

ALTERNATE BEARING IN THE AVOCADO (*PERSEA AMERICANA* MILL.)

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INTRODUCTION

An alternate or biennial bearing tree is one that does not bear a regular crop year after year. Instead, heavy yields are followed by extremely low ones and vice versa. Early literature emphasizes alternate or biennial bearing of deciduous fruit trees. However, this phenomenon is common in widely different families of trees including citrus, apples, mangoes, pistachios, pecans, and avocados⁵².

During a single alternating cycle, the on-year is the year in which trees produce an intense bloom in the spring and a heavy crop load is set and carried through maturity, eventually resulting in a high yield at the time of harvest (on-harvest). An off-year is the year in which the trees produce a light bloom, resulting in a light crop load and a low yield at the time of harvest (off-harvest). Alternate or biennial bearing is not always an every other year cycle. An "extremely" on-year can be followed by one or more off-years and vice versa.

Alternate bearing in avocado is a phenomenon that growers and the industry would like to eliminate because of its economic impact. In on-years, the large number of fruit produced per tree results in smaller individual fruit that are less valuable. In off-years, the fruit are of better size and quality, but the very low yields result in low net dollar return to the grower. Through the law of supply and demand there is a price fluctuation between on- and off-years. In addition, during the years of off-harvest it is frequently necessary to import fruit from other countries. This results in loss of market share.

The initial trigger for the start of an alternating cycle can be an external factor such as frost, lack of pollination, or drought which greatly reduces one year's crop³⁴. Inadequate thinning of the crop in years in which the high temperatures associated with June fruit drop do not occur can also trigger alternate bearing. Once this cycle has started, it usually is amplified annually and becomes self-perpetuating⁶⁸. Delayed harvest referred to as "on-tree storage" or "late hanging of fruit" has been proposed as an additional cause of alternate bearing in the avocado.

The difference in yield between the on-year and the off-year can vary. Reductions of up to almost 100% in yield of the off-harvest relative to the on-harvest have been reported⁷³. Alternate bearing in avocado can occur at different levels. In sub-tropical areas where climatic conditions are more moderated, it usually occurs at the orchard or tree level. However, because the biennial cycle usually starts in response to external factors, in some areas with more extreme climatic conditions alternate bearing occurs in most of the orchards; and it can affect the whole industry of a particular area. In

California, as early as 1947 it was observed that the total production of the state exhibited alternating cycles in which, for a specific year, most of the orchards were in the on-year, followed by a year in which most of them were in the off-year²⁹.

The physiological and biochemical bases for alternate bearing in avocado are not well defined. Research thus far has emphasized two hypotheses to explain the perpetuation of alternate bearing, with little integration between the two. The first hypothesis suggests that flowering, fruit set, and fruit growth utilize large amounts of carbohydrate. Thus, a carbohydrate deficit would limit these processes and eventually result in alternate bearing. It is hypothesized that the heavy crop load in on-years would cause a reduction in the accumulation of carbohydrate during the autumn and winter, resulting in a light bloom the next spring characteristic of off-years. During an off-year, trees would accumulate higher carbohydrate levels during autumn and winter, resulting in an intense bloom the following on-year^{13,25}.

The second hypothesis was proposed by researchers who favor the role of plant growth regulators (PGRs) produced by the seed of the developing fruit, which during the on-year would inhibit flower initiation and cause the light bloom characteristic of the subsequent off-year. The total number of studies on PGRs in avocado is very small, likely due to the difficulties inherent in such studies. Thus, evidence for or against this hypothesis is limited for avocado.

In this paper, the experimental evidence related to alternate bearing in the avocado that is reported in the literature is critically reviewed to determine whether there is sufficient evidence to support one or both of the hypotheses as an explanation for the perpetuation of the alternating cycle of yield. As a result of this critical review, an alternative hypothesis on alternate bearing is emphasized, which takes into consideration the effect of the crop load on the amount of current year summer and fall vegetative shoot growth as the key factor impacting the number of potential flowering points the following spring. In conclusion, a series of tree and orchard management practices are proposed that could be used by growers to eliminate alternate bearing and actually maximize tree yields on an annual basis.

HYPOTHESIS 1: CARBOHYDRATE AVAILABILITY PERPETUATES ALTERNATE BEARING IN AVOCADO.

Starch is the most common and important form of carbohydrate in most higher plants. It can accumulate to concentrations averaging 20% of the dry mass of some tissues. It is the most useful indicator of seasonal fluctuations in carbohydrate in crops and is closely related to aspects of tree performance of interest to horticulturists⁸¹. Starch concentrations in vegetative tissues are greater during the off-year. This has been repeatedly confirmed in apples²⁸, pecans²², and citrus³³.

One of the best known studies favoring the hypothesis that carbohydrate availability is the basis for the perpetuation of alternate bearing was done by Scholefield *et al.*⁵⁹. Their

study identified the seasonal changes in starch concentrations in avocado branches and established that high yields were associated with a high accumulation of starch during the previous winter, yielding high starch levels in the spring at the onset of flowering. Maximum levels of starch occurred in late winter through early spring just before flowering, and declined during flowering, shoot growth, and fruit development to a minimum in late summer and autumn. Starch accumulation began at the time of cessation of vegetative growth and continued over winter and early spring. The heavy crop load in on-years resulted in low concentrations of starch the following winter and spring and a late light bloom, accompanied by much new vegetative growth. Thus, under the conditions where the experiment took place, alternate bearing appeared to be closely related to carbohydrate availability in the tree—contrary to the hypothesis that high carbohydrate concentration is required for floral initiation. The authors suggested that low levels of carbohydrate might have caused the cessation of vegetative growth prerequisite to floral initiation¹⁴. Interestingly, floral initiation was observed to occur at the time of minimum carbohydrate content of the major branches.

