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DEVELOPMENTAL MORPHOLOGY OF THE VEGETATIVE AXIS OF AVOCADO (Persea Americana L.) AND ITS SIGNIFICANCE TO SPACING, PRUNING PRACTICES, AND YIELDS OF THE GROVE

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Although dooryard cultivation of the avocado was practiced in pre-Columbian times in Mexico and Central America, the first systematic commercial plantings date from the beginning of the present century with the establishment of groves in Florida, California, and Cuba. As is usually the case with relatively new crops, there is still a great deal to be learned about the management of the avocado. Certain problems are directly related to growth habit and fruiting behavior, and to fungi which attack the foliage, flowers, and fruits. In the relatively moist climates of Florida and Cuba it has been well established that adequate spray programs during flowering and fruit development are essential to insure sufficient fruit-set and the production of clean commercially-accepted fruits. But adequate spraying is complicated by two characteristics: Many varieties, when planted in grove formation, tend to develop into tall slender trees which quickly grow beyond the practical reach of the spray equipment; and all varieties tend to bear heavily in the upper part of the tree—about two-thirds of the crop is normally produced in the upper third of the crown. Moreover, removing the upper portions of the tree by pruning does not stimulate additional fruit production or branch growth in the remainder. In parts of groves where the upper third of the trees were experimentally pruned prior to flowering, fruit production was reduced by two-thirds as compared to unpruned sections of the grove. Thus the grower confronts conflicting doctrine in the management of avocados: It is desirable to keep the trees rather low and spreading, with rounded crowns, in order to secure adequate spray coverage, without which production is unsatisfactory and harvesting is difficult; yet it is undesirable to control the height of the trees by pruning because of the resulting loss of immediate production. The present study deals with this problem.

This paper correlates a basic study of the developmental morphology of the trunk and branches of avocado with growth responses obtained after different types of experimental pruning, and points out relationships between growth habit, pruning procedures, and planting distances. Recommendations are offered concerning these aspects of grove management.

Growth and Development of the Vegetative Shoot

The basic organization of the avocado shoot is uncomplicated. The leaves spiral around the shoot, with a single leaf borne at each node, and with a single axillary bud in the axil of each leaf. The leaf receives a single large collateral vascular strand from the stele of the shoot, leaving a conspicuous leaf trace gap in the vascular tissue at each node. The axillary bud is supplied with a large vascular strand which separates from the stele as two collateral strands, one to each side of and slightly above the leaf trace gap; these strands unite a short distance away from the stele and are so arranged as to form a lateral stele at the base of the axillary bud.

The rate of shoot growth is not constant, but it may be almost continuous under favorable conditions. Growth occurs in cycles or flushes; each flush is followed by a period of reduced meristematic activity or complete dormancy, but the bark never becomes "tight", i.e., it can always be easily separated from the wood. When the apical meristem becomes dormant, a terminal bud may be formed. Such terminal buds are covered by a type of bud scales; each scale initially contains one axillary bud in its axil. Dormant terminal buds have very short internodes within them. When the terminal bud resumes active growth, the short internodes within the bud do not as a rule elongate appreciably, and the axillary buds of the bud scales usually remain dormant for many years. The major part of the shoot produced during a growth flush is not the result of the enlargement of the reduced members within the bud, rather it is produced by the differentiation of new primordia after the flush has begun.

When a growth flush starts, the bud scales are shed, and the differentiation of new leaf primordia begins. The first leaves formed are more bract-like than leaf-like, with much reduced blades, and the internodes remain relatively short. As additional nodes and leaves are differentiated, there is a progressive change in the morphology of the leaves, from bract-like to leaf-like. This progression is accompanied by an increase in the length of successive internodes; when full-sized leaves are being formed and the apical meristem may be said to have reached maximum activity, the degree of internode elongation usually becomes more or less constant. There seems to be a direct correlation between the rate of meristematic activity in the apical meristem, the size of leaf formed from the leaf primordia, and the degree of elongation of the adjacent internodes.

When the rate of growth in a particular flush slows down, the activity of the apical meristem has already decreased, and the progression of events as described above tends to reverse, i.e., the leaves are reduced in size, internodes are shorter, and in those cases where activity is sufficiently reduced, bractlike leaves may again be formed.

