REVIEW: PHOTOSYNTHESIS OF AVOCADO

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ABSTRACT

To increase avocado yield, the maintenance of high photosynthetic capacity for the production of flowering wood each year is required. A failure to achieve good starch reserves going into flowering is considered to contribute to maintaining an alternate bearing cycle. The accumulation of starch is likely to be linked to photosynthetic activity at all times of the year, most especially during winter when low temperatures could be reducing photosynthesis to very low rates. Under the cool temperatures of a New Zealand winter the photosynthetic apparatus of avocado leaves may experience damage from chilling. A greater understanding of the underlying mechanisms of avocado ecophysiology will allow tree management practices to be developed that increase the accumulation of carbohydrate from photosynthesis. This review summarizes information published on avocado photosynthesis from around the world.

Keywords: *gas exchange, light saturation, stomatal conductance*

INTRODUCTION

The avocado industry in New Zealand comprises of about 3,640 ha of trees 5 years old or older (New Zealand Avocado Growers' Annual Report, 2008). The largest growing area is along the Bay of Plenty coastline, predominantly between Waihi and Te Puke where 64% of the total crop is planted. The Far North and Whangarei regions contribute most of the remaining crop with minor plantings in the rest of New Zealand (South Auckland, Gisborne, Taranaki). The 'Hass' cultivar accounts for almost all avocado fruit exported with exports worth $48.5 million in the 2007/08 season (New Zealand Avocado Growers' Annual Report, 2008). New Zealand avocados are mostly exported to Australia with small volumes heading to the United States, South Korea and Japan. The total New Zealand avocado crop is less than 1% of world production.

The New Zealand avocado industry has set a goal to achieve an average yield of 15 tonnes/ha. Land area planted in productive avocado trees (5 years and older) has increased rapidly from 946ha in 1997 to 3,640ha in 2007/08 (New Zealand Avocado Growers' Annual Report, 2008). Yield per hectare more than doubled between 1996 and 2001, from 3.65 tonnes/ha to 8.86 tonnes/ha, due in part, to the industry wide adoption of phosphorus acid injections as a treatment and preventative of *Phytophthora cinnamomi* root rot. However, yields have not increased significantly since 2001, while alternate bearing has become entrenched on many orchards. To increase profitability to growers and other industry stakeholders, per hectare yields need to increase without a reduction in fruit quality. To achieve increases in yields requires both a greater understanding of avocado physiology and the development of refined methods of avocado production.

Avocado yield can be affected by orchard practices, pest pressure, environmental conditions and tree life history. Low fruit set and poor fruit retention is of concern to the industry as poor yields impose limits on the profitability of individual orchards. In general, the maintenance of high photosynthetic capacity and overall plant carbon assimilation is seen as being central to meeting any yield targets. The best practice recommendations of the New Zealand avocado industry are that avocado growers should aim to maintain robust photosynthetically active leaves and develop trees with sufficient resources to sustain heavy fruit sets to maturity. The availability of good starch reserves going into flowering is considered important for fruit set and retention.

Problems such as alternate bearing may be linked to either excessive demand for carbohydrate or to insufficient carbohydrate reserves (Dixon *et al.*, 2008) that could be expected to be exacerbated by poor photosynthetic capacity during winter.

Surprisingly, considering that avocados have been domesticated for centuries, there appears to be little information about the photosynthetic abilities of avocado leaves. This is particularly so for New Zealand where there have been few studies of leaf gas exchange in orchard conditions. Problems with the photosynthetic processes might be anticipated because the plant is sub-tropical in origin and is thought to be close to its southern climatic limit where it is grown in New Zealand. With an increased understanding of the underlying mechanisms of avocado ecophysiology, improved tree management practices could be used to increase photosynthetic performance. This review aims to provide a summary of the information currently known about the photosynthetic performance of avocados from the scientific literature.

