CHAPTER 3

LEAF AND SHOOT PHYSIOLOGY IN RELATION TO CO_2 ASSIMILATION AND FRUIT RETENTION

The harvest of solar energy by fixation of atmospheric carbon dioxide is one of the most important attributes of plants. Their success as crop plants largely depends on their ability to maintain a photosynthetically efficient canopy, which meets the demands of growth over changing environmental conditions and may shift substantially at both the daily and seasonal level (Long *et al*. 1994). A highland tropical to subtropical, evergreen species from Central America, the avocado is now cultivated over a wide range of environments from cool, semi-arid to humid, tropical climates (Whiley and Schaffer 1994) where it experiences adverse climatic conditions which induce physiological stresses. Photosynthetic activity is influenced by biotic (Wareing *et al*. 1968; Sams and Flore 1982; DeJong 1982; Schaffer *et al*. 1987) and abiotic factors (Ludlow 1983; Bongi *et al*. 1987; Jones, 1992a). This chapter examines some aspects of photo-assimilation of avocado in relation to shoot ontogeny, irradiance, and CO_2 partial pressures. The importance of current assimilate on fruit retention during spring shoot growth was also investigated.

3. 1 DYNAMICS OF GROWTH AND CO_2 ASSIMILATION OF THE FRUITING SPRING SHOOT

3. 1. 1 Introduction

Plant leaves have many functions that include recycling of a portion of the total nutrient stock, storage of carbohydrates, modification for defence purposes (spines) and a direct contribution to the carbon economy (Chabot and Hicks 1982). The product of assimilation rate and longevity ultimately determines the value of the leaf with respect to its carbon contribution, and in general the longer its life the lower its potential A_{max}, i.e. short-lived leaves are more likely to have higher A_{max} than long-lived leaves (Chabot and Hicks 1982). However, it is the CO_2 assimilation dynamics of the whole canopy, and subsequent partitioning of photoassimilate to

photoassimilate to economic end-product which are ultimately related to crop productivity. In this study, aspects of leaf age and the ontogeny of spring-grown, fruiting shoots of cv. Hass in relation to CO_2 assimilation were investigated.

3. 1. 2 Materials and Methods

Net CO_2 assimilation (*A*) measurements were carried out on seven-year-old cv. Hass trees (grafted to seedling 'Edranol' rootstocks), growing in a commercial orchard at Nelspruit, South Africa (latitude 25°S, altitude 660 m). The area has a warm subtropical climate with mean rainfall of 900 mm per annum and a mean min/max temperature of 18.6/29.1°C in January and 6.5/23.3°C in July. The trees were growing in a sandy loam soil with flood irrigation scheduled with a Class 'A' Evaporation Pan to ameliorate the development of water stress.

For this study, three uniform indeterminate flowering terminals on the sun-exposed northern side of each of five trees were selected near the completion of anthesis, and each leaf of the new shoot was tagged and dated as it emerged from the vegetative bud. The first leaf position on the new shoot generally produces a residual leaf and was ignored, with the second leaf designated the first leaf for the purposes of the study. Approximately 10 days after each leaf emerged, its area was measured with a portable leaf area meter (LICOR Model LI-3000) and *A* determined with a LICOR LI-6200 portable photosynthetic meter (see Materials and Methods, Chapter 2). Following the initial measurements, leaf areas were determined every 4 to 8 days until leaves stopped expanding (about 32 days after emergence). Photosynthesis measurements followed a similar schedule until *A* of the youngest leaf was constant (76 days after bud-break). Net *A* of the developing shoot ($\sum$ *A* per area of each leaf) was calculated at each point of measurement.

Ten days after bud-break, fruits set on the tagged indeterminate flowering shoots were counted. Counting was repeated at 7 to 14 day intervals for a period of 76 days after bud-break. Abscised fruit were recovered and microscopically examined for the presence of embryos.

Non-linear regression analyses using TableCurve™ (Jandel Scientific, Calif., USA) were used to correlate *A* to leaf expansion, as well as shoot ontogeny and fruit drop to the time elapsed after bud-break.

3. 1. 3 Results

The mean number of leaves and leaf area per fruiting shoot were 6.9 ± 1.1 and 496.4 ± 141.0 cm^2, respectively. Leaf growth followed a sigmoidal curve (Fig. 10) reaching 50% of full expansion after 18 days with maximum size 31 days after bud-break. There was ca. 10 days difference between full expansion of the first and last leaves on shoots which was related to the time that they developed. Hence leaf ontogeny was approximately the same duration for each position on the shoot.

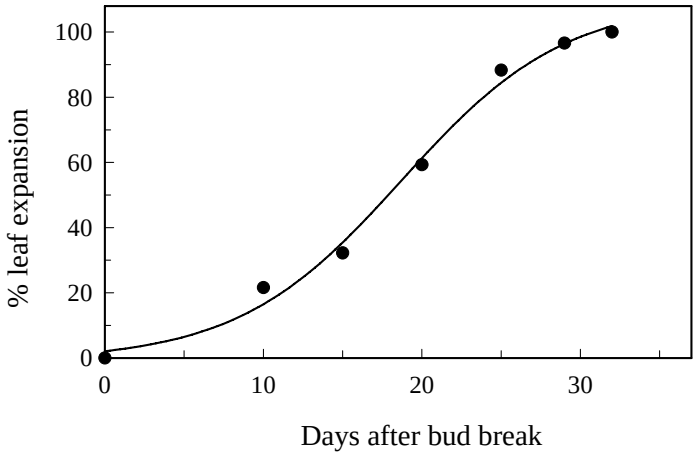

Fig. 10 Expansion of the first leaf on spring-grown fruiting shoots of cv. Hass in relation to bud-break where the regression curve is represented by: y = - 0.776 + 110.475/(1 + exp(-(x - 18.715)/5.168)), r^2 = 0.99**. Data points are mean values from three shoots on each of five trees (n = 5).

Leaves had reached ≈ 20% of their full expansion before they were large enough to fit the LI-6000-11 leaf chamber for the measurement of CO_2 exchange. At this stage of development there was a net CO_2 loss from leaves due to respiration being greater than their capacity for assimilation (Fig. 11). Net CO_2 assimilation increased exponentially as leaves expanded,

however the leaf-age compensation point at saturating PPF was not reached until individual leaves had reached 80% of their final size, i.e. individual leaves underwent the sink/source transition when ≈ 24 days old (Figs. 10 & 11). While leaves reached full expansion ≈ 31 days after bud-break (Fig. 10) they did not attain A_{max} until they were ≈ 50 days old (Fig. 12a). This time frame was approximately the same for each leaf irrespective of when it emerged.

With respect to the gas exchange characteristics of the whole shoot (excluding fruit), during early ontogeny there was a net CO_2 loss as expanding leaves had higher respiratory losses than CO_2 assimilation gains (Fig. 12b). This net CO_2 loss (sink phase) from the shoot continued for

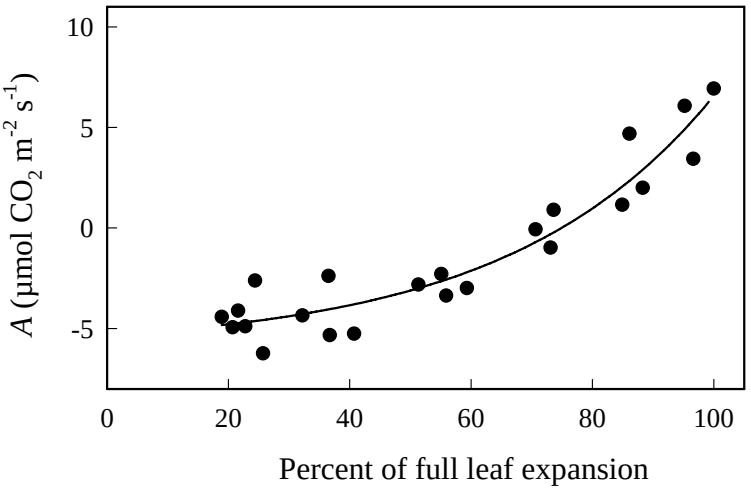

Fig. 11 Effect of leaf age on net CO_2 assimilation (A) of avocado leaves, cv. Hass, represented by the regression y = - 5.967 + 0.652 exp(-x/-33.824), r^2 = 0.88**. Data are means from the first leaf on three fruiting spring-grown shoots on each of five trees (n = 15).

the first 27 days after bud-break after which there was a net gain in CO_2 assimilated, i.e. the shoot as a whole became a source of carbon, with A_{max} for the shoot occurring ≈ 70 days after bud-break.

