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ENVIRONMENTAL REGULATION OF PHOTOSYNTHESIS IN AVOCADO TREES – A MINI-REVIEW

B. Schaffer[1] and A.W. Whiley[2]

[1]Tropical Research and Education Center, University of Florida, 18905 SW 280 Street, Homestead, Florida, 33031

[2]Sunshine Horticultural Services Pty Ltd, 287 Dulong Road, Nambour 4560, Australia

SUMMARY

An important aspect of orchard management is to manipulate and train trees to optimize photosynthesis within the canopy. Knowledge of the impact of environmental factors, such as light, temperature, humidity, flooding, salinity and elevated atmospheric CO_2 concentrations on photosynthesis of avocado trees provides information that can be applied to canopy management and plant selection for specific environments. This mini-review summarizes the current knowledge of the impact of environmental factors on avocado photosynthesis and its implications for crop management plant selection.

Key Words: Avocado, *Persea americana*, photosynthesis, environment.

INTRODUCTION

In avocado (*Persea americana* Mill.) trees, increasing carbohydrate partitioning to flowers and fruit provides a challenge for orchard management, as the tree has a natural vegetative bias resulting in a greater allocation of photoassimilates to shoot growth than to reproductive organs (Whiley et al., 1988b; Wolstenholme, 1990; Schaffer and Whiley, 2002). This vegetative bias, coupled with the relatively short leaf longevity (for a subtropical fruit tree species) results in rapid production of short-lived leaves and increased shading within the canopy that reduces the number of well-lit terminal shoots capable of flowering (Wolstenholme and Whiley, 1999). Leaves of ‘Booth-8’ avocado trees exhibit a net carbon lost (determined by summing photosynthesis and respiration) during the first 21 days of development when they reached 72% of their full expansion (Schaffer et al., 1991). Similarly, there was a net carbon gain for ‘Hass’ avocado leaves only after they reached 80% of full expansion (Whiley, 1990). Thus, the rapid turnover of leaves results in photosynthetically productive leaves being shading by younger leaves, which are sinks rather than sources for photoassimilates. This makes it difficult to train avocado canopies for optimum light interception and carbon assimilation. Thus, a key to improving productivity of avocado is the development of management strategies aimed at increasing the photosynthetic potential and realization by increasing light penetration within the canopy.

A key factor in developing efficient management strategies for avocado orchards is to maximize photosynthetic efficiency within canopies. To do this an understanding of impact of environmental factors on the regulation of photosynthesis is very helpful. The objective of this mini-review is to briefly summarize the current knowledge of the impact of environmental factors on photosynthesis of avocado.

Responses to Light

A key factor to avocado canopy management is to select smaller trees with better overall light interception so that a high percentage of leaves within the canopy are above the light saturation point for photosynthesis (Whiley and Schaffer, 1994; Wolstenholme and Whiley, 1999; Whiley, 2002). To achieve this goal an understanding of irradiance effects on photosynthesis is essential.

In an orchard the light saturation point for photosynthesis of mature 'Hass' avocado trees was determined at a photosynthetic photo flux (PPF) of 1110 µmol quanta m^{-2} s^{-1}

(Whiley, 1994), much higher than the PPF of 400-500 µmol quanta m^{-2} s^{-1} reported for container-grown 'Fuerte' trees (Scholefield et al., 1980). The light saturation of potted 'Edranol' trees was determined at a PPF of 660 µmol quanta m^{-2} s^{-1} (Bower, 1978). The higher light saturation point observed for potted 'Edranol' trees compared to the 'Fuerte' was presumably a result of 'Edranol' photosynthesis being measured in the whole canopy rather than on a single leaf basis as was done with 'Fuerte'. Thus mutual shading of 'Edranol' leaves undoubtedly resulted in a higher light intensity necessary to saturate all of the leaves in the canopy (Schaffer and Whiley, 2002). The much greater light saturation point observed for field-grown trees may have been a result of root restriction in container-grown trees, which limited net photosynthesis to about 7 µmol CO_2 m^{-2} s^{-1} compared to 23 µmol CO_2 m^{-2} s^{-1} for trees in an orchard (Schaffer et al., 1999; Whiley and Schaffer, 1994; Schaffer and Whiley, 2002). Low net photosynthetic rates [7-10 µmol CO_2 m^{-2} s^{-1} (Schaffer et al., 1987; 1991)]of orchard trees in Florida compared to orchard trees elsewhere was attributed root restriction in extremely hard Florida soils, which mimicked root restriction of container-grown trees (Schaffer et al., 1994; Schaffer et al., 1999).