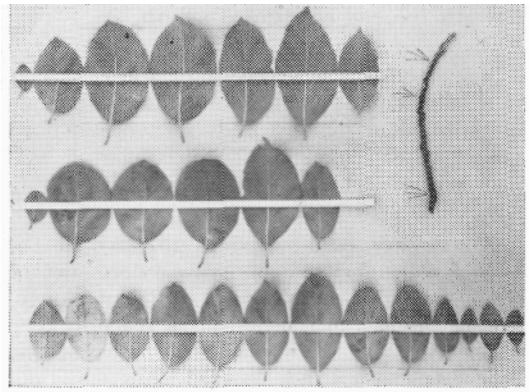

Fig. 1. Variation in leaf size, shape, and number on three flushes of growth made by a Booth 7 shoot in 1954. Flushes marked by arrows on bare shoot. Photograph made March 9, 1955 before new growth had started. Lines are six inches apart.

In Florida and Cuba the tree may make four distinct growth flushes during the year, but in colder climates fewer flushes are produced. The first flush is usually the strongest, and is associated with flowering. The supply of soil moisture, mineral nutrients, and the organic reserves accumulated by the tree all influence the extent of flushing, as does the presence or absence of developing fruit. Only a part of the terminals on a tree become active during a given flush. The position of a terminal bud on the tree may determine whether or not it will flush. Branches in favorable positions grow upright, and growth often continues during the major part of the season without the apical meristem resting as a semi-dormant or dormant bud. Terminal growth may be so vigorous during the growing season that a considerable portion of the branch tip is always too soft and herbaceous to be used for grafting. But some branches (those in unfavorable positions) have only one feeble flush during the whole growing season.

Avocados sometimes tend to bear heavily in alternate years, and in these cases the vegetative activity of the tree is much greater in the less-fruitful year. A tree that has made three or four vigorous growth flushes in a single year has made too much vegetative growth for economical fruit production. During a year of heavy fruiting, good management should include some thinning of young fruits, and perhaps the use of additional nitrogen and potassium to encourage the development of strong new wood for the next year's crop.

Developmental Morphology of the Axillary Buds

The subsequent development of the axillary buds shows great diversity in time sequence, as compared with the development of the axis on which they were initiated.

At one extreme, growth and development of the axillary shoot may proceed immediately from the time the bud primordia are initiated. In these cases, a typical bud structure never exists in the axil of the leaf, as the primordia never pause in its development into a lateral branch. The basal-most internode of this branch is often inordinately elongated. During a particular growth flush, this type of axillary member is formed only during the periods of maximum activity of the apical meristem. Most of them develop into normal branches, but some are abscised within the first year. In such cases, the node from which the branch arose is normally devoid of additional buds, and is incapable of initiating other lateral branches. To the best of our knowledge, this simplified means of lateral branching has never before been described in woody plants, but in addition to avocados we have observed it in many other woody species, including guava (*Psidium Guajava* L.), Ylang-Ylang (*Canangium odoratum* (Lam.) Baill.), Woman's Tongue (*Albizia Lebbek* Benth.), *Ficus* spp., etc.

A bud of similar structure to a dormant terminal is usually differentiated in the leaf axil, and these buds may remain dormant indefinitely or develop into branches during a subsequent growth flush. Branches that arise from dormant buds are much more numerous on the tree than are branches which arise simultaneously with the development of the leaf, as first described. Dormant axillary buds have much reduced internodes, and are cevered with bud scales. This type of bud is normally formed in the axils of the leaves during periods of ascending or descending activity of the apical meristem during a growth flush, and typically accompanies foliage of less than maximum size, other factors being equal.

Fig. 2. Vigorous development from a terminal bud photographed April 30, 1951. The other older leaves were removed. Notice the lateral shoots in axil of leaves, the growth of which was not interrupted by bud formation. The previous flush had produced one lateral of this nature, shown in picture.

When the activity of the apical meristem approaches its maximum during a growth flush, or, during the initial phases of decline, the axillary primordia may show a morphology intermediate between the two extremes which have been described. The bud primordia begins to form a lateral branch, but its initial activity quickly declines, resulting in a bud encased in scale-like organs, but situated on a short pedicel or branch which consists of a single elongated internode, instead of being seated in the axil of the leaf. These buds may resume growth with the next general flush, or they may remain dormant indefinitely. They are frequently abscised, often prior to the abscission of the subtending leaf. When this occurs, that node is thereafter devoid of primordia capable of initiating additional lateral branches.

