

**Role of Plant Growth Regulators
in Vegetative Spring Flush, Flowering, and Fruit Drop
in Avocado (*Persea americana*, Mill.)**

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A Review

by

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Role of Plant Growth Regulators in Vegetative Spring Flush, Flowering, and Fruit Drop in Avocado (*Persea americana*, Mill.)

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Avocado harvests of economic value depend on the balance of vegetative growth flushes, flowering, pollination, and fruit retention. Two endogenous systems affecting the physiology of fruit retention and growth are plant hormones which control growth and fruit development, and nutrients which are utilized as building blocks enabling growth to take place (Bower and Cutting, 1988). Three major areas of opportunities for control of development and growth regulation by plant growth hormones in avocado are vegetative growth control, floral induction, and fruit set and retention (Davenport, 1987). In order for exogenous plant growth hormones to play an important role in maximizing avocado yields, it is essential to understand how the endogenous hormones affect or regulate the stages of plant growth.

Vegetative Flushes

Avocado is an evergreen tree which flowers in the spring from the tip of the previous summer's growth (Whiley *et al.*, 1988). There are two main vegetative growth flushes (root and shoot) per year, one in spring and one in summer. Each flush is followed by a period of enhanced root growth. The spring vegetative flush coincides with the end of flowering and the second, or summer flush, occurs just prior to floral initiation; thus, current root and shoot growth strongly competes with fruit development for plant reserves.

Vegetative flushes occur at a time of falling carbohydrate reserves in the tree (Whiley, *et al.*, 1988). Maximum carbohydrate levels occur in early spring and decline during flowering, shoot growth, and fruit development to a minimum in autumn. Alternate avocado bearing in temperate climates appears to be closely related to the carbohydrate levels in the tree. Higher avocado yields generally follow a higher accumulation of starch (Scholefield, *et al.*, 1985). Carbohydrate accumulation begins at the cessation of vegetative activity and continues over winter until maximum levels are attained in spring. Early fruit development and eventual yield have been correlated to the carbohydrate content of the plant at fruit set (Finazzo and Davenport, 1987). The leaves of the new vegetative flush are a nutrient sink until they reach a length of >40 mm. At this stage, they become a more effective source of photosynthate for the developing fruit than the older proximal leaves (Finazzo and Davenport, 1987).

At present, nitrogen levels in avocado tissues are the producers' most powerful management tool (Whiley, *et al.*, 1988). Nitrogen applications during spring and early summer months stimulate a strong vegetative flush and limit fruit set. Application of nitrogen after fruit set has subsided is the appropriate time for best management practices. Lower concentrations of nitrogen in avocado leaves are associated with lower fruit yields. Maximum production of avocados (Fuerte variety only) occurs when there are moderate levels of nitrogen in the leaves. Embleton, *et al.* (1959) reported that reduced fruit yields occur at nitrogen concentrations above and below this moderate level of 1.8% (dry weight basis). Trees that had the highest percentages of nitrogen in the leaves were the least productive trees, were highly vegetative, and had large, dark-green leaves. Timing of nitrogen fertilizer application in the orchard becomes critical in balancing the tree between reproductive and vegetative growth. Growth and reproduction of avocados is thus a coordination of periodic flushes controlled by specific plant growth hormones which are conducive to production of vegetative structures and a second seed-based hormone system which regulates the reproductive organs (Davenport, 1987).