Avocado presumably evolved as a small gap-colonizing, understorey forest species (Whiley and Schaffer, 1994; Wolstenholme and Whiley, 1999; Wolstenholme, 2002). Several physiological attributes, such as a low light compensation (the PPF level at which net photosynthesis equals 0) and the rapid "turn-over" of relatively short-lived leaves reflect avocado's putative center of origin (Whiley and Schaffer, 1994; Wolstenholme and Whiley, 1999; Wolstenholme, 2002). The light compensation point of approximately 10 mmol quanta m^{-2} s^{-1} for sun-lit leaves in a 'Hass' orchard (Whiley, 1994; Whiley and Schaffer, 1994) would provide an adaptive advantage for harvesting light for photosynthesis in a low-light understorey environment. Additionally, in its native habitat, the vegetative bias due to frequent replacement of short-lived leaves allowed a competitive advantage for maximizing photosynthesis by frequent replacement of excessively shaded leaves. However, in an orchard situation, this vegetative bias results in increased shading of the canopy (Wolstenholme and Whiley, 1999).

Despite a considerable amount of research on management practices for avocado, compared to temperate fruit crops there has been relatively little improvement in tree size control either through breeding or canopy management (Whiley and Schaffer, 1994; Schaffer and Whiley, 2002). Also, light interception within avocado canopies over time has not been sufficiently quantified (Schaffer and Whiley, 2002). Tree spacing, tree thinning, and mechanical or hand pruning techniques must maximize light interception and utilization within avocado canopies. Often a combination of these techniques must be employed to reduce excessive shading, either by over-crowding of trees or excessive vegetative growth within canopies. A study of the dynamics of light interception in a growing orchard and its impact on yield, would contribute significantly to more informed orchard management (Whiley and Schaffer, 1994).

Responses to Temperature

There is a difference in temperature responses among the 3 ecological races (Mexican, Guatemalan and Lowland) of avocado (Krezdorn, 1970; Whiley and Schaffer, 1994). Studies and observations on growth and anatomical damage indicated that Mexican race cultivars are the most cold-tolerant, whereas Guatemalan race cultivars are intermediate in cold tolerance and Lowland (or West Indian) race cultivars are the least cold-tolerant (Schaffer and Whiley, 2002). Although comparisons of photosynthetic responses to temperature among races have not been reported, it stands to reason that the photosynthetic responses would most likely parallel anatomical damage and growth responses to temperature.

Photosynthetic rates of avocado may be significantly affected by slight fluctuations in temperature. For the 'Edranol', a Guatemalan hybrid cultivar (Newett et al., 2002), in containers, the optimum temperature range for photosynthesis was 20-24°C (Bower et al., 1978). Within ± 5°C of this temperature range, net photosynthesis declined by about 20%. For container-grown 'Fuerte' trees (a Mexican x Guatemalan hybrid; Newett et al., 2002), maximum net photosynthetic rates were observed at temperatures of 28-31°C and that rate decline by about 33% at temperatures below 15°C or above 40°C (Scholefield et al., 1980). In an orchard in Queensland, Australia the maximum photosynthetic rate of 'Hass', a predominantly Guatemalan race cultivar with some Mexican genes (Newett et al., 2002), decreased from 19.0 µmol CO_2 m^{-2} s^{-1} during autumn, when minimum daily temperatures were greater than 14°C, to 10.9 µmol CO_2 m^{-2} s^{-1} in winter when minimum temperatures were less than 10°C (Whiley et al., 1999). It was also observed that that temperatures lower than 10°C during winter significantly reduced apparent quantum yield of leaves of field-grown 'Hass' avocado trees from 0.055 µmol CO_2 μmol^{-1} quanta to 0.034 µmol CO_2 μmol^{-1} quanta (Whiley, 1994).

Chlorophyll fluorescence can be used to measure plant stresses caused by temperature extremes. Photoinhibitory damage to Photosystem 2 (PS II) can be quantified by measuring a decrease in the variable to maximum chlorophyll fluorescence (FV/Fm) ratio (Björkman, 1987, Demmig and Björkman, 1987). Whiley (1994) reported that the *Fv/Fm* ratios of avocado were 0.79-0.81 when minimum temperatures in an orchard were above 12.9°C. However, when minimum temperatures dropped below 10°C, the mean *Fv/Fm* ratio was 0.41, indicating cold-induced damage to PS II.

