Architectural analysis of tree form in a range of avocado cultivars

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ABSTRACT

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Shoot growth and tree architecture were examined in five avocado (*Persea americana* Mill.) 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). Cultivars '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. Cultivar '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. Cultivar 'Hass' was intermediate between 'Sharwil' and 'Reed' at the same location. Major differences in tree vigour and number of proleptic shoots were found between locations with 'Hass'; although the basic model of tree architecture was similar at both locations. The data are discussed in terms of the opportunities to manipulate tree growth to enhance fruiting efficiency.

Keywords: acrotony; apical control; apical dominance; avocado; *Persea*; prolepsis; tree architecture.

Abbreviations: AGM=annual growth module; AGS=annual growth section; H:D=height:diameter ratio.
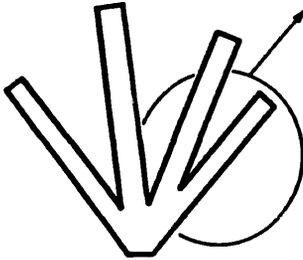
INTRODUCTION

Major advances in temperate tree fruit production have resulted from a detailed knowledge of tree form and how this may be manipulated by tree
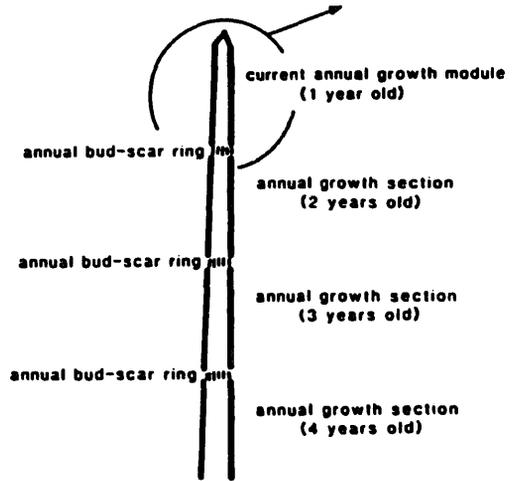
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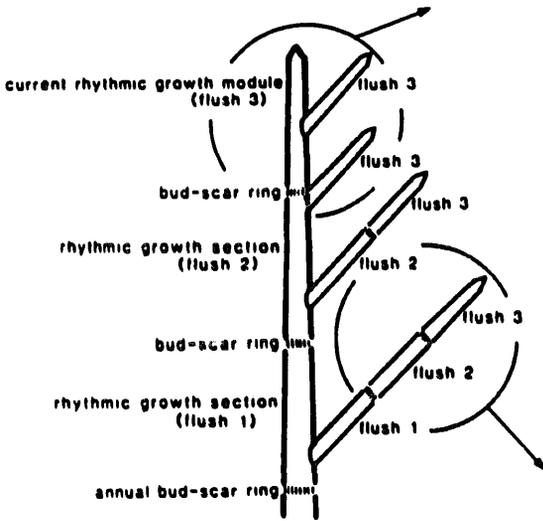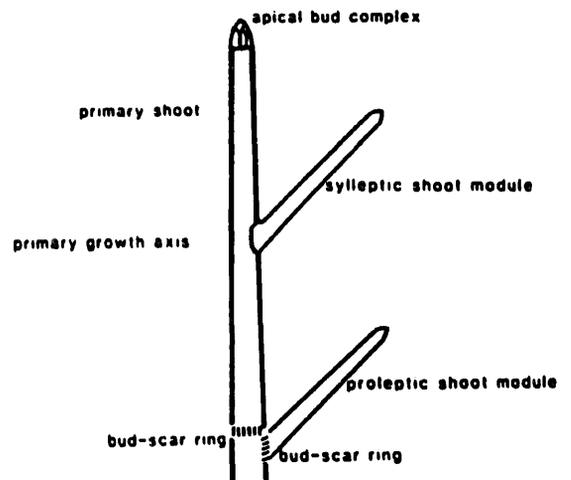
a) Tree
   – major limbs only

