2. Review of vegetative and reproductive growth interactions in avocado.

2.1 Introduction.

The related problems of alternating fruit yields and over-vigorous shoot growth in avocado have been discussed by Whiley et al. (1988b) and Wolstenholme and Whiley (1989) in terms of the plant's phenological cycle. They refer to the energy costs of fruiting and the opportunities to manipulate the balance between vegetative and reproductive growth. In this review I will consider the topic of their discussions in more detail, with specific reference to experimental evidence of the interactions between vegetative and reproductive growth.

This review covers literature available before December 1989, the date the review was completed. References to literature published after that date and up to the end of the project will be included in subsequent discussions. Adato (1990) was made available to me in 1989 so has been included here. A significant component of the literature reviewed here was originally published as student theses or in relatively obscure journals, often in languages other than English. Where full copies of such references were not available and/or the information was "seen" in a separate publication, a specific note of this has been made in the reference list.

2.2 Tree growth.

It is important to first consider the basic components of avocado tree growth, including the major phenological events, before discussing any interactions between the vegetative and reproductive elements of this growth.

2.2.1 Tree architecture.

Avocados exhibit a monopodial, rhythmic pattern of growth, characteristic of the Rauh model of tree architecture discussed by Hallé et al. (1978). The monopodial trunk forms branches that are morphogenetically identical to the trunk, and flowers are borne laterally with no effect on the growth of the shoot system. Although the Rauh model is predominant, some avocado shoots also bear flowers in terminal positions so that subsequent shoot growth is sympodial and characteristic of the Scarrone model (Hallé et al., 1978). The Rauh model is one of the most frequent among trees from temperate and tropical zones. It is a very adaptable model, compared with the unbranched Holtum and Corner models, that enables the tree to respond quickly to environmental cues by reiteration of the monopodial growth model. Reiteration is a specialised environmental response to limb damage or conditions that stimulate resting apical meristems. It is responsible for the formation of multiple trunks in severely pruned trees, e.g. in orchards where young trees have been headed back to encourage formation of scaffold branches.

2.2.2 Shoot growth.

Shoot extension and intervening periods of rest produce the rhythmic pattern of growth included in the Rauh model. From one to six shoot growth flushes per year have been reported with avocados (Adato, 1990; Gregoriou and Kumar, 1982; Kalmar and Lahav, 1977; Köhne and Kremer-Köhne, 1987; Koo and Young, 1977; Scholefield et al., 1985; Whiley et al., 1988b). All of these reports refer to the percentage of shoots in active growth. Many will be axillary, plagiotropic (horizontal) shoots, developing as a consequence of the growth of the parent orthotropic (vertical) axis (Maillard et al., 1989). They may expand at the same time as the parent axis, or they may be in active growth when the parent axis is resting.

Axillary branching on avocado trees may be proleptic, where a shoot develops only after a period of dormancy as a resting bud; or sylleptic, where there is no dormant period and lateral growth is contemporaneous with that of the parent axis (Gregoriou and Kumar, 1982; Hallé et al., 1978; Venning and Lincoln, 1958).

Cladoptosis, the abscission of small branches, is common with avocados (Gregoriou and Kumar, 1982; Scholefield et al., 1985), producing long sections of barren wood. A similar effect results from the rather large number of lateral buds that are shed soon after development. Indeed, most axillary buds have been shed by early autumn (Chandler, 1958; Gur, 1962; Venning and Lincoln, 1958). Only those from the axis of bud scales formed between two growth flushes persist, often for many years. It is these buds that are stimulated to grow by severe pruning (Venning and Lincoln, 1958). The result of prolepsis, syllepsis, cladoptosis and bud shedding is a rather diffuse pattern of axillary branching along the main axes of avocado trees (Hallé et al., 1978).

2.2.3 Leaf growth.

Leaves are critical to the production and partitioning of carbohydrates. Many of the approaches applied to understanding these processes in deciduous fruit trees can be applied to evergreen trees such as avocado (Turner, 1986).

