

SUMMARY

Avocados in Australia are grown across a diverse range of environments ranging from warm, humid subtropical to semi-arid Mediterranean. At present more than 95% of production is consumed on domestic markets. Currently the industry is expanding rapidly and new markets will be required to sustain this growth at profitable levels. Geographical isolation and strong competition from countries with lower production costs (labour) have in the past made export unattractive. However, due to the limited domestic market the industry will need to develop export outlets to ensure future prosperity. To compete effectively the efficiency and reliability of production and quality of fruit must be improved. This can be achieved by the development and adoption of advanced technology to give the Australian industry a competitive edge in export markets.

Pheno/physiological studies of cv. Hass growing in a cool mesic subtropical climate have indicated bimodal periodicity for shoot and root growth over a typical 12 month period. After a period of quiescence during winter and following flowering, indeterminate inflorescences and shoots grew vegetatively for a short time in spring. Cessation of spring shoot growth was followed by a period of root growth (measured at the soil-panel interface of rhizotrons) which then declined prior to an extended period of vegetative flushing during summer through to autumn. Strong root growth occurred from late summer until just before flowering when there was a substantial and rapid decline in white “feeder” roots. The magnitude of root growth, particularly during the winter months was dependant on crop load, with heavy crops significantly reducing root growth. Periods of marked fruit abscission occurred at the end of flowering and again during early summer when fruit had reached 30 to 40% of their final mass.

Rootstock/scion combinations influenced the accumulation of starch in roots and the scion (trunk of the tree). ‘Hass’ grafted to seedling ‘Velvick’, a Guatemalan race rootstock, accumulated double the starch content in roots compared with ‘Hass’ grafted to cloned ‘Velvick’. This relationship was reversed in the scion with the greatest starch content accumulating in ‘Hass’ grafted to cloned ‘Velvick’. Mild incompatibility occurred between the

rootstock and scion of the 'Hass'/cloned 'Velvick' combination which probably accounts for these differences in starch content. Higher starch concentrations in roots were directly related to greater root lengths measured at the soil-panel interface of the rhizotrons. The 'Hass'/cloned 'Velvick' combination produced ca. 20% more of its fruit on determinate terminals, as opposed to indeterminate and had a more efficient fruiting index when compared with the 'Hass'/seedling 'Velvick' combination; viz. $3.57 \pm 0.31 \text{ kg m}^{-3}$ compared with $2.12 \pm 0.42 \text{ kg m}^{-3}$, respectively. These values appear to be associated with the reduced root growth and vegetative vigour of the 'Hass'/cloned 'Velvick' combination.

Seasonal changes in nitrogen, starch and chlorophyll concentrations and CO_2 assimilation (A) of summer flush leaves and their relationship to tree phenology were studied. There was an increase in all of these parameters as leaves matured during late summer and autumn, a period of relative quiescence in the tree. As inflorescences developed from late June leaf nitrogen content dropped sharply, though it partially recovered during the latter stages of anthesis. Starch concentrations of leaves increased rapidly once leaves matured in late summer until just before anthesis, when there was a gradual decline through to leaf senescence in spring. Net CO_2 assimilation was highest during late summer and autumn but declined rapidly when mean minimum temperatures were $< 10^\circ\text{C}$, probably due to photoinhibition. Chlorophyll concentrations followed a similar pattern to A with both making a partial recovery after anthesis.

In studies of leaf and shoot ontogeny of fruiting cv Hass trees it was found that leaves reached full expansion ca. 30 days after bud-break and underwent the sink to source transition when 80% expanded. Maximum A of leaves was reached when they were ca. 50 days old. With respect to whole shoot ontogeny, for the first 27 days after bud-break there was a net carbon loss (sink phase) after which net gains in CO_2 assimilation were made. With respect to fruit retention 86% of fruits initially set had abscised by the time that shoots had reached their CO_2 assimilation compensation point, i.e. respiration loss equalled photosynthetic gains, and a further 6% abscised from this point until the shoot had reached its maximum photosynthetic capacity.

Earlier studies of the gas exchange response of avocado leaves to irradiance have largely been made on container-grown trees and gave relatively low A values. Light saturation of A (Q_A) of mature leaves on field-grown 'Hass' trees was measured at $1270 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ when A was $16.12 \pm 0.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, a much higher value than for container-grown trees. The light compensation point (Q_0) for these leaves was $\approx 30 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Prolonged exposure of leaves to minimum mean night temperatures of $< 10^\circ\text{C}$ caused photoinhibition of photosystem II, reduced Q_A to $1040 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and increased Q_0 to $50 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Cold temperatures also reduced the quantum yield of leaves from 0.0545 to 0.0336. Photoinhibition was reversible with A in leaves making a partial recovery in spring once minimum mean temperatures increased above 10°C .