b) Major limb
   – orthotropic axis only

current annual growth module
(1 year old)

annual bud-scar ring

annual growth section
(2 years old)

annual bud-scar ring

annual growth section
(3 years old)

annual bud-scar ring

annual growth section
(4 years old)

c) Current annual growth module

current rhythmic growth module
(flush 3)

flush 3

flush 3

flush 3

bud-scar ring

rhythmic growth section
(flush 2)

flush 2

flush 3

bud-scar ring

flush 2

rhythmic growth section
(flush 1)

flush 1

annual bud-scar ring

d) Current rhythmic growth module

apical bud complex

primary shoot

sylleptic shoot module

primary growth axis

proleptic shoot module

bud-scar ring

bud-scar ring

e) Shoot modules

apical bud complex

bud-scar ring

terminal shoot

compound shoot
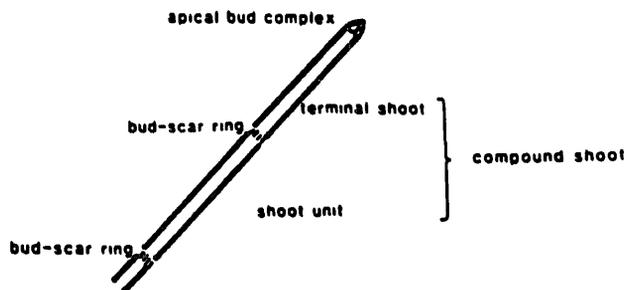
shoot unit

bud-scar ring

Fig. 1. Schematic diagram showing cycles of modular construction leading to the formation of major limbs on avocado.

Fig. 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.

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 fruits have been developed from light interception studies comparing a range of theoretical tree shapes (Oren, 1988; Golomb et al., 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, but 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 paper provides an architectural analysis of avocado tree growth (Fig. 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 (Hallè, 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. 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, Figs. 1 and 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 paper, 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.

MATERIALS AND METHODS

Ten cultivar 'Hass', ten cultivar 'Reed', nine cultivar 'Sharwil' and three cultivar 'Fuerte' trees, grafted on cultivar 'Zutano' seedling rootstocks and growing in the same orchard block at McLaren Vale, South Australia (35.12°S, 138.32°E), an area with a mediterranean climate, were used in this study. All trees were 4 years old in 1989, the first year of this trial, and their growth was monitored over 3 years. In 1990, three 'Gwen' and three 'Hass' trees growing in Maleny, Queensland (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.

In winter 1989 (1990 in Queensland), 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 South Australia and two limbs from two trees and one limb from one tree, i.e. five limbs per cultivar, were selected in Queensland. 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 over-wintering 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 (more than 1.0 m, 0.5–1.0 m and less than 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 below and above bud-scar rings, respectively; and distinct change in leaf size, shape and/or colour (Figs. 1 and 2). Proleptic shoots develped from resting buds, and had a bud-scar ring at their base (Hallé et al., 1978). 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; more than 30 cm, 10–30 cm and less than 10 cm respectively. Number of shoot modules on compound shoots (i.e. those with more than one flush of growth) were also recorded.

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 × shoot type categories were tabulated and a Poisson model was fitted to the data. Where less than five counts were observed per category, Fisher's exact test was used.
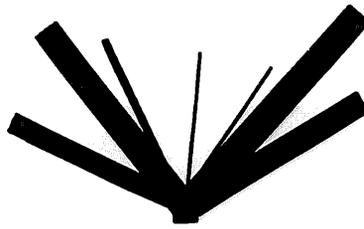
RESULTS