In addition to measuring cold-induced photoinhibitory damage in avocado, chlorophyll fluorescence has been used to indicate the presence of a heat acclimation mechanism in avocado leaves that prevents photo-oxidative damage to PS II over a moderate increase in temperature from 21-35°C (Havaux and Lannoye, 1987).

Responses to Humidity

The leaf water status of fruit crops is strongly tied to the diurnal fluctuations in the evaporative demand of the environment. Thus, leaf water status varies much more in perennial fruit crops than in annual crops, and leaf water stresses may occur under high evaporative demand even if soil water content is adequate (Flore and Lakso, 1989). The effect of humidity on plant photosynthesis is often a result of the effect of vapor pressure deficit. (VPD) on stomatal conductance although there can be non-stomatal photosynthetic responses to changing VPD (Schultze, 1986). Reports of the effects of humidity on avocado have linked decreased photosynthetic responses to decreased stomatal conductance as a result of increasing VPDs (Sterne et al., 1977; Bower et al., 1978; Scholefield et al., 1980). For leaves of 'Fuerte' avocado, stomatal conductance was high shortly after sunrise when VPD was low but decreased significantly during the middle part of the day when VPD was much higher (Whiley et al., 1988a). However, net photosynthesis was not determined in that study. With 'Edranol' trees in containers, however, a 50% reduction in stomatal conductance due to increased VPD resulted in a concomitant 50% decrease in net photosynthesis (Bower et al., 1978).

Responses to Drought

In recent studies, Neuhaus (2003) determined that reduced photosynthesis in avocado as a result of soil water deficit stress is primarily due to reductions in stomatal conductance. Additionally, he determined that stomatal conductance was a more reliable early indicator of water stress in avocado than measurements of leaf water content, leaf water potential, or growth variables.

In avocado, stomatal conductance begins to decline when leaf water potential is ª 0.4 MPa, and continues to decline until stomatal closure occurs at leaf water potentials of 1.0 - 1.2 MPa (Sterne et al., 1977; Bower, 1978; Scholefield et al., 1980; Whiley et al., 1988a). This decline in stomatal conductance is accompanied by a concomitant decline in net photosynthesis (Bower, 1978; Ramadasan, 1980). When water stress is alleviated, leaf water potential has been observed to recover more slowly than net photosynthesis (Ramadasan, 1980) and stomatal conductance (Sterne et al., 1977; Bower et al., 1978; Ramadasan, 1980).

Neuhaus (2003) observed younger leaves of water-stressed plants had less control over water loss and a lower rate of net photosynthesis than older leaves resulting in lower water use efficiency for stressed young leaves. Based on that, Neuhaus (2003) concluded that avocado leaves are more sensitive to water stress during "flushing" when there are a high percentage of young leaves.

Responses to Flooding

Avocado is considered a flood-sensitive species with physiological responses occurring shortly after soils become waterlogged (Schaffer et al., 1992). In flooded soils, the decline in net photosynthesis of avocado is generally accompanied by decreases in stomatal conductance and intercellular partial pressures of CO_2 in the leaves (Ploetz and Schaffer, 1989; Schaffer and Ploetz, 1989). However, the temporal separation between these physiological events has not been defined, 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).

In Krome very gravely loam soil, flooding avocado trees with root systems that were 20% damaged (necrosis) from previous Phytophthora root rot, resulted in almost a complete inhibition of photosynthesis. However, in this same soil non-flooded trees were able to sustain up to 50% root damage from Phytophthora without a decrease in net photosynthesis and up to 90% of the root system damaged with only 65% decrease in photosynthesis (Schaffer and Ploetz, 1989). Thus, although avocado is considered a flood-sensitive species, the negative impact of flooding is greatly exacerbated by the presence of Phytophthora root (Ploetz and Schaffer, 1987, 1988, 1989; Schaffer and Ploetz, 1987; Schaffer et al., 1992). Therefore, in poorly drained soils, flooding-induced inhibition of photosynthesis of avocado may be reduced by properly managing orchards to control Phytophthora root rot.

