4. Preformation of node number in vegetative and reproductive proleptic shoot modules of Persea (Lauraceae).

4.1 Summary.

The number of nodes on primary and axillary shoots were determined in a range of Persea species and cultivars. They were compared with node numbers in apical and axillary buds to investigate whether preformation or neoformation of nodes occurred. Mean number of nodes on single flush primary shoots was 14 for vegetative shoots and 21 for reproductive shoots, and was similar across species, cultivars, rootstocks, locations and climates. In the cultivar 'Hass', numbers of nodes on axillary shoots were variable, and lower than those for primary shoots. There was a mean of 12 nodes for vegetative proleptic shoots, 15 for reproductive proleptic shoots and 6 for sylleptic shoots, invariably vegetative. All nodes were preformed within both apical and axillary proleptic buds. This was not the case in sylleptic buds, which burst contemporaneously with extension of the parent axis. Node initiation occurred first in apical buds, and then successively in axillary buds in an acropetal direction along each shoot. Formation of all nodes of the consequent shoot module was completed within vegetative buds by the time extension of the subtending shoot had ceased, and within reproductive buds by the time of bud break in spring. Node initiation after shoot extension also occurred first in apical buds, but then in a basipetal progression along shoots. Nodes initiated during this second phase of development became part of the apical bud of the consequent shoot, except in the 37% of reproductive buds which formed a terminal inflorescence. In the majority (63%) of reproductive buds, this second phase of node initiation also formed nodes at which a leaf developed during the consequent growth flush. Reproductive shoot modules (compound inflorescences) that developed from reproductive buds, therefore, were determinate or indeterminate. Indeterminate reproductive shoot modules carried 6 basal bud scales, followed by 6 axillary inflorescences and their subtending bracts, and up to 9 true leaves. Each axillary inflorescence terminated with a flower.

4.2 Introduction.

Shoot modules are the basic units of architectural tree models (Watkinson and White, 1985). They are morphologically distinct, single units of extension developed from individual buds or bud primordia. Persea corresponds to the Rauh architectural model, in which the contributing shoot modules are multinodal (Hallé et al., 1978). Module development may be associated with the preformation of nodes within a resting bud, or may result from the neoformation of nodes during shoot extension. Venning and Lincoln (1958) suggested neoformation was predominant in avocado (Persea americana Mill.), although no experimental data was presented in support of this. Subsequent studies have reported relatively constant leaf numbers on avocado shoots from different growth flushes (Gregoriou and Kumar, 1982), suggesting that a constant node number may have been preformed within quiescent buds. Preformation of nodes has been demonstrated in the deciduous woody species Malus domestica (apple) (Fulford 1965, 1966a, b), Pyrus serotina (Japanese pear) (Banno et al., 1985, 1986) and Diospyros kaki (persimmon) (Harada, 1984). In these plants, preformation was generally linked to seasonal factors which caused the cessation of shoot extension and the development of overwintering buds. In the evergreen avocado, two or three growth flushes may occur per year. It is of interest to determine the role of preformation in this more dynamic situation with relatively short rest periods between growth flushes. In this chapter, node formation in the bud is related to growth and morphology of vegetative and reproductive shoots to the stage of early fruit set. In addition to providing basic data on shoot growth in this tropical tree genus, the information will be important in understanding the effects of experimental treatments, such as pruning, to manipulate shoot growth patterns and tree productivity (Mika, 1986).

4.3 Materials and methods.

4.3.1 Plant material.

The Persea species examined were growing in the germplasm collection of the University of California, South Coast Field Station (33.36 N., 117.40 W.). The avocado (Persea americana Mill.) cultivars were from two locations in Australia:

McLaren Vale, South Australia (35.12 S., 138.32 E.); and Maleny, Queensland (26.51 S., 152.51 E.). Details of trees sampled are presented in Table 4.1. Mean annual temperatures (maximum and minimum) and rainfall at meteorological stations nearest to the experimental locations are presented in Table 4.2. South Australia and California have mediterranean climates, whereas Maleny is subtropical.

4.3.2 Shoot morphology.

Node number was determined for reproductive (spring) growth modules collected from the Persea species and cultivars. All nodes on the main axis of each module were counted from the first bud scale or bud-scale scar to the last leaf node below the apical bud. Lengths of primary growth axes of modules were also measured.

Shoot module formation on 7 year old 'Hass' trees were analyzed in detail. All material was selected from the northern aspect of canopy perimeters, 1-2 m above ground level. Fifty-two current annual growth modules were examined during winter 1990: 30 contained modules from spring and summer growth flushes and 22 included spring, summer and autumn modules. Spring, summer and autumn growth flushes occurred in October (1989), January and April (1990), respectively. Flowering coincided with the spring growth flush in October. The material was divided into shoot modules, and node number on individual shoot modules counted. In the subsequent spring (October 1990), 26 reproductive shoot modules were collected from the same trees and their node number was determined.

4.3.3 Bud morphology.

Bud morphology was studied on material collected from 7 year old 'Hass' trees growing at McLaren Vale. Fifteen shoot modules formed during the current or most recent growth flush, were collected each month over a 15 month period. Collections coincided with the major phenological growth stages of bud and shoot development (Aubert and Lossois, 1972; Davenport, 1982). Again, all material was collected from the northern aspect of canopy perimeters, 1-2 m above ground level. Apical and axillary buds were dissected under a light microscope. Node number was determined as the number of bud-scale scars, bud scales and leaf primordia contained in the bud. The developmental stages of axillary meristems at each node were also recorded. Leafless buds and those located in the axils of bud scales near the base of

shoots were not included.

Bud scales and leaf primordia were removed from apical and axillary buds. These were then fixed in 3 % glutaraldehyde in 0.025 M phosphate buffer plus 0.5% caffeine (Mueller and Greenwood, 1978). After dehydration in a graded ethanol series (5, 15, 30, 50, 75, 100 %), the buds were critical-point dried and double coated with gold prior to observation with a Phillips SEM505 scanning electron microscope.