Gibberellins act in controlling the growth of the internodes on the avocado branch (Davies, 1987). High levels of gibberellins in the plant tissue result in heavy growth during the vegetative growth phase. One means of controlling the vigor of the vegetative phase has been by physically manipulating the shoot tip or by girdling the branches, but these practices are very labor intensive (Wolstenholme *et al.*, 1990). The discovery of compounds such as gibberellin inhibitors which act in preventing the synthesis of high levels of gibberellins has been reported to limit the vigorous vegetative growth phase in avocado (Köhne and Kremer-Köhne, 1987; Wolstenholme *et al.*, 1988; Adato, 1990; Wolstenholme *et al.*, 1990). A yield increase by application of the growth retardant paclobutrazol was shown in pears and apples (Raese and Burtz, 1983; Shearing *et al.*, 1985). Foliar paclobutrazol sprays applied at the beginning of the avocado spring flush reduced shoot elongation from 30 to 40% of the control growth and possibly increased fruit set by increasing the dry matter partitioning to the setting fruit. Adato (1990) reported a 3% paclobutrazol spray increased yields by 90%, although other researchers have found no significant yield increase with applications to branches (Köhne and Kremer-Köhne, 1987) or to whole trees (Wolstenholme *et al.*, 1988; Whiley *et al.*, 1988). The positive aspects of application of paclobutrazol in these studies were nearly negated by a heavy summer fruit drop (Wolstenholme, *et al.*, 1988), although application tended to increase yield in the "off" year in these trees (Adato, 1990).

The root system of avocado is shallow and relatively ineffective for water uptake (Whiley *et al.*, 1988). Exogenous auxin addition to the rooting zone of woody plants has resulted in stimulation of lateral and adventitious root formation and shoot growth. Frankenberger and Poth (1987) reported that soil application of low levels 10^{-6} to 10^{-8} M of an auxin precursor, tryptophan, stimulated the growth of potted Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) when monitored for 11 months. The application of the auxin-precursor to the rooting environment increased root growth 1.6-fold and resulted in a 1.28-fold increase in elongation of root tissue. The use of soil-applied auxins or auxin precursors may help increase the root mass of the avocado tree. Root mass increases would improve the uptake ability of the plant for water and nutrients when stress occurs.

While the spring and summer vegetative flushes are competitive with fruit yield, they are essential for the long-term productivity of the tree. Reproductive growth in avocado begins with flowering and is followed by fruit set, development, and fruit maturity.

Flowering

Mature avocado trees have been reported to produce up to 1.6 million flowers with a fruit set of 0.001 to 0.23% (Cameron *et al.*, 1952). The majority of the flowers are shed within a month of anthesis, suggesting inadequate pollination and fertilization (Adato and Gazit, 1977). Floral initiation occurs in autumn with flowering in late winter or early spring. To complete its cycle, the avocado flower opens on two consecutive days. The first day of opening, the flower is functionally female; and the second day, functionally male. Flowering has been shown to occur at a time of minimum carbohydrate content in the major branches. Ethylene has been reported to promote flowering in some tropical plants, such as mangos, that are not exposed to environmental factors such as chilling or day length (Chacko *et al.*, 1974). Flower bud development refers to the growth of the flower panicle from the bud to the stage for the first flower opening.

All avocado inflorescence buds have a vegetative terminal bud which develops into a vegetative shoot following anthesis (Whiley *et al.*, 1988). Application of a gibberellin inhibitor (paclobutrazol) at the swollen bud stage caused a delay in the development of the vegetative shoot of 4 to 5 days when compared to the control plant, which increased the time before shoot growth competed with fruit set (Adato, 1990). When water is limiting, the flower panicles are the first to stress and may suffer permanent damage. The floral organs increased the potential water loss surface of the tree by approximately 90% (Whiley, *et al.*, 1988). Sedgley (1980) reported that 90% of the flowers and fruitlets which abscised during the first week following the end of flowering were unfertilized. Inadequate pollination can be improved by the use of beehives in the groves at the rate of one beehive per ten trees (grower personal communication).

Exogenous application of polyamines (putrescine or spermidine) have been reported to affect flowering in pears by increasing the pollination period through enhancement of ovule longevity (Crisosto *et al.*, 1988). Application of polyamines at flowering has also been reported to increase apple yields (Costa and Bagni, 1983). At present, no research has been documented on flowering and yield enhancement of avocado by application of polyamines, although little scientific evidence has been presented that application of polyamines would have a favorable effect on avocado yields.