Responses to Atmospheric CO_2 Concentration

There have been very few reports on the effects of short- or long-term atmospheric CO_2 enrichment on tropical fruit crops, including avocado. Short-term (5 min) exposure of 'Hass' avocado leaves to increasing atmospheric CO_2 concentrations resulted in net photosynthesis increasing asymptotically as the ambient CO_2 concentration increased until maximum photosynthesis occurred at atmospheric CO_2 to concentrations of 1350-1470 µmol CO_2 µmol^{-1}. There are no reports in the literature on the effects of long-term exposure to increased atmospheric CO_2 on photosynthesis of avocado. However, growing 'Hass' avocado trees for 6 months in a CO_2-enriched environment (atmospheric CO_2 concentration = 600 µmol mol^{-1}) resulted in significantly more dry matter accumulation compared to plants that were grown in a near ambient atmospheric CO_2 concentration (350 µmol mol^{-1}). Although photosynthesis was not measured in that study, it is safe to assume that increased growth in the enhanced CO_2 environment resulted from increased net photosynthetic rates due to constant exposure to elevated CO_2 levels.

Photosynthetic efficiency was higher, although the actual photosynthetic rate was lower in callus-derived, avocado shoot cultures and plantlets grown in ambient atmospheric CO_2 than for cultures and plantlets grown in an enhanced CO_2 environment (Witjaksono et al., 1999). Thus, increasing atmospheric CO_2 concentration during plantlet and shoot development resulted in increased growth. Therefore increasing atmospheric CO_2 concentration during development is a useful technique proliferating enhanced growth of cultured avocado plants

Responses to Salinity

Avocado is considered a salt-sensitive species (Kadman, 1963, 1964; Downton, 1978) and there have been some efforts to select rootstocks for salinity tolerance (Haas, 1950; Embleton et al., 1961; Oster and Arpaia, 1992). Mickelbart and Arpaia (2002) observed that increasing salinity in the root zone from 1.5 to 6.0 dS·m^{-1} resulted in up to a 23% decrease in net photosynthesis of one-year-old 'Hass' avocado trees grafted on 'Thomas', 'Duke 7' (Mexican race cultivars) or 'Toro Canyon' (a Mexican x Lowland race hybrid) rootstocks. There were no consistent differences among cultivars with respect to the impact of salinity on net photosynthesis. Differences in sensitivity to salinity among cultivars were reflected in different growth reductions and leaf necroses among cultivars in response to elevated salt concentrations in the rhizosphere rather than by photosynthetic responses.

CONCLUSIONS

A key factor in developing efficient management strategies for avocado orchards is to maximize photosynthetic efficiency within canopies. Recent orchard studies indicate that under non-stress conditions, the net photosynthetic rate of avocado is considerably higher that what earlier research with potted trees indicated. The continuous growth and rapid turn-over of short-lived leaves in avocado results in a vegetative bias that favors potential shading of photosynthetically efficient source leaves by younger leaves which are sinks for photoassimilates for about 40 days. However, except for spring when shoot growth is synchronised by flowering, not all of the tree flushes at the same time thus, much of the canopy remains well lit. Nevertheless, avocado management should focus on tree shaping that allows a greater proportion of leaves to receive sufficient light to attain their maximum photosynthetic potential. The considerable difference in photosynthetic responses to temperature among the 3 avocado races and the fact that avocado trees can hybridize freely among races (Whiley and Schaffer, 1994), creates a potential for breeding and/or selecting avocado cultivars for almost any environment within the temperature tolerance range for the species. Also, photoinhibition of avocado leaves due to low temperatures can be quickly determined using chlorophyll fluorescence techniques. Thus the potential exists to screen avocado selection for sensitivity to cold temperatures by using chlorophyll fluorescence on young plants or possibly even detached leaves in temperature chambers.

Avocado photosynthesis is sensitive to high evaporative demand and low soil moisture. However, these responses are primarily a result of reductions in stomatal conductance. In fact, stomatal conductance is an excellent early indicator of soil moisture stress in avocado and provides an excellent “tool” for irrigation scheduling in avocado orchards (Neuhaus, 2003).

Avocado trees are sensitive to high salinity and the sensitivity varies among species. Although photosynthetic of avocado is reduced in response to salinity stress, there are not sufficient differences among cultivars to use photosynthesis as an indicator of a cultivars ability to tolerate high salinity.

Enhancing the atmospheric CO_2 concentration reduces the photosynthetic efficiency (amount of carbon fixed per CO_2 molecule) of mature avocado trees and in-vitro plantlets derived from tissue culture. Despite the reduced photosynthetic efficiency elevating the atmospheric CO_2 concentration increases the actual photosynthetic rate due to constant exposure to saturating CO_2 concentrations. This has implications for global climate change, indicating the avocado may thrive under elevated atmospheric CO_2.

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