4.3.4 Compound inflorescence morphology.

The morphology of the inflorescence was studied on material collected from 7 year old 'Hass' trees growing at McLaren Vale, and P. longipes and P. donnell-smithii trees growing in California. The numbers of bud scales, axillary inflorescences, leaves and leaf bracts on inflorescences approaching anthesis were determined. The lengths and maximum basal diameters, number of flowers and early fruit set at one month post-anthesis were determined for inflorescences of 'Hass'.

4.3.5 Statistical analysis.

Pooled- and separate-variance t-tests were used to compare two independent means. Analysis of variance was performed when three or more means were compared, and Duncan's multiple range test were used to separate means when differences were statistically significant ($P < 0.05$). Scheffé's test ($P = 0.05$) was used when sample sizes of compared means were highly variable.

4.4 Results

4.4.1 Shoot morphology.

Various classes of shoot modules were identified. Proleptic shoot modules arose only after a period of dormancy as a resting terminal or axillary bud (Hallé et al., 1978). They had a zone of bud-scale scars at their base (Fig. 4.1). Sylleptic shoot modules did not undergo a dormant period as a resting bud (Hallé et al., 1978). They developed from bud primordia initiated in axillary positions in terminal or axillary buds. Their growth was contemporaneous with extension of the parent axis. They could be identified by the absence of a zone of bud-scale scars at the base of the shoot module. Reproductive shoot modules (compound inflorescences) were proleptic and developed from quiescent buds containing floral initials. The compound inflorescence

comprised a number of individual axillary inflorescences, each derived from a single axillary meristem (Fig. 4.2F). Each axillary inflorescence consisted of numerous individual flowers arranged on second and third order branches of the inflorescence axis. Axillary inflorescences always terminated with a flower but the terminal meristem of the compound inflorescence was either vegetative or reproductive. The compound inflorescence was therefore either indeterminate or determinate. Vegetative proleptic and reproductive shoot modules formed either primary or axillary growth axes in a shoot complex. Sylleptic shoot modules were always axillary. An annual growth module included all the shoot modules formed during an annual growing period, from a single shoot module of the previous year.

The numbers of nodes on primary growth axes of reproductive shoot modules were similar between species and cultivars (Table 4.3). Values ranged from 17.7 for P. americana cv 'Fuerte' to 23.2 for P. floccosa.

Lengths of primary growth axes of modules on 4 year old trees showed little variation between cultivars in the same location (data not shown). Significant differences were found between locations, however. Primary growth axes on annual growth modules of 'Hass' growing in Queensland were twice as long as those on 'Hass' in South Australia (1330 ± 171 and 675 ± 49 mm respectively, $P < 0.01$). Similar numbers of nodes formed on these growth axes, so that mean internode length was greater on 'Hass' in Queensland than in South Australia.

Node numbers on reproductive (spring) shoot modules were significantly higher than on vegetative (summer and autumn) shoot modules. Node number was higher in modules on primary than on axillary growth axes (Table 4.4). Sylleptic shoots had the lowest mean node number (5.9 ± 0.9). Node numbers of equivalent shoot modules were similar irrespective of whether they were from annual growth modules with two (spring and summer) or three (spring, summer and autumn) growth flushes. Reproductive shoot modules collected in the subsequent spring (October, 1990) had 20.8 ± 0.9 nodes.

4.4.2 Bud morphology.

At apical bud swell, outer bud scales began to separate revealing new growth. At this stage, it was not apparent whether buds were vegetative or reproductive. At advanced bud swell, vegetative buds were long and narrow (Fig. 4.2A); whereas reproductive buds were round and plump (Fig. 4.2B). Subsequent development of vegetative buds proceeded from bud break, when

bud scales were completely separate and open, to shoot extension when leaves began to unfold and the young shoot extended with rapidly expanding leaves and internodes (Fig. 4.2C). Shoot extension had generally ceased by the stage of apical bud set (Fig. 4.2D). At this stage, a leaf scale had formed at the first node of the newly formed apical bud. This leaf scale was generally short-lived and soon abscised. At bud break of reproductive buds, inflorescences were visible but protected by bud scales (Fig. 4.2E). At shoot extension, pre-anthesis inflorescence development was complete (Fig. 4.2F). Vegetative terminal meristems of compound inflorescences generally began to extend when extension of the axillary inflorescences was complete (Fig. 4.2F). Vegetative extension began at earlier or later stages of inflorescence development in only a few inflorescences.

Node number was similar in vegetative apical buds on shoots at both shoot extension and apical bud set. At advanced bud swell, however, there were significantly more nodes per bud (Table 4.5). Buds on reproductive shoots collected at bud break had the highest node numbers of all examined. No significant differences in node number were found between comparable buds on spring and summer flush shoots collected at the same phenological growth stage (Table 4.6), or between buds on autumn flush shoots collected in 1990 and 1991. The number of nodes in a vegetative bud at the end of shoot extension (apical bud set), and in a reproductive bud at bud break, matched the number of nodes in shoots derived from similar buds (Table 4.6). This held true for both apical and axillary buds and shoots, and suggests that node formation of the vegetative shoots was completed at a much earlier phenological stage than for the reproductive shoots. Vegetative buds had more nodes at advanced bud swell than they did at the end of shoot extension. These additional nodes represented the commencement of formation of the apical bud of the next shoot module.

Apical buds contained more nodes than axillary buds on the same shoot, at each growth stage (Table 4.5). Axillary bud development initially varied in an acropetal progression along the shoot. Node numbers in axillary buds at shoot extension were higher in basal buds than in buds located towards the shoot apex. At apical bud set, however, all axillary buds contained similar numbers of nodes with the exception of that located immediately below the apical bud. This implies that node production ceased after a fixed number of nodes had been initiated in each bud. A new phase of node initiation occurred in apical and some axillary buds during bud swell, so that at bud break in spring, a

gradient in bud development was apparent along shoot axes. As before, node number was highest in apical buds. In axillary buds at this stage, node number was highest for the second bud down from the apical bud, and then decreased in a basipetal direction along each shoot, in contrast to the acropetal development observed in the first phase of node initiation.

In apical and axillary buds, leaf primordia, bud scales and bud-scale scars were arranged around the bud axis in a Fibonacci spiral (Fig. 4.3). Two sets of contact parastichies, one in each direction were present. One set had parts which differed by 2, the other set by 3, to give a (2 + 3) phyllotactic arrangement (Williams, 1974). The direction of each spiral, that is their left- or right handedness, followed no obvious pattern and was not influenced by bud position on the shoot.

