Fromm and Fei, 1998). For example, stimulation of roots of *Salix viminalis* by the application of nutrients, hormones or changes in pH caused changes in the electrical potential difference between roots and leaves; these changes were followed by a modification of leaf respiration and photosynthetic rates within three minutes after treatments were applied, indicating that changes in the electrical signals may reflect or be a direct mechanism of communication between roots and the leaves (Fromm and Eschrich, 1993). Similarly, osmotic stress suddenly applied to maize (*Zea mays*) roots generated an electrical potential

difference between the roots and the leaves and a concomitant decrease in  $g_s$  (Fromm and Fei, 1998). It has been shown in fava bean (*Vicia fava minor*) that thermal stimulation (scorching) of leaves results in the generation of electrical signals transmitted to distant, non-stimulated leaves which enhance its ethylene emission from those non-stimulated distant leaves (Dziubinska *et al.*, 2003). In response to drought in maize (*Zea mays*), an electrical signal (action potential) was transmitted from the root to the shoot via the phloem (Fromm and Fei, 1998; Grams *et al.*, 2007). This signal initiated stomatal closure and resultant decreases in  $g_s$  and net  $CO_2$  assimilation.

The mechanisms for reductions of  $g_s$  in avocado trees as a result of drought or soil hypoxia have not been elucidated. It is possible that changes in root to shoot electrical voltage differences in response to drought or soil hypoxia may directly trigger stomatal closure which results in reduced  $g_s$  or may indirectly affect stomatal closure by triggering changes in leaf ABA concentrations. Also, factors that stimulate leaf abscission in avocado trees in response to root hypoxia have not been elucidated, but increased ethylene concentrations presumably plays a role and concentrations of ethylene or its precursor, 1-aminocyclopropane-1-carboxylic acid (ACC), may be affected by root-to-shoot electrical signals generated in response to root hypoxia.

## Hypothesis

1) Water relations and leaf gas exchange characteristics of avocado trees are influenced by soil water-to-air ratios. The lower the air content and oxygen diffusion in the soil, the earlier and greater the reduction in leaf gas and water exchange.

2) The injection of hydrogen peroxide ( $H_2O_2$ ) into the soil can counterbalance the negative physiological effects caused by low air content in soil for avocado plants.

3) Differences in electrical voltage between roots and leaves (electrical signal transmission) is a possible physiological mechanism whereby a signal is transmitted from the root to leaves to regulate stomatal opening and closing in response to water stress or root hypoxia.

## Objectives

### General objective

To determine physiological, growth and developmental responses of avocado (*Persea americana* Mill.) to different soil water-to-air ratios and to determine the possible mechanism by which a signal from the root is transmitted to the shoot to stimulate a physiological stress response to water stress or root hypoxia.

## Specific objectives

- 1) To compare the physiological, morphological and growth responses of avocado trees to different soil air conditions.
  
- 2) To determine the effect of hypoxia on plant water status, leaf gas exchange and biomass of avocado.
  
- 3) To determine if the negative effects of low air content in soil on physiology, vascular anatomy and growth of avocado trees can be mitigated by the injection of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) into the soil.
  
- 4) To determine the possible physiological mechanisms involved in root-to-leaf signal transmission that triggers stomatal closure as response to soil drying and root hypoxia.

## References

- Blokhina O, Virolainen E, Fagerstedt KV. 2003. Antioxidants, oxidative damage and oxygen deprivation stress: a review. *Annals Bot* 91:179-194.
- Bower JP. 1978. The effects of shade and water relations in the avocado cv. Edranol. *South African Avocado Growers' Assoc Res Rep* 2: 59-61.
- Davies E, Stankovic B. 2007. Electrical signals, the cytoskeleton, and gene expression: a hypothesis on the coherence of the cellular responses to



- environmental insult. In: Baluska B., Mancuso S., Volkmann D (eds) Communication in Plants, Neuronal Aspects of Plant Life. Springer-Verlag, Heidelberg, Germany, pp 309-320.
- Davies WJ, Zhang J. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annu Rev Plant Physiol Mol Biol* 42: 55-76.
- Davies WJ, Kudoyarova G, Hartung W. 2005. Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought. *J Plant Growth Reg* 24: 285-295.
- Drew MC. 1997. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. *Ann. Rev. Plant Physiol Plant Mol Biol* 48:223-250.
- Düring H, Loveys BR, Dry PR. 1997. Root signals affect water use efficiency and shoot growth. *Acta Hort* 427:1-14.
- Dziubinska H, Filek M, Koscielniak J, Trebacz K. 2003. Variation and action potentials evoked by thermal stimuli accompany enhancement of ethylene emission in distant non-stimulated leaves of *Vicia faba minor* seedlings. *J Plant Physiol* 160: 1203-1210.
- Fromm J, Eschrich W. 1993. Electric signals released from roots of willow (*Salix viminalis* L.) change transpiration and photosynthesis. *J Plant Physiol* 141: 673-680.
- Ferreira R, Sellés G, Celedón J, Maldonado P, Torres A, Gil P. 2007. Effect of the soil air content in the water status and development of avocado. Proc. Sixth World Avocado Congress, Viña del Mar, Chile.

