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CARBOHYDRATE CYCLING IN RELATION TO SHOOT GROWTH, FLORAL INITIATION AND DEVELOPMENT AND YIELD IN THE AVOCADO

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ABSTRACT

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Carbohydrate levels, shoot growth, floral initiation and yield were studied in 10 avocado trees of the cultivar 'Fuerte' over 2 years from March 1976 to April 1978.

There were two main vegetative growth flushes per year, one in spring and one in summer. Floral initiation occurred in autumn, flowering was in late winter/spring and the fruit matured in winter. Thus one vegetative flush coincided with the end of flowering and the other occurred just prior to floral initiation. Carbohydrate levels were lowest after the summer vegetative flush and just prior to floral initiation in autumn. Levels increased over winter during the period of floral development and reached maximum levels in early spring, just prior to flowering. A steep decrease in carbohydrate levels, particularly starch, occurred during flowering, shoot growth and fruit development.

The trees showed a marked biennial bearing cycle. The heavy yield in 1977 followed high levels of starch during the previous year and resulted in much lower levels being accumulated during the following winter and spring. The yields in 1976 and 1978 were low. Biennial bearing appeared to be closely related to the carbohydrate reserves of the trees.

Keywords: avocado; biennial bearing; carbohydrate cycling; floral initiation; *Persea americana* Mill.

INTRODUCTION

Low yields of avocado (*Persea americana* Mill.) are a problem in most production areas, including Australia (Trochoulias and O'Neill, 1976), California (Bergh, 1967), Florida (Ruehle, 1963) and Israel (Lahav et al., 1971). The problem often appears as a biennial bearing cycle where a heavy

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crop one year is followed by a poor yield the following year (Hodgson, 1946; Alexander and Sarooshi, 1980). Many authors have discussed the importance of the relationship between carbohydrate levels, fruits, leaves and flower initiation (see Jackson and Sweet, 1972) and the importance of considering all these factors with respect to yield. Thus all aspects of tree development throughout the year appear to have an effect on yield.

The avocado is grown commercially in a number of countries where the climates vary from temperate through sub-tropical to tropical (Knight, 1980). Under the sub-tropical conditions of Florida, cultivars of Guatemalan and West Indian parentage were shown to have a 3-month development period between floral initiation in winter (December) and anthesis in spring (March) (Reece, 1942). A similar situation was found with Mexican, Guatemalan and Mexican—Guatemalan hybrid cultivars under the temperate conditions of California (Schroeder, 1951), although the development period was generally shorter. In South Africa, 'Fuerte' initiated flowers in autumn (March) and flowering commenced in winter (June), continuing until spring (late September) (Robertson, 1969). Thus in the areas for which information is available there is a 2- to 3-month development period between floral initiation and anthesis.

In this paper we report on the timing of flower bud initiation and development in temperate Australia in relation to yield, vegetative flushes and the carbohydrate status of 'Fuerte' trees.

MATERIALS AND METHODS

Plant material. — Studies were conducted on 10 trees of 'Fuerte', grafted onto Mexican seedling rootstocks, planted in 1968 at a density of 299 trees per ha, irrigated by overhead sprinklers and growing in the CSIRO experimental orchard at Coomealla in the Murray Valley Irrigation Area (latitude 34° S). Avocados are grown commercially in this semi-arid irrigation area of south-east Australia.

Shoot studies. — Six shoots each of two types, originating from the vegetative flush of summer 1976, were selected in autumn 1976 on each of the 10 trees. The two types were long vertically growing shoots and short horizontal shoots. The mean length, leaf number, basal diameter and lateral shoot number of the former were 32.1 cm, 31.5, 0.93 cm and 5.1, respectively, and of the latter 9.8 cm, 8.5, 0.55 cm and 0, respectively, per shoot.

These shoots were observed at regular intervals to determine the times of vegetative growth (flushing), and after each growth flush, measurements were made of shoot extension, leaf number and lateral shoot number. The dates of measurement were 24 March 1976; 2 February, 29 March, 30 November 1977 and 5 April 1978.