General description of *Persea americana*

The avocado tree (*Persea americana* Mill.) belongs to the *Lauraceae* family of which only one other genus, *Cinnamomum* is cultivated. The avocado tree is evergreen, forming a dome canopy up to 30m tall (Scora *et al.*, 2002). Shoot growth occurs in flushes alternating with root flushes. Leaves are arranged spirally along the stem and are variable in both shape and size. The leaf blade is elliptic to lanceolate, ovate or obovate in shape and a smooth entire leaf edge. The veins and midrib are prominent on both the dark green upper waxy surface and the light green hairy (glaucous) lower surface. There are no stomata on the upper surface (Micklebart *et al.*, 2000). Petioles are smooth and green between 3 and 15cm in length. The leaves are often red and soft to touch when young (Whiley and Schaffer, 1994). Avocado trees extend anchoring roots down 3 to 4 metres in deep soils and a shallow root system (feeder roots) provides the primary source of nutrient and water uptake (Whiley and Schaffer, 1994). The feeder roots have no root hairs. The fruit set of avocados is considered to be highly inefficient with estimates of 100 to 300 flowers required to set each fruit (Cameron *et al.*, 1952). Avocado flowering is complex with flowers opening as functionally female or male at different times and flowering branches that can be determinate or indeterminate where a new shoot emerges from the apical compound inflorescence.

Origins of *Persea americana*

Avocado varieties present today are the product of thousands of years of human cultivation. The commercial avocado *Persea americana*, is classified into three subspecies or botanical varieties (also known as horticultural races); *Persea americana americana* or West Indian, *Persea americana gautemalensis* or Guatemalan and *Persea americana drymifolia* or Mexican . The latter two subspecies carry names which are consistent with their accepted original locations. *Persea americana americana* or West Indian sub-species, however, is believed to have originated in the tropical lowlands along the pacific coast of Central America and was moved to the West Indies after the Spanish conquest (Bergh, 1985, 1992; Storey *et al.*, 1986) .

There appears to be little information about the environment of the avocado in its natural habitat. The tree is typical of medium altitude cloud forests in the tropics and sub-tropics with populations existing in highlands of Central America (Wolstenholme and Whiley, 1999). The climate in the presumed native habitat of avocado is summarised in Table 1. The temperature profile of the Bay of Plenty, centred on Tauranga, is easily within the range of temperatures found in the home range of avocado trees. The annual mean temperature for Tauranga was warmer than the highest site in Mexico but with the range between the coldest and warmest months being greater (9.5°C versus 5.9°C) in the Bay of Plenty. The mean temperature of the coldest month was slightly greater at Tauranga than the highest Mexican site but 4.2°C lower than the lowest Mexican site.

Table 1. Microclimate of selected natural avocado growing environments and Tauranga, New Zealand. Data from Praloran (1970) and Mackintosh (2000).

Location	**Altitude (m)**	**Rainfall (mm)**	**Mean temperature (°C)**		
			Annual	**Warmest month**	**Coldest month**
Mexico	1399	1562	17.5	19.8	14.2
	2675	665	12.8	15.6	9.7
Guatemala	1502	1394	19.6		
	2350	671	14.9		
Tauranga[1]	10	1799	15.0	19.9	10.4

[1] Temperature collated from 1994 to 2007 at the Tauranga weather station, on orchard temperatures will generally be greater due to the effective use of shelter.

Table 2. Thickness of the layers in a 'Hass' leaf (Chartzoulakis *et al*., 2002).

Layer	**Dimensions (µm)**
Upper cortex	14.9
Palisade layer 1	72.8
Palisade layer 2	34.0
Spongy mesophyll	65.3
Lower cortex	14.0
Total	203.1

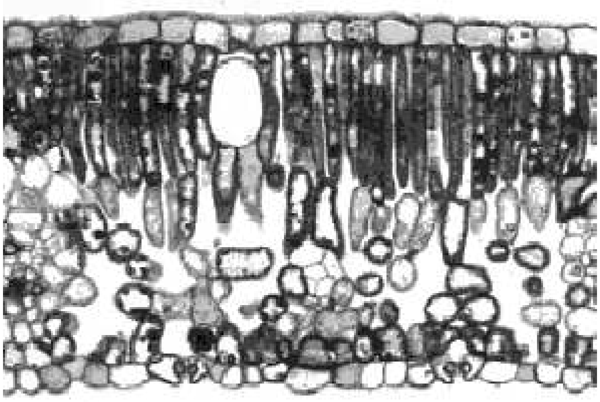

Table 3. Some examples of maximal CO_2 exchange rates (A_{max}) and stomatal conductance.