Apical and axillary meristem development within buds was classified into nine stages. Stage 1 was the formation of a meristem with no lateral primordia apparent (Fig. 4.4A,B). Two bract primordia developed (stage 2), and their tips extended over the meristem (stage 3). Stages 1 and 2 were common to vegetative and inflorescence meristems. At stage 3, however, developing inflorescence meristems were larger and more broadly ovoid than vegetative meristems at the same stage (Scholefield et al., 1985). Vegetative development beyond stage 3 continued with the successive formation of leaf primordia.

Continuing development of floral buds was classified into stages 4 to 9. Bracts were tomentose at stage 4, and elongated at stage 5. Second order branching of developing inflorescences developed at stage 6, with formation of individual flower primordia at stage 7 (Fig. 4.4B). At stage 8, the central axis had started to extend and individual flower buds were visible between bracts at stage 9.

Developing inflorescences at stage 6 were first observed at advanced bud swell and stage 8 at bud break. Doming of the terminal meristem, similar to that observed for axillary inflorescence meristems, indicated the formation of a terminal inflorescence (Fig. 4.4B). In the majority (63%) of shoots, however, the terminal meristem remained vegetative and gave rise to an indeterminate compound inflorescence. Pre-anthesis development of inflorescences was completed in October (spring).

Axillary vegetative and inflorescence primordia in both apical and axillary buds developed acropetally (Table 4.7). In vegetative buds all axillary primordia were vegetative, whereas in reproductive buds the primordia at nodes 1 to 7, remained vegetative, and inflorescence primordia formed at nodes 8 to 15 (Fig.

4.5). Primordia at nodes beyond node 15 in reproductive buds were vegetative, unless a terminal inflorescence formed adjacent to the last axillary inflorescence. Floral development (number of nodes with developing inflorescences at stages 3 - 9, and maximum stage of inflorescence development) was most advanced in apical than in axillary buds on the same shoot (Table 4.8). A gradient in floral development in axillary buds, similar to that observed after the second phase of node initiation in these buds, was apparent along shoot axes such that development was most advanced in the second bud below the apical bud, and then decreased in a basipetal direction along each shoot.

4.4.3 Compound inflorescence morphology.

Basal diameters of extended compound inflorescences were greater on indeterminate inflorescences than on determinate (Table 4.9). Determinate compound inflorescences were more than twice as long as indeterminate, the extra length being due to the length of the terminal inflorescence. Total numbers of flowers per compound inflorescence did not differ significantly between the two types. Determinate and indeterminate compound inflorescences formed 5.8 ± 0.3 bud scales at their base, with the first axillary inflorescence formed at the first node beyond this.

Indeterminate compound inflorescences of P. americana cv 'Hass', P. longipes and P. donnell-smithii all bore similar numbers of nodes (Table 4.10). Whereas P. americana and P. longipes carried significant numbers of leaves beyond the last axillary inflorescence, P. donnell-smithii had an axillary inflorescence at most nodes along the compound inflorescence, so that there were few nodes carrying leaves or leaf bracts alone.

Fruit set was determined one month post-anthesis (Table 4.11). More fruit was set on determinate than on indeterminate inflorescences. Within indeterminate inflorescences, fruit set was greater on those with 4 or more axillary inflorescences than on those with less.

4.5 Discussion.

This study is the first to demonstrate predetermination of node number in both vegetative and reproductive buds of a tropical tree species. Node number was higher in reproductive (spring) than in vegetative (summer and autumn)

shoot modules, the difference being due to a second phase of node formation associated with flower initiation. This finding is in agreement with similar studies on other tree species, including apple (Luckwill and Silva, 1979), Japanese pear (Banno et al., 1986), and loblolly pine (Greenwood, 1980). Node preformation in Persea species results in rhythmic shoot growth, proceeding by the sequential iteration of shoot modules with uniform node numbers. A similar sequence has been described in a range of plant species including apple (Bland 1978, cited by Pratt 1990); Isertia coccinea (Barthelemy, 1986); Alstonia scholaris (Mueller, 1985); Equisetum arvense, (Golub and Whetmore, 1948); and Theobroma cacao (Greathouse et al. 1971). In Persea the process appears to be under strong endogenous control as equivalent modules have similar node numbers regardless of growth flush, cultivar, rootstock, species, sub-genus, geographic location, climate and shoot vigour. The only major species difference observed in module structure was the greater number of axillary inflorescences in the reproductive module of P. donnell-smithii.

An interesting feature of tropical tree growth is the relationship between sylleptic and proleptic shoot growth. Sylleptic shoot modules develop from bud primordia in the axils of leaf primordia contained in resting buds. They are not preformed and have fewer nodes than proleptic shoot modules, possibly because extension growth of the parent bud inhibits neoformation of nodes in the axillary bud primordia. Sylleptic shoots are less common in temperate than in tropical trees (Hallé et al., 1978), and in Persea they produce only vegetative shoots. On reproductive modules, leafy sylleptic shoots occurred at nodes beyond the last axillary inflorescence, except in P. donnell-smithii, where axillary inflorescences formed at each node. On vegetative modules, sylleptic shoots developed at leaf nodes above the basal zone of bud scales and bud-scale scars.

The fact that avocado buds become strongly committed to form a uniform number of nodes infers that shoot modules are developmentally fixed. Control over their formation may occur at an early stage in their development, and be similar to that described for other structures whose development is fixed. In leaves, development is determined at the level of cellular organisation within a meristem (Steeves and Sussex, 1989). In Equisetum, the fixed node number was traced to an apical cell (Gifford, 1983; Gifford and Kurth, 1983). It was suggested that rhythmic growth in these plants was a function of rhythmic activity in the promeristem, wherein they became quiescent at the end of each cycle of leaf initiation. It is possible that a similar developmental pattern may

operate in higher plants, even though their initiating meristems are multi-cellular. Indeed, conflicting theories on zonation in higher plant meristems have been explained in terms of rhythmic activity (Steeves and Sussex, 1989). Hallé and Martin (1968) demonstrated rhythmic mitotic activity in apical meristems of rubber (Hevea brasiliensis), a plant exhibiting strong rhythmic shoot growth. If the duration of rhythmic activity in meristems is tightly controlled, this might determine the number of nodes produced, and so explain the apparent fixed development of subsequent shoot growth.