Floral studies. — Bud samples were collected from these trees at approximately monthly intervals from March 1976 to July 1977. Flowering occurs during the period September to November, so two flowering seasons were studied. Terminal buds and axillary buds from the 1st, 5th and 6th node down from the terminal were sampled from short shoots similar and adjacent to those described earlier and used for the shoot growth studies. All buds were bisected to allow better penetration of the fixative (3% glutaraldehyde in 0.025 M phosphate buffer) before dehydration through an alcohol series and embedding in glycol methacrylate. Longitudinal sections were cut at 5 μm and stained with periodic acid—Schiff's reagent and toluidine blue O (Feder and O'Brien, 1968).

Carbohydrate sampling and analysis. — Four branches (approximate diameter 100 mm) of each of the 10 experimental trees were sampled for carbohydrate analysis. A hole 19 mm diameter and 10 mm deep was cut in the branch, the bark was discarded and the wood was dried (60°C), ground and analysed for total ethanol soluble sugars and starch using α-amylase digestion and the phenol/sulphuric acid method for colorimetric determination of sugars (Dubois et al., 1956) using glucose as a standard. Results were expressed on a starch- and sugar-free residual dry weight basis (Priestley, 1973). Sampling continued for 3 seasons; 1—2 months apart in spring and summer and less frequently in autumn and winter.

Production. — Total yield and average weight of fruits were determined for the experimental trees every year during June to August.

RESULTS

The timing of vegetative flushing, floral initiation, flowering and fruit maturity are shown in Fig. 1.

Shoot growth. — In both seasons, two major periods of vegetative shoot growth (flushing) occurred on the experimental trees between flowering in September and fruit maturity in June (Fig. 1). These growth flushes varied slightly in the time of occurrence and intensity within and between trees, and not all of the observed shoots grew during all of the flushes. For this reason results were pooled for the 10 trees. A higher percentage of all shoots grew in the spring compared with the summer, and at all flushes more long shoots grew than short (Table I). Almost half (26) of the shorter shoots died during the two seasons while only one of the long shoots died.

Both long and short shoots increased in length and lateral number (Fig. 2A). Total number of leaves formed also increased as the shoots grew, but the actual leaf numbers on the shoots (leaves formed minus leaves abscissed) decreased for short shoots over all measurement times, and for long shoots from March 1977 onwards (Fig. 2B). Thus the shoots lost more old leaves

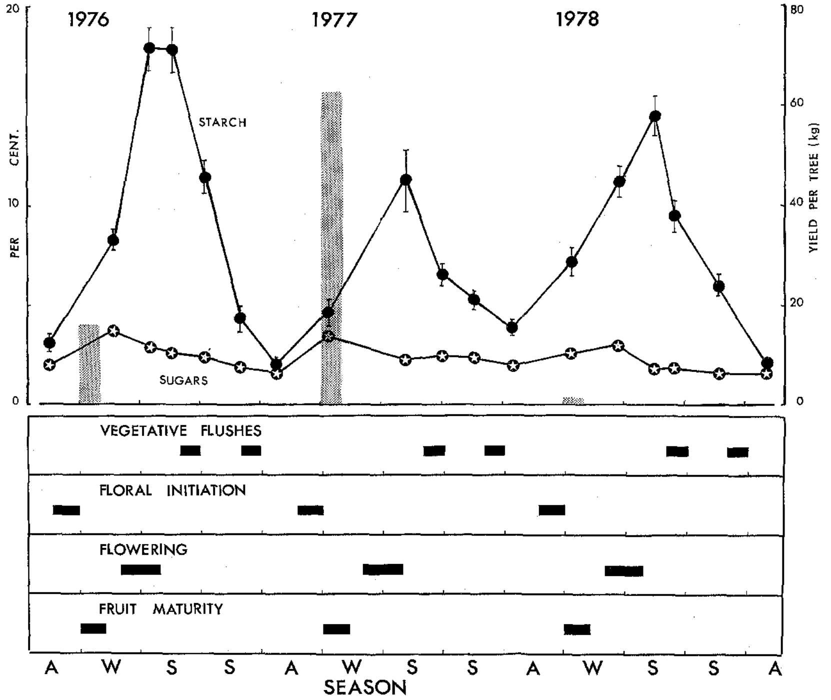


Fig. 1. Diagramatic representation of times of vegetative flushes, floral initiation, flowering, fruit maturity and variations in starch and ethanol-soluble sugars from 'Fuerte' avocado trees from 1976 to 1978. The histograms show the yields of fruit recorded for each year. Bars represent 2 × standard error.