Although avocado trees are evergreen, various degrees of defoliation can occur, especially in spring when most "old" leaves are shed and replaced with "new" season's growth. The main period of leaf drop occurs "during flowering" (Whiley et al., 1988b), or "a few days after flowering" (Cameron et al., 1952). Lahav and Trochoulias (1982) have reported a mean individual leaf area of 60 cm^2 on young 'Fuerte' and 'Hass' trees, while Symons and Wolstenholme (1989) reported 49.7 cm^2 for 'Hass' leaves. Lahav and Trochoulias (1982) found that leaves were smaller in very hot (37/26°C day/night) or cold (17/10° C) temperatures. No accurate data is available on total leaf area on mature trees, except that Cameron et al. (1952) reported two 'Fuerte' trees shed on average 26187 leaves per tree over a 12 month period. Few leaves persist for more than 12 months, so this number of leaves would approximate total leaf number per tree. Using the individual leaf area data of Lahav and Trochoulias (1982), total leaf area per tree would have been approximately 157 m^2. The above trees produced 253 fruit. That is a leaf:fruit ratio of 104:1, or 0.62 m^2 leaf area per fruit. This compares with 0.3 m^2 leaf area per fruit suggested for grapefruit (Fishler et al., 1983); and 0.03 - 0.1 m^2 leaf area per fruit reported for kiwifruit (Snelgar and Thorp, 1988).

Avocado leaves exhibit characteristics of shade plants with maximum photosynthetic rate occurring at 25% of full sunlight (Scholefield et al., 1980). In Israel, the optimal temperature for net photosynthesis was found between 20 and 30°C due to increased stomatal and mesophyll resistance at higher and lower temperatures (Kimelmann, 1979). The presence of fruit increases CO_2 assimilation in proximal leaves, possibly via a carbohydrate-mediated feed-back mechanism (Finazzo and Davenport, 1986; Schaffer et al., 1987).

2.2.4 Root growth.

There have been few scientific examinations of the root systems of mature avocado trees. Most reports refer to root growth on young plants exhibiting continuous growth (see Borys, 1986). Whiley et al. (1988b) reported two periods of root growth on mature avocado trees growing in Queensland, each period of growth occurring at the termination of a vegetative growth flush. In contrast, Gregoriou and Kumar (1982) and Herbert (1989) reported continuous root growth and no relationship with shoot flushing as long as soil conditions were conducive to growth. Gregoriou and Kumar (1982) reported that the taproots of plants they studied were imperfectly formed and became multi-branched a short distance below the soil surface. A very shallow root system with a dense proliferation of fine roots was produced. Salazar and Cortés (1986) reported that with mature trees, up to 75% of root volume consisted of roots with a diameter less than 8 mm. In clay soils, 82 % of root volume was located in the top 60 cm of soil; in sandy soils, 69 % of root volume was located in this zone, with most of these (47 %) located in the top 20 cm of soil. Avocado roots do not have root hairs (Burgis and Wolfe, 1946; Gregoriou and Kumar, 1982).

2.2.5 Flowering and fruit set.

Much attention has been given to understanding the biology of avocado flowering, and the influence of environment on flowering, pollination, fruit set and yield. This work was recently reviewed by Davenport (1986), while Lomas (1988) separately reviewed the effects of high temperatures during flowering on fruit set and yield. Little attention was given in these reviews to factors in the preceding season which effect flower production and the balance between the vegetative and reproductive components of growth, e.g., photosynthetic area and fruit load. These are factors that primarily effect flower induction, but they may also influence subsequent floral development and fruit yield.

Mature avocado trees can produce more than one million flowers (Biran, 1979; Cameron et al., 1952; Lahav and Zamet, 1976a). These flowers are regular, bisexual and trimerous (Reece, 1939), and show marked protogynous dichogamy (Bringhurst, 1952; Papademetriou, 1976; Sedgley, 1985; Sedgley and Grant, 1983; Stout, 1923). They are borne on inflorescences, derived from terminal and subterminal buds on growth from the previous season (Schroeder, 1951; Reece, 1942). Floral buds may be mixed to give indeterminate floral shoots (compound inflorescences), or sometimes not mixed to give determinate floral shoots with a flower in the terminal position (Schroeder, 1944 and 1951).

