7. Summary of avocado tree architecture.

Architectural tree models, defined by F. Hallé, R.A.A. Oldeman and P.B. Tomlinson (1978), are relatively new concepts in plant morphology that have gained wide acceptance in the fields of plant ecology and demography (Fisher, 1984; Tomlinson, 1987; Porter, 1989; Steeves and Sussex, 1989). These concepts also have application in horticulture, but while existing models are adequate for ecological studies, they require further elaboration to be useful to horticultural scientists investigating growth and productivity of fruit trees.

An architectural tree model represents "the fully developed, complex plan of assembly of (growth) modules into a coherent construction" (Hallé, 1986). An architectural analysis of growth, therefore, examines the modular elements of growth. The aim of this chapter is to summarize an architectural analysis of growth and growth processes in avocado, a major fruit crop in tropical and subtropical regions. The discussion is largely a synthesis of information presented elsewhere in this thesis.

The avocado is an example of the Rauh architectural tree model (Hallé et al., 1978). Terminology used here is based mainly upon that of Hallé et al. (1978), but includes some modifications suggested by Watkinson and White (1985). New terminology, derived from this study, to differentiate growth modules and their sequential iteration over seasonal and annual growing periods, is presented in Fig. 7.1. Shoot modules are the lowest order growth modules considered here. They are morphologically distinct, single units of extension, developed from individual buds or bud primordia. Shoot modules are the building blocks of the architectural tree model. Some authors include buds, leaves and flowers as modules (e.g. Hardwick, 1986; Porter, 1989; Williams, 1986), however, most buds on an avocado tree remain dormant indefinitely, or for extended periods and, as with leaves and flowers, contribute relatively little to tree form.

Various definitions of shoot modules have been used in the literature. Hallé et al. (1978) and Barthelemy (1986) defined a module as a shoot with determinate growth, either through apical abortion or conversion of the apex to an inflorescence. However, if growth is purely vegetative over a number of years, then when flowering does occur the resulting "module" may be a large tree and bear little resemblance to a "module" formed after one period of growth. Barthelemy described an Isertia coccinea tree, that had not flowered, to be "not modular, yet conforming to Rauh's architectural model". This statement contradicts the modular definition of the Rauh architectural model. Growth which is apparently continuous is often seen in juvenile plants. In avocado, however, closer examination shows that this continuous growth comprises a regular, rhythmic pattern of rapid (flush) and slow shoot extension (Borchert, 1978). Moreover, vegetative shoots on mature fruiting avocado trees appear to be developmentally fixed as shoots from a single growth flush have uniform node numbers (Chapter 4). Such indeterminate vegetative growth definitely involves the formation of distinct growth modules, although no apical abortion occurs. For this reason, we agree with Watkinson and White's (1985) suggestion that "module" should be replaced with "shoot module ... a reiterated structural unit". This definition incorporates both vegetative and reproductive growth, and indeterminate and determinate growth.

Shoot growth in avocado is dimorphic, with both proleptic and sylleptic shoots (Fig. 7.2), and shoot modules may be defined accordingly. Proleptic shoot modules arise only after a period of dormancy as a resting apical or axillary bud. They are detectable between two successive zones of bud scale scars, the bud-scar ring, which formed part of the resting bud. Bud-scar rings form at the junction between consecutive growth flushes. Sylleptic shoot modules do not undergo a dormant period as a resting bud. They develop from bud primordia in apical or axillary buds, and their growth is contemporaneous with extension of the parent axis. Sylleptic shoot modules do not have a bud-scar ring at their base. They are "units of extension" despite the fact they are not "delineated between two successive zones of bud scale scars", as defined by Hallé et al. (1978). Although both shoot types develop from similar axillary meristems (Wheat, 1980), and they are part of the same growth flush, the distinction between prolepsis and syllepsis is important in physiological studies as the difference in relative timing of each growth form suggests the involvement of separate control mechanisms and has implications for productivity.

Further differentiation of shoot modules is required to distinguish vegetative and reproductive growth. In avocado, one reproductive and generally one or two vegetative growth cycles (flushes) occur each year. Their analysis provides a means of examining conditions required for floral development that is not available with temperate trees which have one major growth cycle per year. In most temperate trees, floral initiation occurs in the interval between successive annual growth flushes. It is of interest, therefore, that floral initiation in avocado does not occur during the interval between all rhythmic growth flushes, even though there are no apparent differences between shoots from each flush (Chapters 4, 5). Floral initiation in avocado trees growing in subtropical and mediterranean climates occurs almost exclusively in autumn, irrespective of shoot age, provided shoots are fully extended and located near the canopy periphery in autumn, and have sufficient vigour to produce new shoot growth in spring. In the lowland tropics of the West Indies, flowering mainly occurs in a single flush during the dry season between February and May, although some cultivars produce their flowers in multiple flushes over a period of up to 8 months (Papademetriou, 1976; Plumbley et al., 1989).

