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EFFECTS OF SOIL OXYGEN DEFICIENCY ON AVOCADO (*PERSEA AMERICANA* MILL.) TREES

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Introduction

In many parts of the world, avocado (*Persea americana* Mill.) tree growth and productivity are negatively impacted by low soil oxygen content. Low soil oxygen content can be the result of poor soil drainage, soil compaction, or flooding of the root zone (Drew, 1997; Fukao and Bailey Serres, 2004; Beigenberger, 2003). Lack of soil oxygen is often referred to as hypoxia or anoxia. Hypoxia refers to the reduction of oxygen below optimal levels and occurs in poorly drained soils or during periods of short-term flooding. Anoxia refers to a complete lack of oxygen that generally occurs in soils after periods of prolonged flooding. All plants are able to survive brief periods of anoxia (Drew, 1996). However, under natural conditions, plant roots rarely are exposed to sudden anoxia. Rather there is a gradual transition from normoxia (an adequate supply of oxygen in the soil) to hypoxia and then to anoxia. Therefore, the gradual transition from normoxia to anoxia provides an opportunity for plants to acclimate to low soil oxygen levels before conditions become lethal to the plant (Drew, 1997). Adaptive mechanisms to increase plant survival under conditions of low soil oxygen have been documented for some subtropical and tropical fruit trees. These include the development of adventitious roots for increased oxygen absorption (e.g., mango; Larson et al., 1993c), development of aerynchyma tissue in the stem for increased internal oxygen transport (e.g., annonas; Nunez-Elisea et al., 1999) and the development of hypertrophic (swollen) stem lenticels which function to increase oxygen absorption and for the excretion of potentially toxic metabolites resulting from anaerobic metabolism in the roots (e.g., mango; Larson et al., 1993a,b,c).   However, to the author's knowledge, none of these anatomical or morphological adaptations have been reported for avocado trees in response to low soil oxygen levels.

In fruit trees, the length of survival is dependant on the species and sometimes the cultivar. For grafted trees, such as avocado, flooding sensitivity is primarily due to the rootstock and not the scion (Schaffer et al. 1992). This provides a particularly difficult situation for both avocado trees grown on clonally propagated rootstocks with little to no tolerance to hypoxic or anoxic soil conditions (e.g., the situation in California) and for avocado trees grown on seedling rootstocks which may show heterogeneous responses within the seedling population to low soil oxygen (e.g., the situation in Florida).

 It was originally thought that damage to avocado trees from excessive water in the root zone was due to increased destruction of roots by the oomycete, *Phytophthora cinnamomi* Rands., the causal organism for Phytophthora root rot (Zentmyer, 1947, 1963,

1980). It was suggested that excess water in the root zone of avocado provides a medium in which the motile spores of *P. cinnamomi* can be readily disseminated and infect plant roots (Zentmyer and Bingham, 1956). However, later studies in California (Stolzy et al., 1967) and Florida (Ploetz and Schaffer, 1987, 1989; Schaffer and Ploetz, 1989) showed that soil flooding and the resultant hypoxia or anoxia can significantly damage avocado roots, even in the absence of *P. cinnamomi*. Also, observations of the clumped pattern of avocado tree mortality in poorly drained soils in Region V of Chile indicated that tree damage was due to root hypoxia or anoxia and not Phytophthora root rot (P. Gil, 2006, personal communication).

