

### **3. Architectural analysis of tree form in a range of avocado cultivars.**

#### 3.1 Summary.

Shoot growth and tree architecture were examined in five avocado cultivars at two locations. Each cultivar had a characteristic form judged on tree height and diameter, and number, frequency and angle of inclination of major limbs. This form was related to differences between cultivars in the number and length distribution of axillary branches, and of the relative dominance of proleptic and sylleptic axillary shoots. These differences were apparently established by the interaction between apical dominance and apical control (acrotony). 'Fuerte', 'Gwen' and 'Reed' displayed weak apical dominance in that they produced large numbers of sylleptic shoots. They also displayed weak acrotony, producing few major limbs, relatively short axillary branching and few proleptic shoots. 'Sharwil' exhibited strong apical dominance with relatively few sylleptic shoots, but strong acrotonous growth with many major limbs, and long and numerous proleptic axillary shoots. 'Hass' was intermediate between 'Sharwil' and 'Reed' at the same location. Major differences in tree vigour were found between locations with 'Hass'. Although the basic model of tree architecture was similar at each location, the number of proleptic shoot modules increased. The data are discussed in terms of the opportunities to manipulate tree growth to enhance fruiting efficiency.

**Abbreviations:** SA = South Australia; QLD = Queensland; AGS = annual growth section; AGM = annual growth module; RGM = rhythmic growth module; H/D = height:diameter ratio.

#### 3.2 Introduction.

Major advances in temperate tree fruit production have resulted from a detailed knowledge of tree form and how this may be manipulated by tree training and pruning to optimise fruit yield and quality (Mika, 1986; Brunner, 1990). However, there are few examples with tropical fruit trees where improvements in yield have been due to the manipulation of tree architecture.

Mechanical pruning techniques in citrus have been developed from light interception studies comparing a range of theoretical tree shapes (Golomb et al., 1988; Oren, 1988), rather than from detailed analysis of citrus tree growth habit (Lewis and McCarty, 1973; Davenport and Codallo, 1990). Detailed studies of leaf formation in banana have provided information useful to increasing fruit yields and manipulating harvest dates with this crop (Robinson, 1981; Turner and Hunt, 1983). Similar developmental studies on tropical fruit trees have examined modular elements of growth. However, these have generally been made only from an ecological viewpoint (Tomlinson, 1987; Porter, 1989). Growth phases of some tropical fruit trees received attention with the phenological cycling approach to tree productivity, outlined by Cull (1986). However, only major phenological events were considered, with no details of tree architecture.

This chapter provides an architectural analysis of avocado tree growth (Fig. 3.1). Shoot growth and tree form are described in the context of the Rauh architectural tree model (Hallé et al., 1978). Growth modules are the basic building blocks of architectural tree models (Watkinson and White, 1985). They represent the genetic blueprint of plant development describing the characteristic tree form for each species (Hallé, 1986). Shoot modules are the lowest order growth modules. They are units of extension developed in a single growth flush from a bud or bud primordium (Chapter 5). In avocado, generally one reproductive (spring) and two vegetative (summer and autumn) growth flushes occur over an annual growing period. The complex of shoots forming on a shoot module during a growth flush is called the rhythmic growth module (RGM, Fig. 3.2). During an annual growing period this complex of shoots is called the annual growth module (AGM). One AGM may contain several RGMs, but only the spring RGM is floral. The main axis of an AGM is called the annual growth section (AGS). The main axis of a major limb comprises one AGS for each year of growth.

In this chapter, factors determining variation in avocado tree habit are investigated by comparing the formation of rhythmic and annual growth modules in a range of cultivars. This information will provide the basis for measurement of the effects of cultural practises in terms of cultivar structure.

### 3.3 Materials and methods.

### 3.3.1 Plant material.

Ten 'Hass', ten 'Reed', nine 'Sharwil' and three 'Fuerte' trees, grafted on 'Zutano' seedling rootstocks and growing in the same orchard block at McLaren Vale, South Australia (SA) (35.12 S., 138.32 E.), an area with a mediterranean climate, were used in this study. All trees were four years old in 1989, the first year of this trial, and their growth was monitored over three years. In 1990, three 'Gwen' and three 'Hass' trees growing in Maleny, Queensland (QLD) (26.51 S., 152.51 E.), an area with a sub-tropical climate, were also studied. They were grafted on 'Hass' seedling rootstocks, and were 4 years old in 1990.