As many axillary buds will be abscised, budding is not a satisfactory method of propagating the avocado unless the propagator is able to distinguish the buds most likely to hold. As a rule, these are the buds formed towards the end of a growth flush.

Dormancy in Avocado Buds

It should be pointed out that dormancy of terminal or axillary buds in avocado need not be a clear-cut phenomenon, and a bud may exhibit varying degrees of activity during the growing season.

An axillary bud seated in the axil of the leaf may undergo a prolonged dormancy if not abscised, but as a rule sufficient elongation of the axis of the bud takes place to keep pace with the increase in diameter of the branch on which it is located, thus maintaining the bud at the surface of the branch or partially submerged in the corky outer layers of the bark.

Dormant axillary buds which survive after their subtending leaves have matured and fallen are usually quite conspicuous for two or three years if the branch has made little increase in diameter. Abscission of buds will have continued along these portions of the branch, so that at the end of two or three years the most common persisting buds are those which were formed in the axils of the terminal bud scales, wherever the branch once formed a terminal bud.

Fast-growing branches of avocado may develop a diameter of two or three inches within the first year. Although the dormant axillary buds on such branches may be considered inactive, the axis of the bud will have grown horizontally an inch or more, thus maintaining the bud itself near the surface of the bark. As the branch continues to increase in diameter, the axis of the bud continues to grow and maintain the bud in the outer bark, but the bud may become almost lost from sight. If after a period of years a portion of the branch is pruned or broken from the tree, some of these buds lying near the injury will sprout. It has sometimes been assumed that these sprouts arise from adventitious buds, but our studies of the tree have shown this to be untrue. By removing the bark from an old avocado branch, these latent buds are revealed as small raised pimples on the surface of the wood. Tangential sections of the wood show the bundle trace leading back to the center of the branch, and confirm that all of the lateral buds on the branch had their inception as axillary buds many years before when the branch was a tender shoot. We have not seen any instances of the formation of adventitious buds in avocado.

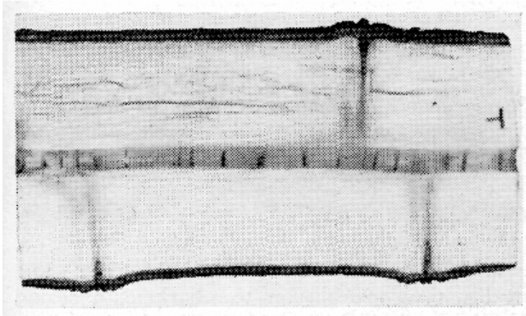

Fig. 3. One year old branch in section with dormant axillary buds, showing their forward growth and the bundle traces back to point of origin. Photographed June 15, 1951.

Dormant axillary buds which have survived on the trunk or large branches will have grown horizontally a foot or more over the years, keeping pace with the increase in diameter of the trunk or branch. On investigating this very slow growth and development of latent buds, we found that many of them consist of a single horizontal axis, as would be expected. When this type of bud is stimulated to sprout, its terminal meristem gives rise to a shoot or branch, and in addition the little axillary meristems in the axils of the bud scales also frequently sprout, so that a cluster of external shoots appears.

In other cases, as the latent bud grows out horizontally to keep pace with the increasing diameter of the trunk or branch, the primordia in the axils of the bud scales may break dormancy and form short lateral branches, each with a scale-enclosed bud at its tip; these buds and branches persist as additional latent axes in or near the surface of the bark. As the trunk or branch continues to increase in diameter, these buds also grow horizontally and keep pace with the radial growth of the mother limb. Over a period of years this phenomenon may occur various times, so that a whole complex of shoots and buds may be found in close proximity to one another surrounding the scar of the original leaf. If, many years later, this bud complex is stimulated to active growth by injury or removal of the distal portion of the branch, it gives rise to many shoots which have been initiated previously and have remained as slowly-growing simple structures within the parent branch. In avocado, this branching of the dormant axillary buds within the secondary wood is a common occurrence.

Concerning the growth habit of the tree as a whole we may generalize that most of the growth of the crown in avocado initiates from the terminal meristems, and that most of the axillary buds either remain dormant or are abscised. In general, lateral buds which were formed during the beginning of or cessation of a growth flush are retained by the tree, whereas the buds formed during periods of high activity of the apical meristem either result in the type of lateral branches first described in this paper, or are for the most part subsequently abscised.