The mean number of fruits set on each shoot was greatest (29.1 ± 6.8) when first recorded ten days after bud-break (Fig. 12b). Fruit numbers declined rapidly as shoot ontogeny advanced with a mean of 1.5 ± 0.6 fruit per shoot remaining 76 days after bud-break. At that time, the number of fruit retained was 5% of the original number set. Of the abscised fruit recovered, 97% had formed normal embryos. From the correlations between fruit number and shoot *A* (Fig. 12b) it was estimated that by the time the shoot compensation point for *A* ($\sum R_l$ and $A = 0$) was reached, 25 fruit per shoot (86%) had fallen. A further 6% of the initial fruit set dropped during the period between the shoot compensation point and reaching shoot $A_{max,}$ and for the remainder of the study period fruit loss was minimal.

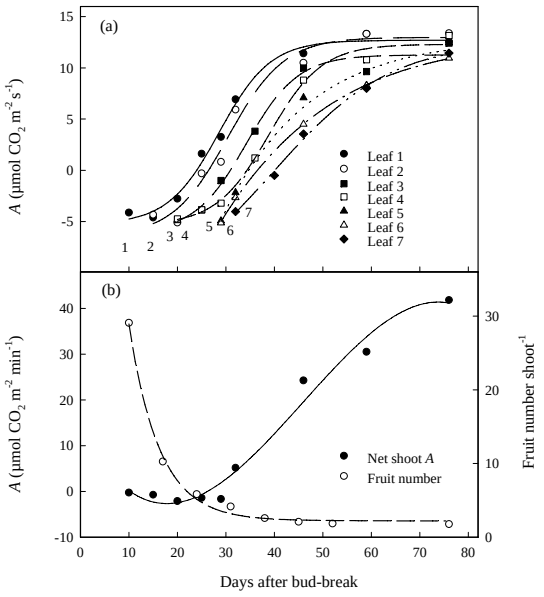

Fig. 12 CO_2 assimilation (*A*) and fruit loss from developing spring shoots where (a) is the *A* of maturing leaves from different positions along the shoot. Equations for each regression are presented below; and (b) the relationship between total *A* of the shoot represented by the regression $y = 13.65 - 1.988x + 0.069x^2 + 0.0005x^3$, $r^2 = 0.98$; and fruit drop represented by the regression $y = 2.213 + 130.39 \exp(-x/6.31)$, $r^2 = 0.99^{**}$. Data points are mean values from five trees (n = 15).

Leaf position	Regression	r^2
1	y = - 6.458 + 19.438/(1 + exp(-(x - 30.47)/5.77))	0.96**
2	y = 6096 + 17.361/(1 + exp(-(x - 34.20)/5.321))	0.96**
3	y = - 5.33 + 17.63/(1 + exp(-(x - 38.91)/5.437))	0.95**
4	y = - 5.264 + 17.96/(1 + exp(x - 28.635)/5.284))	0.96**
5	y = - 209.40 + 222.29/(1 + exp(-(x -+ 11.647)/16.62))	0.97*
6	y = - 119.41 + 132.34/(1 + exp(-(x + 8.697)/20.34))	0.99**
7	y = - 13.158 + 25.764/(1 + exp(-(x - 39.566)/12.23))	0.99*

3. 2 CO_2 ASSIMILATION OF CV. HASS LEAVES IN RELATION TO IRRADIANCE, CO_2 PARTIAL PRESSURES AND TEMPERATURE

3. 2. 1 Introduction

General features of subtropical and tropical fruiting trees include large leaves producing high ratios of leaf area to canopy surface; leaves can be up to 25% of the fresh mass of the tree and can contain a substantial reserve of nutrients and carbohydrate; some species have highly efficient light-harvesting chloroplasts for growth under low photosynthetic photon fluxes (PPF); leaves have a limited vascular network with high stomatal density; *A* commonly saturates at about 20 to 25% of full sunlight, and light compensation points are low (Possingham 1986).

There is still a paucity of published information on leaf gas exchange characteristics of avocado, although some results are available which have similar findings. In separate studies, Bower *et al*. (1978), Kimelmann (1979), Scholefield *et al*. (1980) and Schaffer *et* al. (1987) agreed that A_{max} of leaves was between 6 to 9 µmol CO_2 m^{-2} s^{-1}. There was also general agreement between Bower *et al*. (1978) and Scholefield *et al*. (1980) that light saturation for CO_2 assimilation (Q_A) of avocado leaves was at PPFs between 400 to 500 µmol quanta m^{-2} s^{-1}, i.e. 20-25% of full sunlight. Hence, these results added authenticity to the generally held belief that evergreen species have lower photo-assimilation capacity than deciduous crops (Larcher 1969; Chabot and Hicks 1982; Mooney and Gulmon 1982).

Rate-limitation of photosynthesis is attributed to restricted CO_2 diffusion, either through stomatal resistance or physical resistance through the mesophyll (Wareing *et al.* 1968); leaf age and longevity (Chabot and Hicks 1982; Sams and Flore 1982); sink-limited feedback inhibition (Arp 1991; Thomas and Strain 1991), nutrient deficiencies (Gulmon and Chu 1981; DeJong 1982; Schaffer and Gaye 1989) and water, temperature and light factors (Taylor and Rowley 1971; Kaiser 1987; Anderson and Brodbeck 1988a). Exposure of tropical and subtropical species to temperatures below $\approx 10^{o}C$ is reported to greatly retard or stop growth causing dysfunction of cellular processes. The effects of these temperatures on cellular processes are reversible with limited exposure to temperatures below $10^{o}C$, but ultimately irreversible

leading to cell death (Taylor and Rowley 1971; Powles 1984; Smillie *et al*. 1988). Chill injury results in the inhibition of photosynthetic (Taylor and Rowley 1971; Öquist and Martin 1986) and other metabolic processes (Graham and Patterson 1982), with leaf yellowing (photo-oxidation of chlorophyll) developing after extended exposure to low temperatures (Taylor and Rowley 1971; Taylor *et al.* 1974; Powles 1984; Robinson 1993). Functionally, the consequences of photoinhibition of photosynthesis are a reduction in the maximum quantum yields for CO_2 uptake (Ø) (Powles 1984), and with prolonged exposure to excessive light, a decreased rate of light saturated photosynthesis (A_Q) (Long *et al*. 1983; Powles *et al*. 1983). Damage to leaves from chill stress may be quantified by measuring the decrease in the variable fluorescence (F_v) of photosystem II (PS II) in relation to the maximum fluorescence (F_m), usually parameterised as F_v/F_m, which implies decreased photochemical conversion efficiency of PS II (Krause 1988; Smillie *et al*. 1988). Where persistent low temperatures limit carbon assimilation, decreases in photosynthetic efficiency which may persist for months have been observed in evergreen leaves. The obvious cost is the reduction in efficiency of conversion of intercepted light into plant dry matter, which may affect avocado which is often still committed to fruit development during winter - a time of prolonged low temperature stress.