### 3.3.2 Tree growth.

In winter 1989 (1990 in QLD), tree height and maximum canopy diameters, measured along north-south and east-west transects, were recorded and means calculated. Major limbs with a basal diameter of more than 35 mm were counted, and their length measured from the point of attachment on the trunk or subtending major limb, to the apical bud terminating the main growth axis of the limb. The average angle of inclination of major limbs was determined from the angle of orientation, relative to the vertical, of straight lines drawn from the base of each limb to a series of points along their length.

Two limbs were selected from the northern side of each tree in SA and two limbs from two trees and one limb from one tree, i.e. five limbs per cultivar, were selected in QLD. AGSs on the major axes were identified, and their lengths measured. The junction between AGSs were identified by the presence of a bud-scar ring, a group of bud-scale scars formerly part of the overwintering apical bud complex; change in bark colour and texture; and by the location of fruit and/or floral scars. Axillary branches arising from each AGS were counted and the length of their main axis recorded as long, medium or short (>1.0 m, 0.5-1.0 m and <0.5 m respectively).

On each major limb, the length of the primary growth axis of RGMs forming the most recent AGS were measured. Features used to identify the base of each RGM included: presence of bud-scar ring formed during the interval between successive growth flushes; shortened internodes; location of proleptic and sylleptic shoots above and below bud-scar rings, respectively; and distinct change in leaf size, shape and/or colour (Figs. 3.1 and 3.2). Proleptic shoots developed from resting buds, and had a bud-scar ring at their base (Fig. 3.3). Sylleptic shoots did not develop from resting buds but grew

contemporaneously with extension of the subtending primary growth axis. They had a bulbous base with no bud-scar ring, and a long hypopodium (i.e. length of shoot from shoot base to first node). Number and location of proleptic and sylleptic axillary shoots, and resting buds, along primary growth axes of RGMs were recorded. Length of axillary shoots, their main axis only, were recorded as long, medium or short; >30 cm, 10-30 cm and <10 cm respectively. Number of shoot modules on compound shoots (i.e. those with more than one flush of growth) were also recorded.

### 3.3.3 Statistical analysis.

Analysis of variance and Scheffé's test were used to test for significance of differences between means. The number of observations in the shoot length x shoot type categories were tabulated and a Poisson model was fitted to the data. Where <5 counts were observed per category, Fisher's exact test was used.

## 3.4 Results.

There were consistent differences between cultivars in tree shape, in the fourth year from grafting (Fig. 3.4). These differences were measured in terms of tree height, crown diameter and number of major limbs. 'Reed' trees were very upright with a height:diameter (H/D) of 1.23, and  $2.8 \pm 0.25$  ( $\pm$  standard error) major limbs. 'Sharwil' trees had  $4.2 \pm 0.46$  major limbs, with a spreading tree form (H/D = 0.89). 'Hass' trees in SA were intermediate in form between 'Sharwil' and 'Reed', with H/D = 0.96, and  $3.7 \pm 0.30$  major limbs. The three 'Fuerte' trees in SA had  $3.7 \pm 0.33$  major limbs, and H/D = 0.80. In QLD, 'Gwen' trees were smaller than 'Hass', but had similar H/D (1.63, 1.52 respectively). 'Gwen' trees also had more major limbs than 'Hass',  $3.3 \pm 0.66$  and  $2.0 \pm 0.57$  respectively. In each environment, within-cultivar variation in tree dimensions was low as demonstrated by the low standard errors. There were differences between the environments, however, as 'Hass' trees in QLD were more upright, and had fewer major limbs than 'Hass' trees in SA. Average length of major limbs, on trees in their fourth year from grafting, did not vary between cultivars in SA. However, major limbs on 'Hass' in QLD were longer than those on both 'Gwen' in QLD and 'Hass' in SA (Table 3.1).