Whiley and Wolstenholme⁷¹ found similar seasonal variations in starch levels; *i.e.*, the greater accumulation occurred during autumn and winter reaching the highest concentration just prior to flowering. They also observed a reduction in starch levels during the period of flowering, fruit set, and fruit growth. The minimum starch concentration occurred during the summer. They included these changes in starch concentration in their phenological model for the 'Fuerte' avocado.

The results of Scholefield *et al.*⁵⁹, although better known, were similar to those of a much earlier study by Cameron and Borst¹⁵. They showed that a tree carrying a heavy crop accumulated less starch during the winter and had lower starch levels during summer and autumn than nonbearing trees. They suggested that starch storage during the autumn and early winter was reduced by the demands of the developing fruit. Evidence that crop load reduced carbohydrate availability was provided by the observation that trees produced practically no new vegetative growth during the summer that they were carrying a heavy crop.

In a study done by Van der Walt *et al.*⁶⁸, a close relation between carbohydrate levels and amount of fruit carried by the tree was found. Their data demonstrated the change in carbohydrate status of trees during the transition between an on- and off-year. They observed that the heavy fruit load depleted the carbohydrate reserves of on-trees in November and January, but that these same trees accumulated starch in May as a result of the low demand for carbohydrate by the light bloom and crop of the subsequent off-year. Conversely, off-trees accumulated starch in the winter and showed a sharp decline in the reserve content of carbohydrate during the spring when these trees produced a heavy bloom and set an on-crop.

An additional argument that is used to support the hypothesis that carbohydrate availability perpetuates alternate bearing in avocado is the fact that avocado fruit contain high levels of oil (up to 40% of dry weight in some cultivars), which is obviously energy expensive and requires larger amounts of carbohydrate from the tree compared to sugar storing fruit like apples, oranges, or bananas. The high oil content of the avocado fruit may explain why carbohydrate reserves are severely depleted in an on-year during the period of fruit growth and oil accumulation. Using energy budgets,

Wolstenholme⁷⁸ calculated the potential yield of 'Fuerte' avocados to be only 32.5 tonnes/ha (at 17% oil content) compared to 100 tonnes/ha for apples and 88.5 tonnes/ha for 'Valencia' oranges.

In order to obtain a better price for their fruit, many growers delay harvest to well past the time the fruit first reached maturity (21% dry weight). This has two consequences. First, the fruit continues to accumulate oil; and second, the trees flower and set fruit while still carrying the unharvested crop⁸⁰. Thus, it is anticipated that delayed harvest will exert a pronounced effect on carbohydrate status of the tree and productivity in subsequent years²⁷.

Whiley⁷⁵ tested the effect of delayed harvest and found that it strongly induced alternate bearing in 'Fuerte' trees over a period of five years. He tested the effect of harvesting fruit at different stages of dry weight accumulation. Dry weight is the usual and most practical indicator of maturity for avocado fruit and is correlated with oil content. The treatments were harvesting of all the fruit at either 21%, 24%, or 30% dry weight and harvesting 50% of the fruit at 21% and the rest at 30% dry weight, or 50% of the fruit at 24% and the rest at 30% dry weight. Continued early harvesting of fruit at 21% or 24% dry weight for six years resulted in annual yields where variation was insignificant. Harvesting 50% of the fruit at 21% or 24% dry weight and the rest at 30% dry weight, or harvesting fruit only when they had reached 30% dry weight, resulted in the development of an alternate bearing cycle where the amplitude increased with time.

In a study with 'Hass' trees, Whiley⁷⁵ found that during the first two years yield was greater from late harvested trees (35% dry weight or 50% of fruit harvested at 30% dry weight and the rest at 35% dry weight), but by the third year the yield was higher in early harvested trees (25% dry weight). He noticed that in the third and fourth years there was an indication that treatments were beginning to affect production sustainability, and that in trees harvested at 35% dry weight there were signs of the beginning of a biennial bearing pattern. He concluded that it was necessary to remove fruit from trees when dry matter content was between 21% to 24% dry weight for 'Fuerte' and between 25 to 30% dry weight for 'Hass' in order to sustain production levels. He also observed that, although 'Hass' was more tolerant to delayed harvesting of fruit and took longer to develop alternate bearing cycles, once biennial patterns had developed in the 'Hass' avocado they could not be broken by early harvesting of the fruit and more severe strategies such as fruit thinning or pruning were required to moderate cropping patterns.

In summary, the results of available studies^{15,59,68} provide evidence of a correlation between starch availability and crop load the following season. Trees carrying heavy crops do not accumulate sufficient carbohydrates to support adequate flowering intensity and fruit set the next year, whereas trees carrying a small crop will accumulate enough carbohydrates to produce an intense bloom with high fruit set.

Conversely, there are a number of studies in which there is no correlation between the concentration of available starch and crop load the following season. Kaiser and Wolstenholme³⁶ found similar seasonal changes in the starch levels as those found by Scholefield *et al.*⁵⁹ and Cameron and Borst¹⁵; *i.e.*, maximum levels in spring (just before flowering) and minimum levels in autumn. In their experiments, annual average levels of starch in bark tissues were higher in earlier harvested trees (July) than in late harvested

trees (November). However, flowering and fruit set in November harvested trees were not different from trees harvested at other times, but yields were greater in late harvested trees (which had lower starch levels in October just before flowering) than in early harvested trees (which had higher starch levels prior to flowering). The fact that subsequent yields were not significantly correlated with carbohydrate level and flowering suggests that carbohydrate availability is not the single factor regulating yield and alternate bearing cycles.

Graham and Wolstenholme²⁷ tested the effect of different harvest dates on the 'Hass' avocado at two different locations. Results of this study appear to be contrary to those found by Kaiser and Wolstenholme³⁶ discussed above. Both studies reported similar seasonal changes in the starch levels and that trees harvested early in the season (July) accumulated higher levels of starch than trees harvested later (September to November). However, in the Graham and Wolstenholme³⁶ study differences in starch levels did not affect the bearing behavior of the trees, since trees harvested either in July (high starch levels) or in November (low starch levels) both showed pronounced alternate bearing behavior, independently of the starch levels in the previous winter.