Effect of Low Soil Oxygen Content on Avocado Physiology, Growth, and Yield

Avocado is considered a flood-sensitive tree species with physiological responses occurring shortly after soils become waterlogged (Schaffer et al., 1992; Schaffer and Whiley, 1994). Root hypoxia or anoxia of avocado usually results in inhibition of leaf expansion, a reduction in root and shoot growth, moderate to severe stem and leaf wilting, leaf abscission, and root necrosis (Schaffer and Whiley, 2002). The earliest effects of low soil oxygen content on plants is an alteration of root metabolism when roots of flood-sensitive plants such as avocado are subjected to hypoxic or anoxic soil conditions. When the oxygen concentration in soil is low, there is a reduction in energy (ATP) production during root respiration. In plant cells, both aerobic and anaerobic respiration begin biochemically with glycolysis, where glucose is oxidized to pyruvic acid by a series of reactions. During the conversion of glucose to pyruvic acid, a net total of 2 ATP molecules are produced. After glycolysis, respiration will proceed to aerobic respiration if sufficient oxygen is available or anaerobic respiration (also called fermentation) if oxygen is lacking. There are two types of fermentation, defined by the end product of the chemical reaction; lactic acid fermentation, where the end product is lactic acid and alcohol fermentation where the end products are CO_2 and ethanol. Both types of fermentation do not produce ATP molecules. In the second and third stages of aerobic respiration called the Krebs cycle and the electron transport chain respectively, up to 36 ATP molecules can be produced. Therefore, aerobic respiration produces significantly more energy in the form of ATP molecules than anaerobic respiration, where a total of only 2 ATP molecules are produced during glycolysis.

Root cell death due to a rapid exposure to anoxic conditions has been associated with acidification of the cytoplasm, referred to as cytoplasmic acidosis (Drew, 1997; Felle, 2005; Vartapetian and Jackson, 1997). Sudden exposure to anaerobic conditions results in lactic acid fermentation and the build up of lactic acid which reduces the pH of the cell. After a short time (about 20 minutes), the pH in the cell will stabilize due to a shift from lactic acid fermentation to alcohol fermentation. Thereafter, a second phase of cytoplasmic acidosis occurs due to the loss of protons from the cell vacuole into the cytoplasm. Drew (1997) indicated that under anoxic conditions, cytoplasmic acidosis is the primary determinant of plant cell death. However, Vartapetian and Jackson (1997) and Felle (2005) indicated that there is evidence that cytoplasmic acidosis may not be the primary determinant of cell death as a result of anoxia and still requires further investigation.

The production of potentially toxic metabolites in the roots as a result of anaerobic respiration in anoxic roots has been implicated in plant cell death as a result of soil

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anoxia. Initially, ethanol produced in the roots during alcohol fermentation in anaerobic soil and transported through the xylem was thought to be toxic to the plant (Drew, 1997; Vartapetian and Jackson 1997).   However, it is now realized that the ethanol concentration required to damage plant tissue would be extremely high and ethanol readily diffuses out of plant tissue to the surrounding solution where it is diluted or metabolized by microorganisms (Drew et al., 1997).   The immediate biochemical precursor to ethanol, acetaldehyde, is considerably more toxic to plant cells than ethanol and may be a factor in plant cell death in response to anaerobic root metabolism (Drew, 1997; Vartapetian and Jackson 1997) . The conversion of acetaldehyde to ethanol is catalyzed by the enzyme, alcohol dehydrogenase (ADH).   A significant amount of research with herbaceous plants has shown that increased ADH activity improves a plant's tolerance to anoxia, possibly be avoiding a build-up of acetaldehyde by enhancing its conversion to ethanol under anaerobic conditions.

Metabolic responses to low soil oxygen concentrations and plant metabolic adaptations to root-zone hypoxia and anoxia have been thoroughly reviewed by Malcolm (1997) and Geigenberger (2003). However, studies of the effects of low soil oxygen on plant metabolism have focused primarily on herbaceous plants and published reports are lacking on metabolic responses of fruit trees, including avocado, to low soil oxygen levels.