Fruit Set

Transition from a flower to a developing fruit is termed fruit set and is accompanied by the wilting or abscission of petals and stamens. Avocado trees can be generally classified into two fruit-bearing categories (Davenport, 1987). Type I trees are typified by heavy initial fruit set followed by moderate to heavy fruit drop during fruit development. Type II trees are characterized by light initial fruit set with

little subsequent fruit drop. Davenport (1987) reported that Type II flowers evolved twice the level of ethylene produced by Type I flowers, resulting in loss of large numbers of flowers from the Type II trees. Fruit development is strongly competitive with root and shoot growth in avocado and exerts the most powerful attraction on available resources. There appear to be two main times for loss of set fruit. The first is immediately following fruit set. This drop coincides with the beginning of the spring flush, when fruit and shoot growth are competing for limited tree resources already depleted by flowering. Finazzo and Davenport (1987) reported that the metabolism of new growth and fertilized fruit is directly proportional to their dry mass, indicating that one tissue is not a more competitive sink than the other. Over 90% of the fruitlets which abscised during the first week after the end of flowering were unfertilized and 18% were abnormal (Sedgley 1980). Abnormalities in avocado fruit included ovaries with more than one embryo-sac or ovule with an immature embryo-sac, with an ovule in an abnormal position, or with a deficiency in ovule structure. The majority of fertilized abscised fruitlets had reached a stage corresponding to 14 days after pollination. A comparison of the diameters of the abscised fruitlets with the controls shows that the abscised fruitlets appeared to have ceased growth at least one week before they were abscised. By the fourth week after the end of flowering, all abscised fruitlets were normal, fertilized fruit. Auxins, gibberellins, and cytokinins play important roles in the growth and development of fruit. Lower levels of these hormones were found in abscised compared to non-abscising fruit. When a juvenile fruit is going to abscise, the production of gibberellins and auxins by the seeds has been reported to diminish, and the amount of growth inhibitors, abscisic acid, and ethylene increased in the fruits (Bollard, 1970). Due to the competition between the developing fruit and the vegetative flushes, it is important to limit any stress to the tree during the pollination period. Sedgley (1980) concluded that in the majority of cases, there was no anatomical reason why the fruitlets were abscised. Some undamaged juvenile fruits abscise because of genetic or developmental abnormalities.

Biran (1979) reported that a manual removal of new flushes of avocado growth reduced the vigorous vegetative sink of the spring growth flush which overlapped the fruit set in the Fuerte variety. The removal of the competitive sink led to a several-fold increase in yield. Application of a gibberellin inhibitor, paclobutrazol, resulted in a time lapse of 4-5 days between fruit set and the start of vegetative growth when compared to the non-treated trees, and a yield increase of 90% was reported by Adato (1990) due to paclobutrazol application.

Leopold (1971) reviewed the stages of abscission involved in fruit drop. The first step involves a differentiation of the abscission zone prior to the time of most active growth (Stage 1). Stages 2 and 3 differ only in the ability of auxins to reduce the sensitivity of ethylene to stimulate abscission. In Stage 2, the inhibition of abscission by auxins resulted from the inability of ethylene to induce the differentiation of the abscission zone, and auxins inhibit the passage out of this stage. This stage is a suspended state which ordinarily lasts for the functional life of the organ. In Stage 3, the application of auxins will enhance abscission by stimulation of enzymes involved in the structural deterioration of the separation zone.