Whiley *et al.*⁷³ found that delaying harvest strongly induced alternate bearing, with yield reductions of up to 100% in off-years following on-years in which fruit were left on the tree until they reached 30% dry weight. However, the expected relationship between trunk starch concentrations and tree performance held up only for the first of three years of study. The authors concluded that from their results a direct effect of reduced carbohydrate availability on tree performance or bearing pattern could not be demonstrated.

In the studies discussed above, it was consistently reported that starch accumulation occurred mainly during winter, with maximum levels reached in the spring just before flowering, and that starch levels were reduced during flowering and fruit set. This trend was found in both on- and off-years; the only difference was the magnitude of the accumulation. Whiley⁷⁵ in a study with 'Hass' avocados found a different situation. He observed that maximum starch concentrations did not always occur in the spring just before flowering. In his studies he found that the autumn-winter accumulation of starch did not occur when trees were carrying a heavy crop, and that minimum concentrations occurred just before the flowering period of the off-year. In that year, starch accumulation began during the flowering period and continued during anthesis and fruit set, probably due to the low demand for assimilates by these processes in an off-year. In the off-year, trees accumulated higher starch concentrations during the autumn and winter, and maximum levels were reached in the middle of the flowering period of the on-year, not before the flowering period as other researches reported^{59,71}. However, in the on-year, accumulated starch was utilized during the period of anthesis and fruit set, in a similar way as was reported in previous studies⁰⁹.

In summary, these studies demonstrated a lack of correlation between starch levels and bearing behavior of avocado trees^{27,36-73}. Graham and Wolstenholme²⁷ integrated hypotheses one and two by concluding from their research that induction of meristematic initials sets the potential for development of reproductive or vegetative organs via growth dependent plant growth regulator production, and that assimilate level only influences the extent of their development after induction.

EFFECT OF COMPETITION FOR NITROGEN AND OTHER MINERAL NUTRIENTS ON ALTERNATE BEARING.

Competition for nitrogen and/or other mineral nutrients as a factor involved in the perpetuation of alternate bearing in avocado would seem a logical corollary to competition for carbohydrate; yet, the effects of crop load on tree nitrogen status or of stored nitrogen on the intensity of the subsequent spring bloom have been the subject of limited study. In pistachios it was observed that in on-years there was a strong demand for nitrogen by the developing nuts which resulted in reduced concentrations of stored nitrogen. For avocado there are no studies investigating this competition. However, avocado fruit can contain up to 4.5% protein per gram of dry weight. The 'Hass' avocado contains 2.4% protein which is unusually high for a fruit; e.g., three times as much as mango, orange, peach, and persimmon and six times as much as apricot and apple⁵. Thus, the avocado is not only "carbon expensive" fruit, but also a "nitrogen expensive" fruit. A typical avocado weighs 200 to 300g fresh weight; thus, there are 5.0 to 7.5 g of protein per avocado fruit, which represents 1g of nitrogen per fresh fruit. It was calculated that with a harvest of 10 tonnes/ha of fruit, 28 kg N per hectare was removed⁴⁶. Logically, avocado fruit require large amounts of nitrogen during their development which might result in the competition for this element between developing fruit and vegetative shoot growth.

The period of fruit set which is characterized by competition between young developing fruit and the developing vegetative flush may also be a time when nitrogen is in critical demand. Whiley and Schaffer⁷⁴ showed a figure indicating that there is a sharp decline in nitrogen, and boron, levels in over wintering leaves during flowering. In another study Bar *et al.*⁴ demonstrated that new leaves are a strong sink for nitrogen and that its concentration increased during spring in the first phase of leaf growth. Thus it is possible that setting fruit and new leaves are also competing for nitrogen. In this regard, Kalmar and Lahav³⁷ went so far as to recommend the avoidance of cultural practices that stimulated vegetative growth during the fruit set period.

A similar situation might occur with calcium. Bower and Cutting¹² suggested that nitrogen and calcium levels markedly affect yield, fruit size, and postharvest quality and that the interaction between these two elements influenced the vegetative/reproductive balance in the avocado tree. Calcium concentration gradually increased from leaf emergence to senescence⁴. Witney *et al.*⁷⁶ observed that calcium concentrations in fruit increased during the first six weeks after fruit set in 'Hass' and 'Fuerte' avocados. Thus, it seems probable that competition for calcium between setting fruit and leaves of the spring flush is occurring to the detriment of the small developing fruit which would be weaker sinks compared to the vigorously growing spring shoots. Since calcium is a relatively immobile nutrient with little or no redistribution to new growth, a continuous supply is required⁵⁵.

Additional studies are needed to determine if there is an interaction between stored nitrogen availability and yield during on- and off-years, as well as an effect of time of harvest on the nitrogen status of the tree. The potential competition between fruit and vegetative flushes for other mineral nutrients, as well as the possible role of nutritional

status of avocado trees on alternate bearing await further research.

HYPOTHESIS 2: PLANT GROWTH REGULATORS PERPETUATE ALTERNATE BEARING IN AVOCADO

This hypothesis basically suggests that during on-years the large number of fruit on the tree produces plant growth regulators (PGRs) that inhibit flower initiation. The classic idea is that gibberellins (GA) produced by seeds are responsible for the inhibition of flowering.

Ebert and Bangerth²³, Garcia-Luis *et al.*²⁵, and Jonkers³⁴ all stated that gibberellic acid produced in the seeds of fruit inhibits flower induction. This has led to the hypothesis that biennial bearing cultivars produce more or different gibberellins than regular bearing cultivars⁶⁸. In fact, some of the gibberellins produced by seeds and diffusing into the spurs appeared to be more effective inhibitors of flower initiation than other gibberellins⁵². This argument has been demonstrated to be true in apples by Ebert and Bangerth²³ and Marino and Green⁴⁷. It was found that apple seeds are rich sources of gibberellins, and diffusate experiments demonstrated that gibberellins move from the seeds into the spurs. Similarly more gibberellin activity was found from diffusates of biennial bearing cultivars than in those cultivars which have a regular bearing habit.