Photosynthates and possibly their metabolism from current assimilation had a significant impact on the retention of fruitlets on indeterminate spring shoots. Removal of this resource by defoliation reduced final yield by ca. 400%. Strong competition between the closely coupled reproductive and vegetative sinks on fruiting shoots was also shown in studies on the fruit retention dynamics of indeterminate and determinate flowering terminals. Determinate inflorescences initially set 30% more fruit than indeterminate inflorescences and retained significantly more fruit at the maturation of the indeterminate shoot. Fruit on determinate terminals also grew more rapidly and were larger at maturity than those on indeterminate shoots. Control of the vigour of the spring vegetative flush has been intuitively recommended in the past - these results reinforce the importance of orchard management with respect to spring shoot growth.

Net efflux of CO_2 from attached avocado fruit was measured periodically from three weeks after anthesis to fruit maturity. Net CO_2 exchange was determined in the daylight (light respiration, R_l) at a PPFs $> 600 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, and in the dark (dark respiration, R_d). Dark respiration and R_l were highest during the early cell division stage of fruit growth (about 25 and $22 \text{ nmol CO}_2 \text{ g}_{\text{dw}}^{-1} \text{ s}^{-1}$ respectively) and decreased gradually until fruit maturity to about 1 and $0.5 \text{ nmol CO}_2 \text{ g}_{\text{dw}}^{-1} \text{ s}^{-1}$, respectively. Fruit photosynthesis, calculated from the difference between R_d and R_l , ranged from 0.5 to $3.1 \text{ nmol CO}_2 \text{ g}_{\text{dw}}^{-1} \text{ s}^{-1}$. Net CO_2 assimilation on a fruit dry weight basis was highest during early stages of fruit growth and reached the lowest rate at fruit maturity. Net CO_2 assimilation of fruit exposed to light was 0.4 to 2.5% of that for fully

expanded leaves. Light interception in the fruiting zone of the tree canopy showed sufficient irradiance levels for fruit photosynthesis from fruit set to the end of spring shoot growth. Although the relative amount of carbon assimilated by the fruit was small compared with the total amount assimilated by the leaves, the data indicate that avocado fruit contribute at least marginally to their own carbon requirement, especially in the early critical stages, by means of CO₂ assimilated in the light. However, data were insufficient to quantify this on a percentage basis.

The influence of shoot age on partitioning of ¹⁴C in container-grown avocado trees was determined. The oldest leaf of actively growing shoots and the youngest leaf of the previously matured shoots were exposed to ¹⁴CO₂ 18 and 34 days after bud-break (DABB) of new shoots. At these times, treated leaves had a positive net CO₂ assimilation rate and, therefore, were considered to be net C exporters. Sixteen days after ¹⁴C exposure, separate plant tissues were harvested, dried, weighed, and oxidised. The percentage of ¹⁴C in each tissue was determined by liquid scintillation spectrometry. Photoassimilates were translocated acropetally and basipetally from all treated leaves. However, at 18 DABB, developing leaves of the actively growing shoots appeared to be the strongest sink for carbon assimilated by the oldest leaf of these shoots, whereas the roots were the strongest sink for carbon assimilated by the youngest leaf of the previously matured shoot. By 34 DABB, roots were the strongest sink for carbon assimilated by leaves of both new and previously matured shoots. These data are useful in developing improved management strategies for controlling *Phytophthora* root rot (caused by *Phytophthora cinnamomi* Rands) in avocados by systemic phosphonate fungicides translocated via the photoassimilate pathway.

Translocation of the fungicide phosphonic acid (H₃PO₃) in cv. Hass avocado trees was studied after trunk injection with 20% H₃PO₃, formulated as potassium phosphonate, at three stages of tree phenology during the growing season. Initially, translocation was solely acropetal in the xylem, and H₃PO₃ was detected in the leaves 24 hours after treatment. Several days after injection, H₃PO₃ concentration in the bark of trunks and in roots increased, indicating basipetal phloem transport of H₃PO₃ from leaves. The rate of accumulation and the final concentration of H₃PO₃ in the roots were directly related to the sink: source relationship of the shoot at the time of injection. For example, trunk injection at the beginning of spring growth flush, when renewal shoots were strong

sinks, resulted in low H_3PO_3 root concentrations ($< 9 \text{ mg g}_{\text{fw}}^{-1}$) which peaked about 45 days after treatment. When potassium phosphonate was injected after the transition of spring-grown shoots from sinks to sources, or at summer shoot maturity, root concentrations of H_3PO_3 increased to $\geq 25 \text{ mg g}_{\text{fw}}^{-1}$ by 30 days after treatment. These results, supported by ^{14}C studies, suggest that strategic timing of injections according to phenological events may greatly improve fungicide efficacy when targeting specific organs for protection.

