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Growth and Development of the Fuerte Avocado Fruit[1]

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The growth of fruits is a subject of interest to plant physiologists and may also be of economic importance in understanding associated problems. The investigation reported here was undertaken to ascertain the nature of fruit development in the avocado, with particular reference to cell division and cell size in the pericarp tissues from the time of pollination to horticultural maturity.

Growth of fruit in respect to the development of the component tissues has been studied in the apple in detail (2, 11, 12). It has been concluded in a number of these studies that following full bloom and pollination there is a period of rapid and extensive cell division in all parts of the ovary and associated tissues which comprise the pome fruit extending for approximately three weeks, following which few or no further cell divisions occur. Subsequent increase in fruit size then results entirely from cell enlargement. Variation in size of fruit at maturity is caused mostly by variation in cell number and only to a small extent by variation in mean cell size. Cell enlargement continues throughout the life of the fruit as it remains on the tree.

The peach fruit is characterized by a period of cell division which follows pollination and lasts for about three weeks (1). After thirty days cell division virtually ceases and increase in size of fruit thereafter results from cell enlargement. Intercellular spaces within the peach remain relatively small, never attaining the size of those in the apple. Thus larger areas of cell wall are in contact with adjacent walls; hence the fruit seldom becomes mealy as in the apple.

The situation in the sour cherry (13) differs somewhat from that in the peach. All of the pericarp tissues of the former do not develop simultaneously. There appear to be two stages involved in fruit development— the first, which lasts for twenty days following bloom, in which cells of the stony pericarp increase in number during the first part and enlarge during the second part, and a second stage, which also lasts for about twenty clays, in which cells of the fleshy pericarp increase in number during the first half and double in diameter in the last half. Cell enlargement continues after cell division has terminated. Studies on the developmental anatomy of the date fruit (8) indicate a period of six weeks following bloom in which cell division occurs throughout the mesocarp, in which cell division then ceases. This is followed by the development of a meristematic region as the base of the fruit, which functions for another six weeks. After this period cell enlargement takes place throughout the fruit. The basal meristem then ceases to divide and its cells enlarge. Fruits such as tomato (7, 4), cucurbits (10), and strawberry (6) are characterized by an initial period of cell division followed by cell enlargement, the latter contributing the major portion of fruit size. Certain aspects of the developmental anatomy of the avocado fruit differ from these several other types of fruits.

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MATERIALS AND METHODS

The materials employed consisted of fruits of the Fuerte, the variety of principal importance in the California avocado industry. Collections were made of flowers and fruits at approximately two-week intervals, while measurements for fruit growth curves were made simultaneously on other fruits left on the trees in the Subtropical Horticulture Orchard on the Los Angeles campus. Representative samples of the various sized fruits were selected from the collections.

Samples of entire fruits if small, 0.5 to 2.0 cm in length, or portions of the pericarp wall of larger fruits were killed, fixed and preserved in formalin-aceto-alcohol until ready for use, when they were rinsed in 70 per cent alcohol, dehydrated with normal butyl alcohol, embedded in paraffin, cut on a rotary microtome at 10 microns thickness, and stained with haematoxylin or safranin and fast green. Some large sections of mature fruits were cut on a sliding microtome, fixed in formalin-aceto-alcohol, rinsed and stained. A few sections for various aspects of the study were cut free hand from fresh material, stained with various reagents and examined directly.

The measurement of cross-sectional dimensions of cells was made at 440X at a point 2 mm beneath the epidermis by tracing the cell wall outlines on paper with the aid of a camera lucida which were further magnified, the final drawings being 700X actual size. These permanent records were then measured with a scale and the appropriate calculations made. Since the parenchyma cells are approximately spherical in form, the average diameter was used for calculations. A sample in each tissue area consisted of 20 representative cells in the field. Cell counts along radii were made by drawing and counting all the cells which were bisected by a given radial line in the section.

RESULTS

The normal gross development of the avocado fruit as indicated by the length-width measurements is reflected in a curve of the general S-type, very flat in nature without sharp inflections or marked periods of sudden or rapid growth (9). Increase in fruit size appears to occur in all parts simultaneously and continuously throughout the period while the fruit remains on the tree. Observations by Haas (5) indicated that in those fruits characterized by a prominent neck, relatively greater length growth may occur in the basal third of the fruit, as determined from reference points marked on the epidermis and by the ultimate distribution of stomata.

Plotting the average diameter of cortical parenchyma cells against the size of fruit indicates that following blossoming and fruit set there is a short period during which rather marked increase in average cell size is evident, extending over a period of time until the fruit reaches half its ultimate length, approximately 55 to 60 mm (Figs. 1—5). Thereafter the average cell size of pericarp parenchyma remains practically constant, between 50-60 throughout the subsequent life of the fruit.