The exact timing of floral induction, the event triggering transcription and expression of flowering genes, is not known with avocados (Davenport, 1986). The first visible sign of flower development, floral initiation, occurs in autumn in subtropical climates (Reece 1942; Scholefield et al. 1985), four to five months before anthesis in spring (Alexander, 1975 and 1983; Lichou and Vogel, 1972; Whiley et al., 1988b). In the lowland tropics of the West Indies, anthesis occurs during the dry season between February and May (Papademetriou, 1976; Plumbley et al., 1989).

Duration of flowering is cultivar and temperature dependant. In tropical regions, flowering may continue for from 1-2 to 7-8 months depending on the cultivar (Papademetriou, 1976; Plumbley et al., 1989). With a different set of cultivars growing in subtropical and Mediterranean climates, the flowering period was 1-3 months (Alexander, 1975 and 1983; Lichou and Vogel, 1972; Whiley et al., 1988b). In controlled conditions, high temperatures reduced the number of flowers, and the flowering period, of young 'Fuerte' and 'Hass' trees (Buttrose and Alexander, 1978; Sedgley, 1977; Sedgley et al., 1985).

Cross pollination appears to be an important factor in successful avocado production, although good yields have been obtained from single cultivar blocks (Davenport, 1986). There is increasing evidence, however, that fruit set from out-crosses are retained in preference to those from self-pollination (Degani et al., 1986 and 1989; Degani and Gazit, 1984; Gafni, 1984; Vrecenar-Gadus and Ellstrand; 1985), and out-cross pollen from some parents is more effective than from others (Argaman, 1983; Degani and Gazit, 1984; Gafni, 1984; Goldring et al., 1987). Gafni (1984) reported metazenia, although this was determined from the size of fruitlets, and not the mature fruit.

2.2.7 Fruit growth and maturity.

Bower and Cutting (1988) have reviewed avocado fruit growth and development "as a background to ripening physiology...and long-term storage".

Avocados follow a single sigmoid pattern of growth (Blumenfeld and Gazit, 1974; Schroeder, 1953). Increase in fruit size results from cell division and expansion in the early period of growth, but cell division is the main component of growth in the latter stages of fruit development, apparently continuing throughout the time the fruit is on the tree.

Whiley et al. (1988b) refer to two major periods of fruit drop in Australia. One occurring in September and October, four to six weeks after anthesis; the second in January. Davenport (1985) has suggested that avocados be divided into Type I cultivars that initially set a high number of fruit, most of which are subsequently shed; and Type II cultivars that initially set only a few fruit and these are mostly retained until maturity.

Avocado fruit yields typically alternate between heavy and light crops (Table 2.1). This is a major concern of avocado growers. Fruit may be plentiful in an on-year, but economic returns are generally low due to an oversupply of small fruit in particular. In off-years, prices may be better and fruit larger, but these are of little consequence if only a handful of fruit are harvested from each tree. Crop alternation appears to be an inherent feature of fruit trees (Monselise and Goldschmidt, 1982), and a more detailed discussion of its implications to fruit production are included later in this review.

Avocado fruit are recognised for their high oil content, ranging from 15 to 30% on a fresh weight basis (Ahmed and Barmore, 1980; Biale and Young, 1971). Horticultural maturity of avocados is determined on a dry weight basis - an indirect measure of flesh oil content (Lee et al., 1983; Underraga et al., 1987). Fruit of different cultivars attain horticultural maturity at different stages of their phenological sequence (Alexander, 1983; Plumbley et al., 1989). Harvest of "early" cultivars generally coincides with the period of flower initiation in winter, whereas "late" season cultivars may be harvested in the following summer, after flowering. These relationships appear to be temperature dependant as fruit may mature earlier in warmer climates, but flowering may be less affected (Alexander, 1983).

2.3 Vegetative and reproductive growth interactions.

In the previous section I have summarised information that describes the "normal" pattern of avocado growth. In the second part of this review, I will consider published evidence of interactions within and between the vegetative and reproductive components of growth, and examine some of the methods used to manipulate growth and their effect on tree productivity. Vegetative growth is primarily concerned with survival of the individual, and in this context includes both shoot and root growth. Reproductive growth, however, concerns the flow of genetic information from one generation to the next, and includes the production of flowers and seed bearing fruit.