Adato and Gazit (1977) demonstrated that seed abortion and abscission occur at the greatest rate when the fruit are the smallest, and gradually decrease in rate as the fruit enlarge. Davenport and Manners (1982), in the evaluation of fruit abscission in avocado, concluded that events preliminary to avocado fruitlet abscission included senescence of the nucellus and the seed coat. (See *Figure 1* in the glossary for a diagram of the avocado fruit anatomy.) They described four stages of seed coat deterioration. Stage 0 was described as having a white to slightly green nucellus and a bright white seed coat. Stage 1 was characterized as the nucellus now acquiring a gray cast, but with no color change in the seed coat. Stage 2 results when both nucellus and seed coat become slightly brown. Stage 3 has the nucellus and seed coat a distinct brown color. Determination of ethylene production rates by avocado fruitlets sampled directly from trees clearly indicated that sound, firmly attached fruitlets produced trace or undetectable amounts of ethylene. At the first sign of nucellus senescence (Stage 1), the nucellus-seed coat produced a temporary burst of ethylene. Of the four stages monitored, fruitlets exhibiting nucellar senescence in Stage 1 produced the most ethylene. All fruitlets underwent nucellar degradation prior to abscission. The transition from Stage 0 to Stage 1 was approximately 33 hours after excision of an avocado branch, and a 100% abscission was noted at approximately 99 hours. The burst of ethylene begins to occur at the time that nucellus senescence begins, suggesting that ethylene production is a consequence of the senescence process and not involved in the inductive mechanism of the process.

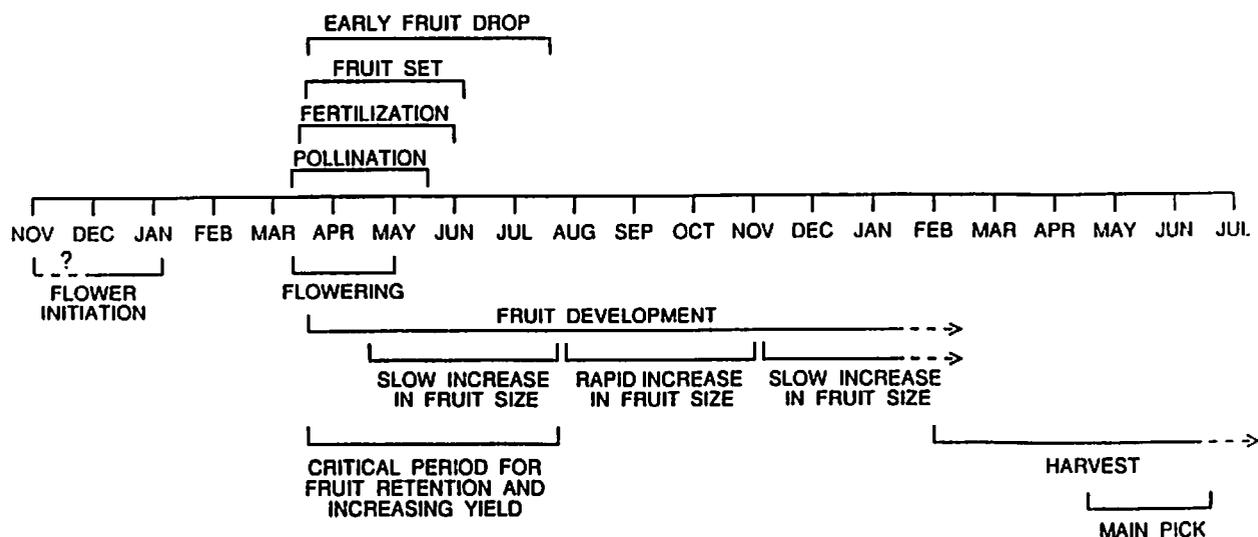
Sedgley (1980) suggested that inefficient distribution of water and nutrients to the fruitlets, rather than low availability, may be part of the reason for the cessation of growth that precedes nucellus senescence. On the plant, the fruitlet receives water, nutrients, and photosynthate by means of a network of vascular tissue. The vascular tissues of the plant connect the leaves and other parts of the shoot with the root. The vascular system is composed of two kinds of conducting tissue: the phloem, through which organic materials are transported; and the xylem, which is the conduit for water and soil nutrients (Aloni, 1987). Auxins have been reported to be involved in the efficiency of water and nutrient assimilation (Aloni, 1987). The phloem is induced at low auxin levels, where there is a need for higher auxin levels for xylem differentiation (LaMotte and Jacobs, 1963). The higher levels of auxins also increase the differentiation and result in a greater vascular vessel density. At present, no investigations have been reported on application of auxins for retention of fruit in avocado production.