It has been shown that applications of gibberellins reduce flowering in subtropical and tropical evergreen trees^{35,51}. In their study, Scholefield *et al.*⁵⁹ mentioned that flower initiation occurred as a consequence of cessation of vegetative growth due to reduced carbohydrate levels. It could be possible that cessation of vegetative growth is related to a decrease in the production of gibberellins by the growing shoots, allowing flower initiation.

Recent research by Salazar-Garcia and Lovatt⁵⁷ suggested that gibberellins are not typical inhibitors of flowering in avocado, and that the effect of applications of GAS to 'Hass' avocado trees depends on the time of the application. The main effect of applications of GAS to avocado resulted in early bud break and growth of the shoot apex at whatever stage of development it had reached at the time of the application. If applications were made early enough so that most buds contained only partially formed inflorescences, floral intensity was reduced. But if the application was made in December or later, when most of the buds contained all the secondary axes primordia, there was no effect on floral intensity and fully formed inflorescences were produced. It is important to mention that these results are the responses to applications of exogenous GAS. No studies have quantified fruit export of GA or the accumulation of GA at the time of flower induction or flower initiation when trees are carrying on- or off-crops.

There is little doubt that roots play an important role in the regulation of flowering and promotion of bud development through the timely supply of growth regulators³⁰. Initially, cytokinins were not thought to play a role in flower induction; more recent evidence has indicated that cytokinins can overcome the inhibitory effects of GA4+7 on flowering in apples⁴⁹. Roots are the primary source of cytokinins which contribute to the floral stimulus of the apical buds. Arpaia *et al.*², showed that root growth is depressed and that it actually stopped during the winter months in on-years compared to a continuous

growth during the entire year in trees carrying a regular or light crop. Thus, poor root growth in an on-year, resulting in reduced cytokinin supply, may well be a factor contributing to the reduced flowering in the following off-year⁷.

Bower *et al.*¹³ proposed a model in which root physiology is a key factor because roots are the source of cytokinins and abscisic acid (ABA). They suggested that in the absence of low temperature or water-deficit stress, an alternating pattern of shoot and root growth prevails, which is normally regulated by cytokinins produced by the roots and gibberellins produced by the shoots. With low temperature and water-deficit stress the same happens, but there is an additional production of ABA by the roots in response to the stress. The ABA causes the cessation of the vegetative shoot growth necessary for the transition of the vegetative apex to a floral apex and thus, regulates floral shoot development under stress.

In avocado, ABA levels in the fruits rise as the fruit mature^{18,77}. This means that in on-years, by the time of flower induction ABA levels would be higher than in off-years. Therefore, it is possible that high concentrations of ABA in on-years could exert inhibitory effects on flower induction. It has also been demonstrated that another inhibitor accumulates as the fruit mature (1-acetoxy-2,4-dihydroxy-n-heptadeca-16-ene), which could also exert inhibitory effects on flower initiation^{6,26}. Further research is needed to determine whether ABA, or other compound, is an inhibitor of flowering in avocado trees.

While for some fruit trees it has been clearly demonstrated that alternate bearing is caused by plant growth regulators produced by the developing embryo^{23,34,61}, there is no clear evidence that this happens in avocado trees. The avocado seed coat and endosperm have high concentrations of growth promoting substances like gibberellins, cytokinins and auxins during the early stages of development, with concentrations of all PGRs studied higher in the seed than in the mesocarp^{10,77}. However, levels of these substances were reduced as the fruit matured^{8,10,18,26,77}. This may be explained by several facts. During the first two to three months after fruit set the endosperm is present and envelops the embryo but subsequently disappears⁸. Shriveling of the seed coat starts at the same time the embryo stops growing⁹. Shriveling of the seed coat seems to be strongly related to growth processes and fruit maturation. The vascular system in the seed coat also dries and is incapable of transferring materials between the embryo and the pericarp¹¹. No measurable gibberellin-like activity was found in the embryo or mesocarp¹⁰.

Floral induction in avocado occurs some time during mid to late autumn^{48,59}. By this time levels of gibberellins in the fruit are low, since by this time the endosperm is no longer present and the seed coat has shriveled. From another viewpoint, embryo development, which is a period associated with high levels of growth promoting PGRs, occurs several months before flower bud induction. Thus, a direct relationship between the developing embryo and flower bud induction is unlikely. For most deciduous trees, embryo growth occurs during the period of flower bud induction and thus, a direct relationship between the developing fruit and floral differentiation is feasible and a direct hormonal effect on the process possible^{44,67}.

VEGETATIVE GROWTH AND ALTERNATE BEARING IN AVOCADO

In general, fruiting has a strong effect on assimilate partitioning and tends to antagonize vegetative shoot and root growth which are weaker sinks, especially roots^{16,82}. The order of priority among sinks is typically seeds>fleshy fruit parts = shoot apices and leaves>cambium>roots storage¹⁶. In avocado, the amount of assimilates is distributed in direct proportion to the dry mass of the sink tissues²⁴. In addition, there is an in-built tendency for trees to crop in an alternating pattern of high and low crops that amplifies over time, because when vegetative shoot apices transition to floral apices it is at the expense of the continued vegetative growth of the tree. When vegetative apices do not transition to floral shoots, it is at the expense of flowering and fruit set^{14,45}.

The polyaxial, pseudo-terminal flowering architecture of avocado, dictates that the tree must continue to grow in size to remain productive. However, vegetative vigor is a serious problem in many avocado growing areas, particularly when alternate bearing trees are in their off-year¹⁹. In subtropical climates, where sustainable yield in intensively managed mature orchards may exceed 20 tonnes/ha, typically there are two major periods of shoot growth during a fruiting cycle, one in spring and another in summer^{69,74}. In some growing areas like California, a third vegetative flush may occur in autumn. Heavy crops suppress vegetative growth^{3,42}. Wolstenholme *et al.*⁸³ reported that fruiting shoots were 24% and 55% shorter than non-fruiting shoots in 'Hass' and 'Fuerte', respectively. In moist subtropical climates, two to four growth flushes per year may occur in non-fruiting shoots, while fruiting shoots may flush only once during spring. This results in a composite canopy with leaves and branches of various ages⁵⁸.