TABLE I

Number of shoots and percentage flushing for long and short shoots between Spring 1976 and Summer 1978

	Shoot type			
	Long		Short	
	Number	Flushing (%)	Number	Flushing (%)
Spring 1976	60	96.7	59	69.5
Summer 1977	60	75.0	57	24.6
Spring 1977	60	88.3	47	68.1
Summer 1978	59	61.0	34	29.4

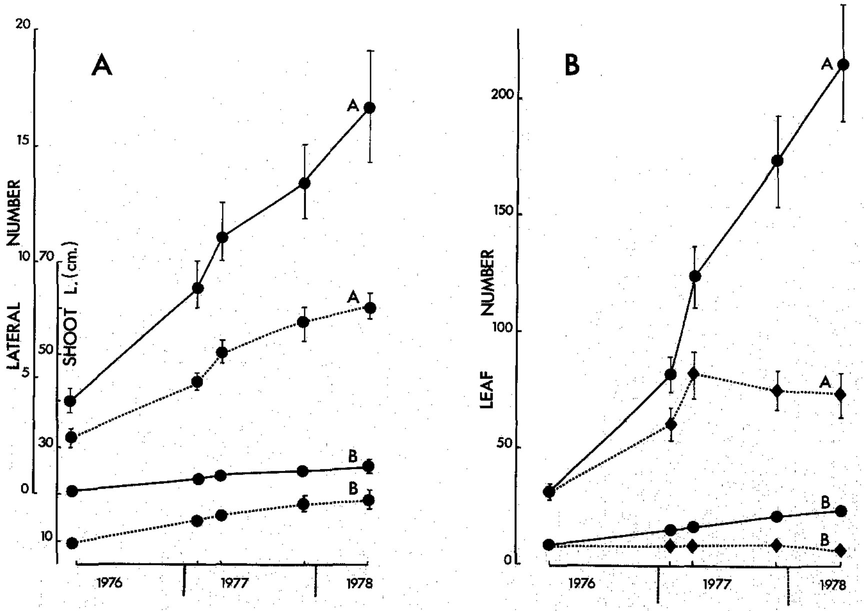
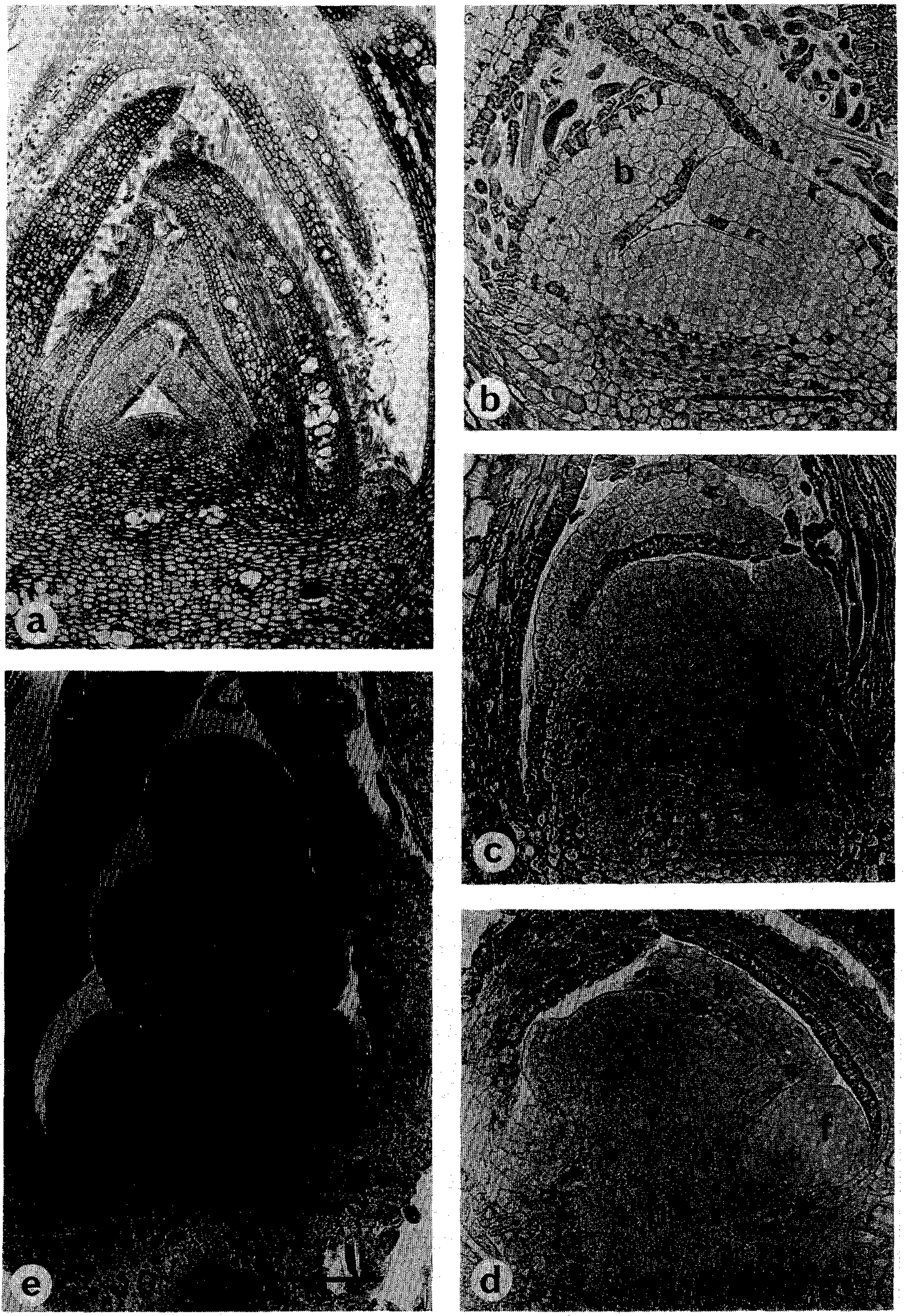