In avocado, a reproductive shoot module is a proleptic shoot module that has developed from a resting bud containing floral initials. It forms a compound inflorescence with individual inflorescences mainly located axillary to the primary axis. In many plants, including avocado, reproductive shoot modules are formed from two phases of apical activity, the floral initials forming during the second phase (Chapter 4). Such biphasic development contrasts with Hallé's (1986) definition that reproductive modules (or units of morphogenesis *sensu* Hallé) are delineated by a single cycle of mitotic activity.

Interesting physiological information may be gained from a separate study of prolepsis and syllepsis. For example, Zieslin (1992) proposed that the transition to the floral state in rose plants is due to the elimination of inhibitory factors, as evidenced by the transition from proleptic to sylleptic axillary growth. In avocado, sylleptic shoot modules are always vegetative, but they may play a role in reproductive development as although the compound inflorescence is a proleptic shoot module, individual inflorescences are sylleptic (Hallé et al., 1978) and may be homologous with sylleptic vegetative shoots. Individual axillary inflorescences on reproductive shoot modules develop at equivalent times and locations as sylleptic shoots on vegetative modules. If the homology is accepted, then it would seem that the switch to floral development also involves a switch which prevents leaf development, as avocado inflorescences do not carry true leaves.

Comparison of sylleptic and proleptic development in avocados has revealed important cultivar differences in tree shape (Chapter 3). Strong proleptic growth was linked with an open spreading tree habit (e.g. 'Sharwil') while high rates of syllepsis were observed in cultivars with a more upright compact growth habit (e.g. 'Gwen' and 'Reed'). Certain plant growth regulators (e.g.

Cytolin) have been shown to encourage compact sylleptic branching in avocado, and increase fruit set (Chapter 6). No doubt future studies involving similar comparisons of tree growth would also benefit from separate analysis of proleptic and sylleptic shoot growth.

The above differentiation between proleptic and sylleptic shoot modules is consistent with the premise that a shoot module develops from a single growth flush associated with a single bud or bud primordium, respectively. The next order of growth module, called the rhythmic growth module, describes shoot growth (proleptic and sylleptic) developed during a single growth flush on a shoot module formed during a previous growth flush. In avocado, cultivar differences in tree habit may be observed in the relative strength of prolepsis and syllepsis in rhythmic growth modules (Chapter 3). The term rhythmic growth module is used to emphasise the strong endogenous control over shoot growth. Although growth in natural situations is often linked to seasonal fluctuations in temperature or rainfall, in more constant environments, growth is rhythmic and under endogenous control (Greathouse et al., 1971; Borchert, 1978).

The primary growth axis in a rhythmic growth module is the dominant growth axis. This differentiation is important in strongly growing modules of avocado, as the primary growth axis generally exhibits orthotropic development, compared with the plagiotropic development of axillary axes. Orthotropy is the gravitational response which produces a vertical axis with radial symmetry; plagiotropy produces a horizontal axis with dorsiventral symmetry (Hallé et al., 1978).

When more than one major growth flush develops over an annual growing period, as in tropical and subtropical genera, the combination of rhythmic growth modules, thus formed, is called the annual growth module. This is a collective term for all shoot modules formed during an annual growing period on a single shoot module of the previous year's growth. In avocado, floral development occurs mainly in apical and axillary buds on the last formed shoot of a particular growth axis. The earlier formed, subtending modules (shoot units), are therefore non-fruiting structural units. The ratio between these fruiting and non-fruiting shoot modules is important to the overall productivity of annual growth modules. Maximising this ratio may be an important step to improving productivity in avocado.

Modular analysis of tree growth is a reductionist approach, but its strength lies in the fact that it retains an appreciation of the holistic growth model

(Tomlinson, 1987). This is the first time architectural tree models have been applied in horticultural science. Similar concepts of modular analysis would benefit research in other fruit trees. However, to achieve this requires a consistent terminology for describing and/or quantifying growth. The terminology discussed here has been developed for avocados, it should also be useful for describing growth in other plants. Modular analysis is a simple means of describing tree growth, that should enable a more sophisticated understanding of whole-canopy architecture, and facilitate comparison of growth among plants from widely different genera.

Figure legends

Figure 7.1 Schematic diagram summarising modular construction in avocado.

Figure 7.2 Distinguishing features of sylleptic and proleptic shoot modules in avocado.