The effect of harvest time in relation to subsequent yield and fruit size, and the seasonal dynamics of starch concentration flux were studied for an early ('Fuerte') and late ('Hass') maturing cultivar over 3 to 6 consecutive seasons. Harvesting fruit at or shortly after reaching legal maturity sustained yield while delayed harvesting resulted in alternate bearing patterns. Delayed harvesting resulted in a significant reduction of accumulated yield over a number of years with both early and late maturing cultivars. When strong alternate bearing patterns had developed they could not be alleviated by early-harvesting fruit at minimum legal maturity. There was a tendency for delayed harvesting of 'Fuerte' to significantly ($P \leq 0.05$) increase fruit size but this did not occur every year. This effect was less pronounced with 'Hass' with almost significant ($P \leq 0.06$) increases in size only recorded in the "off" year of cropping. Seasonal starch concentration fluxes in the trunks of 'Fuerte' trees were small ($< 30\%$) and gave no indication of potential cropping in subsequent seasons. Starch fluxes were much greater in 'Fuerte' shoots (600 to 700%) but were also a poor indicator of yield in the following season. Seasonal starch concentration fluxes in shoots and trunks of 'Hass' trees were greater than in 'Fuerte' and followed more predictable patterns. July concentrations of starch in 'Hass' were directly related to subsequent yield and have potential for use as a prediction index for crop estimation.

Reduced fruit size and yield are problems with 'Hass' growing in warm, subtropical climates. Low A of over-wintered leaves was identified at flowering and fruit set, a time of assimilate demand by competing reproductive and vegetative sinks on indeterminate terminals. Enhancement of nitrogen content of these leaves while simultaneously restricting shoot growth with the growth inhibitor paclobutrazol (PBZ), was investigated over two seasons as a means of increasing the assimilate supply to developing fruitlets during the critical first 12 weeks of ontogeny. Forchlorfenuron (CPPU) a chemical with cytokinin-like activity with the potential to increase cell division was also

evaluated for its potential to increase fruit size. Pre-anthesis soil nitrogen applications together with mid-anthesis foliar sprays of PBZ (2.5 g a. i. l⁻¹) or mid-anthesis foliar sprays of PBZ alone (2.5 g a. i. l⁻¹) significantly increased *A* (ca. 10.8 and 9.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively) compared with control trees (ca 7.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). These treatments and mid-anthesis foliar sprays of PBZ at 1.25 g a. i. l⁻¹ significantly increased accumulative fruit yield over two consecutive years. Nitrogen plus PBZ also increased the storage life of fruit held at 7°C by six days. CPPU sprayed on trees at either 10 or 20 mg a. i. l⁻¹ when fruit was in the first two weeks of ontogeny had no effect on fruit size or yield. Further research is needed before possible orchard adoption of this manipulative strategy.

The plasticity of the light response of avocados identified in this thesis together with morphological characteristics reported in the literature provide evidence that ecologically avocado has evolved as a small gap species in the subtropical and highland tropical rainforests of Central America. The tree has normally been classified and usually behaves as an evergreen species, albeit with remarkably short-lived leaves. However, many of the physiological characteristics of avocado identified in research reported herein are more typical of those described for deciduous species. In subtropical climates the avocado exhibits wintergreenness, replacing the over-wintered canopy after a cohort of new leaves in spring. However, in harsher environments and under *Phytophthora* root rot or other severe stresses the tree may become “near deciduous”, thereby relieving stress until more favourable conditions return.

The detailed pheno-physiological studies reported in this thesis involve research conducted since 1989 and in particular over the period 1991 through 1994. However, the conceptual framework was developed over a longer period. The author’s studies have thrown more light on the ecological, physiological and ultimately genetic constraints on the performance of currently available cultivars/composite trees, and helped to explain relatively low commercial orchard yields. However, the resultant more sophisticated understanding of the tree has led to opportunities for tree manipulation to improve leaf (and fruit) photosynthetic efficiency, increased carbon partitioning to roots and fruits, control of vegetative:reproductive competition at critical periods in the phenological cycle, and improved efficacy of translocated fungicides. The data base for managing the avocado tree has been considerably expanded.