2.3.1 Root and shoot growth.

There is little detailed information on the interaction between root and shoot growth in avocados, or in many tropical trees exhibiting rhythmic growth (see Maillard et al., 1989). Whiley et al. (1988b) provided some evidence of an alternating pattern of root and shoot growth in mature avocados, but this has not been confirmed with experimental evidence. With other plants, rhythmic growth has been described as an endogenous growth process, controlled by a feed-back mechanism operating between shoot and root growth (Borchert, 1978), possibly involving an interaction between shoot produced auxins and root produced cytokinins (Tamas, 1987). Endogenous factors controlling root and shoot growth are thought to be more important in trees of tropical origin that have had fewer exogenous constraints placed upon them, than in trees of temperate origin (Borchert, 1978). Exogenous factors, in particular climate, will modify the expression of rhythmic growth. Fruit can also be regarded as an exogenous factor, located external to the vegetative system. Fruit may affect the proportion of assimilate allocated to reproductive compared with vegetative growth, however, it does not alter the root:shoot ratio (Richards, 1986) unless at very high fruit loads (Landsberg, 1986).

All plants appear to have a characteristic root:shoot ratio, responding to alterations of this ratio with compensatory growth to restore the characteristic balance between roots and shoots (Marini and Barden, 1987; Mika, 1986). Controlling root growth, by root restriction or root pruning techniques, is an important means of controlling vegetative growth in temperate fruit trees (Richards, 1986). Similar techniques may not be appropriate for avocados as the inevitable root damage would make treated trees more susceptible to root rots such as Phytophthora cinnamomi.

Rootstocks and interstocks have important effects on tree growth and productivity (Rom and Carlson, 1987). Wutscher (1989) has reviewed avocado rootstock effects in relation to tree nutrition, but does not relate this information to shoot growth or fruitfulness. High yield variability between trees grafted onto seedling rootstocks has been reported (Gillespie, 1952; Ben-Ya'acov, 1973), suggesting a rootstock effect on productivity. Apart from general tree performance, the major economic factors determining avocado rootstock choice are resistance to Phytophthora cinnamomi and tolerance to saline or alkaline soils (Ben-Ya'acov, 1987 and 1989; Brokaw, 1987; Coffey and Guillemet, 1987; Kadman and Ben-Ya'acov, 1981). Borys (1986), Borys et al. (1985) and Flores et al. (1988) indicated differences between West Indian, Mexican and Guatemalan races of avocado used as rootstocks in terms of root orientation and the relative dimensions of roots and shoots. But this was for young trees exhibiting juvenile growth characteristics (Borchert, 1978). Bergh et al. (1988) reported that mature 'Hass' trees were larger on P. nubigena rootstock than P. americana, with no significant difference in yield. No data on root growth was given.

Dwarfing rootstocks and interstocks have been reported for avocados (Bergh and Whitsell, 1962; Hernandez and Gallegos, 1982; Lopez and Barrientos, 1987; Barrientos et al., 1987). None are used in commercial plantings, however, and their effects on tree productivity have yet to be determined.

2.3.2 Alternate bearing and shoot growth.

Alternate (irregular) bearing is a commonly cited example of the close relationship between shoot and reproductive growth. Monselise and Goldschmidt (1982) have reviewed alternate bearing in fruit crops, including avocados. They suggest that regular cropping cultivars, selected for in most fruit breeding programmes, have efficient self-thinning mechanisms to maintain consistent fruit loads. With avocados, genetic selection may be an important part of such a self-thinning mechanism. This is indicated by reports mentioned previously in this review that suggest preferential retention of fruit set from out-crosses rather than from self-pollination, and from some out-cross pollen sources in preference to others. The very marked pattern of alternate bearing in avocado cultivars, however, may indicate that this self-thinning mechanism is relatively inefficient. The advantage of regular yields and the annual dispersal of seed bearing fruit may be compromised by the avocado's investment in geneflow via pollen rather than seed transfer (Janzen, 1977a,b), as evidenced by the extremely high number of flowers produced.

Monselise and Goldschmidt (1982) emphasized "fruit overload" as an important cause of alternate bearing in fruit trees. They proposed that with a heavy crop of fruit, excess accumulation of the hormonal inhibitor abscisic acid (ABA) in maturing fruits, leads to inhibition of floral development in axillary buds, and so a reduction in next years crop. Cutting et al. (1986) have since reported increased ABA concentration in the flesh of avocados as the fruit approached maturity, which is approximately the time of flower initiation. Furthermore, unusually high levels of ABA have been reported in avocado fruit due to stress in the early stages of fruit growth (Bower and Cutting, 1987). The presence of a flowering inhibitor in avocados, this time produced by young leaves, has also been suggested by Ben-Tal (1986).