- Fromm J, Fei H. 1998. Electrical signaling and gas exchange in maize plant in drying soil. *Plant Sci* 132: 203-213.
- Fromm J, Lautner S. 2007. Electrical signals and their physiological significance in plants. *Plan Cell Environ* 30:249-257.
- Grams TE, Koziolok C, Lautner S, Mayssek R, Fromm J. 2007. Distinct roles of electric and hydraulic signals on the reaction of leaf gas exchange upon re-irrigation in *Zea mays* L. *Plant Cell Environ* 30: 79-84.
- Hartung W, Sauter A, Hese E. 2002. Abscisic acid in the xylem: where does it come from, where does it go to? *J Exp Bot* 53: 117-124.
- INE-ODEPA, 2007. VII Censo Nacional Agropecuario y Forestal. [www.censoagropecuario.cl/noticias/07/11/13112007.html](http://www.censoagropecuario.cl/noticias/07/11/13112007.html)
- Kozlowski TT. 1997. Response of woody plants to flooding and salinity. *Tree Physiol Monograph* 1:1-29.
- Labanauskas CK, Stolzy LH, Zentmyer GA, Szuskiewicz TE. 1968. Influence of soil oxygen and soil water on the accumulation of nutrients in avocado seedlings (*Persea americana* Mill.). *Plant and Soil* 29:391-406.
- Lahav, E, A.W. Whaley. 2002. Irrigation and mineral nutrition. In: *Avocado: Botany, Production and Uses*, AW Whaley, B Schaffer and B N Wolstenholme (eds). CABI Publishing, Wallingford, UK.
- Letey J. 1961. Aeration, compaction and drainage. *California Turfgrass Culture* 11:17-21.
- Munns R, King R. 1988. Abscisic acid is not the only stomatal inhibitor in the transpiration stream of wheat plants. *Plant Physiol* 88:703-8.

- Perks M, Irvine J, Grace J. 2002. Canopy stomatal conductance and xylem sap abscisic acid (ABA) in mature Scots pine during a gradually imposed drought. *Tree Physiol* 22:877-83.
- Ploetz RC, Schaffer B. 1987. Effects of flooding and Phytophthora root rot on photosynthetic characteristics of avocado. *Proc. Fla. State Hort. Soc.* 100:290-294.
- Ploetz, R.C., Schaffer B. 1992. Effects of flooding and Phytophthora root rot on net gas exchange of avocado in Dade County, Florida. *Proc. Second World Avocado Congress.* p. 111-117.
- Sauter A, Davies WJ, Hartung W. 2001. The long-distance abscisic acid signal in the droughted plant: the fate of the hormone on its way from root to shoot. *J Exp Bot* 52:1991-7.
- 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 RC. 1989. Net gas exchange as damage indicator for Phytophthora root rot of flooded and non-flooded avocado. *HortScience* 24:653-655.
- Schaffer B, Whiley AW. 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 PC, Ploetz RC. 1992. Responses of fruit trees to flooding. *Hort. Reviews* 13:257-313.

- Scholefield PB, Walcott JJ, Kriedemann PE, Ramadasan A. 1980. Some environmental effects on photosynthesis and water relations of avocado leaves. *California Avocado Soc Yrbk* 64:93-105.
- Schwartz M, Ibarra K, Adam CW. 2007. Indicadores de competitividad de la industria exportadora chilena de palta (aguacate). *Proc. Sixth World Avocado Congress*, Viña del Mar, Chile.
- Sterne RE, Kaufmann, MR, Zentmyer GA. 1977. Environmental effects on transpiration and leaf water potential in avocado. *Physiol Plant* 41: 1-6.
- Stolzy LH, Zentmyer GA, Klotz LJ, Labanauskas CK. 1967. Oxygen diffusion, water, and *Phytophthora cinnamomi* in root decay and nutrition of avocados. *Proc. Amer. Soc. Hort. Sci.* 90:67-76.
- Waissbluth R, Valenzuela J. 2007 Determinación del porcentaje mínimo de materia seca para autorizar la cosecha de paltas cv. Hass para ser exportadas. *Proc. Sixth World Avocado Congress*, Viña del Mar, Chile.
- Whiley AW, 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.
- Whiley AW, Chapman KR, Saranah JB. 1988a. Water loss by floral structures of avocado (*Persea americana* Mill.) cv. Fuerte during flowering. *Aust J Agric Res* 39: 457-467.
- Whiley AW, Saranah JB, Cull BW, Pegg KG. 1988b. Manage avocado tree growth cycles for productivity gains. *Queensland Agric J* 114: 29-36.

Zappi M, White K, Hwang HM, Bajpai R, Qasim M. 2000. The fate of hydrogen peroxide as an oxygen source for bioremediation activities within saturated aquifer systems. *J. Air Waste Manage. Assoc.* 50:1818-1830.

Zhang J, Schurr U, Davies WJ. 1987 Control of stomatal behavior by abscisic acid which apparently originates in the roots. *J Exp Bot* 38:1174-81.