Although two to four vegetative flushes may occur during a single season, the potential contribution of each flush to fruit production is not the same. Autumn flushes are capable of producing inflorescences, but floral intensity is low because these shoots predominantly produce single terminal inflorescences and no lateral inflorescences. Summer flushes produce greater floral intensity because they produce a significant number of lateral inflorescences and thus are more important in terms of crop production⁶³. It is worth noting that during an on-year, the growth of the summer flush is the most severely reduced, which results in a reduction of the fruiting points for the following year, and thus in an off-year. Whiley⁷⁵ reported that crop failure was most often related to poor flowering with either a reduced number of floral sites or decreased expression of floral intensity. During off-years, the opposite occurs; there is a large amount of vegetative shoot growth due to the small crop load, which results in the production of a large number of potential flowering points and in intense bloom the next spring.

A reduction in vegetative shoot growth during on-crop years could be due to reduced availability of carbohydrates caused by the high assimilate demand of the developing fruit. A possible role of PGRs from fruit in regulating the summer vegetative flush is unlikely. The highest concentrations of the growth-promoting substances gibberellins, auxins, and cytokinins were shown to occur during the two to three months after fruit set, the time at which the summer vegetative flush would be starting to form. Thus, in on-years when the concentration of growth-promoting PGRs would be higher, the growth of the summer flush should be greater; but this is not the case. In on-years, the summer flush is reduced.

The possibility that other factors are limiting summer vegetative shoot growth during on-years requires further research. Nitrogen is likely to be a critical factor since, as mentioned before, avocado fruit is nitrogen expensive and competition for nitrogen between developing fruit and vegetative shoot growth is possible.

Observations reported by Davie and Van der Walt²⁰ indicate that for older avocado trees it is usually the size of the tree frame (trunk and main branches) and root system that play the most important role in providing sufficient reserves of carbohydrate and plant growth regulators to sustain regular yield. Lovatt⁴⁶ showed that small branches (<5.0 cm in diameter) were the greater source of stored nitrogen. Younger trees have a better canopy to root and frame ratio, which probably accounts for their more regular production pattern. The authors concluded that a reduction in the canopy to root and frame ratio would have a beneficial effect on production, fruit quality, and size by restoring a better leaf to fruit ratio, and would thus modify biennial bearing.

Another aspect of vegetative growth that might be related to alternate bearing is the contribution made by leaves which over-winter to flowering and fruit set. In humid subtropical regions, over-wintered leaves provide a photosynthetically active canopy during anthesis and fruit set which results in sustained high yields annually. In contrast, in cool, semiarid climates, there is a great potential for over-wintered leaves to abscise during and immediately following anthesis. It is likely that the photoassimilation efficiency of the remaining over-wintered leaves is low during the critical period of fruit set and early fruit growth that occurs prior to the expansion of the spring flush leaves^{74,75}.

Further research to determine the importance of the reduction of the summer vegetative shoot flush on the number of potential flowering points in on-years and subsequent crop load the following year, should include experiments with the objective of stimulating the growth of that flush whether by pruning, fruit thinning, or application of PGRs or extra doses of nitrogen at critical times. Conversely, a practical method for controlling the extent of vegetative shoot growth in off-years should be evaluated.

ORCHARD MANAGEMENT AND ALTERNATE BEARING IN AVOCADO

Delayed harvest. For other fruit crops as well as avocado the picking date has been reported to have an effect on yield. In a study with apples, fruit were picked over an eight week period from when they were judged to have reached maturity until they had begun to fall naturally from the trees. It was shown that fruit set the following spring was highly correlated to the harvest dates of the previous year. Early picking promoted more flower clusters which consequently set more fruit (Williams *et al.*, 1980). Similarly, harvest time has been shown to affect cropping patterns of 'Valencia' oranges. After a 14-year study, Jones *et al.*³² concluded that late picking decreased the following year's yield and increased the severity of alternate bearing.

While the results are not in total agreement, the majority indicate that delayed harvest of avocados contribute to alternate bearing. Therefore, in orchards where biennial bearing is not a problem, it is highly recommended that fruit be harvested as soon as they reach

legal maturity. For the 'Hass'¹ cultivar, harvest should be done when fruit have reached a maximum of 30% dry weight and for 'Fuerte', a maximum of 25% dry weight⁷⁵.

Graham and Wolstenholme²⁷ suggested that in avocado a heavy crop is likely to result in increasingly later fruit maturity, increasingly slower rates of fruit growth, and increasingly smaller energy costs per avocado fruit. Conversely, fruit from trees bearing relatively lighter crops, in terms of fruit number per tree, generally grow faster than those on more heavily bearing trees. Hence, it is likely that fruit on trees in a heavy year, generally require a longer time to reach a desired size than those from trees in a light year. In order to obtain the desired size on a sufficiently large number of fruit to make a profit, fruit thinning and cyclical picking should be employed. This involves harvesting fruit that have reached the desired size as early as possible, especially from on-trees, in order to reduce the crop load and to stimulate the growth of the remaining fruit, to obtain enough flowers in the next year, and to help modify alternate bearing. Removing fruit will help to restore a better leaf to fruit ratio.

Pruning avocado trees. If avocado yields are to be further increased, tree manipulation is necessary to control tree architecture and complexity, and increase fruitfulness as is successfully done with deciduous trees¹⁹. In some situations, yields of 20 tonnes/ha have been sustained for a number of years; but inevitably tree size becomes excessive and management strategies which result in a major yield loss for a number of years are necessary⁷⁵. Pruning methods employed in temperate fruit trees stimulate unfruitful vigorous growth when applied to subtropical/tropical evergreen trees such as avocado. Light pruning that redistributes growth is generally a preferred option, limiting primary extension and stimulating growth of axillary buds. A high rate of syllepsis, occurring independent of shoot growth vigor, should be an important selection criterion in future avocado breeding and pruning programs, with the final goal being to increase the number of fruiting points⁶⁴.