Alternate bearing may also be influenced by availability of growth factors, e.g., carbohydrates, minerals and plant hormones (Monselise and Goldschmidt, 1982). Compared with other crops, fruiting is relatively energy expensive in the avocado due to the high flesh oil content (Wolstenholme, 1986), and is likely to contribute to "fruit overload" during on-years. Although it is possible that the high leaf area:fruit ratios mentioned before, and the evergreen nature of avocados, could increase photosynthetic capacity to compensate for the high energy outlay. Causal relationships between availability of growth factors and alternate bearing in avocados have been indicated by various pruning trials that removed competing vegetative sinks (Biran, 1979; Farré et al., 1987; Zilkah et al., 1987), girdling trials that maintained artificially high levels of growth factors in treated branches (Hodgson, 1947; Lahav et al., 1971, 1972 and 1986; Ticho, 1971; Trochoulias, 1973 and 1977; Trochoulias and O'Neill, 1976); studies of carbohydrate cycling (Cameron and Borst, 1938; Rodrigues and Ryan, 1960; Scholefield et al., 1985); and plant growth regulator treatments that caused large numbers of seedless fruit to set, in addition to the normal crop of seeded fruit (Stewart and Heild, 1951).

The high level of flowering does not appear to be an important cause of alternate bearing in avocados (Cameron et al., 1952), although flowering in itself is likely to be a large drain on tree resources (Whiley et al., 1988a), in particular iron (Lahav and Zamet, 1976b). With healthy trees, more flowers do not automatically mean more fruit (Farré et al., 1987; Lahav and Zamet, 1976a; Papademetriou, 1976). Trees which produce too few flowers to set a crop of fruit may induce alternate bearing, but it is more likely that a previous heavy crop of fruit was the first to initiate the cycle of irregular fruit yields.

Pruning can reduce alternate bearing in avocados. Pre-bloom, tip-pruning treatments of Farré et al. (1987) and Miller (1960) applied prior to an expected on-year, increased fruit yields in the following off-year. Miller's treatment reduced fruit load in the current on-year and this may have contributed to increased yields in the off-year. Farré's treatment, however, did not reduce yields in the on-year. Increased shoot growth and total leaf area were observed in response to Farré's treatments. Possibly the resultant increase in photosynthetic area contributed to increased yields in the off-year, as Rodrigues and Ryan (1960) and Scholefield et al. (1985) have suggested that the summer growth flush in avocados helps restore carbohydrate reserves required for floral initiation and development of next years crop. Stephenson and Cull (1986) have also emphasized the importance to macadamia nut yields, of a strong summer flush and the resulting higher potential photosynthetic capacity. In deciduous trees, early defoliation drastically reduces carbohydrate reserves, especially in the roots, and can also reduce flower formation (Oliveira and Priestley, 1988). A check of the carbohydrate status in winter of pruned versus un-pruned avocado trees, in their on-year, may confirm the role of the summer flush in reducing the effect of "fruit overload".

Lahav and Kalmar (1977) found that irrigation influenced the degree of alternate bearing in avocados. More frequent irrigation, that applied more water, exaggerated the difference between yields in on- and off-years. This resulted in higher average yield over the six year period, but it also increased fruit size in the on-year. Little treatment effect was found on tree size, but more frequent irrigation increased the number of growth flushes from one to two, to three or four per year (Kalmar and Lahav, 1977). Increasing irrigation only in on-years may reduce alternate bearing by increasing the summer growth flush, while also increasing the size of otherwise small fruit.