Cell number increase, as indicated by the number of cells bisected by a radius in a given fruit, apparently is continuous throughout the life of the fruit. As the size of fruit increases there is an increase in number of cells along the radius (Fig. 2). The increase in thickness of the fruit wall thus does not result entirely from cell expansion. A fruit 20 mm in length may have a pericarp wall 3.5 mm thick, composed of a layer of

approximately 145 cells. A mature fruit 120 mm long with a wall thickness of 14 mm may have 300 cells or more than twice as many cells along the radius. The approximate average cell diameter of the former fruit is about 30 microns and the latter about50 microns. It appears in general that increased pericarp wall thickness and hence fruit size in the avocado results from both cell division throughout the fruit life and cell expansion, the latter more pronounced during the first half of fruit development before maximum cell size is attained. Mitotic figures and other evidence of current and recent cell division can be observed in mature fruits.

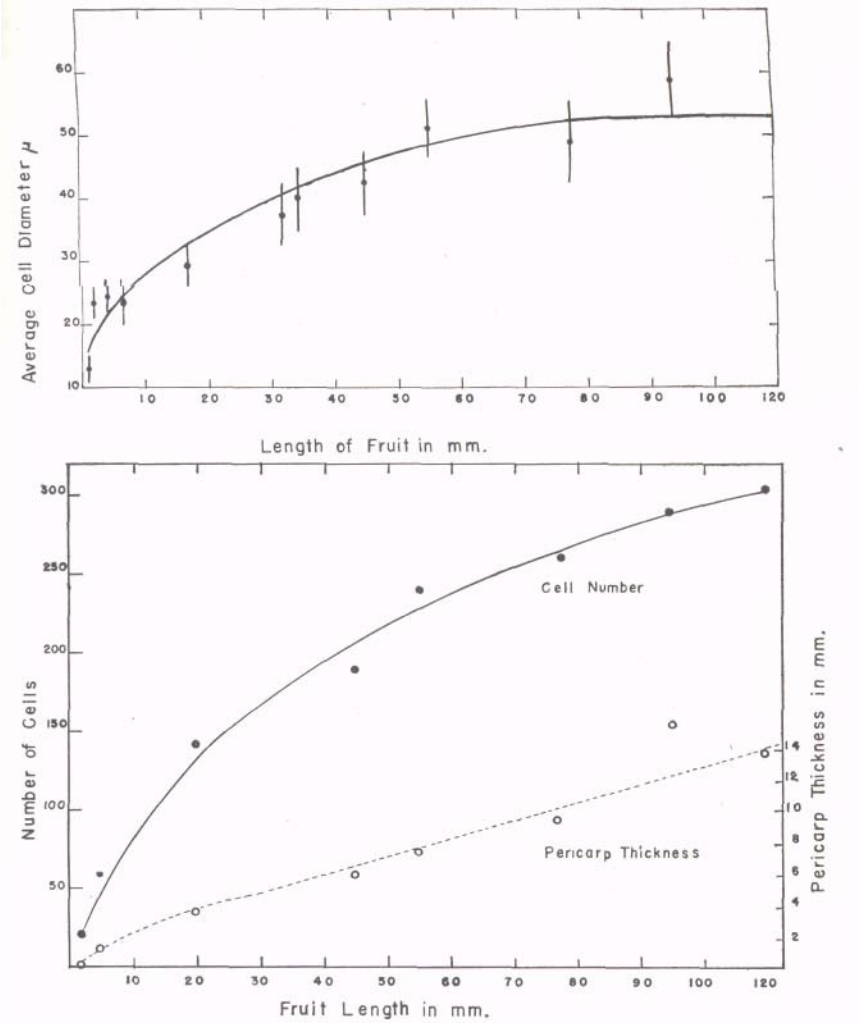

FIG. 1. Above: Cell diameter plotted against size of fruit in Fuerte avocado. Vertical lines represent standard deviation of measurements.

FIG. 2. Below: Cell number and pericarp thickness plotted against size of fruit in Fuerte avocado.