There were consistent differences between cultivars in tree shape, in Year 4 from grafting (Fig. 3). These differences were measured in terms of tree
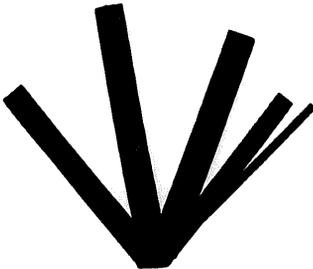
South Australia
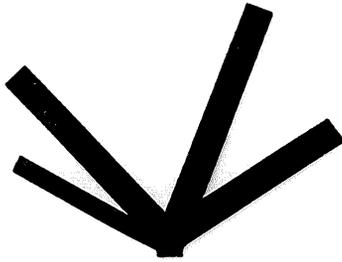
'Fuerte'

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)	
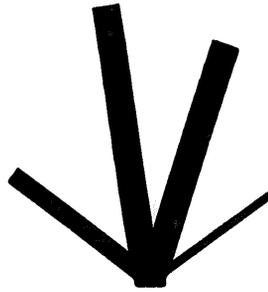
'Reed'

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

Queensland
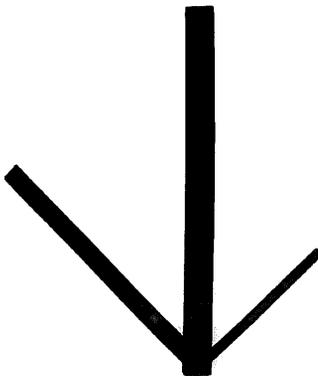
'Hass'

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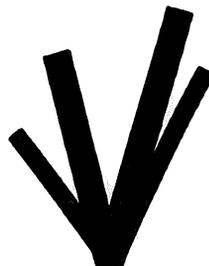
'Gwen'

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

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±0.25 (± standard error) major limbs. 'Sharwil' trees had 4.2±0.46 major limbs, with a spreading tree form (H:D=0.89). 'Hass' trees in South Australia were intermediate in form between 'Sharwil' and 'Reed', with H:D=0.96, and 3.7±0.30 major limbs. The three 'Fuerte' trees in South Australia had 3.7±0.33 major limbs, and H:D=0.80. In Queensland, '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±0.66 and 2.0±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 Queensland were more upright, and had fewer major limbs than 'Hass' trees in South Australia. Average length of major limbs, on trees in their fourth year from grafting, did not vary between cultivars in South Australia. However, major limbs on 'Hass' in Queensland were longer than those on both 'Gwen' in Queensland and 'Hass' in South Australia (Table 1).

Not all limbs had the same number of AGSs because some grew from buds on 1 or 2 year old wood (Table 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 South Australia, the length of AGSs of the same age were not significantly different among cultivars, although 'Sharwil' tended to be the longest. In Queensland, the lengths 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). This trend correlated di-

TABLE 1

Length (±s.e.) of major limbs of avocado cultivars growing at two locations. All trees were in Year 4 from grafting

	South Australia				Queensland	
	'Fuerte' (11)[1]	'Sharwil' (38)	'Reed' (28)	'Hass' (37)	'Hass' (6)	'Gwen' (10)
Average length (m)	2.1±0.12	2.1±0.08	2.2±0.09	2.2±0.05	2.7±0.36	2.0±0.12

[1]No. of limbs sampled.

Fig. 3. Tree habit of five avocado cultivars growing at two locations; all trees in Year 4 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.

TABLE 2

Length (mm) of annual growth sections on major limbs of avocado cultivars growing at two locations

Year growth	Tree age	South Australia				Tree age	Queensland	
		'Fuerte'	'Sharwil'	'Reed'	'Hass'		'Hass'	'Gwen'
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	–[1]	830	2	720	575
s.e.(n)		59(6)	59(18)		60(20)		131(5)	250(2)
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)			

[1]No data.