The phytohormone, ethylene, has been implicated in a wide range of plant responses and/or adaptations to root zone hypoxia and anoxia including development of aerenchyma and hypertrophic lenticels in stems, development of adventitious roots, and leaf epinasty (Drew, 1997; Morgan and Drew, 1997; Vartapetian and Jackson, 1997; Visser and Voesenek, 2004).   Hypoxia generally increases ethylene production, stimulating anatomical or morphological adaptations to low soil oxygen including development of hypertrophic stem lenticels and aerenchyma formation. Anoxia, on the other hand, decreases ethylene formation due to the requirement of oxygen for the conversion of aminocyclopropane-1-carboxylic acid (ACC) to ethylene, the final step in the biosynthesis of ethylene (Yang et al., 1980). Although ethylene has been shown to have an important role in flooding symptomotology of several herbaceous and some woody plants, trying to establish a relationship between the symptomotology of fruit trees exposed to low soil oxygen and ethylene concentration has had mixed results (Schaffer et al., 1992) and more work is needed to clearly characterize the role of ethylene in responses of fruit trees, including avocado, to soil hypoxia and anoxia.

In addition to metabolic and hormonal effects, other effects of root-zone hypoxia and anoxia on fruit trees include electrolyte leakage (Schaffer et al, 1992) and root mortality. In studies with seedling trees of 'Mexicola' avocado, low soil oxygen content due to poor soil drainage combined with Phytophthora root rot caused significant root decay. There was also considerable root mortality in saturated soil with low levels soil oxygen, even in the absence of Phytophthora root rot (Stolzy et al., 1967). Thus a direct growth effect of root zone hypoxia or anoxia on avocado trees is root mortality. Shoot damage as a result of low soil oxygen is an indirect effect due to less efficient root metabolism, a loss of root function (e.g., water uptake), or a reduction of root biomass.

In hypoxic or anoxic soils, one of the earliest detectable changes in avocado trees is a decline in net CO_2 assimilation which is generally accompanied by decreases in stomatal conductance, transpiration, and intercellular partial pressure of CO_2 in the leaves

(Ploetz and Schaffer, 1989; Schaffer and Ploetz, 1989). In south Florida soils, the reduction in leaf gas exchange due to flooding was greatly exacerbated by Phytophthora root rot (Fig. 2). The temporal separation between these physiological events has not been determined, which would be useful for determining if flood-induced reductions in photosynthesis in avocado are due to stomatal or non-stomatal factors (Schaffer et al., 1992).
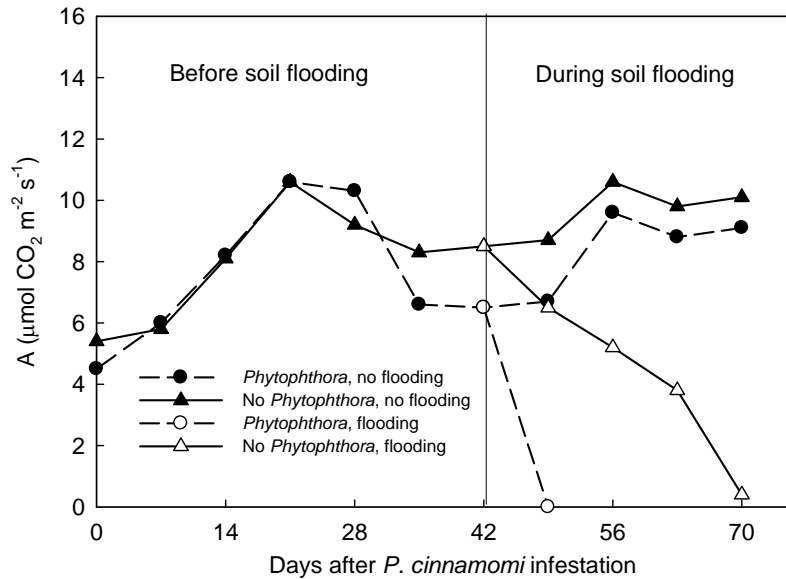
Figure 1. Effects of soil flooding and *Phytophthora cinnamomi* on net CO_2 assimilation (A) of 'Simmonds' avocado scions on 'Waldin' rootstock growing in a calcareous soil. Forty two days after infesting soil with *P. cinnamomi*, infested and non-infested plants were flooded. Redrawn from Ploetz and Schaffer, 1989.