If more fruit and less leaves are produced as a result of growth inhibitor treatments then this could seriously overload the tree, reducing next season's crop. Paclobutrazol is a triazole derivative that inhibits shoot extension in a wide range of species (Davis et al., 1988), including avocado (Adato, 1990; Köhne and Kremer-Köhne, 1987; Symons and Wolstenholme, 1989; Wolstenholme et al., 1988; Whiley et al., 1988c). While a reduction in shoot length is universally observed, there are few reports which describe the effects of paclobutrazol on features such as internode length, leaf area or branching. Symons and Wolstenholme (1989) observed shortened internodes, reduced total leaf area and decreased branching on young potted plants after treatment with paclobutrazol as a soil drench. If similar treatments, applied to mature fruiting trees, caused a change in leaf area:fruit ratios and patterns of light interception within treated canopies, then it would be of interest to examine the effects of these changes on tree productivity.

2.3.3 Manipulation of shoot growth.

There are numerous management options available that alter the balance between vegetative and reproductive growth. Reproductive growth is commonly manipulated with various flower and fruit thinning techniques. Pruning, however, is the most important management technique for regulating fruit load. Pruning is a direct manipulation of shoot growth, and involves an immediate alteration of root:shoot ratios.

The physiological responses of fruit trees to pruning have been reviewed by Mika (1986), and Marini and Barden (1987). In temperate trees, dormant pruning is generally thought to stimulate shoot vigour whereas summer pruning may reduce shoot vigour and induce fruiting. With avocados, most authorities recommend minimum pruning and then only as necessary to provide access to trees and in some cases reduce tree height, as "pruning stimulates shoot growth at the expense of fruiting" (Beck, 1952; Koch, F.D., 1983; Kotzé, 1982; McCarty et al., 1962; Smoyer et al., 1951). However, relatively few detailed avocado pruning trials have been reported in the scientific literature. Gaillard (1971) reported the start of a detailed tree training investigation involving complex cordon and palmette systems. Notably, no yield data has been forthcoming from this work.

Various tip-pruning treatments have been evaluated (Biran, 1979; Farré et al., 1987; Miller, 1960; Montgomery, 1955). These have mostly involved cutting back the current, or most recent, growth flush. Biran (1979) reported that weekly removal of young growth from selected 'Fuerte' branches during flowering caused a 50 % increase in fruit set and 20 % increase in fruit weight. Repeating the trial on whole trees, produced a x10 to x21 increase in fruit yield. Biran believed the effect was due to removal of vegetative sinks that would otherwise compete for assimilates with developing fruitlets. Paclobutrazol apparently has a similar effect by shifting the onset of the spring vegetative flush away from the period of fruit-set (Adato, 1990; Köhne and Kremer-Köhne, 1987). Bar-On (1986) found an equivalent situation in a study of high and low yielding 'Fuerte' trees. In this study, onset of vegetative growth, after flowering, occurred five days later in high-compared with low-yielding trees. It has also been suggested that determinate floral shoots, with no terminal vegetative flush, have better fruit set than indeterminate shoots (Bertling and Köhne, 1986). It is not clear what conditions promote formation of determinate floral shoots. However, conditions that promote vegetative growth appear to result in more leaves (and less flowers?) on indeterminate floral shoots (Salomon, 1984).

Important cultivar differences are apparent in the response to tip-pruning and growth inhibitor treatments. With 'Fuerte', best results were obtained if paclobutrazol was applied as the first few flowers reached anthesis (Adato, 1990), or at full-bloom (Köhne and Kremer-Köhne, 1987). Results from similar applications to 'Hass' trees, however, have been less consistent (Whiley et al., 1988c). Adato (1990) suggested the full-bloom timing may not be appropriate for 'Hass', as vegetative growth is not simultaneous with fruit-set in this cultivar. Whiley et al. (1988c) said their full-bloom applications coincided with the onset of vegetative growth - a better effect may have been obtained if their applications were made at an earlier stage. Similar inconsistencies have been observed in response to tip-pruning trials. Yields in the year of pruning (expected on-year) were either increased (Biran, 1979), not effected (Farré et al., 1987), or reduced (Miller, 1960). The differences may have been due to the timing of pruning treatments. Farré et al. (1987) and Miller (1960) tip-pruned their trees before flowering, whereas Biran (1979) did this during the flowering period. The differences may also have been cultivar related as each trial involved a different cultivar and the relative timing of anthesis and rapid shoot growth may vary among cultivars. Unfortunately, no studies have compared the timing of onset of spring shoot growth relative to flowering with different cultivars, or with the same cultivar in different climates and/or growing conditions.