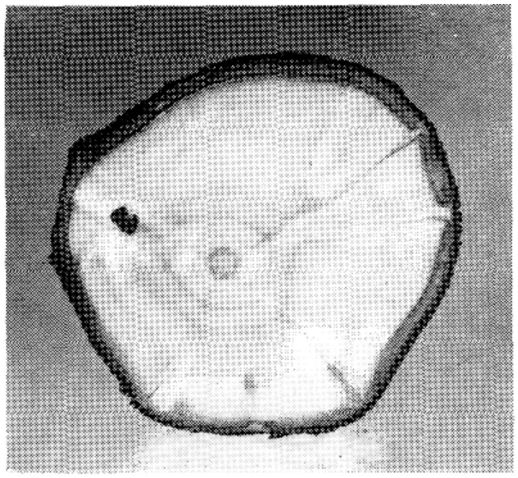

Fig. 4. Branch in section with dormant axillary buds showing their bundle traces, and how the axis of one had branched in this plane.

The slender pyramidal growth habit of seedling avocados and the relatively limited development of the laterals suggest that the apical meristems exert considerable dominance over the development of lateral buds and branches. Once a lateral branch begins development, the developments of the laterals on this branch are again inhibited. The results of pruning experiments imply that powerful axial gradients operate to control the development of all secondary organs. The marked exception occurs during the height of a growth flush, when the meristematic primordia in the axils of very young leaves never form axillary buds but immediately give rise to axillary branches. In an attempt to gain some understanding of this behavior, terminal meristems showing this type of development were collected and serial sections were made and studied. These slides revealed that when the activity of the apical meristem is at a high level, those portions of this primordia which give rise to the leaves and axillary buds have high meristematic activity and are physically still contiguous with the lateral portions of the apical meristem when they begin to form the new leaf and lateral branch. Subsequent expansion and differentiation of the pith and cortical parenchyma in the node delimits the procambial strands of the leaf and its axillary branch. In other words, during these periods the usual progression of differentiation of ground tissue deposited by the apical meristem in relation to the degree of activity of the primordia of the lateral organs is upset, and although the basic morphological design of the shoot remains unchanged, the axillary branches possess for a time the physiological characteristics that would result were the apical meristem to branch dichotomously.

Effect of Pruning on Dormancy and Subsequent Growth

Unlike many other trees, pruning the distal portion of the trunk or branch of avocado does not stimulate the buds along the remainder of the pruned member; only the buds at the first few nodes below the cut are stimulated. In the case of old branches or trunks, these buds emerge as a complex of shoots because of the branching the axillary bud has undergone while remaining within the parent limb. The subsequent development of these shoots is distinctly vertical, and tends to replace those portions of the tree which were removed; a general "filling-out" of the remainder of the branch or tree, which would be desirable, does not occur and the unpruned part of the tree remains in form much as before. Pruning is further complicated by the fact that most of the lateral buds may have been abscised along certain portions of the branch. Pruning then stimulates the dormant buds at the uppermost nodes which have retained lateral buds, and this is often found to be from one to three feet below the actual pruning cut. It is then necessary to make a fresh cut just above the region where the new sprouts are emerging in order that the cut surface is offered some chance to heal over, and this must be done before the emerging shoots have developed or they interfere with the sawing operation. If not done, this "stump" quickly decays, and the decay extends far down into the branch, weakening or eventually killing it. If it becomes necessary to prune the distal portion of a branch, the cut should be made immediately above the region where a growth flush terminated and the branch once formed a dormant terminal bud. These regions are readily recognizable on the bark as a series of closely-placed scars (from the bud scales) which are distributed around the branch, but care must be taken not to mistake a band of flower-branch scars for bud scale scars. Many dormant axillary buds are found in association with the bud scale scars, and the necessity for removing a second portion of the branch after the buds sprout is eliminated. In all cases where lateral buds are stimulated to produce branches after many years of dormancy, the juncture between the new branch and the parent member is structurally imperfect and inherently weak. The base of the branch expands rapidly, and its wood usually unites satisfactorily with that of the parent branch on the lower side, but it does not develop contiguously with the wood of the parent on the upper side; instead, the base of the lateral expands over the bark of the parent member, and a sheet of bark is thus embedded in the crotch of the branch, between the wood of the branch and its parent. Such branches have little resistance to stress, and are easily split off by wind or an excess of fruit. All of these characteristics lead to the conclusion that pruning the mature avocado tree is neither satisfactory nor desirable, and that insofar as possible it should be held to a minimum such as the removal of dead or damaged branches.