The developmental fixation of buds and shoot modules at an early stage in their development does not explain which buds develop as new shoots. The dominant new shoot on practically all shoot modules was that which developed from the apical bud of the previous module. Exceptions were due to physical damage, or to abnormal development associated with high temperatures (Sedgley, Scholefield and Alexander, 1985). The apical bud was the largest and oldest bud, and the first to initiate new nodes prior to bud burst. Initial development of axillary buds then occurred acropetally along each shoot, as does leaf and internode extension in many plants (Brown and Sommer, 1992).

In spring, the second phase of node formation in buds, and associated floral development, also occurred first in the apical bud, but then in a basipetal direction in axillary buds along the shoot. This shift in development gradient in axillary buds produced a bud hierarchy along the shoot resulting in a pattern of axillary shoot growth in which proleptic axillary shoots developed from buds proximal to the apical bud. This pattern of branching is termed acrotony (Troll, 1937), and results from the combined effects of basipetal inhibition and acropetal stimulation of axillary buds on shoot axes (Champagnat, 1978). In avocado, these two stem effects and the bud hierarchies they produce, do not appear to operate until the second phase of node initiation. That is, after preformation of the fixed node number characteristic of vegetative shoots and when extension growth of the parent shoot axes has ceased.

In Persea, 21 nodes were produced in reproductive buds. A similar number is preformed in apple fruit buds (Pratt, 1988) following two phases of node initiation in the resting bud (Luckwill and Silva, 1979). In apple, the first phase is purely vegetative, but the second forms a terminal inflorescence and is absent from vegetative buds. There was a similar differentiation between avocado buds, although floral development occurred at nodes produced during the first phase of node initiation. The second phase of node initiation either

produced a terminal inflorescence or vegetative nodes which formed part of the apical bud of the next shoot module.

Inflorescences are described here as determinate or indeterminate, depending upon the absence or presence of a terminal leafy shoot. Alternative, more specific terms are anthotelic and blastotelic respectively (Briggs and Johnson 1979, Weberling 1989). The indeterminate condition is predominant in Persea, and inflorescences are generally axillary and subterminal on the parent compound inflorescence (Allen, 1945; Kopp, 1966; Reece, 1942; Scholefield et al., 1985). In avocado, individual axillary inflorescences are determinate and paniculate.

In avocado, growth of the terminal vegetative flush on indeterminate compound inflorescences has been postulated to compete with floral development and to lead to reduced fruit set (Biran, 1979). Comparison of fruit set on determinate and indeterminate compound inflorescences (Table 4.11) provides evidence for this.

In the Persea species studied here, shoot modules with uniform node numbers are the precision building blocks of the Rauh architectural tree model. While such developmentally fixed shoot modules may infer a lack of plasticity in plant development, in fact they explain the orderly way in which plants react to physical and environmental disturbances. An understanding of their structure offers a framework against which manipulation of tree structure and physiology can be measured.

Table 4.1 Details of Persea (Clus.) trees used in this study.

	Location[1]	Age (yrs)	No. of trees	Rootstock
Sub-genus Eriodaphne				
P. donnell-smithii Mez	C	21	1	P. borbonia L.
P. indica L.	C	>10[2]	1	own roots
P. longipes Schlecht.	C	18	1	P. americana Mill.
Sub-genus Persea				
P. floccosa Mez	C	19	1	P. americana Mill.
P. schiedeana Nees	C	6	5	own roots
P. schiedeana Nees x P. americana Mill.	C	7	5	own roots
P. americana Mill. cv				P. americana Mill. cv
'Fuerte'	SA	4	3	'Zutano'
'Sharwil'	SA	4	9	'Zutano'
'Reed'	SA	4	10	'Zutano'
'Hass'	SA	4;7	10;12	'Zutano'
'Hass'	Q	4	3	'Hass'
'Gwen'	Q	4	3	'Hass'

[1] C : California, SA : South Australia, Q : Queensland.
[2] Exact age not known.

Table 4.2 Mean annual temperatures (maximum and minimum) and rainfall at meteorological stations nearest to locations used in this study. SA : South Australia, Q : Queensland. (Sources: Climatic Averages Australia, Meteorological Summary July 1988, Bureau of Meteorology, Australian Government Publishing Service; Queensland Department of Primary Industries, Nambour; University of California, Riverside).

Location	Temperature (C)		Rainfall (mm)
	Max.	Min.	
Australia			
McLaren Vale (SA)	19.9 [1]	7.9 [1]	826[2]
Maleny (Q)	25.5 [3]	13.6 [3]	2792[4]
California			
South Coast Field Station	23.3 [5]	10.5 [5]	328[5]

[1] 10 year mean (1976-86); [2] 15 year mean (1971-86); [3] 21 year mean (1965-86); [4] 3 year mean (1987-90); [5] 10 year mean (1981-1990).

Table 4.3 Node number (mean ± s.e.) of primary growth axes of reproductive (spring) shoot modules of Persea species and cultivars.

	Species	Location[1]	Node number[2]	No. of shoots
Sub-genus	Eriodaphne			
	P. donnell-smithii	C	19.3 ± 0.9	10
	P. indica	C	21.9 ± 2.0	10
	P. longipes	C	21.4 ± 0.7	10
Sub-genus	Persea			
	P. floccosa	C	23.2 ± 1.1	10
	P. schiedeana	C	20.7 ± 1.4	10
	P. schiedeana x P. americana	C	19.1 ± 0.6	10
	P. americana cv			
	'Fuerte'	SA	17.7 ± 2.3	3
	'Sharwil'	SA	18.4 ± 1.2	18
	'Reed'	SA	18.8 ± 1.1	20
	'Hass'	SA	20.2 ± 1.2	18
	'Hass'	Q	19.8 ± 1.9	5
	'Gwen'	Q	18.8 ± 3.0	4

[1] C : California, SA : South Australia, Q : Queensland.
[2] Analysis of variance found no significant differences between means ($P < 0.05$).