The tip-pruning treatments of Farré et al. (1987) and Miller (1960) also significantly reduced the number of flowers, but apparently this had no effect on fruit yield. Neither did removing 80% of flowers (Papademetriou, 1976), or thinning young fruitlets soon after flowering effect final yield (Farré et al., 1987). This suggests that the strength of competing vegetative sinks is more important to fruit set than competition among reproductive sinks.

There is no doubt that young leaves on a developing growth flush are net importers of assimilates (Finazzo and Davenport, 1987a), and therefore compete with young fruitlets. But these leaves quickly become net exporters and start contributing to fruitlet growth. Indeed, Finazzo and Davenport (1987a) believe that leaves and fruitlets are equal sinks at an early stage, providing further indication of the importance of timing manipulative treatments to take advantage of phenological events determining relative sink-strengths. Carbon partitioning could be studied in shoots/inflorescences at different phenological stages, to establish exactly when flowers and leaves become competing sinks in a range of cultivars and conditions.

Topping, to reduce the height of tall, upright growing cultivars produces a severe alteration in the root:shoot ratio and may encourage greater assimilate allocation to fruit growth. Warneke et al. (1972) reported yields of young 'Bacon' trees were reduced after topping. In mature trees, yields were effected in the year of pruning, but were almost back to normal in the year following. It is not clear if tree size was also "back to normal". And no information was included on the fruit bearing habit of un-pruned portions to indicate the reasons for reduced yield. Was it simply due to reduced fruiting surface, or was vegetative re-growth stimulated at the expense of fruiting? In contrast to the results of Warneke et al. (1972), a general increase in yield from topping 'Lula' trees has been reported by Bertin (1976), with a 5 t/ha yield increase after 3 years of pruning. The degree of mutual shading before topping may determine the effect on subsequent yields as Goodall (1954) reported topping reduced avocado yield more if trees were crowded before pruning, than if they were widely spaced. Ashenkasi (1984) recommends annual topping at 6.5 m for 'Hass' and 'Ettinger' trees, arguing that without tree topping the fruiting canopy becomes isolated at the top of trees, due to shading of lower branches, and fruit become difficult and expensive to harvest.

Re-growth from topped 'Bacon' trees has been successfully suppressed with formulations of Naphthaleneacetic acid (NAA) (Boswell et al., 1972). Unfortunately no information was included to indicate if this pruning and subsequent growth suppression affected fruit yields.

Nitrogen is an important management tool for manipulating shoot growth. Bower and Cutting (1988) considered the effects of nutrition in general in their review of fruit development and ripening, and Embleton et al. (1959) have reported on nitrogen fertilization trials with avocados. The general observation is that nitrogen promotes vegetative flushing in the spring, and so reduces fruit yields in the following season. It is recommended, therefore, that nitrogen should not be applied to avocados close to flowering (Kotzé, 1982; Whiley et al., 1988b), and only sufficient amounts should be applied to maintain tree health. There is some evidence, however, that nitrogen can be an effective tool in increasing fruitfulness of avocados, although responses will depend on the level of tree nutrition. Abou Aziz (1975) reported that, in Egypt, nitrogen applied between March and June increased fruit yield of 'Fuerte'. This is the flowering period of 'Fuerte' in Corsica (Lichou and Vogel, 1972), which has a climate similar to that in Egypt. Nevin and Lovatt (1987) have postulated a more direct role of nitrogen in controlling flowering. They have suggested increased nitrogen in autumn, combined with minimal stress, e.g., low temperature (Nevin and Lovatt, 1988 and 1989) or salt stress (Ayers et al., 1951; Downton, 1978), may be a way to maximise flowering in avocado. Their working hypothesis is that ammonia accumulation is an essential component of flower induction. Autumn nitrogen fertilization has been shown to increase carbohydrate reserves in deciduous fruit trees by delaying leaf fall (Oliveira and Priestley, 1988). This factor may be worth considering in similar trials with avocados.

2.3.4 Axillary branching.

Reduced vegetative vigour is generally regarded as a fundamental step to improving avocado orchard productivity (Wolstenholme, 1988), and trials involving growth inhibitors and dwarfing rootstocks have been discussed earlier in this review. Vegetative vigour, however, can be interpreted in different ways. Increased vigour may materialize as longer shoots with longer internodes and/or increased nodes. It may also appear as increased axillary branching.