Fig. 2. A. Length of shoots (• - - - •) and number of lateral shoots (•——•). B. Total number of leaves formed (•——•) and net number of leaves present (♦ - - - ♦) for the long (A) and short (B) shoots over the 5 times of measurement. Bars represent 2 × standard error.

due to abscission than were produced on new shoot extensions during this period, probably due to the high salinity of the irrigation water.

Floral studies. — The results were similar for 1976 and 1977. From December to April all buds had a vegetative terminal with undifferentiated meristems in the axils of the bud bracts (Fig. 3a). In some cases these axillary meristems had produced one or two bracts (Fig. 3b). The first stages in floral development were observed during April and May. The axillary meristems elongated (Fig. 3c) into secondary axes, but the first definite appearance of a floral meristem was the production of tertiary axes in the axils of the bracts (Fig. 3d). Each secondary axis continued to elongate (Fig. 3e) and was determinate in development. The apex of each axis developed into a flower (Fig. 4a,b) and further flower and axis primordia were produced basipetally. The apex of the meristem became flattened and the first perianth and stamen primordia (Fig. 4c) were observed in May. The most advanced buds had pistil primordia (Fig. 4b) by June and were fully developed by September (Fig. 4d). In all cases observed, the terminal apex of the bud remained vegetative and up to 10 floral axillaries were present (Fig. 4a). Each floral axillary developed into an inflorescence.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b
b
c
e
f
d