Each grower should develop his own pruning strategy depending on local circumstances with the goal of achieving an adequate balance between vegetative and reproductive growth. Once trees are in a biennial bearing cycle, pruning should be aimed to increase the fruiting points prior to an off-year and to reduce them prior to an on-year. Further research is needed to determine the optimal time of pruning and the type of cuts to be done. In this paper, pruning strategies are presented because they are likely to be useful, but it does not mean that they will work in all circumstances.

Cutting *et al.*¹⁹ tried two different types of pruning cuts, one through the bud ring and the other below the bud ring, midway down the previous growth flush. The pruning was carried out on current season (previous flush) wood in late summer or late autumn. There were significant differences in the responses due to type of cut and, to a lesser extent, time of cut. The cut through the bud ring resulted in many buds breaking, with the growth of the resulting shoots controlled by competition, so that the induced vigorous response was diluted. The cut midway down the previous growth flush resulted in one bud or none breaking during the eight month period after the cuts were made. This study showed that pruning an avocado tree to increase tree complexity is possible. Increasing complexity in trees is important for increasing the number of flowering points

and for maximizing the advantages of precocity in high density plantings before tree removal becomes necessary. The authors suggested that the time of pruning needs to be accurately related to tree phenology rather than to chronological time.

Snijder and Stassen⁶⁰ suggested several strategies for the renewal of an older unproductive avocado orchard with encroachment problems. First, pruning back must be done in such a way that a pyramidal shape is created. Second, horizontal branches are "encouraged" into flowering units by tipping them. This causes these shoots to develop side shoots, thus creating a complex branching framework. It is evident that the avocado tree can be managed in such a way as to retain the right size and shape to increase the yields of the orchards.

Miller⁵⁰ pruned vigorous terminal twig growth and branches which extended out, away from the general contour of the tree. At the end of a four year period, the cumulative yield was the same in pruned and unpruned trees. He concluded that a severe pruning prior to an anticipated heavy fruit set will reduce the crop for the current season and increase the crop for the following season. It may also increase the size of the fruit by eliminating the very small fruit, which are often produced with heavy crops, and hasten maturity since small fruit are often slower to mature.

Thinning avocado orchards.

In California, high density planting and progressive tree removal is advocated. This provides for precocity in the early years of the orchards and sustained production at maturity. Failure to thin high density orchards results in a decline in yield once tree crowding begins⁵⁴. In South Africa, thinning has been recommended when 90% of the orchard floor becomes shaded. When alternate diagonal rows were removed in a 6X6m planting, yields increased 50% the following year, compared with trees that remained at the original planting density⁶⁶.

Tree thinning results have shown that thinning does not decrease the rate of return per acre; rather, by improving fruit quality and lowering harvest cost the net return is actually increased. Removing every other tree provides better results than removing every other row. Also, limited pruning of the tree can not replace whole tree removal because the rate of avocado growth is so rapid².

It appears that the main effect of tree thinning on alternate bearing is that it prevents the loss of the fruiting points on the lower canopy of the trees. Thinning should be done as soon as crowding occurs. Otherwise, thinning itself might induce a alternate bearing cycle in the remaining trees, which, once receiving enough light, may set a very heavy crop after several years of small crops caused by crowding.

Girdling. Hodgson⁶⁵ tested several horticultural practices that might affect the alternate bearing pattern of avocado trees. His best treatment was early harvesting of the fruit plus girdling. Early harvesting alone did not cause the same beneficial results.

Girdling is more frequently applied as final act aimed at achieving one final good yield from a tree before it is cut down and removed⁴⁰. However, researchers in California,

Israel, and Australia were able to increase fruit yield to a greater or lesser extent and, in some cases, managed to maintain these higher yields for a maximum period of three years by successive annual girdling of the same tree²¹. In a study comparing girdling and scoring of a number of branches per tree, Davie and co-authors²¹ preliminary recommendation was to score (not girdle) alternate branches of a tree that has set a good crop at the end of November in the southern hemisphere (equivalent to mid-spring in the northern hemisphere). The main goals of scoring were to induce the tree to set fruit even after a bumper crop; and in this way break the alternate bearing cycle, or to stop the tree from over-producing in the on-year.

Ticho⁶⁵ found that ringing the same branch for two successive years gave positive results, although in the second year results were less striking than in the first year. He stated that the prolific cultivar 'Hass' does not need to be girdled.

Girdling should be done on only a few branches in the same tree in order not to affect root growth and uptake of water and mineral nutrients. It is likely that girdling a tree prior to an off-year may produce more flowering and fruit set and also a reduction of vegetative growth in the following year, which with time might result in a more regular bearing pattern.

Irrigation. Irrigation practices influence every factor related to tree performance; *e.g.*, flowering, fruit set and growth, vegetative shoot and root growth, etc. It has been estimated that flowering increases the available canopy surface area for water loss by 90%, and 13% of total transpirational-water loss is attributable to floral organs⁷⁰. Preliminary soil matric potential measurements in the avocado tree root zone have shown a rapid depletion in soil water as flowering begins. Hence, with the significant increase in canopy surface area, water requirements of well-foliated, flowering trees will rise, especially in environments experiencing periods of high evaporative demand⁷⁰.