The effects of flooding on net gas exchange of avocado trees can be greatly increased by Phytophthora root rot (Ploetz and Schaffer, 1987, 1989; Schaffer et al., 1992, 2006; Schaffer and Whiley; 2002; Whiley and Schaffer, 1994). Trees in porous calcareous soil that was pre-inoculated with *P. cinnamomi* showed large reductions in net CO_2 assimilation, stomatal conductance and transpiration within one week after roots were inundated (Ploetz and Schaffer, 1989) and all infected, flooded trees died within two weeks of continuous flooding. Non-infected avocado trees in a porous, calcareous soil that were flooded did not show a significant decrease in leaf gas exchange until more than 45 days after roots were flooded (Ploetz and Schaffer, 1989). Also, for avocado trees in calcareous soils in containers, 25-30% root necrosis from pre-inoculating plants with Phytophthora root rot resulted in almost a complete inhibition of photosynthesis after soils were flooded for one week. However, in the same soil, nonflooded trees were able to sustain up to 90% root necrosis with only a 65% decrease in net CO_2 assimilation (Schaffer and Ploetz, 1989; Schaffer et al., 1992; Schaffer and Whiley, 2002; Whiley and Schaffer, 1994). In the porous limestone soils of south Florida, hypoxia or anoxia results from flooding due to heavy rains and a high watertable.

In contrast, in soils where hypoxia results from slow or inadequate soil drainage, hypoxia alone in the absence of Phytophthora root rot may result in a rapid decline in leaf gas exchange of avocado. For example, in recent studies in a potting media with a high organic matter content, avocado trees not infected with *P. cinnamomi* showed a decline net CO_2 assimilation, stomatal conductance and transpiration within 11 days after roots were flooded (P. Gil and B. Schaffer, 2006, unpublished data; Fig. 2).
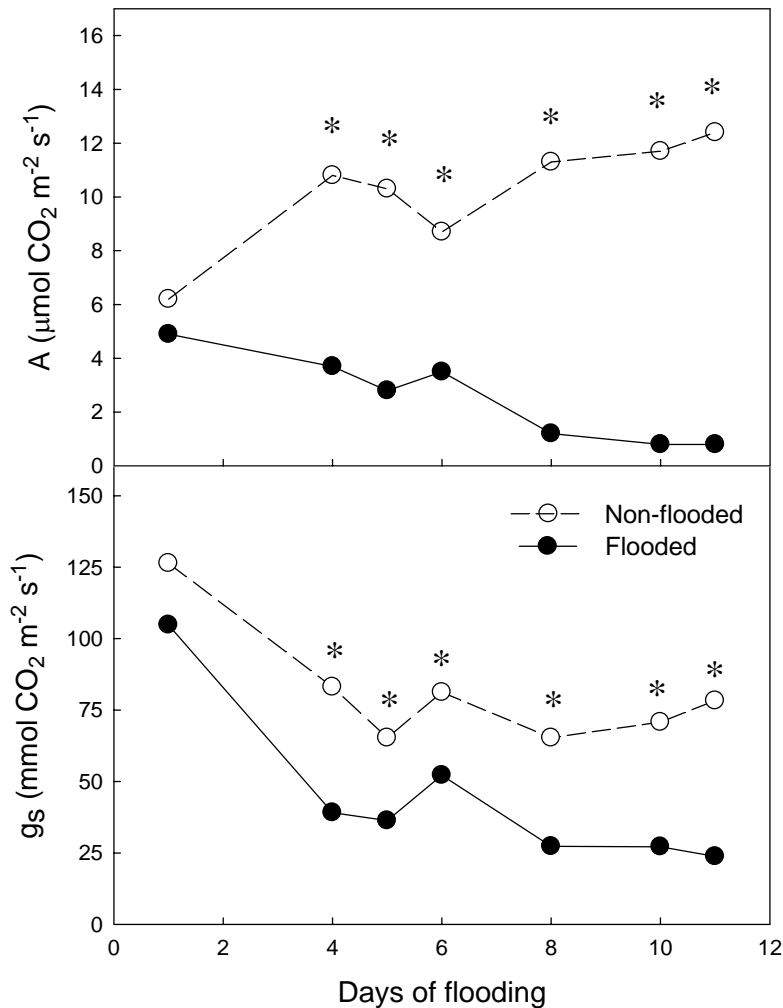