There was a progression in development down the shoot. The terminal bud of a shoot became floral before the buds at Nodes 1, 5 and 6 down from the terminal. In addition, the axillary apices in the upper bracts of a bud became floral ahead of those in the lower bracts of the same bud. Moreover, the terminal flower produced by each mersitem was always the most advanced developmentally. However, the apical meristem of a bud, either terminal or from Nodes 1, 5 and 6, always remained vegetative. There was no difference in anatomy between the terminal bud of a shoot and those buds at Nodes 1, 5 and 6 down from the terminal except that the terminal was larger and, for a given sampling, more advanced developmentally. Not all buds became floral; some buds from Nodes 1, 5 and 6 remained vegetative.

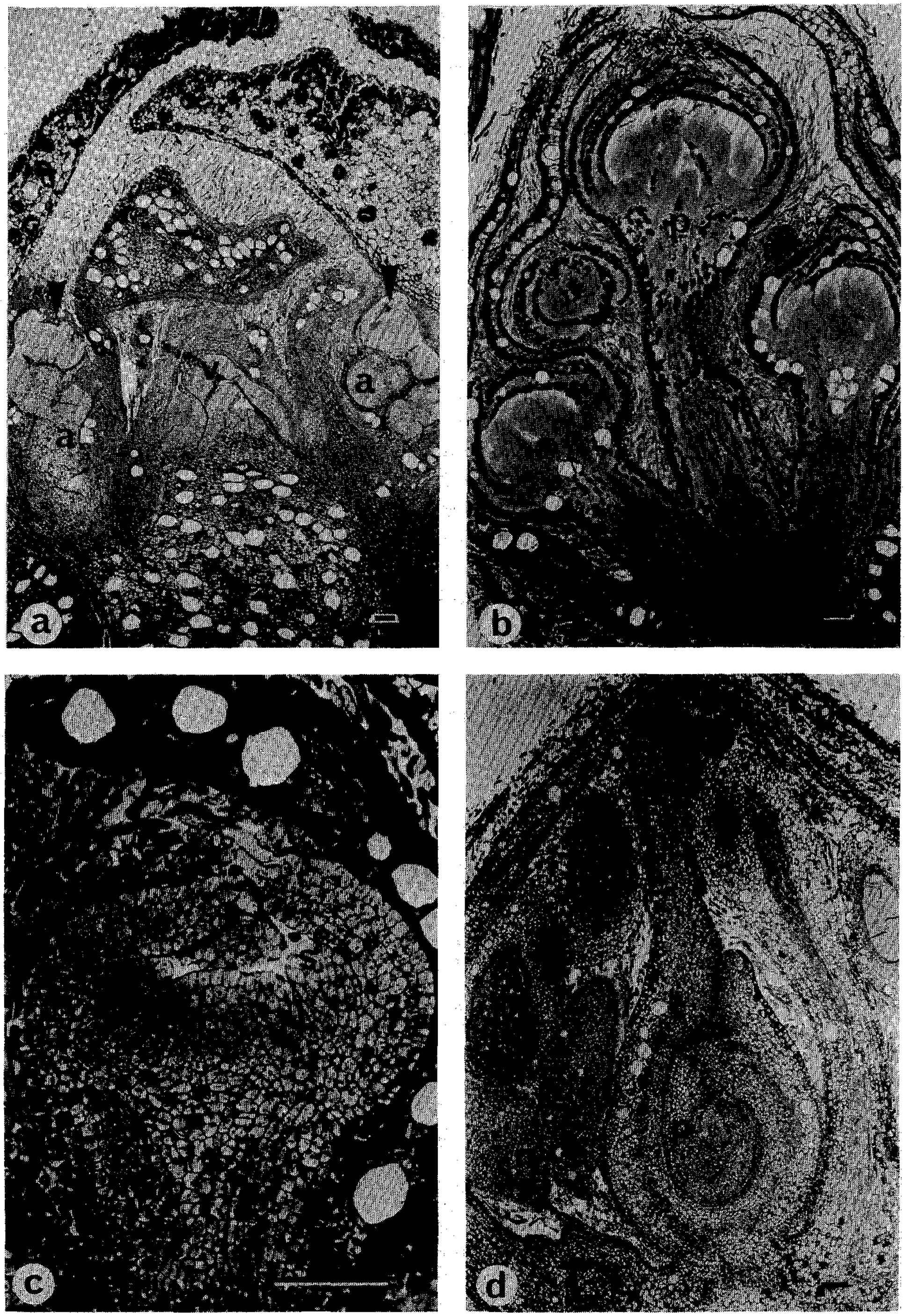
Carbohydrates. — The concentration of sugars was maximum in winter and declined through spring and summer to a minimum in autumn, corresponding to minimum levels of starch (see Fig. 1). Maximum levels of starch occurred in early spring and decreased sharply from then until autumn. During this period of rapid decline of carbohydrate reserves, flowering and early fruit growth were taking place as well as two vegetative growth flushes. Vegetative growth ceased and fruit development was almost completed by late autumn and the reserves of starch began to accumulate rapidly through autumn and winter to reach maximum levels again in spring.