The shaping of the trees, if done by pruning, is preferable while they are young, with the frequent removal of succulent terminal initials. The ideal is to develop a tree with a multiple trunk if the variety in question tends toward strong vertical growth.

Fig. 5. A vigorous Lula tree's response to pruning done the year before. It was headed back to two lateral branches at A and B. Dormant bud sprung on each of the lateral and outgrew them in a few months. These are the uprights near pruning wounds. Buds also sprung on pruned branches below pruning wounds. Those on side B made two strong upright branches. The effect was all close to the pruning cuts. (Photographed by J. C. Noonan)

Effect of Light on Development The incident illumination has significant effects on the development of avocado, and the spacing of the grove will greatly influence the ultimate form of the mature tree. For example, seedlings grown indoors in dim light develop long whip-like or vine-like stems, with much elongated internodes, reduced linear leaves, and few or no branches. At the opposite extreme, avocado seedlings which have developed under the high illumination of the pacific slopes of Central America show a compact bushy habit. It has been possible to make a number of observations in Florida and Cuba concerning the growth habit of avocado in relation to exposure to light. Although many varieties show the tendency when young to develop into tall slender pyramidal trees, old individual trees in Cuba, if not closely surrounded by other trees and receiving more or less uniform illumination on all sides, invariably present dense rounded crowns; the pyramidal habit of the young tree gives way to this more desirable form, in which the crown is usually not over one-third higher than broad, and frequently no higher than broad.

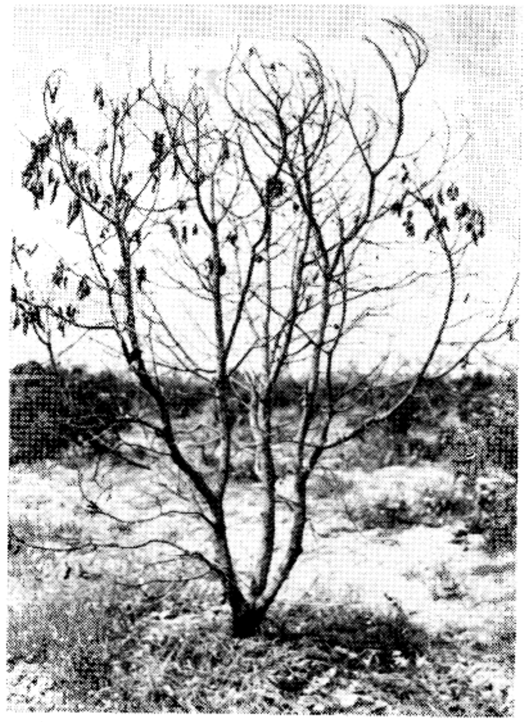

Fig. 6. A multiple trunk tree five years old which had a light heading back pruning the year before. The tree was killed by a flood. It had not borne fruit.

From studies of the development of unpruned trees of various ages planted at distinct spacings, some generalizations are possible at the present time:

When conditions for the growth of the tree are good and the spacing is close (under 25 feet) and the sides of the trees begin to shade or interfere with one another, further horizontal growth is inhibited, but vertical growth continues indefinitely, and the upper portions grow beyond the practical reach of the spray equipment. The lateral branches tend to have an upright growth; the lower shaded laterals which do not assume upright growth become unproductive and may eventually die; such lateral buds on the lower portions of the tree that sprout are unable to prosper in the low light intensity which reaches them.

With wider spacing (30 feet or more), the growth rate of the main axis in relation to the growth of the lateral branches becomes proportionately reduced as the tree reaches a height of 15 to 20 feet. The position of the principal lateral branches tends to be more open and gradually ascending. When these trees have reached a height of between 25 and 30 feet, growth in height takes place slowly and the crown becomes rounded from the continued development of laterals, provided the sides of the tree receive adequate sunlight. In southern Florida, where the spacing in many avocado groves is somewhat less than 25 x 25 feet, one observes considerable contrast between the slender form of the trees within the grove and the more rounded denser crowns of the trees in the border rows. In Cuba, the minimum spacing necessary to achieve desirably-shaped trees without pruning is about 30 x 30 feet, with a spacing of 35 x 35 or even 40 x 40 even more desirable. Using a triangular planting scheme rather than a square provides a more efficient use of the planting area in relation to the development of the trees.

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