Figure 2. Effects of soil flooding on net CO_2 assimilation (A) and stomatal conductance of CO_2 of 'Beta' avocado scions on 'Waldin' rootstock growing in a potting mix with a high organic matter content. Asterisks indicate a significant difference between flooded and non-flooded plants ($P \leq 0.05$). From P. Gil and B. Schaffer, 2006, unpublished data.

The reductions in transpiration caused by flooding in avocado trees not infected with *P. cinnamomi* are most likely the result of reduced stomatal conductance rather than a hydraulic effect because there was no significant difference in leaf water potential

between flooded of avocado trees not infected with *P. cinnamomi* and non-flooded avocado trees that were not infected with the pathogen (Schaffer et al., 1992; Fig. 3).
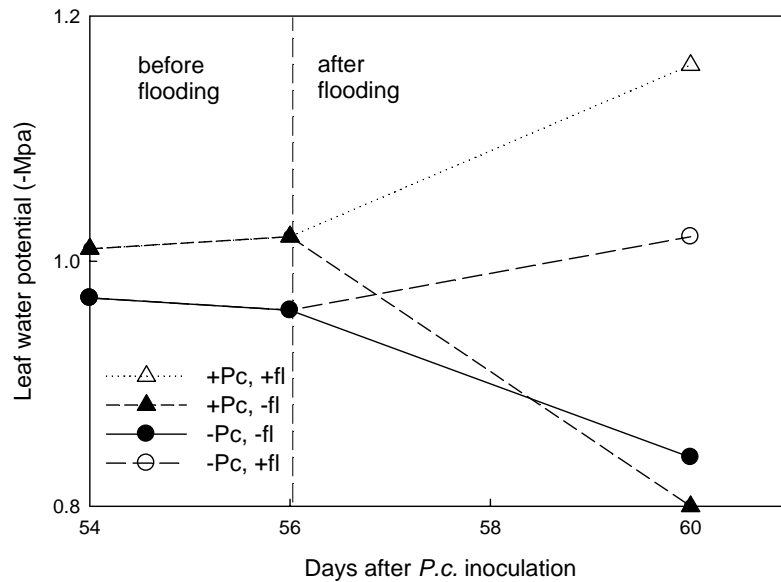
Figure 3. Leaf water potential of avocado ('Simmonds' scions on 'Waldin' seedling rootstock) 56 days after planting in soil infested (+Pc) or non-infested (-Pc) with *Phytophthora cinnamomi* and either flooded (+fl) or non-flooded (-fl). Leaf water potentials were determined immediately prior to flooding and four days after flooding. Different letters indicate significant differences (P $\leq$ 0.05). Redrawn from Schaffer et al., 1992.

Low soil oxygen content affects the nutrient content of avocado trees. In 'Hass' on Duke or Topa Topa rootstock, leaf concentrations of N, P, K Ca, Mn and Cu were lower in avocado trees grown in soil with 2% oxygen than in trees grown in soil with 21% oxygen (Labanauskas et al., 1978; Slowick et al., 1979). In contrast, low soil oxygen content resulted in increased leaf concentration of Fe in 'Hass' avocado (Labanauskas et al., 1978) and Fe and Mn in seedling trees of 'Mexicola' avocado (Stolzy et al., 1967), which was attributed to Fe and Mn being reduced in hypoxic soil to forms that are readily absorbed and metabolized by plants (Stolzy et al., 1967, Labanauskas et al., 1978). Concentrations of N, K, and Mg in the roots were lower in avocado trees grown in soil with 2% oxygen than in soil with 21% oxygen. However, concentrations of Na, Cl and Zn in avocado roots were higher in plants in soil with the low oxygen content then in soil with the higher oxygen content (Labanauskas et al., 1978).