Documented research on *A* of avocado was carried out on container-grown trees (Bower *et al*. 1978, Kimelmann 1979, Scholefield *et al*. 1980) or field-grown trees (Schaffer *et* al. 1987) where soil conditions imposed severe root restriction (Crane *et al.* 1994). Arp (1991) and Thomas and Strain (1991) reported reduced photosynthetic capacity in a number of species grown in pots where roots had become pot-bound. They attributed this effect to end product-inhibition caused by the sink-limitation of restricted root systems. In view of these recent findings it is pertinent to re-examine the relationship between PPF and the CO_2 assimilation responses of avocado under field grown conditions.

The availability of reliable portable photosynthetic meters in the 1980s has advanced the study of CO_2 assimilation of plants in natural environments. This study investigates the response of leaves on mature, field-grown avocado trees to light and CO_2 partial pressures before and during extended cold temperature stress over winter.

3. 2. 2 Materials and Methods

Five year old cv. Hass trees grafted to seedling 'Velvick' rootstocks (see Chapter 2), growing in a commercial orchard with a cool, mesic subtropical climate at Maleny were used in this study. Irrigation was provided by two under-tree sprinklers each delivering 10 l hr^{-1}, and watering was scheduled with permanently installed tensiometers at frequencies to ameliorate development of water stress (Banks 1992). An automatic weather station (Monitor Sensors, Caboolture, AUS.) in the orchard provided minimum and maximum temperature data for the duration of the study. For each set of gas exchange measurements, mature summer-grown leaves from at least three non-fruiting shoots on three trees were selected at a time when shoot growth and floral development were quiescent. Measurements of *A* and intercellular partial pressures of CO_2 (Ci) under variable PPFs and ambient CO_2 partial pressures were made in May 1994 on non-cold stressed (NCS) leaves, and repeated at the end of July 1994 on cold stressed (CS) leaves after prolonged exposure to orchard night temperatures < 10^oC (Table 3). In each case measurements were made between 0800 and 1030 h to reduce the effect of diurnal variation on *A* and Ci. Leaf cuvette temperatures and VPD's during pre- and post cold stress measurements were 25 to 27^oC and <1.0 kPa and 21 to 24^oC and < 1.2 kPa, respectively. To characterise potential chill damage to PSII, chlorophyll fluorescence of leaves was measured using a BioMonitor Stress Meter (BioMonitor SCI, Umeå, Sweden). Measurements were taken monthly starting in April when summer growth had matured and concluded prior to anthesis in August. A further set of measurements were taken at the end of October during the rapid growth stage of fruitlets and spring shoots. Measurements were taken on 4 to 5 sunlit leaves proximate to where gas exchange determinations were carried out on the same three trees. Cuvettes were attached to leaves on each side of the midrib between 0900 and 1000 h and chlorophyll fluorescence measurements taken after 30 mins of dark adaptation followed by two secs irradiation with 400 µmol quanta m^{-2} s^{-1} of blue light (320-550 nm).

Fluorescence was quantified as the F_v/F_m ratio where:

F_0 = initial constant yield fluorescence

F_m = maximum fluorescence recorded

Variable fluorescence (F_v) was calculated as described by Öquist and Wass (1988); where:

$$F_v = F_m - F_0$$

For the light studies, PPF was manipulated by the use of 1 m^2 frames with a polythene mesh (Sarlon Industries, Sydney, AUS.) of different light transmission properties, i.e. by varying mesh size and density. Measurements were made on cloud-free days to ensure acclimation of leaves to a range of PPFs under stable irradiance conditions. Frames were erected 0.5 m from the tree canopy and the leaves allowed to acclimate to the new PPF conditions for at least 30 mins prior to taking measurements. Determinations of *A* and Ci were made with a LICOR Ll-6200 portable photosynthetic meter (see Materials and Methods, Chapter 2). Readings of *A* taken at zero PPF were obtained by wrapping the leaf cuvette in a black cloth and waiting until CO_2 evolution stabilised.

Measurements of the responses of *A* to CO_2 partial pressures were made at saturating PPFs (Whiley and Schaffer 1994) using a CIRAS-1 portable photosynthesis meter (PP Systems, UK) configured as an open system. This equipment facilitates delivery of variable ambient CO_2 partial pressures to the leaf cuvette via compressed CO_2 cartridges. Determinations were made approximately 3 to 5 min after placing the leaf in the cuvette when *A* had stabilised.

Data were fitted to non-linear regression models (TableCurve™, Jandel Scientific, Calif., USA) and the light compensation (Q_O), and light (Q_A) and CO_2 (C_A) saturation points for *A* were predicted (Q_A and C_A = 0.9 of the maximum *A* [A_{max}]; Osman and Milthorpe 1971). Quantum yield (Ø) was estimated from the slope of the linear portion (at low PPFs) of the *A* vs. PPF curve.

3. 2. 3 Results

Mean monthly minimum and maximum air temperatures for the experimental site are presented in Table 3. During April and May when the first leaf measurements were made the mean minimum air temperatures were > 12°C. There were 22 and 21 nights in June and July respectively, when minimum temperatures were < 10°C. The coldest temperatures registered were 4.7 and 4.6°C for each of the months, respectively. Mean minimum temperatures remained below 10°C until September when they increased to 11°C.

Table 3 Mean monthly temperatures in the orchard at Maleny for 1994.

Months‡	Mean temperature (°C)	
	min.	max.
Jan	19.2	28.1
Feb	17.6	24.5
Mar	16.1	23.3
Apr	14.0	22.0
May	12.9	21.1
Jun	9.2	19.1
Jul	8.0	18.0
Aug	8.3	19.1
Sep	10.0	23.6
Oct	12.5	24.2

‡ F_v/F_m ratios were determined in May and July 1994.

Chlorophyll fluorescence

Mean min/max temperatures for the five days preceding *A* measurements were 12.7/20.2^{o}C and 5.5/18.8^{o}C in May and July, respectively. The F_v/F_m ratios in April and May were 0.81 ± 0.02 and 0.79 ± 0.01, respectively (Table 4) indicating that leaves had not been exposed to damaging low temperatures and photosynthetic processes were functioning normally (Öquist and Wass 1988). In June, minimum temperatures dropped below the critical threshold where chill injury may occur (Table 3) and this was reflected in a substantial decrease in the F_v/F_m ratio (Table 4). By late July, following a period of low temperatures, a few north-facing leaves had visible signs of chlorophyll photo-oxidation (Fig. 13), a condition caused by low temperatures and high PPFs (van Hasselt 1974). At this time the F_v/F_m ratio was 0.41 ± 0.03 indicating cold-induced stress. Increased mean minimum temperatures in August were concomitant with a higher F_v/F_m ratio, and substantial improvement was measured ca. eight weeks later (31 October) when the F_v/F_m ratio was 0.67 ± 0.01. The October measurement of the F_v/F_m ratio suggests that the photoinhibition that developed during the winter months in these leaves was reversible and is further supported by the seasonal changes in *A* reported on the same trees in 1992 (see Fig. 8, Chapter 2).

Table 4 Seasonal variation in chlorophyll fluorescence (F_v/F_m) measured on field-grown cv. Hass trees growing at Maleny. Data are mean values (± SEs) of 4 to 5 leaves from each of three trees.