Lahav and Kalmar⁴³ also suggested that during flowering transpiration exceeds water uptake and translocation from the soil, and a negative water balance develops in the avocado canopy during the day. They tested different irrigation intervals based on tensiometer readings obtained at a depth of 30 cm. For an on-year, the optimal interval in the summer was 14 days; and in an off-year, the interval was 21 days. In their experiment, which was conducted for seven years, higher yields were obtained from trees irrigated with a dry-wet regimen (50 cbar in spring and 25 cbar in autumn). The irrigation treatments used had no effect on the alternate bearing habit of the 'Hass' avocado. For the conditions where the experiment was conducted, it was recommended that the irrigation interval be shortened in July-August when fruit growth rate is rapid, in order to increase fruit size. Shortening the irrigation interval in the spring provided no advantage. An irrigation regimen which dries the soil preserves the soil structure, whereas destruction of the structure can be caused by short irrigation intervals which represent, in fact, a regimen without any drying. In addition, frequent irrigation can invigorate vegetative growth to such a degree that trees do not transition to floral (reproductive) growth. Conversely, once pre-dawn leaf water potential, which reflects cumulative drought stress on particular trees, falls to -2.5 MPa or thereabouts, floral and fruit development become seriously impaired⁴¹.

Whiley and Schaffer⁷⁴ mention that 7-day intervals resulted in a strong alternate cropping pattern in 'Hass' compared with other irrigation regimes. Schedules with longer than 7-day intervals between irrigation probably reduce potential fruit set, thereby limiting yield, thus causing accumulation of stored assimilates for later contribution to the energy requirements of the flowering and fruit set events of subsequent crops. This irrigation schedule could be used to reduce potential yield of on-years.

Kalmar and Lahav³⁷, however, found that there were three or four vegetative flushes on the trees irrigated at 7- and 14-day intervals, compared with only one or two flushes in trees irrigated at 21- or 28-day intervals. Relatively small trees were obtained by irrigating every 21 days. This treatment did not result in lower yields and compared favorably with the other treatments tested. In the same experiment, trees in the 7-day interval tended more toward alternate bearing, whereas trees in the 14-day interval treatment had the more regular bearing behavior. However, cumulative yield over six years was only reduced by the 28- day interval treatment with no significant differences between the other treatments. The authors recommended the 21-day interval for their growing conditions. This confirms that irrigation treatments influence growth and may in the course of years affect the productivity potential of the tree and its bearing pattern⁴².

Adato and Levinson¹ also reported that trees responded to reduced watering levels with a reduction in vegetative shoot growth. In their experiments, they tried two intermittent irrigation regimes: one wet in which trees receive 0.64 mm per irrigation, and one dry in which trees received 0.46 mm per irrigation. The effect of the irrigation regime was more pronounced during the on-year. Trees in the dry treatment averaged for the five harvests thirty-six (15%) more fruit per tree than the wet treatment. This was equal to 13 kg (20%) more fruit per tree per year than in the wet treatment.

From the current literature it can be seen that shorter irrigation intervals are more likely to induce alternate bearing. However, adequate water should be provided during flowering, keeping in mind that the surface area for transpirational loss is greater during this period. During off-years, the amount of water supplied to the trees could be reduced in order to reduce vegetative vigor since fruit size may not be seriously affected due to the reduced fruit number. During on-years the amount of water supplied to the tree should be greater, in order to promote fruit and vegetative growth. In orchards where the alternate bearing cycle has not been established, irrigation intervals should be as long as possible, but care must be taken to avoid any stress that might affect productivity.

Fertilization.

Lovatt⁴⁶ found that the activity of glutamate synthetase, the primary enzyme of ammonia assimilation, was typically lower in leaves of avocado scion varieties, especially 'Hass' and 'Bacon', than in the roots of avocado rootstock varieties. The relatively higher concentration of nitrogen metabolism in the roots than in the leaves of avocado suggests that the rootstock may be a more important factor in nitrogen nutrition than the scion, and thus, emphasizes the importance of good root health to avocado production. Results from an on-going experiment provide evidence that in an off-year, 'Hass' avocado trees benefit from receiving extra nitrogen in April, the time of fruit set and

vegetative shoot development in southern California. No benefit was derived from the extra nitrogen provided in this experiment during the on-year. However, the possibility that nitrogen was still limited and that an even greater amount should have been supplied to support the large crop and vegetative shoot growth of the on-year can not be ruled out.

Boron is essential for pollen germination, for successful growth of the pollen tube through the stigma, style, and ovary to the ovule, and the mitotic divisions necessary to produce the sperms¹⁷. Jaganath and Lovatt⁴⁶ tested the effect of pre-bloom foliar applications of boron and low-biuret urea at the cauliflower stage of inflorescence development on pollen tube growth, ovule viability, and yield. They found that boron and low-biuret urea increased the number of pollen tubes reaching the ovary by 2.5- and 2.0-fold, respectively, in a field experiment. These treatments increased the cumulative yield over the three years of experiment by 25% and 23%, respectively. However, they emphasized that these results were found only in an orchard with low to adequate tree boron status. In an orchard characterized by excess leaf boron concentrations, which yielded better than the orchard with low to adequate boron levels, the cumulative yield for the two years of the study tended to be reduced by the boron or low-biuret urea applications, the reductions were not statistically significant. The results indicated that foliar applications of boron or low-biuret urea during the bloom period should not be used indiscriminately or prophylactically. Robbertse *et al.*⁵⁶ found that optimal pollen tube growth was obtained when the concentration of boron in the flowers was 50-75 ppm, suggesting that the value proposed by Wolstenholme⁷⁹ of 35 ppm is far too low. Leaf spraying supplied more free boron to the leaves than soil application.

Thus, fertilization should also be managed according to crop load. During an on-year, nitrogen levels should be high enough to ensure adequate fruit and vegetative growth. During an off-year, additional amounts of nitrogen pre-bloom may be beneficial to increase yield. Nitrogen applications could be timed to stimulate summer vegetative growth during on-years; this would lead to more source leaves for the current fruit and more flowering points the following spring.