Table 4.4 Comparison of node numbers for vegetative and reproductive proleptic shoot modules, on primary and axillary axes of current annual growth modules on 7 year old 'Hass' avocado trees growing at McLaren Vale, South Australia.

Proleptic shoot module	Growth axis	No. of shoot modules	Node number (mean ± s.e.)	
Reproductive	primary	52	20.9± 0.4	c[1]
	axillary	65	14.8± 0.4	b
Vegetative	primary	74	14.1 ± 0.3	b
	axillary	103	11.9± 0.2	a

[1] Mean separation between means by Duncan's multiple range test (P = 0.05)

Table 4.5 Node numbers (mean ± s.e) (including leaf primordia, bud scales and bud-scale scars) of apical and axillary buds of avocado shoot modules at major phenological growth stages.

Growth stage:	shoot extension	apical bud set	advanced bud swell	advanced bud swell	bud break
Growth flush:[1]	V	V	V	R	R
Apical bud	13.0 ± 0.2	13.1 ± 0.3	17.3 ± 0.4	16.3 ± 0.6	22.8 ± 0.5
Axillary buds[2]	7.4 ± 0.2	9.3 ± 0.2	10.9 ± 0.6	11.8 ± 0.3	15.8 ± 0.7
	8.6 ± 0.3	10.4 ± 0.3	13.1 ± 0.5	12.1 ± 0.3	17.9 ± 0.6
	9.3 ± 0.2	10.7 ± 0.3	13.7 ± 0.4	12.7 ± 0.4	17.2 ± 1.0
	10.5 ± 0.2	11.5 ± 0.3	13.7 ± 0.5	12.6 ± 0.5	16.2 ± 0.8
	10.6 ± 0.2	12.0 ± 0.3	14.1 ± 0.3	12.3 ± 0.4	14.8 ± 0.7
	11.2 ± 0.2	11.5 ± 0.1	14.0 ± 0.4	12.1 ± 0.3	13.7 ± 0.6
	11.5 ± 0.2	11.5 ± 0.2	13.4 ± 0.4	12.8 ± 0.5	13.4 ± 0.4
	11.4 ± 0.2	11.3 ± 0.5	13.1 ± 0.4		11.8 ± 0.8
	11.2 ± 0.7	11.4 ± 0.7	13.3 ± 0.5		
		11.6 ± 0.9	14.3 ± 0.3		

[1] V : Vegetative, R : Reproductive.
[2] Presented in the sequence they occur below apical bud.

Table 4.6 Comparison of node numbers of apical and axillary buds at three stages of development, with number of nodes on shoots developed from similar buds.

	Number of nodes per bud at			Number of nodes on shoots in next flush	
	apical bud set	advanced bud swell	bud break		
Growth flush	Apical buds			Terminal shoots	
Spring	13.1 a	17.3 b	-	Summer	14.5 a
Summer	13.4 a	18.0 b	-	Autumn	13.4 a
Autumn (reproductive)	-	16.3 a	22.8 b	Spring (reproductive)	22.0 b
	Axillary buds			Axillary shoots	
Spring	10.8 a	13.1 b	-	Summer	11.5 ab
Summer	11.5 a	13.7 b	-	Autumn	10.6 a
Autumn (reproductive)	-	12.3 a	16.4 b	Spring (reproductive)	14.8 b

- No data.
Values with different letters show significant differences across columns by Scheffé's test (P = 0.05). Minimum of 15 observations per reading.

Table 4.7 Stages of vegetative and inflorescence primordia development (1 - 9)[1] (mean ± s.e.) at axillary nodes in apical buds on 'Hass' avocado shoots (n = 15) at major phenological growth stages. Node 1 is the first formed node, at the base of the bud.

Table 4.7

Growth stage	Apical bud set	Advanced bud swell		Bud break
Growth flush[2]	V	V	R	R
Node				
24	-	-	-	0
23	-	-	-	0.1 ± 0.1
22	-	-	0	0.3 ± 0.13
21	-	-	0	0.4 ± 0.19
20	-	-	0	0.5 ± 0.22
19	-	0	0.5 ± 0.14	0.9 ± 0.26
18	-	0	0.8 ± 0.21	1.5 ± 0.31
17	-	0.1 ± 0.07	1.6 ± 0.20	2.0 ± 0.28
16	-	0.3 ± 0.12	2.2 ± 0.26	2.7 ± 0.34
15	-	0.3 ± 0.13	2.6 ± 0.20	3.4 ± 0.27 F
14	0	0.7 ± 0.19	3.3 ± 0.29 F [2]	4.1 ± 0.35 F
13	0	1.1 ± 0.19	3.6 ± 0.25 F	4.9 ± 0.37 F
12	0	1.4 ± 0.16	4.2 ± 0.24 F	5.7 ± 0.36 F
11	0.1 ± 0.09	1.7 ± 0.12	4.8 ± 0.28 F	6.4 ± 0.29 F
10	0.5 ± 0.13	1.9 ± 0.09	5.4 ± 0.23 F	7.2 ± 0.28 F
9	0.9 ± 0.09	2.0 ± 0.10	5.1 ± 0.31 F	6.3 ± 0.62 F
8	1.2 ± 0.11	2.1 ± 0.07	3.1 ± 0.31 F	4.3 ± 0.73 F
7	1.5 ± 0.13	2.2 ± 0.11	2.4 ± 0.23	2.5 ± 0.40
6	1.9 ± 0.07	2.2 ± 0.11	2.2 ± 0.15	2.0 ± 0
5	2.1 ± 0.07	2.5 ± 0.13	2.1 ± 0.07	2.0 ± 0
4	2.4 ± 0.13	2.9 ± 0.09	2.6 ± 0.14	2.0 ± 0
3	2.9 ± 0.07	3.3 ± 0.12	3.0 ± 0	2.8 ± 0.11
2	3.1 ± 0.07	3.7 ± 0.12	3.1 ± 0.07	3.0 ± 0
1	3.9 ± 0.17	4.1 ± 0.07	3.9 ± 0.07	4.0 ± 0

- Node not present.