F_v/F_m ratio					
April	May	June	July	August	October
0.81 ± 0.02	0.79 ± 0.01	0.51 ± 0.05	0.41 ± 0.03	0.48 ± 0.03	0.67 ± 0.01

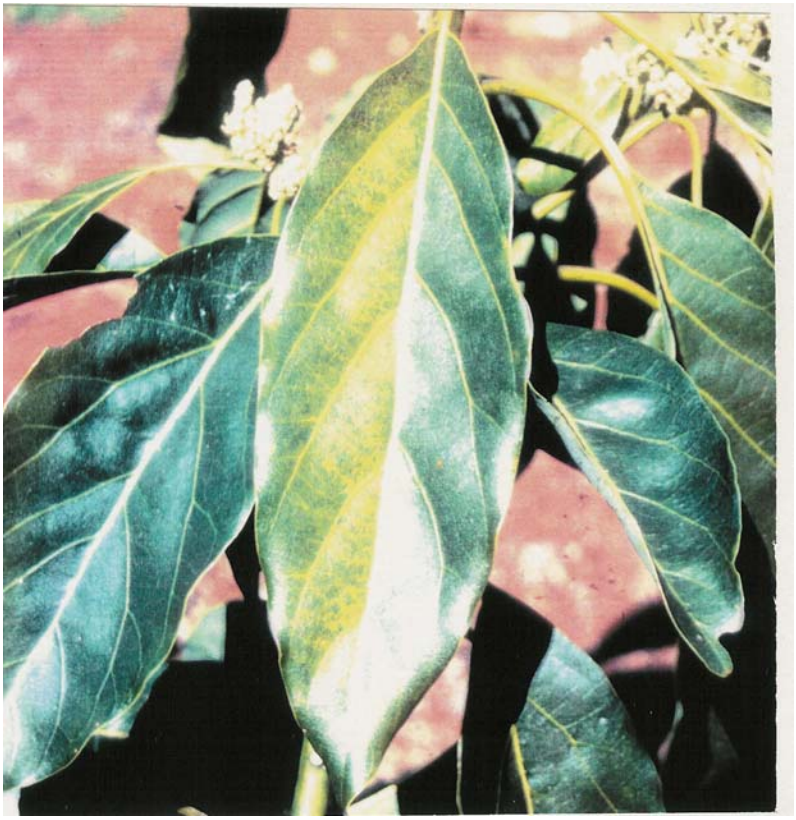

Fig. 13 Photo-oxidation of the chlorophyll of a cv. Hass avocado leaf following extended exposure to night temperatures < 8°C and PPFs > 1600 µmol quanta m^{-2} s^{-1}. The decline in total chlorophyll concentration in 'Hass' leaves during winter is shown in Fig. 8b (Chapter 2).

Response of A and Ci to PPF

The photosynthetic rate increased asymptotically in response to increasing PPF, irrespective of the pre-conditioning temperatures to which the leaves had been exposed (Fig. 14a). Exposure to temperatures < 10°C reduced A_Q from the NCS leaf value of 16.12 ± 0.26 µmol CO_2 m^{-2} s^{-1} to 11.1 ± 0.29 µmol CO_2 m^{-2} s^{-1}, and reduced Q_A from 1270 µmol quanta m^{-2} s^{-1} to 1040 µmol quanta m^{-2} s^{-1}. The Q_0, estimated from regression curves, was ≈ 30 µmol quanta m^{-2} s^{-1} for NCS leaves and increased to ≈ 50 µmol quanta m^{-2} s^{-1} after leaves had been exposed to cold temperatures.

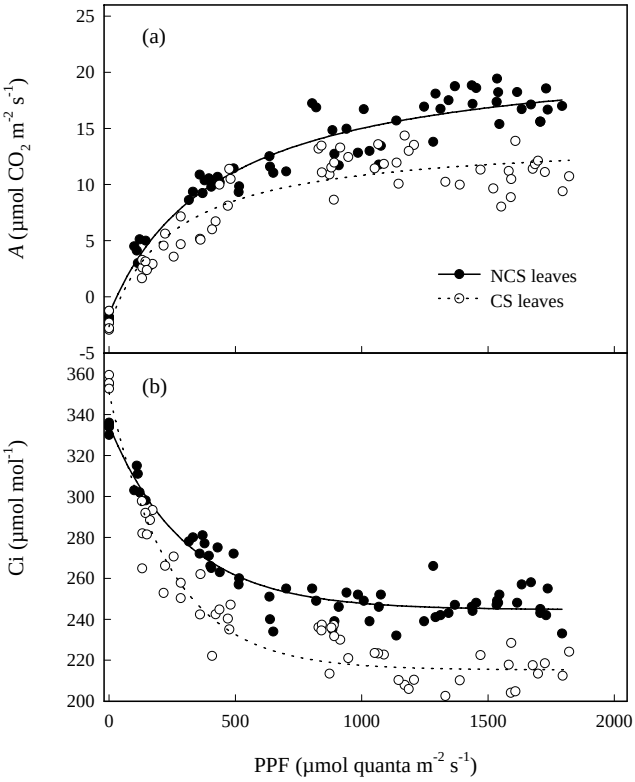

Fig. 14 Responses of CO_2 assimilation (*A*) and intercellular partial pressures of CO_2 (Ci) in leaves of field-grown avocado trees cv. Hass, to varying photosynthetic photon flux (PPF). Data points are for single leaves. The regression line for *A* of non-cold stressed (NCS) leaves is represented by (a) y = 22.08 ((-30.67 + x)/(427.43 + x)), $r^2 = 0.94$**; and cold stressed (CS) leaves by y = 14.17((-46.72 + x)/(250.05 + x)), $r^2 = 0.86$**; the regression line for Ci of NCS leaves is represented by (b) y = 244.65 + 90.2 exp(-0.0034x), $r^2 = 0.94$**, and CS leaves by y = 215.28 + 135.52 exp(-0.0041x), $r^2 = 0.92$**.

For NCS and CS leaves Ci initially declined rapidly and then levelled as leaves were removed from darkness and exposed to increasing PPFs (Fig. 14b).

Q½, representing the PPF when Ci is reduced by 50% was calculated from:

$Q½ = \ln(0.5)/-k$ where *k* is the third constant in the standard decay curve fitted to the data (adapted from Jones 1992b)

Calculated values of Q½ indicate that NCS leaves had a higher light requirement (207 µmol quanta m^{-2} s^{-1}) compared with CS leaves (167 µmol quanta m^{-2} s^{-1}) to reduce Ci by one-half. Thus the Q_A of NCS leaves will be higher than that for CS leaves so long as stomatal conductance is not a limiting factor, supporting the information presented in Fig. 14a.

Cold temperatures significantly reduced Ø from 0.0545 µmol CO_2. µmol $quanta^{-1}$ to 0.0336 µmol CO_2. µmol $quanta^{-1}$ (Fig. 15).

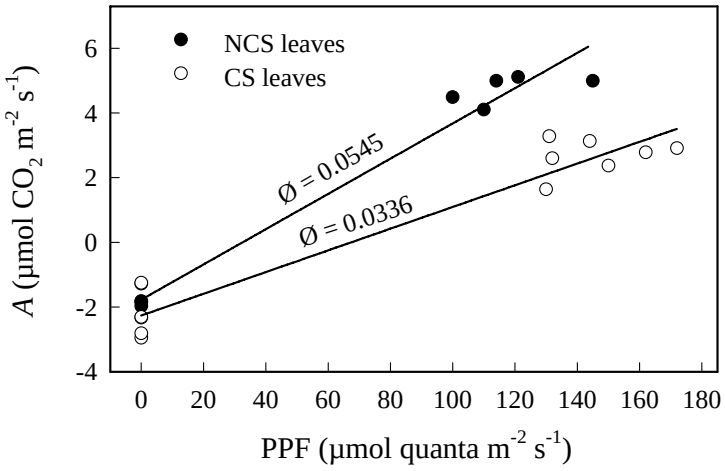

Fig. 15 Quantum yield (Ø) of non-cold stressed (NCS) and cold-stressed (CS) leaves on field-grown cv. Hass trees. Data points represent values of single leaves and CO_2 partial pressure was 330 µmol mol^{-1} at the time of measurement. Ø differ significantly ($P < 0.01$) as judged by a *t* test comparing the slopes.