Authors	A_{max} (µmol m^{-2} s^{-1})	Stomatal conductance (mmol m^{-2} s^{-1})	Comments
(Mickelbart and Arpaia, 2002)	7 - 8		California Container grown
(Heath *et al*., 2005)	Up to 20	300	California Orchard grown
(Schaffer, 2006)	10 - 12		Queensland
(Whiley *et al*., 1999)	19		Queensland
(Schaffer *et al*., 1991)	9		Queensland
(Kimelmann, 1979)	6		Israel
(Heath *et al*., 2005)	20		New Zealand
(Heath *et al*., 2005)	9	150	

These data suggest that if there is a temperature limitation to the performance of avocado at the Bay of Plenty site then it is most likely to be in the winter.

Leaf Adaptation

Wolstenhome and Whiley (1999) have characterised the leaves of avocado as being low sun/low stress according to the classification of Smith *et al.* (1989). Such leaves are large, laminar broadleaf, relatively thin (less than 400 µm), with a single palisade layer held horizontal and medium to low maximal photosynthetic potential (Table 2). The leaf characteristics describe a tree considered to be a small gap coloniser or under story tree within forests with exposure to fluctuating light intensity (cloudy to full sunlight) that can potentially damage leaf function. In such a situation the avocado leaf cannot be completely adapted to either shade or full sunshine and must be able to handle large and rapid changes in its environment.

Leaf Gas Exchange

There have been a small number of detailed studies into the gas exchange of the avocado leaf, the main findings of which are summarised in Table 3.

Many of the early measurements of CO_2 exchange rates were made on plants grown in containers. The plants in containers appear to have suffered from root restriction and had substantially lower CO_2 exchange rates than trees in the orchard (Whiley *et al.*, 1999). Under optimal conditions CO_2 exchange rates have been measured as high as 15 to 20 µmol m^{-2} s^{-1}. The single data point available from New Zealand (Heath *et al.*, 2005) of 20 µmol m^{-2} s^{-1} is estimated from a response curve of CO_2 exchange rates to CO_2 concentration.

Avocado leaves have often been referred to as shade leaves because of their low light saturation level for photosynthesis of around 20 to 33% of full sunlight (Whiley, 1994). These studies, however, were on container grown plants and studies of orchard trees suggest that saturation can be at much higher photon flux density (PFD) of around 1100 µmol m^{-2} s^{-1} or over 50% of full sunlight (Wolstenholme and Whiley, 1999). This suggests that avocados are closer to being sun adapted plants. It is generally accepted that there is a strong linear or near linear link between stomatal conductance and net photosynthetic rate (Heath *et al.*, 2005). It has not been determined if stomatal conductance controls net photosynthesis or is controlled by photosynthesis in avocado leaves.

Leaf Age and Photosynthetic Capacity

The avocado is an evergreen tree with a leaf longevity of 10 to 12 months in Australia and South Africa (Wolstenholme and Whiley, 1999). This is a relatively short leaf life span compared to other evergreen fruit trees such as citrus and mango (Whiley and Schaffer, 1994). Leaf growth in New Zealand occurs during two distinct flushes, one in spring and the other in summer/autumn with most leaves abscising during the subsequent year's growth (Dixon *et al.*, 2006). As leaves grow and age, physiological changes alter the photosynthetic performance as the leaf passes from a sink to a source of photoassimilates.

In leaves of field grown 'Booth-8' and 'Peterson' cultivars net CO_2 assimilation increased until about 42 days after bud-break and then levelled off (Schaffer *et al*., 1991). Maximum CO_2 assimilation was approximately 5 µmol m^{-2} s^{-1} for 'Booth-8' and 8 µmol m^{-2} s^{-1} for 'Peterson'. The increase in CO_2 assimilation as leaves age was not due to changes in stomatal conductance as this remained relatively constant with leaf age. Whole leaves continue to be a sink for photoassimilates until about 40 days after bud break (Schaffer and Whiley, 2003). For field grown 'Hass' leaves in California, maximum CO_2 assimilation occurred 50 days after bud-break corresponding to when leaf colour developed to dark green (Liu *et al.,* 1999). For individual leaves, net CO_2 assimilation became positive after 17 days when the previous season's leaves were at 50% of their previous maximum net CO_2 assimilation. Whole tree net CO_2 gain was achieved 20 days after new leaves fully expanded (Liu *et al.,* 1999). Although older leaves play an important role in carbohydrate supply (Liu *et al.,* 1999) during the shoot flush the new leaves shade the older leaves reducing overall carbohydrate gain across the tree (Schaffer and Whiley, 2003).