In some avocado productions areas throughout the world, many growers have observed tree and/or crops losses in their avocado orchards due to poor soil aeration or flooding. For example, flooding of orchards from heavy rains, tropical storms or hurricanes caused many avocado growers in Florida to make insurance claims because of significant tree and/or yield losses (J.H. Crane, 2006, personal communication). However, there is little published information quantifying the effects of poor soil aeration

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on avocado crop yield. In a 3-year-old 'Hass' and 'Ettinger' avocado orchard in Israel, standing rainwater in troughs between plating ridges resulted in 40 percent fewer 'Hass' fruit on trees next to the flooded troughs compared to trees next to nonflooded troughs, although yields of 'Ettinger' were too low for comparisons between wet and dry sites (Zamet, 2001). Collection of detailed avocado tree growth and yield data along with information about the oxygen content of the soil in orchards with slow drainage or flood-prone soil would provide valuable information for selection of avocado germplasm tolerant of low soil oxygen concentration.

Possible Solutions for Growing Avocado Trees in Poorly Aerated Soils

Perhaps the best long-term solution for growing avocado trees in poorly drained or flood-prone soils is the development of flood-tolerant rootstocks. However, most avocado rootstock selection and development has focused on developing Phytophthora-resistant or salt-tolerant rootstocks and there has been little research on identifying, selecting, or developing avocado rootstocks solely for their ability to tolerate poorly aerated soil conditions (Ben-Ya'acov and Michelson, 1995). In poorly-drained soils where *P. cinnamomi* is prevalent, the development of Phytophthora-resistant avocado rootstocks should help alleviate flood-induced stress due to the strong interaction between flooding and Phytophthora root rot. Moderately Phytophthora-resistant avocado rootstocks such as 'Duke 7' and 'Martin Grande' have been developed in California (Coffey and Guillemet, 1987; Pegg et al., 2002) and current efforts are underway to select Phytophthora-resistant rootstocks in Florida (Ploetz et al., 2002; R. Ploetz, University of Florida and R. Schnell, 2006, personal communication) and Australia (A.W. Whiley, 2006, personal communication). Selection of such rootstocks should aid in increasing productivity and reducing tree mortality in poorly drained soils where *P. cinnamomi* is prevalent.

In a review of avocado rootstocks in 1995, it was stated that "avocado production has almost disappeared from most sites where aeration is limited, and it seems that soils rather than rootstocks should be selected to overcome this problem" (Ben-Ya-acov and Michelson, 1995). However due to the rapid expansion of avocado production in some countries such as Chile in recent years, it is inevitable that production will expand into areas with poorly aerated soils. Therefore, there is a need for selection and/or development of avocado rootstocks that can tolerate poorly aerated soil conditions in addition to the on-going selection and development of Phytophthora-resistant rootstocks.

During the past ten years there have been considerable advance in understanding molecular genetics related to plant flood tolerance (Dennis et al., 2000; Fukao and Baily-Serres, 2004). For example, a gene variant has just been identified that promotes flood tolerance in rice by promoting the production of ADH and ethylene. When this gene is inserted into flood-sensitive rice cultivars, they survive up to two weeks completely submerged in water (Xu et al., 2006). However, similar molecular genetics advances for avocado are a long-way off at best. There have been attempts to improve tolerance of avocado trees to poor soil aeration and Phytophthora root rot through molecular breeding. Some species in the genus *Persea* other than avocado are tolerant of poorly-drained soils and Phytophthora root rot but are not sexually or graft compatible with *Persea americana* (Witjaksono, 1997). For example, *Persea borbonia* a species native to southern Florida and is moderately tolerant to soil flooding and also resistant to Phytophthora root rot.