Response of A and Ci to increasing partial pressures of CO_2

Net CO_2 assimilation showed a typical asymptotic response to increasing partial pressures of CO_2 for both NCS and CS leaves (Fig. 16a). After short term exposure to increasing partial pressures of CO_2, the A_{max} estimated at 2100 µmol mol^{-1} CO_2 for NCS and CS leaves, was 54.1 ± 3.7 and 42.1 ± µmol CO_2 m^{-2} s^{-1}, respectively. Exposure to temperatures < 10°C decreased the CO_2 saturation point (C_A,) from ≈ 1320 µmol mol^{-1} CO_2 for NCS leaves to ≈ 1260 µmol mol^{-1} CO_2, and reduced the saturated CO_2 assimilation rate (A_C) of 48.7 ± 2.7 µmol CO_2 m^{-2} s^{-1}

for NCS leaves to 37.9 ± 2.4 µmol CO_2 m^{-2} s^{-1}. Ci in leaves from both treatments increased in a linear relationship as the CO_2 partial pressure increased and was non-limiting for *A* (Fig. 16b).

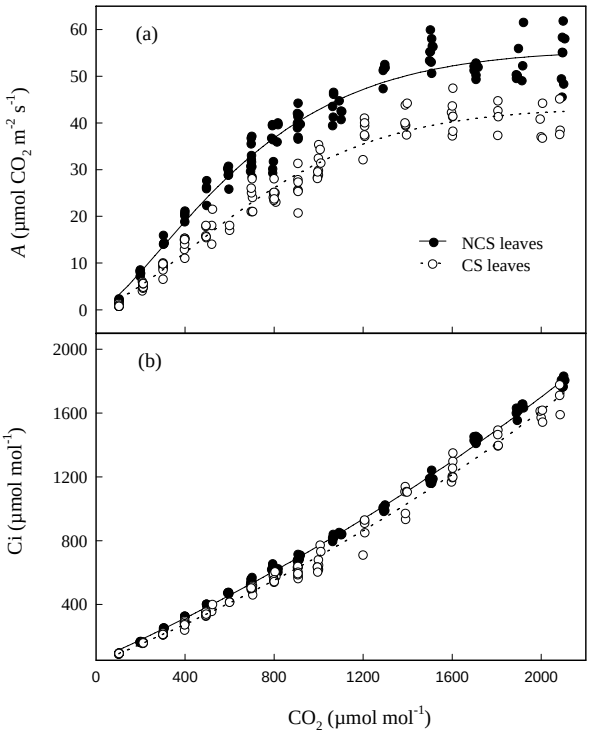

Fig. 16 Responses of CO_2 assimilation (*A*) and intercellular partial pressures of CO_2 (Ci) in leaves of field-grown avocado trees, cv. Hass, to increasing partial pressures of CO_2. Data points are for single leaves. The regression line for *A* of non-cold stressed (NCS) leaves is represented by (a) $y = 55.61(1-\exp(-((x + 745.02\ \ln(2)^{1/1.354}-578.39)/745.02)^{1.354}))$, $r^2 = 0.96$**; and for cold stressed (CS) leaves is represented by $y = 43.2-\exp(-((x + 880.14\ \ln(2)^{1/1.583}-659.07/880.14)^{1.58}))$, $r^2 = 0.96$**; and the regression line for Ci of NCS leaves is represented by (b) $y = -2372.91 + 2421.79 \exp(-x/-3845.81)$, $r^2 = 0.99$**, and for CS leaves is represented by $y = -1818.11 + 1850.45 \exp(-x/-3235.892)$, $r^2 = 0.99$**.

3.3 EFFECT OF PRE-ANTHESIS DEFOLIATION OF TREES AND THE INFLUENCE OF INDETERMINATE AND DETERMINATE INFLORESCENCES ON FRUIT RETENTION

3. 3. 1 Introduction

Pre-flowering concentrations of stored carbohydrates have been positively related to yield in several fruit crop species (Hilgeman *et al.* 1967; Goldschmidt and Golomb 1982; Scholefield *et al.* 1985; Worley 1979). Based on a three-year study, Scholefield *et al.* (1985) reported that pre-flowering concentrations of trunk starch in 'Fuerte' avocado trees were directly related to subsequent yield. During flowering and fruit set these trees lost most of their leaves with no effective source of current photo-assimilates available until the maturation of the new growth in spring. Possibly as a consequence, strong biennial cropping patterns developed because fruit set and retention were dependant on a 'pool' of stored carbohydrate which did not accumulate in sufficient quantity during seasons of heavy cropping. Maximum levels of starch accumulation in 'Hass' avocado trees in subtropical production areas of Queensland, Australia and Natal, South Africa do not reach the same magnitude as those reported by Scholefield *et al.* (1985) and trees in Queensland and Natal retain their over-wintered leaves during anthesis and fruit set (Kaiser and Wolstenholme 1994; Chapter 3).

Avocado conforms architecturally to Rauh's model wherein the majority of inflorescences are compound indeterminate (Reece 1942; Halle *et al.* 1978). However, departures from this model can occur with the production of determinate inflorescences at varying frequencies (Thorp *et al.* 1994; Whiley and Schaffer 1994). Close coupling between fruit and shoot growth from indeterminate inflorescences is thought to be partially responsible for the low fruit retention characteristic of avocado. Removal of the terminal shoot during early development has been shown to increase fruit retention and yield (Biran 1979; Cutting and Bower 1990). A similar result has been achieved with the use of strategically timed foliar applications of the growth inhibitor paclobutrazol to 'Fuerte' (Adato 1990) and 'Hass' trees (Wolstenholme *et al.* 1990; Whiley *et al.* 1991). The dynamics of fruit set and retention on naturally occurring

determinate inflorescences of avocados has not previously been reported in detail and may provide additional information on the mechanisms of fruiting in avocados.

The objective of this study was to investigate the role of over-wintered leaves produced mainly during the summer (current photoassimilate supply) on fruit set and retention during spring shoot ontogeny of cv. Hass, and to compare the dynamics of fruit set and retention of indeterminate and determinate inflorescences.

3. 3. 2 Materials and Methods

Four-year-old cv. Hass trees grafted to 'Velvick' seedling rootstock and growing in a commercial orchard at Maleny, S.E. Queensland, were selected for the defoliation study which was carried out on the same trees over two cropping cycles. The block was not irrigated but annual rainfall is very high and trees were mulched from their trunks to the drip line with barley straw (100 mm deep) and fertilised and sprayed for pest and disease control according to standard commercial recommendations (Banks 1992). Initial tree selection was made at the completion of summer growth with care being taken to select trees of similar size and appearance in relation to tree vigour. Six uniform trees were chosen and immediately prior to flower development, all leaves were hand-stripped from three of the trees which then had their trunks and limbs coated with a white acrylic-based paint on the upper and north-western surfaces to protect against sunburn. Ten shoots, between 1 and 2.5 m above soil level, were labelled on the northern side of each of the six trees. As soon as indeterminate shoots could be identified, five uniform shoots were selected from the original group chosen on each tree. The start (first flower open) and termination (last flower open) of anthesis were recorded on the selected shoots on each tree.

The number of fruits set on each of the selected shoots was counted at the end of anthesis. Nine and 18 days after bud-break of the terminal vegetative bud, fruit on each shoot were counted again and to judge shoot development, the length and breadth of youngest leaves

measured. Thereafter fruit counts and leaf measurements on each of the shoots were repeated at 3 to 4 day intervals until shortly after the youngest leaf reached full expansion.

'Hass' trees grafted to cloned 'Velvick' rootstocks were chosen at the same location for the studies on fruiting characteristics of determinate and indeterminate inflorescences. These trees were growing in the rhizotron facility under conditions already described (Chapter 2). Three terminals of each inflorescence type were selected for uniformity on each of five trees near the completion of anthesis. The mean date of bud-break of the terminal vegetative bud on indeterminate inflorescences was used as the reference point for fruit numbers on each terminal. From 12 days after bud-break fruit were counted on each terminal at weekly intervals for eight weeks with a final count being made two weeks later.

Climatic data for the duration of the experiment were recorded on an automatic weather station (Monitor Sensors, Caboolture, AUS.) near the experimental site.

TableCurve^{TM} (Jandel Scientific, Calif., USA) was used for non-linear regression analyses to model the growth of the youngest leaf and the loss of fruit in relation to shoot ontogeny.