Not all limbs had the same number of AGSs because some grew from buds

on one or two year old wood (Table 3.2). On 'Reed', only current AGSs were measured in 1989 and 1990 as no obvious changes in bark morphology were present to reliably identify AGSs from previous years. In SA, the length of AGSs of the same age were not significantly different among cultivars, although 'Sharwil' tended to be the longest. In QLD, length of 'Gwen' and 'Hass' AGSs were similar in 1988, and 1989. In 1990, however, AGSs were significantly longer on 'Hass' compared with 'Gwen'.

The number and length of axillary branches on major limbs contribute to overall limb dimensions. 'Fuerte' had more branches per major limb than 'Hass', which had more than 'Sharwil' (Table 3.3). This trend correlated directly with the relative percentage of short branches for each cultivar. In SA, 'Sharwil' had more branches in the medium length category than 'Hass' and 'Fuerte'. In QLD, 'Hass' had more branches in the long and medium categories than 'Hass' in SA, and 'Gwen' had predominantly short branches.

The total number of nodes, i.e. shoots + buds, was not significantly different among cultivars, and between locations, on current AGSs with 3 growth flushes (Table 3.4). Length of primary growth axes and pattern of axillary shoot formation on each RGM, were similar within cultivars. Only data from the complete AGS are presented. The numbers of axillary shoots on AGSs were inversely related to the numbers of resting buds. 'Fuerte' and 'Gwen' tended to have more shoots and fewer resting buds than the other cultivars. The relative dominance of proleptic and sylleptic axillary shoots varied among cultivars. 'Fuerte', 'Gwen' and 'Reed' produced more sylleptic and fewer proleptic shoots than the other cultivars. On 'Gwen' and 'Reed', shoots were nearly all in the short category. 'Sharwil' and 'Hass' had similar proportions of each shoot type, but there were more proleptic than sylleptic shoots in the longer shoot categories for 'Sharwil' ( $X^2 = 11.29$  on 2 df,  $P < 0.01$ ), and more sylleptic than proleptic shoots in the longer categories for 'Hass' in SA ( $X^2 = 18.98$  on 1 d.f.,  $P < 0.001$ ). The difference was not significant for 'Hass' in QLD as there were more proleptic shoots on 'Hass' in QLD than in SA. Shoot length data were not recorded for 'Reed', but field observations indicated that nearly all axillary shoots were in the short category with this cultivar. 'Fuerte' in SA, and 'Gwen' and 'Hass' in QLD produced more shoot modules per AGS than the other cultivars (Table 3.5). In 'Fuerte' and 'Gwen' this difference was due to higher numbers of axillary shoots, with 'Hass' in QLD it was due to higher numbers of shoot modules per axillary shoot. On compound shoots, only shoots in terminal positions on their respective axes generally became floral, so their

number indicated the floral potential of trees. 'Hass' in QLD had significantly more terminal shoots than 'Hass' in SA.

Data collected from current AGMs on trees in SA, and presented above, are for 1989 only. Comparable data from subsequent years showed trends similar to those outlined above, although the number and length of new shoot modules decreased as trees became older.

### 3.5 Discussion.

This study has demonstrated important cultivar differences in the number of major limbs, their angle of divergence, and the relative dominance of axillary shoot growth. These differences have implications for both the form of the tree and its bearing capacity. The relative number and length of proleptic and sylleptic axillary shoots in RGMs were characteristic for each cultivar. Similar patterns of dominance were apparent in current AGMs, and there was a corresponding hierarchy of branches on AGSs formed in previous years on major limbs. 'Sharwil', for example, had relatively long proleptic shoots on RGMs and current AGMs, and relatively long branches on major limbs. 'Gwen', however, had mainly short sylleptic shoots on RGMs and current AGMs, and short branches on major limbs. The results of any applied cultural manipulations, such as pruning, may therefore be analyzed in terms of their effect on the basic shoot system of these growth modules.

The control of shoot formation in plants has been traditionally considered in terms of apical dominance, where an active terminal bud inhibits the growth of axillary buds beneath. This concept is inadequate to explain the development of shoot systems beyond the first growth cycle in woody perennial plants. Brown and his co-workers introduced the term "apical control" to help explain excurrent versus decurrent growth habit in trees (Brown et al., 1967; Brown, 1971). Apical control (*sensu* Brown) is the release of resting buds in subsequent years. A tree with one trunk is under strong apical control, and a tree with no clearly defined single trunk, but several large scaffold branches (major limbs), exhibits weak apical control. In both situations, however, each trunk may exhibit strong apical dominance. Champagnat (1978) adopted the term acrotony, a specific form of apical control which involves the release of subterminal axes that allows them to become dominant. Thus the formation of a single dominant trunk, as in 'Reed' avocados was due to weak acrotony,

whereas in 'Sharwil', strong acrotony resulted in the formation of several trunks or major limbs.