The interrelationship between auxins and ethylene metabolism in fruit retention supports the view that auxins are important in fruit retention. During two years of field experiments conducted by W. T. Frankenberger's laboratory at the University of California at Riverside, increased yield in seeded and seedless watermelons ranged up to 85% and 56%, respectively, by a one-time addition of a soil drench of auxins (10^{-6} to 10^{-9} M) to the young seedling before transplant into the field. A synchronization effect by addition of the auxins was also determined with up to 93% of the melons harvested at one time. Observational analysis indicated that the treated plants first flowered 7 to 10 days before nontreated plants. The cost of the optimum auxin application (reagent price) was about \$0.05 per 100 acres. Additional field experiments conducted in Yuma, Arizona, showed that an

auxin soil drench to drilled cantaloupe resulted in a yield increase of up to 138%. This yield enhancement was due to a noticeable synchronization of yield under tremendous white fly pressure which limited yields of the control plants. Honeydew melons have also been found to show a yield enhancement of up to 90% due to a one-time application of auxins at the young seedling stage. Experiments with application of ¹⁴C labelled indole-3-acetic acid (IAA) to the rooting zone in sterile nutrient solution, or sterile soil and nonsterile soil, showed that wheat roots will assimilate a portion of the added label. Martens and Frankenberger (1993) found that IAA and other auxin derivatives were not tightly bound to soil colloids and varied in persistence in soil with measured half-life (t_{1/2}) values of 36 to 125 hours. These results showed that auxins can persist for extended periods in the soil and can diffuse through the soil to the actively growing assimilating roots. Most of the label assimilated was recovered as amino acid conjugates of IAA in the shoot tissue. These experiments showed that IAA added to the root zone of plants was translocated and increased the auxin content in the aerial portion of the plant tissue. It is anticipated that application of auxins to the avocado root zone by a drench, or more effectively by a dripline application, would also increase the levels of auxins in the plant; and, as a result, may increase fruit retention. *Figure 2* shows the flowering, fruit set, and fruit development in the 'Hass' avocado based on southern California environmental conditions. The diagram indicates a critical time frame for fruit retention is during the fruit set and the slow increase in fruit size before the later rapid increase. Timing of this auxin addition to the rooting zone appears to be one of the most important factors for increased retention of fruit by auxin addition.

Figure 2.

FLOWERING, FRUIT SET, AND FRUIT DEVELOPMENT IN THE 'HASS' AVOCADO*



*BASED ON SAN DIEGO - RIVERSIDE ENVIRONMENTAL CONDITIONS

(Courtesy of Dr. Carol Lovatt, Department of Botany and Plant Sciences, University of California, Riverside, CA)

Fruit Development

Fruit growth occurs both by cell division and by cell expansion. In most fruits, cells divide for only a short period after fruit set (Nitsch, 1965), the fruit growth after this period being due to cell expansion. Avocado is an exception, in that cell division continues as long as the fruit is attached to the tree (Schroeder, 1958). Avocado fruit growth is defined by three periods of growth. An initial period of slow growth, a period of exponential growth, and a period of declining growth are often referred to as Phases I, II, and III, respectively (Denne, 1960). Phase I is characterized by an increase in cell number. In Phase II, cells enlarge rapidly and resources accumulate in both the seed and the pericarp. Phase III is characterized by the changes associated with ripening. Fruit flesh softens, storage material such as starches and oils convert to sugar, astringent secondary compounds and organic acids decrease, and epidermal pigments change. Fruit abscission usually occurs in one or more distinct periods of abortion that precede the rapid growth phase of fruits (Phase II).

Developing seeds produce pulses of plant growth hormones that are believed to control growth and differentiation in the young fruits. Hormones produced by the seed also play a leading role in the mobilization of resources into the developing fruit (Biale, 1978). It is generally accepted that the seed controls fruit growth by synthesizing or attracting plant growth hormones, which then become available to the fruit flesh. (Wolstenholme *et al.*, 1985). Nutritive endosperm of the seed is a potent source of auxins, gibberellins, and cytokinins, and is the main source of these compounds in the first months after fruit set. When the endosperm has been used up, the testa becomes a very prominent plant growth hormones source, together with the embryo of the seed. The seed is a strong physiological sink from which the flesh benefits.