3. 3. 3 Results

Defoliation studies

There was no difference in the time of the anthesis period among the selected shoots (data not presented) which occurred from 27 August to 9 October 1991 and 2 September to 6 October 1992. In both years the main period of flowering occurred during September when mean min/max temperatures were >10 and 20°C, respectively (Table 5), which are non-restrictive for floral dichogamy, pollination and fertilisation of 'Hass' trees (Sedgley and Annells 1981).

Patterns of fruit set and drop and leaf expansion were similar for both years of the study so only data for 1992 are presented. Also, as there was no temporal separation in leaf development on shoots from either treatment, the 1992 data have been pooled for regression analysis.

Table 5 Mean monthly maximum/minimum temperatures recorded in the orchard at Maleny during anthesis in 1991 and 1992.

Months	Rainfall (mm)		Temperature (°C)			
	1991	1992	1991		1992	
			min.	max.	min.	max.
Aug	0.3	34.6	10.0	21.2	9.1	19.9
Sep	4.8	54.8	11.5	24.7	11.0	22.1
Oct	82.6	15.2	13.7	24.9	12.2	23.9

was no significant difference in the initial number of fruits set on shoots of defoliated trees compared with control trees; these being 20.88 ± 2.04 and 22.50 ± 1.96, respectively. However, subsequent fruit loss from shoots on all trees was high, although it became greater on defoliated trees as shoots approached maturity (Fig. 17).

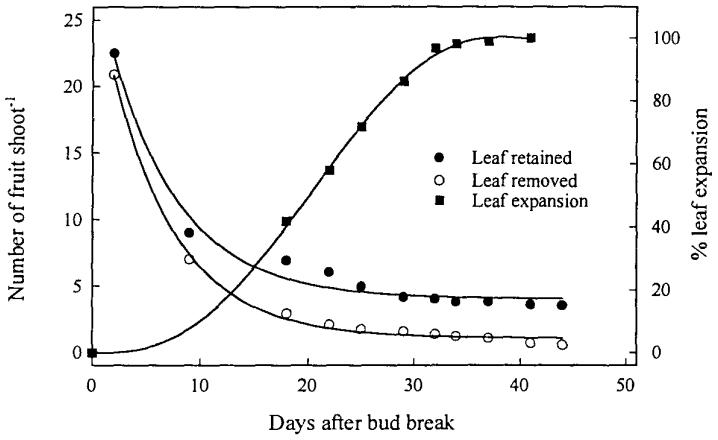

Fig. 17 Spring leaf expansion and fruit loss from shoots on trees where the mature, over-wintered leaves were either retained or removed prior to anthesis. The model for expansion of the youngest leaf is represented by $y = -2.132 + 106.44/(1 + \exp(-(x-20.274)/5.397))$, $r^2 = 0.99^{**}$ (data are mean values from six trees, n = 30); the model for fruit loss from shoots on trees where leaves were retained is represented by $y = 4.02 + 24.83 \exp(-0.154x)$, $r^2 = 0.98^{**}$, and for fruit loss from shoots on trees where leaves were removed by $y = 0.79 + 26.36 \exp(-0.136x)$, $r^2 = 0.99^{**}$. Fruit drop curves are significantly different in placement as judged by t test ($P < 0.01$). Fruit data are mean values for from three trees (n = 3).

Shoots were judged mature when the last-formed leaf reached full expansion, which was ≈ 37 days after bud-break (Fig. 17). With respect to the time for full expansion of leaves, the results from this study were in agreement with those reported with 'Hass' in South Africa (Chapter 3. 1. 3). At this stage of shoot development it was estimated from the regression models that defoliated trees had retained 1.1 ± 0.16 fruits shoot ^{1} while the control trees had retained 4.1 ± 0.38 fruits shoot^{-1}.

Dry matter accumulation was significantly different between shoots from the two treatments when measured at shoot maturity (60 days after bud-break). Shoots on defoliated trees produced ca. 37% more dry matter than shoots on trees where over-wintered leaves were retained (Table 6). In shoots from the control trees, 93.5% of the dry matter was partitioned to the vegetative component of the shoot with the remaining 6.5% partitioned to fruit. However, in shoots from defoliated trees 98.4% of the dry matter was partitioned to the vegetative component of the shoot with only 1.6% distributed to fruit.

Table 6 Effect of pre-anthesis defoliation on the distribution of dry matter in mature springgrown fruiting shoots of cv. Hass trees. Data are mean values ± SEs of five shoots from each of three trees. Percentage allocation of dry matter within shoots are indicated in parenthesis.

Shoot component	Dry weight (g shoot^{-1})	
	Untreated	Pre-anthesis defoliation
Leaf	8.84± 0.22 (82.8)	11.57 ± 0.08 (79.3)
Stem	1.14± 0.35 (10.7)	2.79 ± 0.35 (19.1)
Fruit	0.70± 0.18 (6.5)	0.23 ± 0.20 (1.6)
Total shoot	10.68± 0.25	14.59 ± 0.21

With respect to final yield there was a significant reduction in both fruit number and total weight on trees defoliated prior to inflorescence development (Table 7). Based on the

cumulative yield for the two years of the experiment, pre-flowering defoliation reduced fruit numbers and yield by ca. 77%.

Table 7 Effect of pre-anthesis defoliation on the cumulative fruit numbers and yield (1992 & 1993) of cv. Hass trees. Data are mean values ± SEs of three trees.

Treatment	Fruit number ($tree^{-1}$)	Fruit weight ($kg\ tree^{-1}$)
Pre-anthesis defoliation	24.67 ± 3.93	6.73 ± 0.74
Control (retention of leaves)	111.00 ± 2.08	30.63 ± 0.94

Fruit retention on indeterminate and determinate inflorescences

There was an exponential loss of fruit over time from set to spring shoot maturity from both types of terminals (Fig. 18). Initial fruit set was considerably higher on the determinate terminals (62.5) compared with indeterminate terminals (46.2). At the completion of spring shoot growth (ca. 40 days after bud-break) an average of only 1.7 and 0.4 fruit remained on determinate or indeterminate terminals, respectively. This was equivalent to 2.7% of the initial set on determinate, and 0.9% for indeterminate terminals.

3. 3. 4 Discussion

Leaf ontogeny and A characteristics

Young leaves are heterotrophic, i.e. sinks, depending to a greater or lesser extent on photoassimilates imported from other regions of the plant for growth. However, by full expansion they are autotrophic (or sources), exporting products of photosynthesis to support growth and development in the total plant (Dale 1985; Turgeon 1989; Kozlowski 1992). The sink-source transition in leaves has been the subject of many studies, with leaves

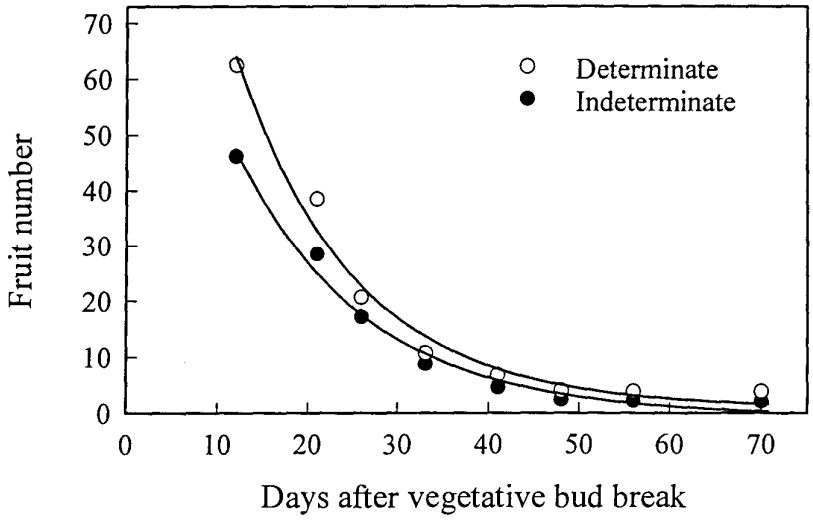

Fig. 18 Fruit loss from indeterminate and determinate flowering terminals from fruit set to maturity of the spring shoot. The regression model for fruit loss from indeterminate terminals is represented by the equation $y = -0.509 + 109.664(0.933^{x})$, $r^2 = 0.99$; and for determinate terminals is represented by the equation $y = 0.907 + 156.42(0.927^{X})$, $r^2 = 0.98$. The curves are significantly different in placement as judged by *t* test ($P < 0.01$). Data points are mean values of fruit numbers from three terminals on each of five trees.