TABLE II

Mean number and weight of avocados per tree and per hectare for the experimental trees for the seasons 1975—1979

	Fruit number per tree	Yield	
		kg/tree	t/ha
1975	222 ± 31	63.9 ± 8.2	19.1
1976	48 ± 8	16.1 ± 2.4	4.8
1977	278 ± 27	62.6 ± 5.9	18.7
1978	4 ± 3	1.2 ± 0.9	0.4
1979	112 ± 29	29.4 ± 7.5	8.8

Fig. 3. Progression of avocado buds from vegetative to floral. (a) Node 1 bud collected 18 March 1976 showing vegetative apex, v, and undifferentiated axillary meristem, a. (b) Terminal bud collected 4 May 1976 showing axillary mersitem which has produced some bracts, b. (c) Terminal bud collected 4 May 1976 showing elongated axillary meristem. (d) Terminal bud collected 4 May 1976 showing axillary meristem with floral axes, f, in the axils of bracts, b. (e) Terminal bud collected 4 May 1976 showing elongated axillary, a, secondary meristem with floral, f, tertiary meristems. Bar represents 100 μm.


a
a
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d

Productivity. — The mean number and weight of fruits for the 10 experimental trees for the seasons 1975 to 1979, inclusive, are presented in Table II. The results for 1975—1979 are presented because this series of yields shows the biennial nature of cropping in the trees.

DISCUSSION

Alternate bearing in the avocado in temperate southern Australia appears to be closely related to the carbohydrate levels in the tree. High yields follow a high accumulation of starch during the previous winter and result in low levels of starch during the following year. Maximum carbohydrate levels occur in early spring and decline during flowering, shoot growth and fruit development to a minimum in autumn. Accumulation begins at about the time of cessation of vegetative activity and continues over winter until maximum levels are attained in spring. Cameron and Borst (1938) reported similar fluctuations in carbohydrates in young avocado trees grown in California and showed differences between fruiting and non-fruiting trees. The large branches (and presumably the trunk and large roots) store considerable amounts of starch, with the concentration varying between 3 and 20%. High winter levels of sugars are often associated with a conversion of starch to sugars at low temperatures (Priestley, 1962), but in this case starch levels increased at the same time as sugars. Throughout the year, sugars varied less than starch, indicating that sugars were not a major storage carbohydrate but constituted a ‘pool’ for immediate use within the tree. It appears that under the cool winter conditions of temperate southern Australia (average minimum winter temperature 4.8° C), the winter is an important period for the accumulation of reserves. The success of grafting has been related to the carbohydrate reserves of the shoot selected for scion wood (Garner, 1979). Our experiences in propagating avocados have indicated that the best period for grafting is in late winter, and this coincides with the highest levels of starch within the tree.