Increase in shoot length is not wanted by the grower wishing to contain tree size, but an increase in axillary branching could have positive effects through increased leaf area. As mentioned before, increased photosynthetic capacity in an on-year may increase fruit yield in the subsequent off-year (Farré et al., 1987). Timing is likely to be important. Rapid shoot growth, too late in the summer, is likely to be damaged by autumn frosts and poor floral initiation will result (Montgomery, 1955; Newman, 1972). High rates of shoot growth in spring may be antagonistic to fruit set (see above), and are likely to reduce fruit calcium content with negative effects on fruit growth and post-harvest quality (Bower and Cutting, 1988).

Reports of nutrition, irrigation and pruning trials, mentioned previously in this review, that have increased shoot growth, have included no information of treatment effects on axillary branching. There have been some reports, however, that plant growth regulators may affect the pattern of axillary branching. McCarty et al. (1971) increased the number of sylleptic shoots on young avocado seedlings by applying the auxin transport inhibitor TIBA (2,3,5-triiodobenzoic acid). Haas and Brusca (1954) produced a similar effect when they applied 2,4-D to the soil around young 'Fuerte' trees growing on 'Caliente' rootstocks. Unfortunately, both of these treatments increased the length of primary shoot axes as well as increasing lateral branching. No treatments have been reported that increased the number of proleptic shoots. The pattern of axillary shoot formation may also be altered by preventing the abscission of lateral buds. Gur (1962) has reduced bud abscission on detached avocado shoots by dipping them in 50 ppm IAA (indoleacetic acid), but few details were provided.

Apart from increasing photosynthetic area, increased axillary branching on young trees may increase the number of potential fruiting points, and bring these trees into production sooner than trees with few axillary shoots (Köhne, 1986). Manipulating the ratio of sylleptic and proleptic shoots may also lead to increased productivity. The development of proleptic and sylleptic shoots are temporally separated on a growth flush. Proleptic shoots produced during the first growth flush may compete for resources with flowers, whereas sylleptic shoots develop later in the growth flush and may be antagonistic to fruit set. A genetic relationship may also exist between axillary branching and tree size. With young seedling avocados, branched trees were shorter than single axis trees (Barrientos and Sanchez, 1982). Fruit breeders may be able to exploit this factor.

Increased axillary branching will most likely increase leaf production, however, leaf retention patterns may also be affected. Scholefield et al. (1985), working with 'Fuerte', reported shedding of old leaves took place throughout the year on short shoots, and from late summer on long shoots (mean shoot length 9.8 and 32.1 cm respectively). Although saline water was likely the major cause for high rates of premature leaf-shed in this trial, it does indicate that some shoots have a competitive advantage over other shoots. Manipulating the type of axillary branching may improve leaf retention and hence the photosynthetic capacity of avocado trees.

2.4 Conclusions.

In reviewing the literature on the vegetative and reproductive interactions of avocados it was notable that reproductive development has been well researched and reported, but vegetative growth, both above and below-ground, has received only cursory attention. This is surprising considering the often cited, dominating effects of shoot growth over flowering and fruit yields. Shoots and roots comprise large pools of carbohydrates, yet relatively little is known about their interactions in avocado. There is still no clear evidence for an alternating pattern of shoot and root growth. Nor are we familiar with the effects of fruit removal on shoot and/or root growth, and the implications for subsequent fruit yields. The concepts of "good fruiting wood" have not been developed to the extent they have been in other fruit crops. Light interception within the tree canopy, and the accumulation of carbohydrate and mineral reserves and plant hormones, required for the formation of next years crop, need to be researched in this context. More careful examination of shoot growth is required. Rather than investigating treatments that simply reduce vegetative vigour, all factors that modify the expression of rhythmic growth, or that cause a shift in the timing of major phenological events, should be considered. Critical to such investigations will be the development of a sophisticated understanding of tree architecture incorporating both the temporal and spatial features of shoot growth.

Table 2.1 Example of alternate bearing in 'Fuerte' avocado trees (from Scholefield et al., 1985).

Season	1975	1976	1977	1978	1979
Fruit yield (kg/tree)	64	16	63	1	29