expansion (Turgeon 1989). However, they continue to import photoassimilates from nearby source leaves for a period after beginning the export of their own carbon-based products (Fellows and Geiger 1974; Ho and Shaw 1977; Anderson and Dale 1983). It is likely that the longevity of leaves influences the stage of development at which they undergo the sink-source transition. For instance, leaves with a life span of less than eight months reach the sink-source transition at 25 to 50% of full expansion *(Cucumis sativis,* Hopkinson 1964 and Ho *et al.* 1984; *Vitis vinifera,* Bernard 1985; *Actinidia chinensis,* Lai *et al.* 1988), while in evergreen species it is delayed until leaves are near full size *(Citrus spp.,* Kriedemann 1969a; *Persea americana,* Buchholz 1986).

In this study, 'Hass' avocado leaves reached full expansion 31 days after bud-break which is similar to the 27-28 days reported by Schaffer *et al.* (1991) for leaves of the West Indian cvs. Booth-8 and Peterson in a warmer climate. Although a net gain in A of 'Hass' leaves in this study was recorded at 80% of full leaf expansion (24 days old), ^{14}C studies by Buchholz (1986) suggested that avocado leaves do not become an effective source until fully expanded. i.e. when about 28-30 days old. This transition period from photosynthetic competency to net exporter of assimilates supports results reported for other species (Fellows and Geiger 1974; Ho and Shaw 1977; Anderson and Dale 1983) and may be due to the requirements of growth and R_d exceeding the initial supply of photosynthetic products.

Twenty days after full leaf expansion there was a two-fold increase in A with A_{max} occurring 50 days after bud-break. This result contrasts with those reported by Kozlowski (1992) in his review where the attainment of A_{max} in leaves occurred between 35 to 90% of full expansion. However, these values refer to herbaceous dicotyledonous species with a leaf age span of less than five months *(Phaseolus vulgaris L.,* Fraser and Bidwell 1974; *Fragaria virginiana,* Jurkin *et al.* 1979). Schaffer *et al.* (1991) found that A_{max} for the West Indian cvs. Peterson and Booth-8 was not reached until ca. 60 and 80 days after bud-break, respectively. The longer time taken to reach A_{max} in avocado leaves is probably a function of increasing chlorophyll and nitrogen concentrations which continue to rise until some time after full leaf expansion (Fig. 8) (Schaffer *et al.* 1991). Furthermore, avocado leaves are relatively large and more sclerophyllous than those of most other evergreen fruit trees.

The A_{max} measured on spring grown leaves reported herein (13.1 µmol CO_2 m^{-2} s^{-1}), is considerably higher than previously published values for the Guatemalan race cv. Edranol (9.1 µmol CO_2 m^{-2} s^{-1}, Bower *et al.* 1978), the Mexican cv. Fuerte (6.2 µmol CO_2 m^{-2} s^{-1}, Scholefield *et al.* 1980) and the West Indian cvs. Peterson and Booth-8 (5.5 and 8.0 µmol CO_2 m^{-2} s^{-1}, Schaffer *et al.* 1991). The higher A in this study may be due to more favourable environmental conditions during measurements; the effect of enhanced sink strength from the developing fruit on these shoots (Hansen 1970; Ghosh 1973; Fujii and Kennedy 1985); and/or most likely freedom from sink-limited feedback inhibition. The lower values reported from previous studies were measured on container-grown and on field-grown trees where

growth was probably restricted by the container or soil factors (Arp 1991, Crane *et al.* 1994). This can suppress A due to limited root sinks and an accumulation of photoassimilates in leaves (Schaffer *et al.* 1987; Arp 1991). Schaffer *et al.* (1994) provide a more detailed discussion on the effect of sink-limitation on A with respect to container-grown vs. field grown trees.

In the second study defining the response of single 'Hass' leaves to increasing PPF (3. 2), the A_{max} of non-stressed leaves in full sunlight (1800 µmol quanta m^{-2} s^{-1}) was measured at 17.54 ± 0.39 µcool CO_2 m2 $^{s-1.}$ This was determined on mature summer-grown leaves, following a period of quiescence in the tree when leaves attain their maximum nitrogen content for the year (Fig. 8). Net CO_2 assimilation rates of this magnitude for single 'Hass' leaves have been measured on field-grown trees by the author for a number of years during the late summer/autumn period, using both LI-COR 6200 and CIRAS-1 photosynthetic meters (unpublished data). These data are contrary to the long-accepted contention that evergreen trees have lower A's than deciduous trees (Larcher 1969; Chabot and Hicks 1982). Indeed, the A_{max} measured for 'Hass' avocado in this study is similar to that reported for almond (18.0), apple (15.7 ± 5.6), pecan (14.5 ± 2.1) and sweet cherry (17.9 ± 5.3) (Flore and Lakso 1989).

The quantum yield (0) of non-stressed 'Hass' leaves was determined at 0.0545 µmol CO_2 µmol $quanta^{-1}$ and approximates the range defined for C_3 plants (0.0524 ± 0.0014; Ehleringer and Bjorkman 1977). The 30 µmol quanta m^{-2} s^{-1} value determined as the light compensation point for A falls within the upper end of the range defined for shade tolerant species (Thompson *et al.* 1992) indicating the ability of avocado leaves to exploit low levels of incident light. Together with the high A_Q (16.12 µmol CO_2 m^{-2} s^{-1}), it demonstrates the plasticity of this species in its response to the light environment. Net CO_2 assimilation at light saturation has been reported for a diversity of rainforest tree species which range from ca. 2.4 to 12.1 µmol CO_2 m^{-2} s^{-1}, depending on their ecological niche in the forest canopy (Langenheim *et al.* 1984; Oberbauer and Strain 1984; Chazdon and Pearcy 1986; Doley *et al.* 1988;Thompson *et al.* 1992). The A_Q for avocado is considerably higher than the aforementioned range and the ecological significance for

The *A* rates resulting from short-term exposure of single avocado leaves to enriched partial pressures of CO_2 are unlikely to be sustainable. Research with other species has shown a downward rate adjustment after long-term exposure to elevated CO_2. Although reasons for this decline have not been fully elucidated it has been suggested that it may be due to a decline in carboxylation efficiency due to reduced Rubisco activity; suppressed sucrose synthesis caused by an accumulation of starch; inhibition of the triose-P carrier; limitation of daytime photosynthate export from sources to sinks; or insufficient sinks in the plants (Guinn and Mauney 1980; DeLucia *et al.* 1985; Koch *et al.* 1986; Fetcher *et al.* 1988; Sage *et al.* 1989). Short-term CO_2 enrichment of 'Hass' leaves at saturating PPFs increased A by ca. 300% compared with ambient CO_2 partial pressures. An increase of similar magnitude was reported by Garcia *et al.* (1994) for *Pinus eldarica* in response to atmospheric CO_2 enrichment. They were able to continuously measure whole tree A at enriched CO_2 partial pressures for 4 to 5 days and found that C_A increased from 25.1 to 77.5 μmol CO_2 $tree^{-1}$ s^{-1} when CO_2 partial pressures were raised by 450 μmol mol^{-1}. These preliminary results with 'Hass' however, indicate high carboxylation efficiency, particularly when compared with the response of mangosteen (a shade-tolerant tropical rainforest species) to CO_2 enrichment (Wiebel *et al.* 1993).