TABLE 3

Axillary branch length distribution on major limbs of avocado cultivars growing at two locations. All trees in Year 4 from grafting. Length categories: long, > 1.0 m; medium, 0.5–1.0 m; short, <0.5 m

Cultivar	Percentage of branches in each category			Mean no. of branches per limb
	Long	Medium	Short	
South Australia ($\chi^2 = 42.02$ on 4 d.f., $P < 0.001$)				
'Fuerte' (6)[1]	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 ($\chi^2 = 65.50$ on 2 d.f., $P < 0.001$)				
'Hass' (5)	16.8	42.0	41.2	23.8
'Gwen' (5)	2.0	6.9	91.1	20.2

[1]No. of limbs sampled.

rectly with the relative percentage of short branches for each cultivar. In South Australia, 'Sharwil' had more branches in the medium length category than 'Hass' and 'Fuerte'. In Queensland, 'Hass' had more branches in the long and medium categories than 'Hass' in South Autralia, 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 three growth

flushes (Table 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' ($\chi^2 = 11.29$ on 2 d.f., $P < 0.01$), and more sylleptic than proleptic shoots in the longer categories for 'Hass' in South Australia ($\chi^2 = 18.98$ on 1 d.f., $P < 0.001$). The difference was not significant for 'Hass' in Queensland as there were more proleptic shoots on 'Hass' in Queensland than in South Australia. Shoot length data were not recorded for 'Reed', but field observations indicated that nearly all axillary shoots were in

TABLE 4

Numbers (±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 Year 4 from grafting, and annual growth modules were formed from three growth flushes

	South Australia				Queensland	
	'Fuerte' (3)[1]	'Sharwil' (18)	'Reed' (20)	'Hass' (18)	'Hass' (5)	'Gwen' (4)
Sylleptic shoots (P<0.001)[2]						
	29.0 c	7.9 a	14.3 b	10.7 ab	7.8 ab	24.5 c
	±5.6	±1.0	±1.0	±1.5	±3.0	±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
	±2.0	±0.7	±0.6	±0.8	±1.5	±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
	±3.1	±1.5	±1.2	±1.5	±1.2	±1.8
Total shoots[3] + buds (NS)						
	57.0	53.1	52.9	53.4	55.4	56.8
	±3.2	±1.8	±1.3	±1.3	±4.5	±3.3

[1]No. of limbs.
[2]Mean separation within rows by Scheffé's test ($P=0.05$)
[3]Does not include Flush 1 proleptic shoots as these arise from resting buds on previous annual growth section.

TABLE 5

Numbers (±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 Year 4 from grafting. Only growth modules formed from three seasonal growth flushes were included

	South Australia			Queensland	
	'Fuerte' (3)[1]	'Sharwil' (18)	'Hass' (18)	'Hass' (5)	'Gwen' (4)
Shoot modules (P < 0.001)[2]					
	59.3 ab ± 12.8	25.1 a ± 2.7	25.5 a ± 3.1	64.0 b ± 18.9	59.5 b ± 9.2
Shoot modules per axillary shoot (P < 0.001)					
	1.9 a ± 0.3	1.8 a ± 0.1	1.8 a ± 0.1	3.7 b ± 0.5	2.2 a ± 0.2
Terminal shoot modules (P < 0.001)					
	–[3]	19.0 ab ± 1.8	18.0 a ± 2.2	49.0 c ± 12.3	38.0 bc ± 6.3

[1]No. of limbs per cultivar.
[2]Mean separation within rows by Scheffé's test ($P = 0.05$).
[3]Data not recorded.

the short category with this cultivar. 'Fuerte' in South Australia, and 'Gwen' and 'Hass' in Queensland produced more shoot modules per AGS than the other cultivars (Table 5). In 'Fuerte' and 'Gwen' this difference was due to higher numbers of axillary shoots, with 'Hass' in Queensland 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 Queensland had significantly more terminal shoots than 'Hass' in South Australia.

Data collected from current AGMs on trees in South Australia 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.