Many investigators believe that the inability of a fruit to garner adequate resources promotes the production of growth inhibitors, resulting eventually in fruit abscission (Addison and Lyon, 1973). Auxins can increase the sink strength of the fruit and regulate endosperm development (Gazit and Blumenfeld, 1972; Cutting *et al.*, 1985). Gazit and Blumenfeld (1972) found auxin activity in young fruit with higher levels of auxin in seed and testa at all stages of fruit development than in the surrounding flesh. In whole fruit samples, IAA peaked in late spring. The concentration fell rapidly in summer and then fell more slowly at the end of summer. It was presumed that most of this activity was associated with seed components. The seed gave the highest reading in mid-January, declining steadily by the end of March. The testa was very prominent and fleshy until late summer. Auxins are also important in Ca^{2+} allocation to developing tissues (Banuelos *et al.*, 1987). Low levels of Ca^{2+} in avocado fruit have been associated with rapid softening after harvest and an increased susceptibility to chilling injury (Cutting and Bower, 1989). Calcium content is also related to ripening rates in avocado. Tingwa and Young (1975) found that avocado with higher endogenous levels of calcium had slower rates of ripening. Gazit and Blumenfeld (1970) found that high levels of cytokinins in avocado fruit served to increase the sink strength of the fruit for nutrients and promoted fruit growth. High levels of cytokinin-like activity were found in both embryo and testa of avocado with levels declining as the fruit approached matu-

ity. Gazit and Blumenfeld also found that cytokinin concentrations in avocado positively related to fruit growth rates and cellular division. Additional evidence for the involvement of cytokinins in the regulation of assimilate partitioning has been presented by Richards (1980) and Goussard (1981).

The second fruit drop occurs during early summer. This drop is also associated with a major vegetative flush resulting in competition between the two growth forms for tree resources. At present, management of fruit growth and fruit retention is achieved by timing fertilizer applications, irrigation practices, and the maintenance of a healthy root system. Stimulation of vigorous vegetative growth during these critical periods usually results in excessive fruit shedding. The second fruit drop stage of the growth cycle is the most critical period for water management. Fruit maturation is selective. When resources are limited, the reproductive structures located farthest from the source of resources are shed first. In general, because flowering occurs over a period of two to three weeks, avocado fruit in a range of sizes will occur on a branch. Also, when pollinated flowers and immature fruits compete for limited resources, the ones most likely to mature are those that set first or result from outcrosses (Stephenson, 1981); although tagging experiments in orchards revealed that large avocado fruit in a cluster were just as likely to drop as small ones. Competition between fruit within a cluster was apparently not dictated by avocado fruit size (Davenport and Manners, 1982).

Fruit Maturity and Ripening

The avocado seed is important in fruit development by influencing growth, size, shape, and maturation. Auxins, gibberellins, and abscisic acid interact with or influence production and effects of ethylene on the fruit senescence or maturity (Dilley, 1969; Leopold, 1971). Avocado is an example of a climacteric fruit. The onset of ripening corresponds to a marked rise in respiration. The key element for normal ripening of climacteric fruit is the initiation of ethylene formation (Yang, 1981). The rate of ethylene production rises dramatically at or before the time at which the respiration is climacteric and the onset of ripening changes are initiated to reach a peak, and then its production is maintained at a reactively high rate throughout the period of ripening. A peak in ethylene production can, depending on the fruit involved, coincide with the peak in respiration. Auxins have been reported to be the agent to be responsible for the inability of avocado fruit to ripen on the tree (Twinga and Young, 1975). The endogenous levels of fruit auxins represent a resistance factor in ripening which must be deactivated before ripening can occur (Frenkel and Dyck, 1973). If exogenous auxins are applied to the surface of the fruit, ethylene levels are stimulated and fruit ripening is accelerated; but if auxins are infused into the fruit tissue by the vascular system, ethylene levels are limited and ripening is inhibited. Ethylene production during ripening may act to promote the activation of the IAA oxidase, resulting in lower auxin levels in the fruit tissue. Adato and Gazit (1976) found application of gibberellins to avocados had no influence upon fruit abscission or ripening. The application inhibited ethylene production but not fruit abscission. Blumenfeld and Gazit (1970) noted high levels of gibberellin activity in seed testa of developing avocados, decreasing with fruit growth; but no measurable gibberellin-like activity was noted in the fruit flesh or in the embryo. They suggested that the testa was the site of production of gibberellins in