Water Relations and Photosynthetic Performance.

During drought conditions and in unirrigated orchards, soil water potential can become sufficiently reduced so as to limit photosynthesis by reducing stomatal conductance. Avocado plants can be stressed by moderately dry soil conditions (Bower, 1978a). Stomatal conductance was not reduced until soil moisture potential fell below -40kPa in South Africa (Bower *et al.*, 1977) and stomata become completely closed by about -80kPa soil moisture potential. Container grown 'Fuerte' and 'Hass' plants with a wet irrigation regime and irrigation at -0.5MPa had reduced stomatal conductance and photosynthetic performance in the water stressed trees by 5 days after withholding water (Chartzoulakis *et al.*, 2002). By day 12, photosynthesis of the leaves had reduced by 27% in 'Fuerte' and 35% in 'Hass' (Chartzoulakis *et al.*, 2002). 'Fuerte' leaves recovered to the pre-water stress photosynthetic rate and stomatal conductance 2 days after irrigation, while in 'Hass' plants values remained 20% lower than the controls after irrigation (Chartzoulakis *et al.*, 2002). Stomatal conductance and photosynthetic rate can have a very rapid response to water stress as demonstrated on 2 year old potted 'Fuerte' plants where 5 hours after discontinuing irrigation, maximum net photosynthesis reduced from 3.6 µmol m^{-2} s^{-1} to 1.3 µmol m^{-2} s^{-1} (Ramadasan, 1980). The decline in photosynthetic rate and stomatal conductance was related in a linear manner during the period of water stress (Chartzoulakis *et al.*, 2002). The decline in photosynthesis corresponded with an almost 3 fold decrease in stomatal conductance. Stomatal conductance increased by 50% one hour after irrigation was restored and net photosynthesis had returned to pre-drying levels after 4 hours. It should be noted that these studies used potted plants that would have had a low volume of exploitable soil. Avocado trees in orchards have a much greater volume of soil from which to extract water and can tolerate water restrictions more effectively than potted plants through maintaining a high level of stomatal conductance through high root hydraulic conductivity and elastic leaf mesophyll cells (Sharon *et al.*, 2001) .

Based on the observations reported above, root rot due to *Phytophthora cinnamomi* infection is likely to reduce net CO_2 assimilation by limiting stomatal conductance through reduced water uptake ability (Schaffer and Ploetz, 1989). Therefore maintaining good root health is important to sustain good photosynthetic productivity. For example, in potted 'Simmonds' avocado trees with Phytophthora root rot necrosis of = 20%, net CO_2 assimilation and stomatal conductance decreased when the plants were flooded (Schaffer and Ploetz, 1989). In contrast, the plants that were not flooded, net CO_2 assimilation and stomatal conductance was only reduced when root rot necrosis was greater than 65% (Schaffer and Ploetz, 1989). When measuring photosynthetic performance of avocado leaves root health must be considered as a confounding factor.

Relationship between temperature and photosynthesis

Optimum Temperature

The three ecological races of avocado have been observed to have different temperature tolerances where the Mexican race cultivars are the most cold-tolerant, Guatemalan race cultivars are intermediate and West Indian race cultivars are the least cold-tolerant (Krezdorn, 1970; Whiley and Schaffer, 1994). There are no published comparisons of photosynthetic responses to temperature between the races but it is likely that photosynthetic performance of each race would be similar to the cold damage and growth responses differences to temperature (Schaffer and Whiley, 2002) .