Leaves of evergreen plants grown in the subtropics are often exposed to conditions during winter that favour photoinhibition due to low temperatures interacting with excess incident light. Chill injury in plants which develop photoinhibition, characteristically results in a reduction of Q_A and Ø (Powles *et al.* 1983). The reduced carboxylation efficiency of cold stressed leaves in this study was most likely due to photoinhibition following exposure to temperatures < 10°C. Indeed, this is indicated by the reduced F_v/F_m ratio of 'Hass' leaves, suggesting a lower capacity of PS II for electron transport resulting in a significant decline in 0. However, rate limitation of photosynthesis may also be attributed to lowered stomatal conductance (Flore and Lakso 1989) which can occur following chilling temperatures (Wilson 1979). In this study it is unlikely that this factor was a major contributor to reduced *A* under light saturating conditions. When leaves were exposed to non-limiting partial pressures of ambient CO_2 and saturating PPFs, Ci increased in a linear relationship indicating unrestricted diffusion of CO_2 through the mesophyll tissues. The photoinhibition that occurred was

reversible with leaves recovering substantially (as determined by the F_v/F_m ratio) by the end of October.

Carbon balance of the fruiting shoot

Crop yields for many subtropical and tropical evergreen tree fruit species, e.g. avocado, litchi, macadamia, and mango, are low compared with "similar" temperate species. In some cases environmental conditions at critical stages of floral biology limit fruiting. However, for the most part fruit set is prolific but is followed by a heavy drop during the first few weeks of ontogeny. This normal process of yield adjustment establishes a sink/source balance, i.e. fruit/leaf ratio. In many instances this adjustment favours the vegetative bias of these trees which have not undergone the intensive selection and development programs of temperate fruit crop species. For instance, mango has had a long history of cultivation in India where it was grown for the Rajahs but selected on quality rather than yield criteria, and the large scale production of grafted avocado and macadamia as orchard trees has only occurred from the 1920s in spite of a long period of utilisation of the former. Thus, improvement of the harvest index of these crops through manipulation of resource allocation is of primary concern to the horticulturist.

With avocado the study of spring shoot ontogeny indicated that the greatest loss of fruit coincided with the period during which the shoot was a strong sink (i.e. net A loss) with 60% of the initial fruit set abscising during the first 27 days after bud-break. The youngest leaves of the shoots were sinks for another 15 days (42 days after bud-break) during which time a further 22% of the fruits were lost. Fruit retention stabilised at the time that spring shoots reached maximum source strength. It has also been shown that dry matter gain of individual fruit is minimal during the period of net leaf carbon loss but becomes substantial as the spring shoot approaches maximum source strength (Whiley 1990).

Previous research with avocado has suggested that the fruit and shoot components of spring growth are competitive sinks for available assimilate. Tipping during the early stages of shoot growth or chemically retarding spring shoot growth (especially indeterminate fruiting shoots)

has been effective in retaining more fruit on shoots and increasing final yield (Biran 1979; Blumenfeld *et al.* 1983; Kohne and Kremer-Kohne 1987; Adato 1990; Cutting and Bower 1990; Wolstenholme *et al.* 1990). In recent studies with partitioning of ^{14}C-photosynthates during flowering and fruit set of avocado, Finazzo *et al.* (1994) reported that the sink strength of floral, fruitlet and vegetative organs was similar on indeterminate inflorescences. They concluded that neither developing fruitlets or shoots were limited for assimilates during the critical period of fruitlet abscission as assimilate was "available" for distribution from other areas such as branch tissues. These conclusions are against the weight of evidence in the literature and it may be argued that branches themselves are strong sinks for photoassimilates. Shoots of avocado are succulent and somewhat brittle and are thicker than young shoots of most other evergreen fruit tree species (Chandler 1958). Their strength is due to a rapid increase in thickness rather than the nature of the wood suggesting that they are important sinks for assimilates (Chandler 1958). In ^{14}C-photosynthate studies with non-fruiting containergrown avocados Whiley and Schaffer (1993) found that when leaves were exposed to $^{14}C0_2$ when either shoots or roots were sinks, > 40% of the recovered ^{14}C was from trunk/shoot organs. Studies in other crops with ^{14}C-photosynthate report a high percentage (up to 76%) of the recovered ^{14}C from shoots at times of sink activity in other portions of the plant, suggesting that the "pool" of photosynthates in shoots may not be available for re-translocation (Dickson and Larson 1981; Dickson *et al.* 1990). However, the Finazzo *et al.* (1994) experiments were carried out on trees growing in soils which restrict root growth (Crane *et al.* 1994) and these conditions are known to influence some physiological responses of trees (Schaffer *et al.* 1994) and may explain their different results.

The study on the dynamics of fruit abscission from indeterminate and determinate shoots also supports the hypothesis that fruit loss is at least to some extent influenced by the closely coupled spring shoot. Not only were more fruit lost from indeterminate terminals during the first 70 days of spring growth (Fig. 17) but fruit grew faster on determinate shoots (Fig. 7) and were larger at maturity. Previous studies with 'Hass' have also shown that increased fruit size at spring shoot maturity is expressed in larger fruit at harvest (Wolstenholme *et al.* 1990; Whiley *et al.* 1991). Recently completed ^{14}C studies with developing avocado shoots (Whiley and Schaffer 1993) confirmed that expanding leaves

supports the concept of competitive vegetative sinks during the first 42 days after bud-break, i.e. incomplete temporal and spatial separation of vegetative and reproductive growth, especially in indeterminate fruiting shoots. It is suggested that the size of the assimilate pool (stored and current from existing mature leaves) and the strength of the shoot sink (i.e. vigour of growth) largely determines the success of fruit retention during the first 60 days after budbreak.

While initially competitive, renewal shoot growth during spring is necessary for the secondary development of avocado fruit. Wolstenholme *et al.* (1990) demonstrated that with severe retardation of spring shoot growth of cv. Hass with paclobutrazol sprays, fruit dry mass at flush maturity was significantly reduced compared to other treatments resulting in less growth suppression. This was reflected in lower yield at fruit maturity. Similar results were reported by Quinlan and Preston (1971) from shoot tipping and removal studies with apples. Despite the necessity of spring shoot growth, the opportunity remains to manipulate the vegetative reproductive balance to give a more favourable economic yield. Whiley *et al.* (1991) have shown that a low concentration foliar spray of paclobutrazol (Cultar) at full bloom, which slightly suppresses shoot growth of cv. Hass, significantly increased fruit yield. Correct timing of fertilisation with nitrogen can also assist in controlling spring flush vigour thus favouring greater fruit retention and yield (Whiley *et al.* 1988a). "Fine-tuning" of competitive vegetative: reproductive growth interactions at this critical juncture has major horticultural implications, which are becoming increasingly recognised by progressive growers.

These studies have also highlighted the importance in the summer rainfall subtropics of the over-wintered leaf canopy, a variable mixture of spring and summer leaf flush cohorts (presumably of varying overall A), to fruit retention during the development of the renewal spring shoot. As fruit loss was higher from shoots on defoliated trees (Fig. 17), it is not surprising that more dry matter was allocated to the combined leaf and stem components of the shoot. However, with the loss of a net source of current assimilate during the first 25 days of shoot development (Chapter 3.1) it is surprising that these shoots accumulated more dry matter than those shoots on trees where a full canopy was retained. This may be attributed to the additional respiratory loss of carbon from fruiting shoots during early

Whiley (1995) report R, and R_d of young 'Hass' fruit at ca. 12 and 14.5 CO_2 m^{-2} s^{-1}, respectively. This is approximately three times greater than the maximum R_d of 4.6 CO_2 m^{-2} s^{-1} reported for 'Peterson' avocado leaves (Schaffer *et al.* 1991).