There was a positive relationship between apical dominance and acrotony such that 'Gwen' and 'Reed' had weak acrotony and weak apical dominance; and 'Sharwil' had strong acrotony and strong apical dominance. These relationships may be interpreted in terms of the concepts of prolepsis and syllepsis. Acrotony generally refers to a resumption of growth by a resting bud, as with proleptic shoot growth. Apical dominance, however, means suppression of axillary buds at growth, and therefore involves inhibition of syllepsis. Thus weak apical control (i.e. strong acrotony and prolepsis) coincided with strong apical dominance and hence weak syllepsis, and strong apical control was associated with weak apical dominance and hence strong syllepsis. 'Gwen' and 'Reed' displayed strong apical control, producing few major limbs, relatively short axillary shoots and few proleptic shoots. They also displayed weak apical dominance in that they had large numbers of sylleptic shoots. In contrast, 'Sharwil' exhibited strong apical dominance with relatively few sylleptic shoots, but strong acrotonous growth with many major limbs, and long and numerous proleptic shoots. In SA, 'Hass' was intermediate between 'Sharwil' and 'Reed', and so were the relative influences of apical dominance and apical control on axillary shoot formation. This information supports the hypothesis that cultivar differences in tree habit are established by factors controlling prolepsis and syllepsis in rhythmic growth modules.

Architectural tree models provide information which can be used by plant breeders and horticulturists to improve crop production. More compact growth habit, e.g., 'Gwen' compared with 'Hass', appears to be linked with weak apical dominance and high syllepsis (Fig. 3.5). Plant growth regulators and certain rootstocks may be useful to encourage this type of growth. Previous attempts have concentrated on reducing shoot growth, with little consideration of the effects on modular construction. It is possible that plant growth regulators which increase the number of axillary shoots, e.g. formulations of gibberellins and cytokinins (Miller, 1988), may also increase productivity of current AGMs. More axillary shoots would mean more leaves and possibly more terminal shoots, i.e. potential floral shoots, per AGM. Pruning is routinely employed in temperate fruit crops to manipulate apical dominance and apical control (Mika, 1986; Brunner, 1990). No similar methods have been adopted by avocado growers. Pruning, to rejuvenate modular construction on older trees, may improve average module productivity. Removal of vigorous proleptic

shoots from young 'Sharwil' trees may encourage more compact modular growth with this cultivar. Analysis of modular construction is a simple means of interpreting effects of growth treatments and will have universal application with other tropical trees which exhibit rhythmic growth.



Table 3.1 Length ( $\pm$  s.e.) of major limbs of avocado cultivars growing at two locations. All trees were in their fourth year from grafting.

	South Australia				Queensland	
	'Fuerte'	'Sharwil'	'Reed'	'Hass'	'Hass'	'Gwen'
n	11	38	28	37	6	10
Average length (m)	2.1 $\pm$ 0.12	2.1 $\pm$ 0.08	2.2 $\pm$ 0.09	2.2 $\pm$ 0.05	2.7 $\pm$ 0.36	2.0 $\pm$ 0.12

Table 3.2 Length of annual growth sections on major limbs of avocado cultivars growing at two locations.

Year of growth	Tree age	South Australia				Tree age	Queensland	
		'Fuerte'	'Sharwil'	'Reed'	'Hass'		'Hass'	'Gwen'
		Length (mm)				Length (mm)		
1990	5	289	559	353	341	4	1330	950
s.e.(n)		77 (6)	50 (18)	23 (20)	27 (20)		171 (5)	86 (5)
1989	4	765	700	608	645	3	880	960
s.e.(n)		128 (6)	28 (18)	21 (20)	49 (20)		97 (5)	108 (5)
1988	3	773	890	- <sup>1</sup>	830	2	720	575
s.e.(n)		59 (6)	59 (18)		60 (20)		131 (5)	250 (5)
1987	2	502	687	-	612		-	-
s.e.(n)		37 (6)	77 (9)		55 (18)			
1986	1	475	-	-	350		-	-
s.e.(n)		15 (2)			42 (4)			

<sup>1</sup> No data

Table 3.3 Axillary branch length distribution on major limbs of avocado cultivars growing at two locations. All trees in their fourth year from grafting. Length categories: long, >1.0 m; medium, 0.5-1.0 m; short, <0.5 m.