the avocado fruit.

Abscissic acid (ABA) levels were nearly constant during avocado fruit maturation but rose dramatically during ripening, apparently as a result of synthesis rather than release from the bound form (Cutting *et al.*, 1985). The trend was for ABA levels in whole-fruit samples to increase with time. Cutting (1984) found that stress induced increased abscissic acid concentrations, creating an irreversible loss in fruit growth which is thought to involve the interaction of abscissic acid and cytokinins reducing the rate of cell division (Hill, 1980). Warner and Leopold (1971) noted that ABA could act as an inhibitor of auxin-induced cell expansion, and it has been observed to inhibit cytokinin metabolism (Letham and Palni, 1983). ABA levels in young abscissing fruit were seven times higher than in normal fruits. A steady increase in ABA concentration in fruit flesh was found in late summer and autumn where levels were in excess of those of the embryo.

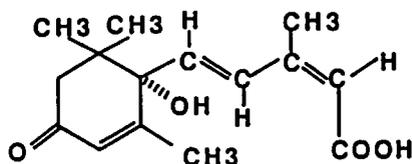
These results again emphasize the vital importance of the seed in avocado fruit maturation. Once the seed is mature (testa dries), the potential for further fruit growth is limited. Slow fruit growth certainly occurs, as many studies have shown. This slow cell division is possible as long as the fruit is firmly attached to the tree. This cell division is possible by the self-sufficiency of the flesh at this time for low concentration of promotive plant hormones—especially cytokinins, which are, however, antagonized by the buildup of ABA, particularly under moisture stress conditions.

As this review shows, our knowledge of the actions of growth hormones is comparatively larger than our knowledge of the effects of applications of exogenous growth regulators on plant development. The increased retention of fruit by application of auxins to the rooting zone could result in a healthier tree, producing more and larger fruit. This may result from an enhanced root system, enhanced vascular development in fruitlets, and increased time to maturation. The interaction of the hormones discussed here in avocado production may necessitate applications of several plant hormones at various times during the growing season to promote maximum yields.

Glossary

A glossary of some terms discussed throughout this review is included to facilitate a better understanding of this complicated interactive system.

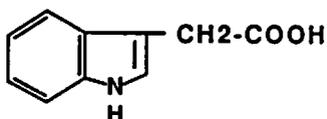
Abscissic acid. Plant growth regulator involved in stomatal closing during water stress, inducing transport of photosynthates toward developing seed and inducing storage protein synthesis in seeds. Abscissic acid is synthesized from mevalonic acid.



ABSCISIC ACID

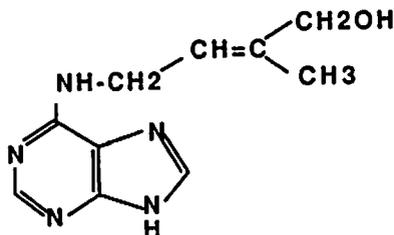
Abscission. A specialized senescence in which death of defined cells is associated with the breakdown of adjoining cell walls and the formation of an abscission zone. Auxins, cytokinins, light, and good nutrition tend to reduce or delay abscission. Possible auxin gradient that maintains the abscission zone in a nonsensitive state. Reduction or reversal of this auxin gradient makes the abscission zone sensitive to ethylene.