[1] 1 = meristem formation, 2 = first bract primordia, 3 = bract primordia extended over meristem, 4 = bract primordia tomentose, 5 = bud elongates, 6 = first branch primordia, 7 = first flower primordia, 8 = axis extends, 9 = flower primordia visible. Commitment to floral development occurs at Stage 3.

[2] V : Vegetative, R : Reproductive, F : inflorescence primordia.

Table 4.8 Development (1 - 9)[1] of inflorescence primordia in apical and axillary buds on 'Hass' avocado shoots (n = 15) at bud break, in spring.

	No. of floral nodes (mean ± s.e.)	Maximum stage of primordia development (mean ± s.e.)
Apical bud	8.2 ± 0.4	7.5 ± 0.2
Axillary buds[2]	3.5 ± 0.8	3.5 ± 0.7
	5.5 ± 0.6	5.3 ± 0.5
	4.9 ± 0.7	4.6 ± 0.7
	4.0 ± 0.7	3.8 ± 0.6
	2.9 ± 0.7	3.1 ± 0.7
	1.9 ± 0.8	2.0 ± 0.7
	0.4 ± 0.3	0.7 ± 0.4

[1] 1 = meristem formation, 2 = first bract primordia, 3 = bract primordia extended over meristem, 4 = bract primordia tomentose, 5 = bud elongates, 6 = first branch primordia, 7 = first flower primordia, 8 = axis extends, 9 = flower primordia visible. Commitment to floral development occurs at Stage 3.
[2] Presented in the sequence they occur below the apical bud.

Table 4.9 Basal diameter, length and number of flowers (mean ± s.e.) on determinate and indeterminate compound inflorescences of 'Hass' avocado.

Inflorescence type	Determinate	Indeterminate	
No. in sample	47	41	
Diameter at base (mm)	4.9 ± 0.1	5.9 ± 0.2	***[1]
Length (mm)	130 ± 4.5	66 ± 6.2	***
No. of flowers	73 ± 4.4	80 ± 8.6	NS

[1] Paired t-test carried out for each variate (NS = not significant, *** = $P < 0.001$).

Table 4.10 Numbers of bud scales, axillary inflorescences, leaves and leaf bracts (mean ± s.e.) along primary axes of indeterminate compound inflorescences in three Persea species.

	P. Americana cv 'Hass'	P. longipes	P. donnell-smithii
n =	41	10	10
No. of leaves and leaf bracts	9.2 ± 0.4 b	7.6 ± 0.9 b	0.2 ± 0.1 a
No. of axillary inflorescences	6.5 ± 0.3 a	9.9 ± 0.7 b	12.9 ± 1.3 c
No. of bud scales	5.7 ± 0.3 b	3.8 ± 0.4 a	6.2 ± 1.0 b
Total	21.4 ± 0.6	21.3 ± 0.7	19.3 ± 0.9

Values with different letters show significant differences across columns by Scheffé's test (P = 0.05). Difference between totals was not significant.

Table 4.11 Early fruit set (mean ± s.e.), one month post-anthesis, on indeterminate and determinate compound inflorescences of 'Hass' avocado.

	Indeterminate		Determinate
Axillary inflorescences	< 4	> 4	
n =	84	471	322
No. of fruit set per compound inflorescence	0.08 ± 0.03 a[1]	0.22 ± 0.02 b	0.36 ± 0.03 c

[1] Mean separation by Scheffé's test (P = 0.05).

Figure legends

Figure 4.1 Basal portion of proleptic vegetative shoot module of Persea americana showing bud-scale scars (arrows) and proleptic (P) and sylleptic (S) axillary shoots.

Figure 4.2 Growth stages during development of vegetative and reproductive buds and shoot modules in Persea americana cv 'Hass': A, vegetative bud at advanced bud swell; B, reproductive bud at advanced bud swell; C, vegetative module during shoot extension, with two proleptic axillary shoots (P); D, vegetative module at apical bud set; E, reproductive bud at bud break with inflorescences (I) developing in axils of bud scales; F, pre-anthesis inflorescence, with terminal vegetative meristem (V) at shoot extension.

Figure 4.3 Arrangement of bud parts (1 is the youngest) in an apical (A) and axillary (B) reproductive bud of Persea americana cv 'Hass'. Bud scales and leaf primordia have been removed to show (2 + 3) Fibonacci phyllotaxis. Scale = 1 mm.

Figure 4.4 A : Avocado bud, showing apical meristem (a) and stages 1 - 3 (numbered) of vegetative axillary meristem development. Scale = 1 mm. B : Determinate reproductive bud of avocado, showing development of terminal inflorescence (t), and axillary inflorescences at developmental stages 1 - 4, and 7 (numbered). Bracts of inflorescence at stage 7 have been folded back to expose terminal flower primordium (f). Scale = 0.1 mm. Stage 1 = meristem formation, 2 = first bract primordia, 3 = bract primordia extended over meristem, 4 = bract primordia tomentose, 7 = first flower primordia. Commitment to floral

development occurs at stage 3.

Figure 4.5 Avocado bud morphology in diagrammatic longitudinal section showing foliar appendages and inflorescence primordia (not drawn to scale): A, vegetative bud; B, reproductive bud (indeterminate); C, reproductive bud (determinate) with terminal inflorescence. Bud scales, solid black; leaf primordia, outlined; inflorescence bracts, stippled.

Fig. 4.1 Basal portion of proleptic vegetative shoot module of avocado cv 'Hass' showing bud-scale scars (arrows) and proleptic (P) and sylleptic (S) axillary shoots.