Management of spring vegetative growth. In avocado it has been observed that the spring vegetative flush competes with setting fruit for available assimilates, which causes a reduction in fruit set^{7,82}. This competition has been studied using different approaches. Avocado trees usually produce two types of inflorescences, determinate inflorescences, which end with a flower, and indeterminate inflorescences, which end with a vegetative shoot. In terms of fruit set, determinate inflorescences are more successful than indeterminate inflorescences, but the bulk of the production is produced from indeterminate inflorescences since trees produce a much higher proportion of this type of inflorescence (Salazar-Garcia and Lovatt, unpublished). Zilkah *et al.*⁸⁴ demonstrated that by de-shooting indeterminate inflorescences the amount of initial fruit set was increased by a factor of 2.2, when compared with fruit set on intact indeterminate inflorescences. Thus far, no yield increases have been reported by de-shooting indeterminate inflorescences.

An additional strategy is the use of plant growth regulators to inhibit the growth of the

vegetative shoot of indeterminate inflorescences. In this regard, the most studied growth regulator is the anti-gibberellin paclobutrazol^{38,39,62,72,75,83}. Paclobutrazol can not be used in the United States on avocado trees, but results of its use are presented as general information to show potential results that might be obtained with other growth retardants in the future. The results of most of the studies showed an increase in fruit set and yield due to applications of paclobutrazol targeted to retard the growth of the spring vegetative shoot flush, whether as a foliar spray, trunk injection, or soil drench. The main effect was a reduction in the length of the vegetative shoot and a presumed decrease in competition. Thus, Wolstenholme *et al.*⁸³ proposed the use of paclobutrazol in the spring of off-crop years to increase fruit set and yield, but not in on-crop years.

The effect of these applications on the second vegetative flush in summer has not been extensively studied. Wolstenholme *et al.*⁸³ proposed that a final opportunity for adjustment of avocado crop load, especially in a heavy cropping season, is provided by competition between rapidly growing fruit and the second (summer) vegetative shoot flush. They proposed that carbohydrate stress may be the most important cause of summer fruit drop when fruit have reached 10-40% of their potential individual mass. Avocado photosynthesis is relatively inefficient, and the period of rapid growth and oil accumulation places heavy energy demands on the tree coinciding with higher summer temperatures and often higher evaporative demands. Thus, paclobutrazol might be useful if targeted to reduce the growth of the summer flush to reduce fruit drop. However, in on-years, if not excessive, summer fruit drop should be tolerated to increase the following season's yield. Paclobutrazol applications made to reduce the growth of the summer flush may reduce fruit drop, but will also reduce the number of potential flowering points the next spring (off-year); summer shoots produce the most flowers and set the most fruit in avocado trees⁶³. Therefore, paclobutrazol (or any other growth retardant) should only be used in off-years targeted to the spring flush with the objective of increasing fruit set and yield.

Gibberellic acid (GA₃) application prior to flowering of citrus has been shown to reduce flowering intensity in on-years, but has proven of commercial value only in Australia⁵³. This approach is being tested to determine whether it can be used as a tool to reduce alternate bearing cycles in avocados⁵⁷. The effects of other plant growth regulators on avocado tree productivity and phenology have not been investigated.

Thorp and Sedgley⁶⁴ found that cytolin (6-benzyladenine and gibberellins4+7) applied in late spring to shoots that had just completed shoot extension (i.e., before extension of the summer growth) produced an increase in the number of sylleptic shoots, which led to increased fruit set the following year. Cytolin significantly increased vegetative shoot growth when applied on other dates.

CONCLUSIONS

Alternate bearing represents an economic problem for growers and the industry affecting fruit size and net economic return, causing a price fluctuation between on- and off-years, and the loss of market share during off-years that is not always regained in the following on-year. The two main hypotheses to explain the perpetuation of alternate bearing were critically reviewed.

It is difficult to find a hypothesis that explains all aspects involved in alternate bearing. A hypothesis involving growth regulators other than gibberellins translocated from developing fruit is more likely to explain the role of plant growth regulators in the perpetuation of alternate bearing in avocado trees. A possible role of ABA in the inhibition of flower initiation in on-years was proposed, but as of yet there is no experimental evidence regarding ABA. It was also suggested that competition between developing fruit and new vegetative shoot growth for carbohydrate and other nutrients, especially nitrogen, might play an important role in the biennial bearing pattern of avocado trees. While plant growth regulators promote root and shoot growth, fruit set, and fruit growth, all these processes can only be expressed fully if carbohydrate, nitrogen compounds, water, and nutrients are available in sufficient quantity^{13,27}.

It was demonstrated that a heavy crop load strongly reduced the summer vegetative shoot flush, which is the most important in terms of productivity. It is the main contributor of glucose for the synthesis of the starch that accumulates during the autumn and winter, and it provides most of the flowering points the next spring. It was proposed that variation in amount of this flush may be an additional explanation for the perpetuation of alternate bearing. Additional research is needed to determine the concentration of plant growth regulators in buds at the time of flower induction and initiation, the effect of carbohydrate deficit on summer vegetative growth in on-years and on floral intensity the following year, and the role of nitrogen in the perpetuation of alternate bearing.

Orchard management practices can be used to successfully eliminate alternate bearing and to sustain regular and economic yields year after year. These should be done according to the size of the crop:

- Harvesting of the fruit should be done as soon as they reach legal maturity, avoiding delayed harvest, (before 25% dry weight in 'Fuerte' and before 30% dry weight in 'Hass').
- Manipulation of tree architecture and complexity is required and additional pruning strategies need to be developed.
- Tree thinning should be done when 90% of the orchard floor is shaded.
- Girdling should be done in trees that are going to be removed prior to thinning and/or in alternate branches for a maximum of three consecutive years or only prior to an off-year.
- Irrigation intervals should be as long as possible, taking care not to stress the trees mainly in the critical periods of flowering and fruit set; e.g., pre-dawn leaf water potential should never decrease to -2.5MPa.
- Applications of N at bloom during off-years could give positive results as well as N applications in the summer to promote vegetative growth in on-years.
- The use of growth retardants to reduce vegetative shoot growth should be limited to off-years.

Research in specific areas is needed in order to fine-tune orchard management practices that growers can use to eliminate alternate bearing and to sustain regular and

economic yields year after year.

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