Location Cultivar	% of branches in each category			Mean no. of branches per limb
	Long	Medium	Short	
South Australia ( $X^2 = 42.02$ on 4 df, $P < 0.001$ )				
'Fuerte' (6) <sup>1</sup>	9.8	9.5	80.7	45.8
'Sharwil' (18)	8.8	26.2	65.0	34.0
'Hass' (20)	9.3	16.3	74.4	39.9
Queensland ( $X^2 = 65.50$ on 2 df, $P < 0.001$ )				
'Hass' (5)	16.8	42.0	41.2	23.8
'Gwen' (5)	2.0	6.9	91.1	20.2

<sup>1</sup> No. of limbs sampled

Table 3.4 Numbers ( $\pm$  s.e.) of resting buds and axillary shoots on main axis of the current annual growth module of major limbs of avocado cultivars growing at two locations. All trees were in their fourth year from grafting, and annual growth modules were formed from three growth flushes.

	South Australia				Queensland	
	'Fuerte'	'Sharwil'	'Reed'	'Hass'	'Hass'	'Gwen'
no. of limbs	3	18	20	18	5	4
Sylleptic shoots (P <0.001) <sup>1</sup>						
	29.0 c	7.9 a	14.3 b	10.7 ab	7.8 ab	24.5 c
	$\pm 3.6$	$\pm 1.0$	$\pm 1.0$	$\pm 1.5$	$\pm 3.0$	$\pm 1.0$
Proleptic shoots (P <0.001)						
	2.0 a	9.3 bc	5.1 a	7.2 ab	12.6 c	4.3 a
	$\pm 2.0$	$\pm 0.7$	$\pm 0.6$	$\pm 0.8$	$\pm 1.5$	$\pm 1.2$
Resting buds (P <0.01)						
	27.0 a	39.3 b	36.8 ab	38.8 ab	38.6 ab	30.0 ab
	$\pm 3.1$	$\pm 1.5$	$\pm 1.2$	$\pm 1.5$	$\pm 1.2$	$\pm 1.8$
Total shoots <sup>2</sup> + buds (NS)						
	57.0	53.1	52.9	53.4	55.4	56.8
	$\pm 3.2$	$\pm 1.8$	$\pm 1.3$	$\pm 1.3$	$\pm 4.5$	$\pm 3.3$

<sup>1</sup> Mean separation within rows by Scheffé's test (P = 0.05).

<sup>2</sup> Does not include flush 1 proleptic shoots as these arise from resting buds on previous annual growth section.

Table 3.5 Numbers ( $\pm$  s.e.) of shoot modules borne by current annual growth modules on major limbs of avocado cultivars growing at two locations. All trees were in their fourth year from grafting. Only growth modules formed from three seasonal growth flushes were included.

	South Australia			Queensland	
	'Fuerte'	'Sharwil'	'Hass'	'Hass'	'Gwen'
no. of limbs per cultivar	3	18	18	5	4
Shoot modules ( $P < 0.001$ ) <sup>1</sup>					
	59.3 ab	25.1 a	25.5 a	64.0 b	59.5 b
	$\pm 12.8$	$\pm 2.7$	$\pm 3.1$	$\pm 18.9$	$\pm 9.2$
Shoot modules per axillary shoot ( $P < 0.001$ )					
	1.9 a	1.8 a	1.8 a	3.7 b	2.2 a
	$\pm 0.3$	$\pm 0.1$	$\pm 0.1$	$\pm 0.5$	$\pm 0.2$
Terminal shoot modules ( $P < 0.001$ )					
	- <sup>2</sup>	19.0 ab	18.0 a	49.0 c	38.0 bc
		$\pm 1.8$	$\pm 2.2$	$\pm 12.3$	$\pm 6.3$

<sup>1</sup> Mean separation within rows by Scheffé's test ( $P = 0.05$ ).