A
B
C
P
P
D
E
I
I
F
V

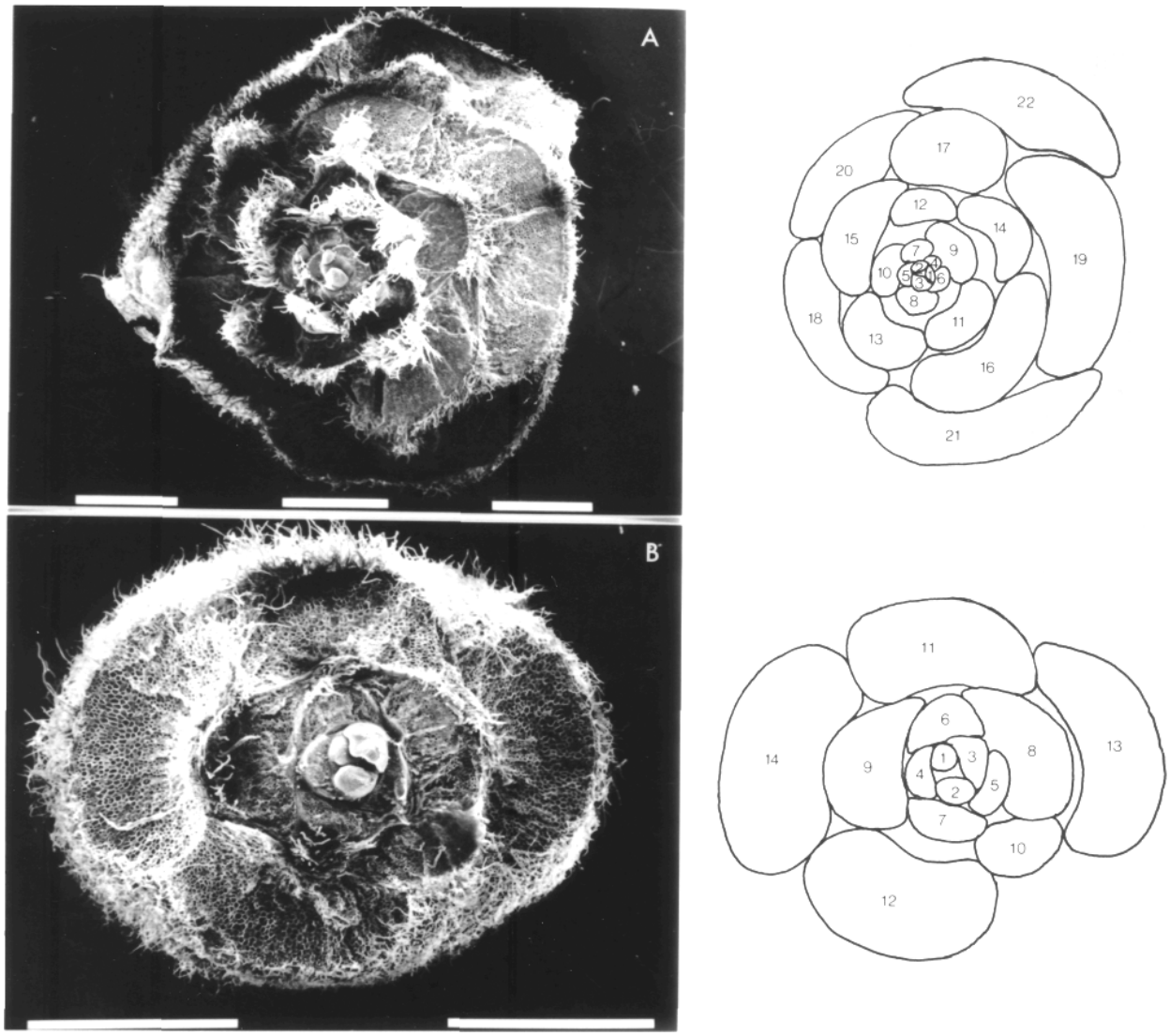
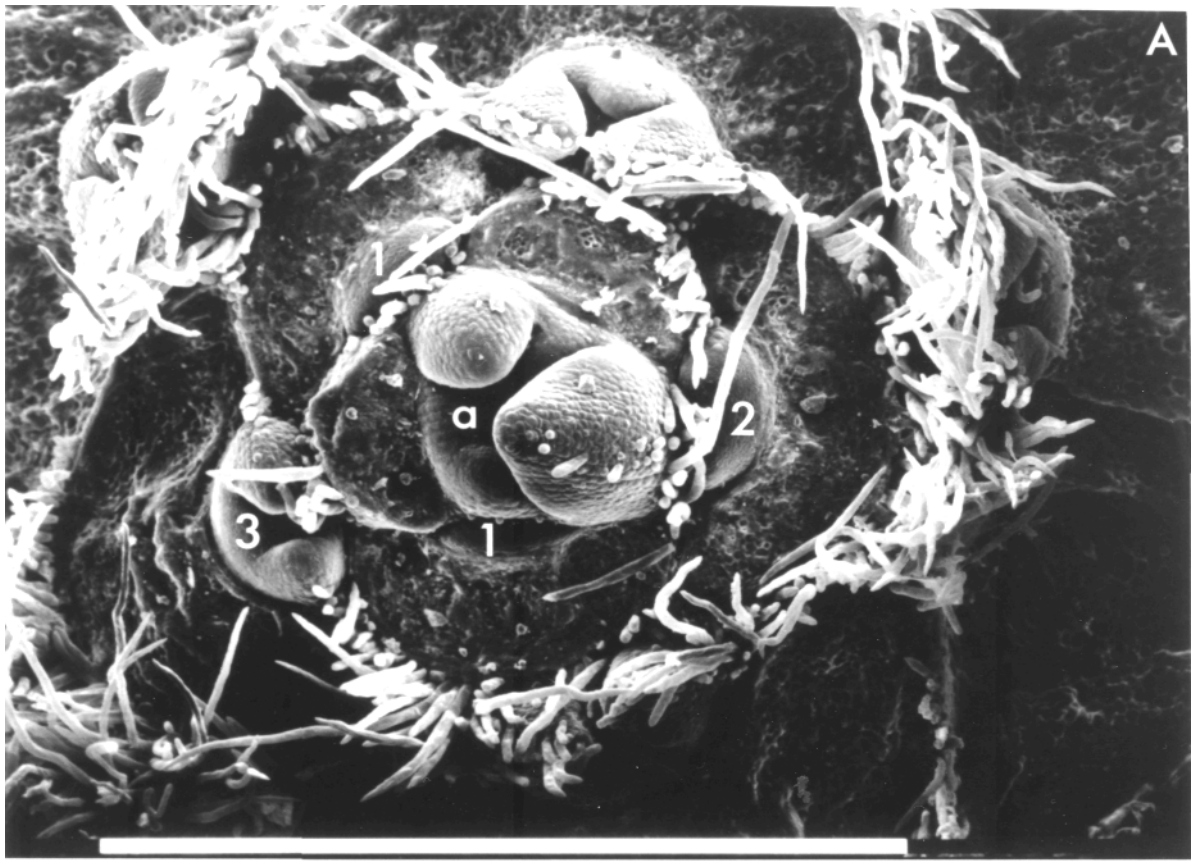
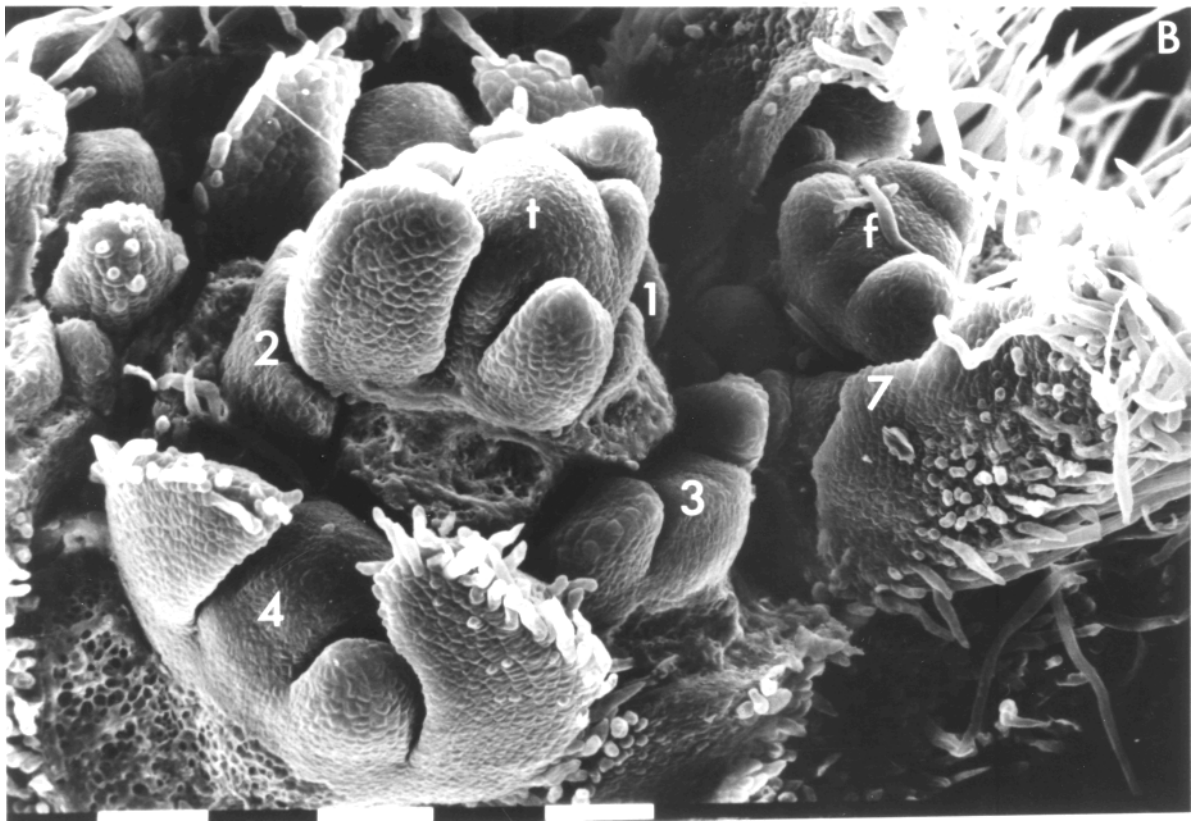