Auxin. Plant growth regulator involved with cell enlargement and stem growth. Auxins are also involved in differentiation of phloem and xylem tissue, delay in leaf senescence, inhibition of leaf and fruit abscission, stimulation of growth of flower parts, and may delay fruit ripening. Auxins are synthesized from tryptophan primarily in leaf primordia, young leaves, and in developing seeds. Indole-3-acetic acid is the most important physiological auxin in plant tissue.



INDOLEACETIC ACID

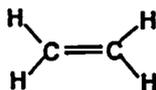
Cytokinin. Plant growth regulator based on adenine which affects cell division, release of lateral bud from apical dominance, delays senescence, and enhances stomatal openings. Zeatin is an active cytokinin.



ZEATIN

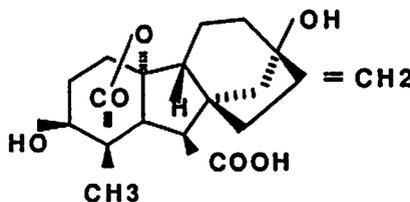
Endosperm. The nutritive protein material within the embryo sac of seed plants.

Ethylene. A gaseous plant growth regulator involved in differentiation of shoot and root growth; flower, leaf, and fruit abscission; flower opening; and fruit ripening. Ethylene is synthesized from the amino acid methionine in response to stress.



ETHYLENE

Gibberellins. Plant growth regulators involved in growth promotion of stems by stimulation of both cell division and elongation. Gibberellins also regulate fruit set and growth and are synthesized from mevalonic acid in tissues of the shoot and the developing seed.



GIBBERELLIN (GA1)

Gibberellin inhibitors. Compounds such as paclobutrazol that interfere in the synthesis of gibberellins, resulting in lower gibberellin concentrations in the plant tissue.

Mesocarp. The middle layer of the wall of the fruit (pericarp).

Plant growth hormones. Naturally occurring organic substances that influence plant physiological processes at low concentrations. Plant growth hormones include auxins, gibberellins, ethylene, cytokinins, abscisic acid, and polyamines.

Polyamines. Aliphatic compounds with unusual amino acid structures which appear to be essential for cell division and normal morphologies. Polyamines are synthesized from arginine (putrescine) and methionine (spermine).



PUTRESCINE



SPERMINE

Senescence. The terminal phase of development of a biological structure, whether it be the plant as a whole or a single leaf.

Testa. The seed coat.

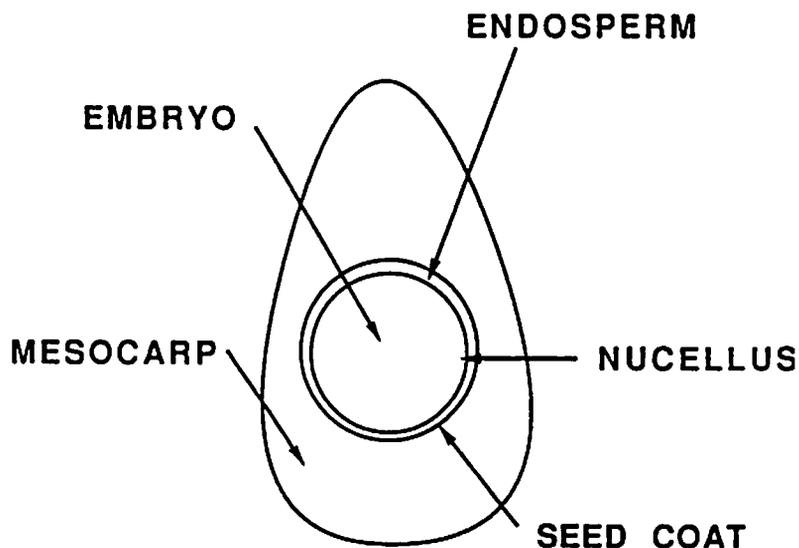


Figure 1. AVOCADO FRUIT ANATOMY

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