## 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$^{\circ}$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).

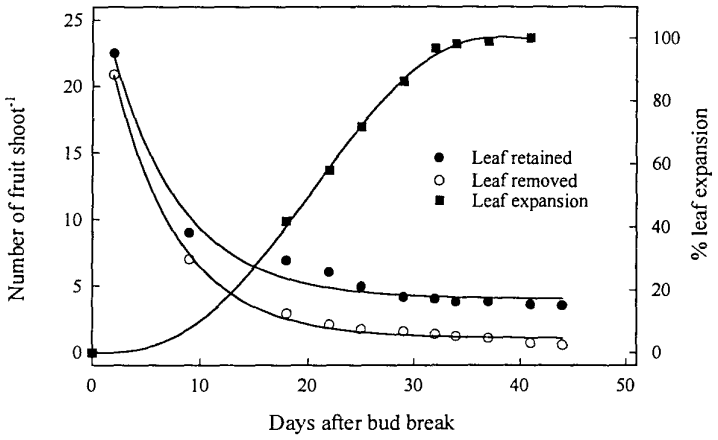


**Fig. 17** Spring leaf expansion and fruit loss from shoots on trees where the mature, over-wintered leaves were either retained or removed prior to anthesis. The model for expansion of the youngest leaf is represented by $y = -2.132 + 106.44/(1 + \exp(-(x-20.274)/5.397))$, $r^2 = 0.99^{**}$ (data are 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

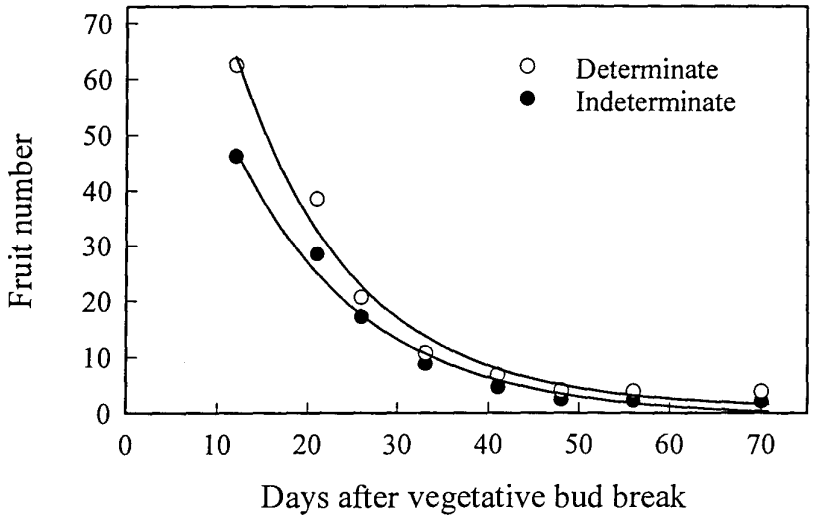


**Fig. 18** Fruit loss from indeterminate and determinate flowering terminals from fruit set to maturity of the spring shoot. The regression model for fruit loss from indeterminate terminals is represented by the equation $y = -0.509 + 109.664(0.933^{x})$, $r^2 = 0.99$; and for determinate terminals 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).