8. General discussion

This thesis has been primarily concerned with investigating tree growth in avocado, a major fruit crop in tropical, subtropical and mediterranean regions. A structured approach has been adopted to quantify this growth in terms of its separate elements. Central to this research has been an examination of bud morphogenesis and flowering, and the roles they have in determining the observed patterns of shoot formation.

Axillary shoot growth in plants is generally described in terms of apical dominance, whereby an active terminal bud imposes dormancy on the axillary buds beneath. Classical demonstrations of this in herbaceous plants have involved the decapitation of a plant and observations of the regrowth from the bud nearest to the cut surface (Thimann and Skoog, 1933, 1934; Went, 1939). Since this early work, apical dominance has become a general term to cover the formation of a meristem, the imposition and/or release of inhibition at that meristem, and the relative dominance of subsequent growth. Unfortunately, it is the latter two of these events, that is the release of buds from inhibition and the length of the subsequent growth, which have gained prominence in the literature (Cline, 1991). A plethora of theories pertaining to apical dominance in both herbaceous annuals and woody perennials have been proposed. Plant hormones, in particular auxins and cytokinins, availability of nutrients, and environmental factors such as light and gravity have been implicated (Cline, 1991; Martin, 1987; McIntyre, 1977; Tamas, 1987). Not surprisingly, in attempting to incorporate features of all hypotheses, general unifying hypotheses have been proposed (Martin, 1987). These attribute apical dominance to several different factors, the relative importance of each being determined by the stage of bud or shoot development. Martin (1987) went on to suggest that researchers have been mistaken in looking for "a simple solution for a phenomenon (apical dominance) that embraces most physiological events occurring in plants". An alternative viewpoint is that researchers have attributed too many physiological events to apical dominance. Possibly the mechanism imposing dormancy is unrelated to the mechanism releasing buds from dormancy. Indeed, apical dominance may involve only a single step, the imposition of dormancy, and not the myriad of hormonal, environmental and physical factors which influence subsequent growth of resting and active growth axes. Should a more restrictive definition of the term apical dominance be advocated? It is difficult, if not impossible, to get a restrictive definition of a term accepted once a more general definition has become accepted. Use of the term in the restrictive sense then becomes clouded by misunderstanding. Possibly the introduction of new unambiguous terms should be advocated to differentiate the growth processes more generally defined as apical dominance. Such new terms could be developed from the various types of dormancy (Lang et al., 1987) and correlative inhibitions (Champagnat, 1989) recently defined.

Relatively few studies have been made on the imposition of dormancy in the bud (Cline, 1991), however, the gene-controlled ratio between auxins and cytokinins would seem to be the most plausible mechanism imposing this dormancy and hence controlling apical dominance (Klee and Estelle, 1991). If it is accepted that apical dominance involves the imposition of dormancy at growth, then in avocado at least, this involves the control of sylleptic shoot growth. In plants with no syllepsis, with axillary shoot growth only after a period of rest, complete apical dominance can be assumed (Hallé et al., 1978; Tomlinson, 1983, 1987). On the other hand, apical dominance may be absent during inflorescence development in which all secondary axes are sylleptic. A similar observation led Zieslin (1992) to suggest that floral development in rose plants is regulated by apical dominance. In this study with avocado, strong apical dominance resulted in few sylleptic shoots and weak apical dominance gave many sylleptic shoots. The overall effect of strong apical dominance was an open, spreading growth habit with relatively numerous major limbs, whereas trees exhibiting weak apical dominance formed a single dominant axis with numerous small axillary axes. Most horticulturists would incorrectly attribute this latter growth form to strong apical dominance. Such anomalies have long been recognized by tree physiologists who differentiate between apical dominance, the suppression of axillary buds by the apical bud from which they developed, and apical control, the mechanism determining relative dominance of growth axes (Brown et al. 1967, Brown, 1971). Clearly, the pre-disposition to growth of resting buds, that contributes to the wide range of architectural tree models described by Hallé et al. (1978), develops independently of apical dominance.

Flowering also determines shoot morphogenesis. The most obvious being the distinction between vegetative and reproductive shoot modules. In seasonal climates, reproductive modules on avocado trees appear mainly in spring. If they could be encouraged to develop during summer or autumn, to produce out-of-season flowering, then this would reduce the dominance of vegetative growth (Wolstenholme, 1988). Advances made with promoting out-of-season flowering in a range of fruit and vegetable crops (Chang and Bay-Peterson, 1990), suggest that a similar outcome could be achieved with avocado. Competition between vegetative and reproductive growth in avocado (P. americana) is most apparent during the development of indeterminate compound inflorescences. Here, rapid extension of terminal vegetative axes coincides with anthesis and early fruit growth, and leads to reduced fruit set (Biran, 1979, Zilkah et al., 1987). A sequence of vegetative development, more conducive to fruit set, was observed with P. donnell-smithii. In avocado, an inflorescence bract forms at the base of individual axillary inflorescences. In P. donnell-smithii, however, each inflorescence was subtended by a true leaf which was fully developed by the time the adjacent inflorescence reached anthesis. Furthermore, an inflorescence formed at all nodes beyond the basal bud scales, so that even though the apical bud remained vegetative, there was no terminal vegetative flush to compete with floral development and early fruit set. Morphogenesis of compound inflorescences therefore involves control over leaf development as well as control over formation of inflorescence meristems. If a "leaf" gene could be activated in avocado, it could be possible to increase fruit yields by reproducing the leafy compound inflorescence of P. donnell-smithii. A temporal separation between leaf growth and flowering, similar to that in P. donnell-smithii, has been observed by the author in 'Hass' avocado. In this case, leaf growth typical of that observed on vegetative shoots occurred during shoot extension in summer, and axillary inflorescences in the axils of these leaves extended in the next (autumn) flush. Further investigation into the control of these atypical growth patterns may hold the key to increased productivity in avocado.

Stebbins (1992) argues that the genetic basis of plant morphogenesis is epigenetic, involving a balance between gene-controlled suppression and activation of growth processes. Tree architecture can be considered in similar terms, especially if modular analysis is employed. Strong apical dominance, for example, appeared to involve suppression of axillary bud development during initiation of shoot modules. Vegetative shoot modules had suppressed development of inflorescence and hence floral meristems. Reproductive shoot modules in avocado had suppressed leaf meristems when inflorescence meristems were activated at the same nodes, while in P. donnell-smithii, no similar leaf suppression was observed. Molecular genetic techniques have already enabled important advances towards the reliable control of apical dominance (Klee and Estelle, 1991), and inflorescence and floral meristem development (Coen, 1991). Control over leaf development could also be achieved with similar techniques. Although there are still major problems to be solved before such approaches can be adopted in research with perennial fruit trees, it is apparent they will soon be overcome (Schaff, 1991; Scorza, 1991). When this occurs, gene transfer techniques will play a major role in the manipulation of tree architecture to the benefit of fruit production. A clear understanding of modular growth will assist the development of well-targeted research using these techniques, and communication of the results.