Persea borbonia is not sexually or graft compatible with *P. americana*. However, there has been some success in somatic hybridization of *P. borbonia* with *P. americana* (Litz et al., 2005, Witjaksono, 1997). *Persea borbonia* and *P. americana* have been successful hybridized by protoplast fusion, with resulting plantlets developed in tissue culture. However, this is at best a long-range solution because plants have yet to be screened for flood-tolerance and Phytophthora root rot resistance, and even resistant plants would need to be field-tested for several years to determine if they have characteristics suitable for horticultural production.

Ideally, planting sites for avocado should be selected that have well-drained soil with no history of flooding. However, in areas that are prone to flooding due to heavy rains, tropical storms, or hurricanes, planting trees on beds or mounds will help to minimize tree damage and mortality from low soil oxygen. In flood-prone areas of southern Florida it is recommended that homeowners plant individual avocado trees on mounds 0.61 to 0.91 meter high and 1.21 to 3.03 meters in diameter (Crane et al., 2005) and that commercial growers plant trees on beds that are 0.91 meter high and 0.91 to 1.5 meters wide (Balerdi et al., 2003).

For new potential planting sites that may be prone to flooding or poor soil drainage, pre-planting techniques such as deep soil tillage or dragging (where a plow-like implement is pulled through the soil profile at about one meter below the soil profile) and/or installation of a tile drainage system may enhance soil aeration and water drainage.

If avocado roots experience sudden hypoxia from soil a result of sudden heavy rains, tropical storms or hurricanes, removing a portion of the tree canopy after the flood-water subsides may save trees that would otherwise be severely damaged from soil hypoxia or anoxia (Balerdi et al., 2003). As stated earlier, after brief periods of soil hypoxia or anoxia due to flooding, the metabolic activity of the roots is reduced because anaerobic metabolism is less energy efficient than aerobic metabolism (Drew, 1997). Removing a portion of the canopy will reduce total leaf water loss and transpirational demand on the stressed roots. Removing a portion of the canopy after flood waters subside will prevent that the remaining leaves from desiccating and dying and reduce the overall stress to the tree (Balerdi et al., 2003).

In orchards planted in soils that are easily compacted or are naturally slow to drain, proper irrigation management is critical for maintaining adequate soil aeration and preventing tree damage and mortality. Irrigation frequency and timing must be fine tuned in slow draining avocado orchards to prevent soil hypoxia and maintain adequate soil moisture. In poorly drained soils, soil water monitoring, possibly coupled with phytomonitoring techniques can help to fine-tune irrigation management and maintain soil water content below saturation but at an adequate level for optimum plant growth and productivity. Simple soil monitoring devices such as tensiometers are relatively inexpensive and can help growers to maintain soil water content below the water saturation point where the soil environment has become hypoxic. However, tensiometers must be maintained and checked periodically which is time consuming. In south Florida, the use of multi-sensor capacitance probe systems (i.e., EnviroScan, Sentek Sensor Technologies, PTY, Australia) has been useful for continuously monitoring soil water content in avocado orchards to maintain soil water content below the saturation point but at an adequate level for good plant growth (Nuñez-Elisea et al., 2001; Zekri et. al., 1999).

However, these devices are relatively expensive. In Israel (Ton et al., 2003) and Chile (Gurovitch and Saggé, 2005), the use phytomonitoring techniques such as dendrometers to measure small changes in stem diameter as a result of changes in irrigation, in combination with soil water monitoring devices, has been useful for fine-tuning irrigation scheduling in avocado orchards and may be helpful for managing irrigation to reduce the potential for soil hypoxia. Regardless of the technique used, basing irrigation scheduling on quantitative measures of soil water content and/or plant water status may be critical for providing sufficient water and adequate root aeration in avocado orchards that are planted in poorly-drained or flood-prone soils.

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