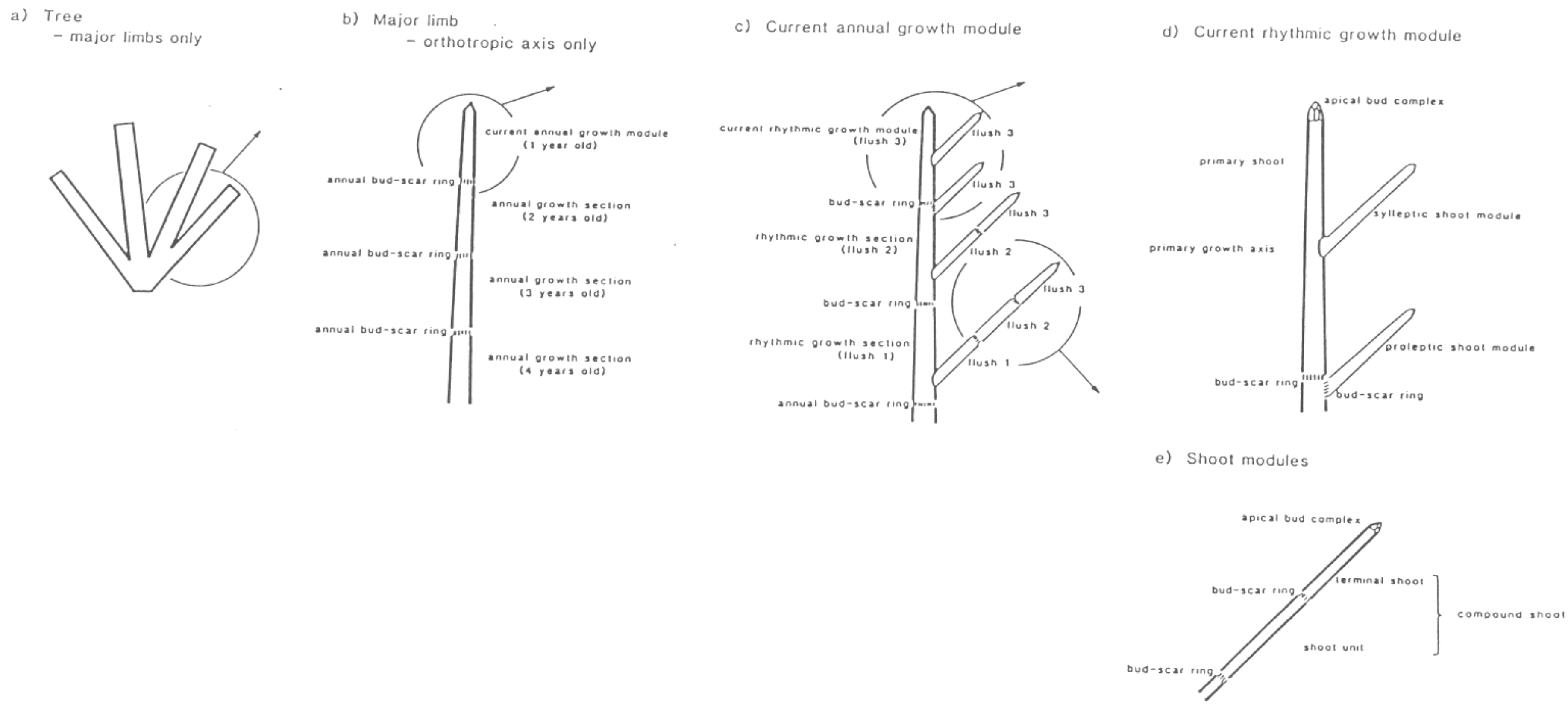
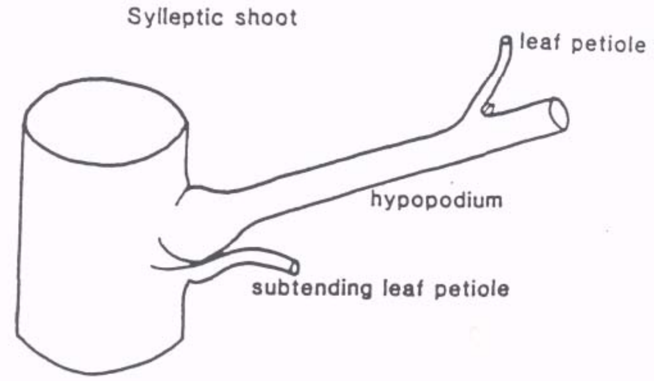


Fig. 7.1 Schematic diagram summarising modular construction in avocado.



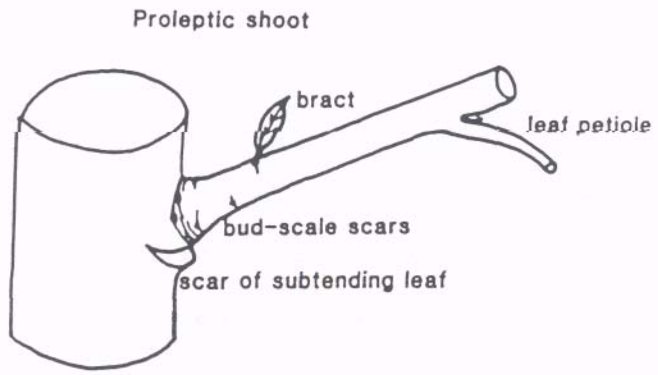


Fig. 7.2 Distinguishing features of sylleptic and proleptic shoot modules in avocado