Fig. 4.3 Arrangement of bud parts (1 is youngest) in an apical (A) and axillary (B) reproductive bud of avocado cv 'Hass'. Bud scales and leaf primordia have been removed to show (2•3) Fibonacci phyllotaxis. Scale : 1 mm.


A
1
a
2
3
1


B
t
f
1
2
7
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4

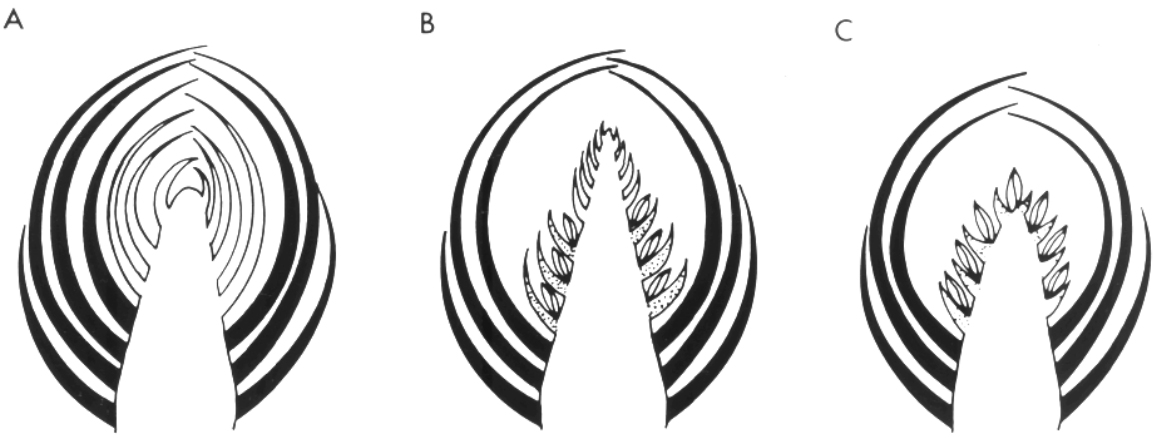

Fig. 4.5 Avocado bud morphology in diagrammatic longitudonal section showing foliar appendages and inflorescence primordia (not drawn to scale): A, vegetative bud; B, reproductive bud (indeterminate); C, reproductive bud (determinate) with terminal inflorescence. Bud scales, solid black; leaf primordia, outlined; inflorescence bracts, stippled.