<sup>2</sup> Data not recorded.

## Figure legends

Fig. 3.1 Schematic diagram showing cycles of modular construction leading to the formation of major limbs on avocado.

Fig. 3.2 Rhythmic (seasonal) growth module of 'Hass' avocado, showing location of bud-scar ring (arrow), and proleptic (P) and sylleptic (S) axillary shoots. Note new spring growth flush (f) forming on terminal shoots.

Fig. 3.3 Distinguishing features of sylleptic and proleptic axillary shoots of avocado.

Fig. 3.4 Tree habit of five avocado cultivars growing at two locations; all trees in their fourth year from grafting. Major limbs were grouped according to length such that the longest limb on each tree was placed in group 1, the second longest in group 2, etc. Each line represents a group of major limbs, showing average length and angle of inclination. Line thickness indicates the relative number of limbs in each group. Data in brackets represent 1 s.e.

Fig. 3.5 Annual growth module of 'Hass' (a) and 'Gwen' (b) avocado, four years from grafting, growing in Queensland. Arrows indicate base of main axis of each module.

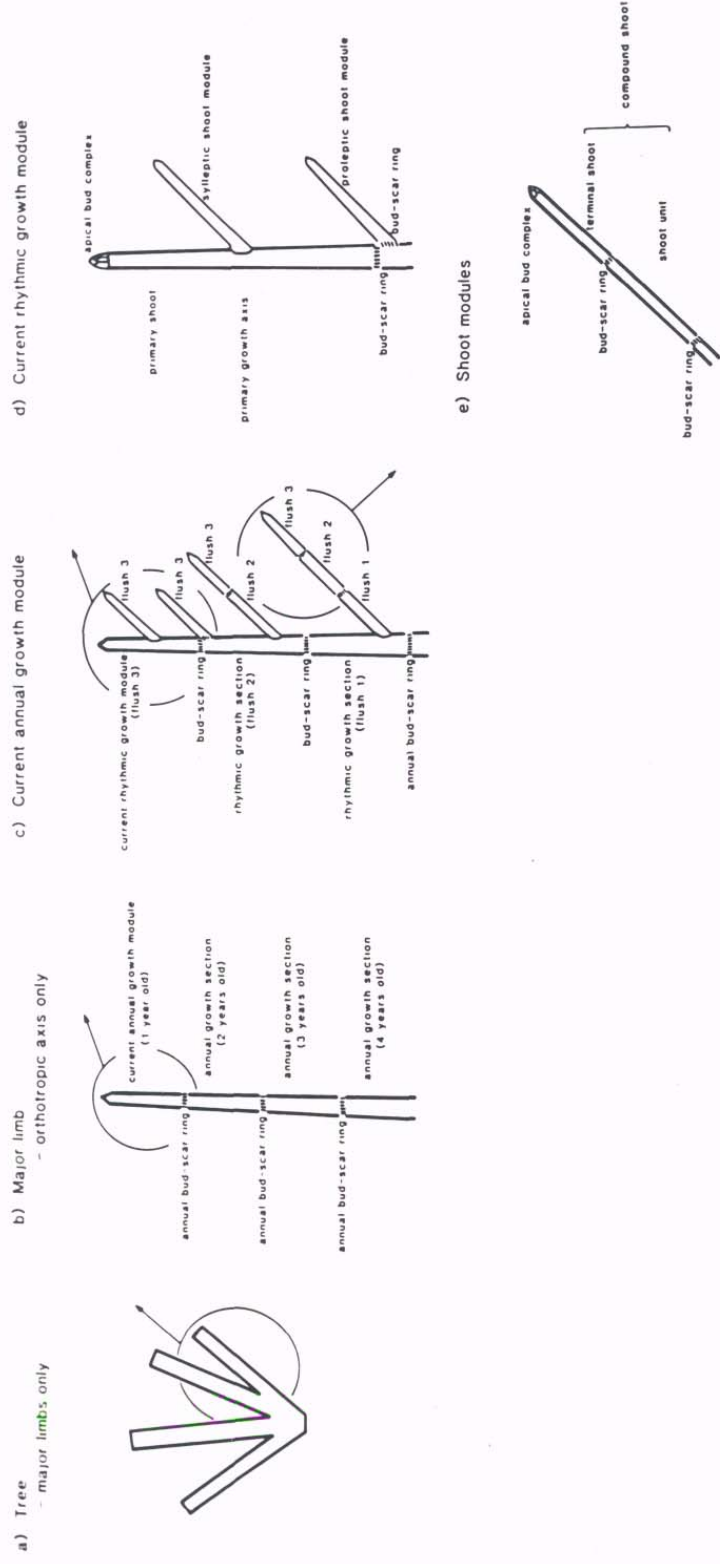


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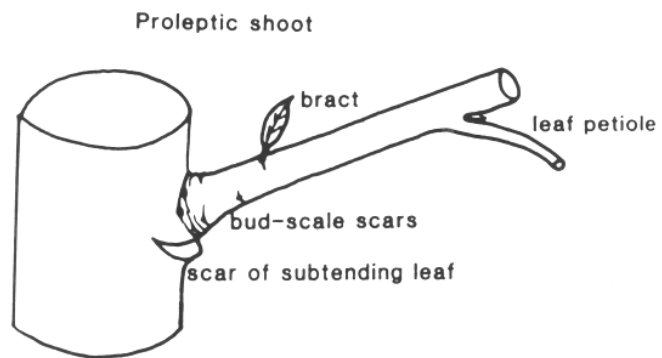
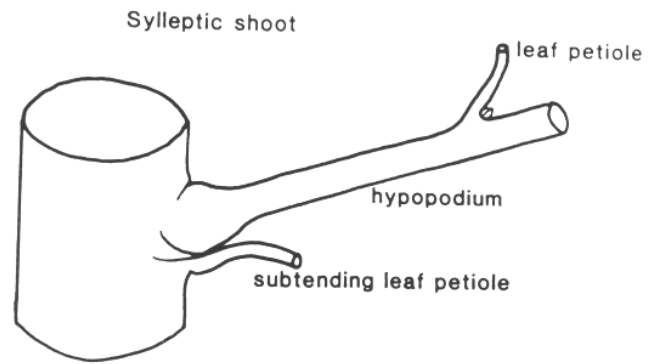


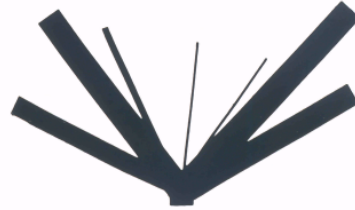
Fig. 3.3 Distinguishing features of sylleptic and proleptic axillary shoots of avocado.

## South Australia



'Fuerte'

Tree height (H) 2.4 m (0.11)  
diameter (D) 3.0 m (0.06)  
H/D 0.80 (0.02)  
(n 3)



'Sharwill'

2.2 m (0.15)  
2.5 m (0.18)  
0.89 (0.07)  
(n 9)



'Hass'

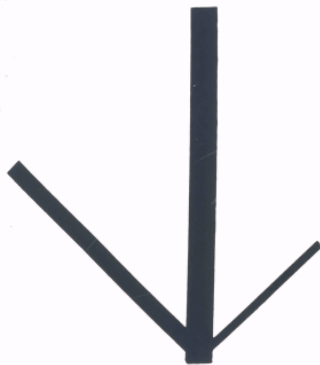
Tree height (H) 2.4 m (0.08)  
diameter (D) 2.5 m (0.07)  
H/D 0.96 (0.03)  
(n 10)



'Reed'

2.5 m (0.05)  
2.1 m (0.07)  
1.23 (0.05)  
(n 10)

## Queensland



'Hass'

Tree height (H) 3.5 m (0.22)  
diameter (D) 2.3 m (0.22)  
H/D 1.52 (0.22)  
(n 3)



'Gwen'

2.6 m (0.15)  
1.6 m (0.15)  
1.63 (0.06)  
(n 3)



Fig. 3.5 Annual growth module of 'Hass' (a) and 'Gwen' (b) avocado, four years from grafting, growing in Queensland. Arrows indicate base of main axis of each module.