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 South Autralia, '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 sup-
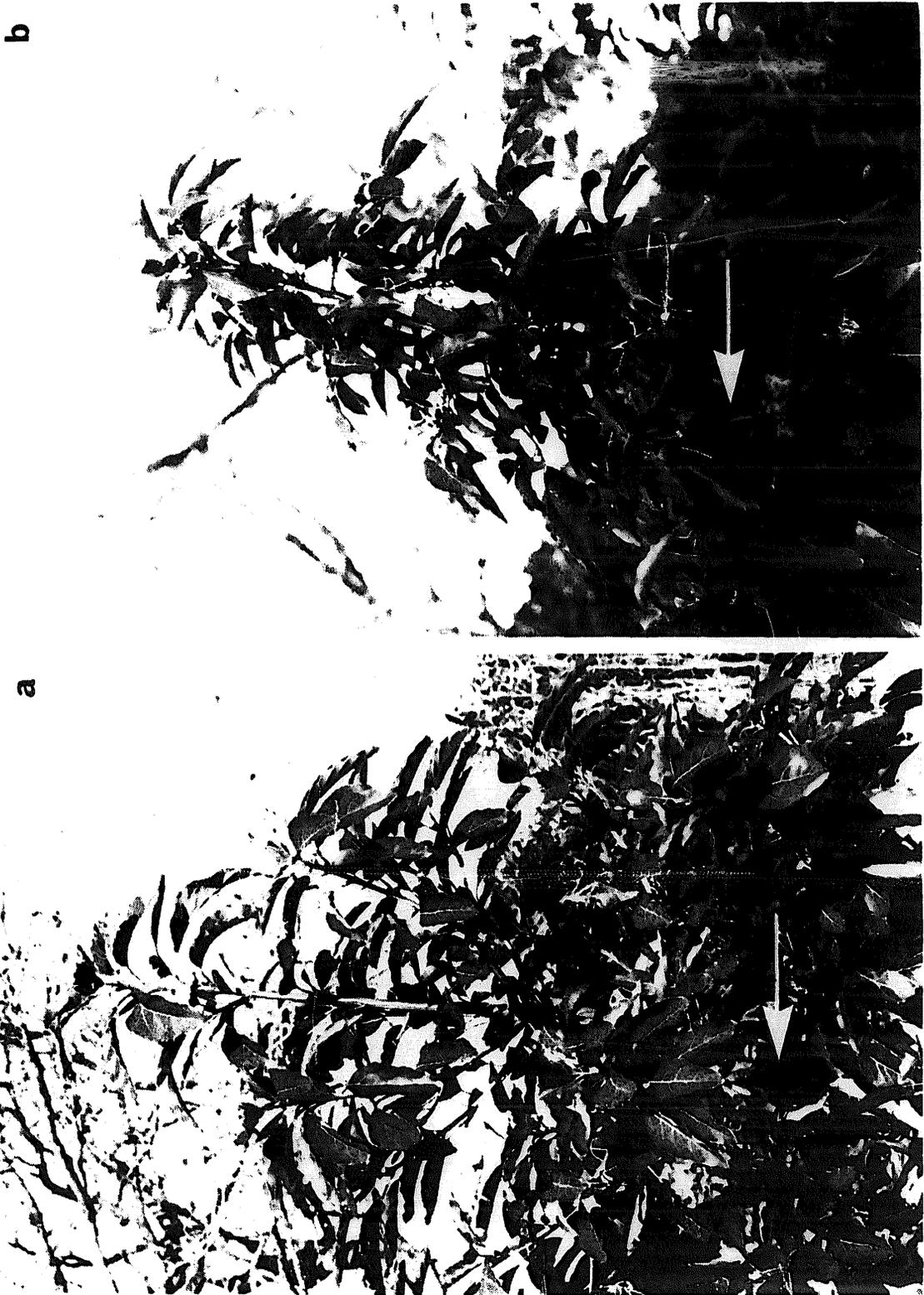
Fig. 4. Annual growth module of (a) 'Hass' and (b) 'Gwen' avocado, 4 years from grafting, growing in Queensland. Arrows indicate base of main axis of each module.

ports 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. 4). Plant growth regulators and certain rootstocks may be useful to encourage this type of growth (Miller, 1988). Pruning, to rejuvenate modular construction on older trees, may improve average module productivity. For example, 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.

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