Floral initiation has been shown to occur at a time of minimum carbohydrate content of the major branches. Therefore, it seems unlikely that the level of carbohydrate causes floral initiation. Rather, low levels of carbohydrate may cause a cessation of vegetative activity and this fact may be more related to floral initiation. Floral development in avocados growing

Fig. 4. Flower development in floral avocado buds. (a) Node 5 or 6 bud collected 11 June 1976 showing vegetative apex, v, and floral axillary meristems, a. The apex of each axillary meristem is a flower primordium (arrowhead). (b) Terminal bud collected 9 July 1976 showing floral axillary meristem with pistil primordium, p, in the developing flower at the apex of the meristem. (c) Terminal bud collected 29 July 1977 showing developing flower with perianth, pe, and stamen, s, primordia. (d) Node 5 or 6 bud collected 20 September 1976 showing flower just prior to anthesis with pistil, p, anthers, an, nectaries, n, and perianth, pe. Bar represents 100 μm.

in temperate Australia showed a similar sequence to that described previously in other parts of the world. In general, the period between floral initiation and anthesis was longer than that observed in Florida (Reece, 1942), California (Schroeder, 1945, 1951) and South Africa (Robertson, 1969), probably due to the cooler winter experienced in southern Australia. No differences were observed in the numbers of flowers produced per inflorescence each year.

There were two vegetative growth flushes per year, one in spring and one in summer. Floral initiation occurred in autumn, flowering was in late winter/spring and the fruit matured in winter. Thus one vegetative flush coincided with the end of the flowering period. All inflorescence buds had a vegetative terminal which developed into a vegetative shoot following anthesis. It is possible that this vegetative flush competes with the developing fruits for available reserves. This is particularly likely as the vegetative terminal is apical and the fruiting branches are axillary. Certainly post-pollination fruit drop is a major problem in the avocado (Sedgley, 1980; Kotze, 1982) and the vegetative flushes occur at a time of falling carbohydrate reserves in the tree as a whole. The summer growth flush does not appear to affect yield to the same extent and may be the more important of the two flushes as it precedes the winter increase in carbohydrate reserves. In this study the spring flush was the strongest in both years of observation. It is possible that management practices which reduce the post-anthesis flush may improve yields in avocado and reduce biennial bearing. This flushing pattern varies with both cultivar and environment. In more sub-tropical and tropical environments, vegetative flushes on avocado trees are less uniform and more frequent than observed here. Similarly, preliminary observations on carbohydrate accumulation in a sub-tropical area at Alstonville, New South Wales (S.E. Australia, latitude 29° S) showed less fluctuations of carbohydrate reserves throughout the year than at Merbein (T. Trochoulias and P.B. Scholefield, unpublished data, 1978). However, it is not possible to say whether this leads to less biennial bearing.

Both the long shoots and the short shoots had two distinct growth flushes during each year of observation. The longer shoots were responsible for most of the extension growth of the tree. The short shoots appeared to be shaded by the more vigorous long shoots and many died during the experimental period. There does not appear to be any functional difference between the shoots with regard to flowering, as is the case in some temperate species. It is possible that the short shoots provide a short-term increase in leaf area to maximise the photosynthetic capacity of the tree. Avocados are very sensitive to chloride ions (Ayers et al., 1951). Maximum monthly salinity of the irrigation water reached over 800 EC units during some months of the period of observations, and these levels are thought to have caused the considerable leaf drop in spring 1977 and the low yields in 1978.

In general, the flush behaviour and carbohydrate fluctuations throughout the annual growth cycle of the avocado are similar to those described in citrus (Cameron, 1932; Sauer, 1951). Goldschmidt and Golomb (1982) reported large fluctuations in starch in mandarin trees, particularly in the trunk and roots, between the "on" and "off" bearing cycle. Citrus and avocado are both sub-tropical evergreen species and show more similarities to each other than to the deciduous species for which most information is available. Nevertheless, the deciduous species show a similar general pattern to the avocado, but without the large accumulation of carbohydrate during winter (Priestley, 1960). In all cases there appears to be a close relationship between yield and the carbohydrate reserves of the tree. However, the question of which factor triggers the biennial bearing cycle, the yield, or the level of reserves, and what causes the imbalance in the first place is still unclear.

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