Photosynthetic rates of avocado leaves have been reported to be affected by slight fluctuations in temperature. For potted 'Edranol' trees the optimal temperature range for photosynthesis was 20-24°C (Bower, 1978b). Within plus or minus 5°C of this temperature range net photosynthesis declined by about 20%. For container-grown 'Fuerte' trees, maximum net photosynthetic rates were at temperatures of 28-31°C (Whiley and Schaffer, 1994) and that rate declined by about 33% at temperatures below 15°C or above 40°C (Scholefield *et al.*, 1980). In field grown 'Hass' avocado trees, temperatures lower than 10°C during winter reduced apparent quantum yield of leaves from 0.055 µmol CO_2 per μmol^{-1} quanta to 0.034 µmol CO_2 per μmol^{-1} quanta (Whiley, 1994). In warm climates such as Florida and California, peak summer temperatures limit photosynthetic performance. Net photosynthesis was reduced to near zero in Californian grown 'Hass' trees when leaf temperature was between 35°C and 40°C; this correlated strongly with a reduction in stomatal conductance (Liu *et al.*, 2002). Photosynthesis was found to be maintained at 33% of maximum levels for temperatures above 40°C (Scholefield *et al.*, 1980; Whiley and Scheffer, 1994). Such temperatures are very rare in New Zealand avocado orchards therefore upper temperature limits to photosynthesis are unlikely to be of concern for 'Hass' trees growing in New Zealand.

Low Temperatures

Avocados are affected by cold temperatures either by physical freezing damage caused by frosts or chilling damage caused by temperatures above freezing point but below 13°C.

Freezing Temperatures

Avocado trees are sensitive to frosts in line with their subtropical origins. Frost damaged leaves become bronzed and dry up quickly, leaving branches defoliated (Scorza and Wiltbank, 1975); in severe frost events damage to stems and branches can cause whole plant death (Witney and Arpaia, 1991). The negative impact of freezing and chilling may be altered by the condition and pre-treatment of the plants. Cultivar, time of year, location, ice nucleating temperature, orchard conditions, leaf nitrogen content, root rot infection, tree size, tree age, leaf age and drought can influence the cold hardiness of avocado leaves (Krezdorn, 1973; Mckellar *et al.*, 1983, 1992; Witney and Arpaia, 1991). The high level of damage on frosted leaves indicates that there will be little photosynthetic activity following a damaging frost.

Chilling Temperatures

Chilling refers to non-freezing temperatures of 0°C to 12°C that can be relatively common in temperate regions, even in the growing season, and can substantially reduce photosynthetic productivity (Allen and Ort, 2001). Exposure to chilling temperatures can disrupt all major components of photosynthesis including thylakoid electron transport, the carbon reduction cycle and control of stomatal conductance. Avocado leaves that experience cold nights at around 8 to 10°C have been reported to show substantial declines in net photosynthesis from 19 to 10 $\mu mol\ m^{-2}\ s^{-1}$, apparent CO_2 quantum efficiency, and optimal quantum efficiency of photosystem II (F_v/F_m) from 0.81 to 0.41 (Whiley *et al.*, 1999). It is reasonable to expect that avocados in the New Zealand growing areas are negatively impacted by winter temperatures when the mean daily temperatures can be below 10°C for up to two months of the year.

CONCLUSIONS

Production by the New Zealand avocado industry has not increased significantly since 2001 and has failed to exceed 8.86 tonnes/ha. To achieve the industry target of an average yield of 15 tonnes/ha a greater understanding of carbohydrate assimilation is required. The regions of New Zealand where avocado trees are grown commercially are considered by some to be at the southern climatic limits for good yields. On this basis a potential cause of low production is poor photosynthetic capability during winter that commonly manifests as damage to the photosynthetic apparatus visible as leaf-yellowing. Leaf yellowing appears to follow periods of cold temperature in winter and is perceived to be an indication of a decline in leaf chlorophyll content, resulting in a large reduction in net photosynthetic rate and consequential decline in starch production. A lack of sufficient starch accumulation during winter may be important in determining a poor fruit set in an 'off' flowering year where a heavy crop of fruit grows in size and increases in oil content over the winter months. Low temperature damage to the photosynthetic apparatus could be an important problem as the damage would restrict leaf longevity and reduce overall plant resources for the coming spring flowering. Research findings from overseas suggest that the productivity of avocados in the major growing areas of New Zealand could be severely depressed by winter chilling. Maintaining a strong carbohydrate productive base through high rates of photosynthesis in the avocado tree all year round is needed when new methods of managing trees for smaller size without compromising yields are used. Determining the photosynthetic capability of leaves as they emerge, grow and age in relation to position on the tree, crop load and exposure to light alongside New Zealand phenological information is essential to understand how to achieve consistent and greater yields.

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