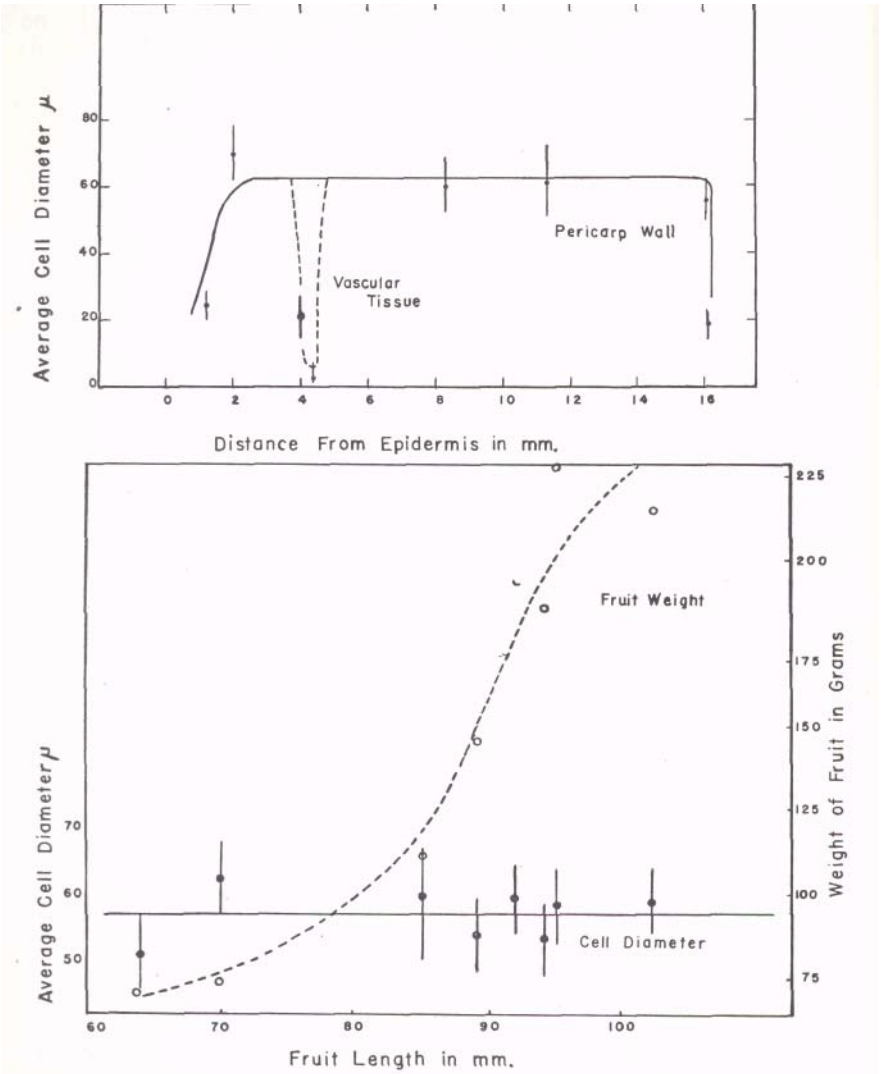

FIG. 3. Above: Average cell diameter of parenchyma at various points along the radius of mature Fuerte avocado fruit. Vertical lines represent standard deviation of measurement.

FIG. 4. Below: Relationship of average cell size to size (length and weight) of horticulturally mature Fuerte avocado fruits. Vertical lines represent standard deviation of measurements.

Preliminary observations (3) indicated that the texture and morphology of the pericarp wall is homogeneous, except for vascular tissue, in all parts of the mature fruit. Sections taken from the "cheek," the point of greatest diameter of a fruit, extending from the skin to the seed cavity, were prepared as permanent slides. Measurements were then made of fields of cells at various points in the pericarp wall along a radius at the equator from skin to carpel cavity. The mean cell diameter was then plotted against the distance along the radius (Fig. 3). The cells immediately beneath the epidermis are usually rather small and elongated somewhat in a tangential direction. Passing inward a distance of 1 to 1.5 mm, the parenchyma cells increase in size and become isodiametric to spherical in form, reaching a maximum size which remains practically constant throughout the

remainder of the pericarp wall except when in the region of vascular bundles, which are scattered throughout the pericarp wall, where the average cell size diminishes. As the seed coat is approached, the cell size also diminishes abruptly. Cells of the innermost pericarp parenchyma tend to be somewhat elongated in a tangential direction.

Uniformity of cell diameter along a radius becomes constant only after the fruit has attained approximately half of its ultimate length. Examination of cell size gradients in small developing fruits indicates that the average diameter of the cells in the outer pericarp is greater than those toward the inner portion near the seed cavity. While such a gradient appears in fruits ranging from 1.5 to 32 mm in length, these differences in cell size disappear in fruits 55 mm long and larger. The existence of such marked gradients in smaller fruits indicates that intensive growth as cell division probably occurs more rapidly and for a longer period of time in the inner portion of the carpellary wall, and that the outer peripheral portion attains maturity more quickly in respect to cell size and reduced meristematic activity. Evidence to support this frequently is observed in some fruits which have long rows of cells resulting from active or recently active cell division near the seed cavity.

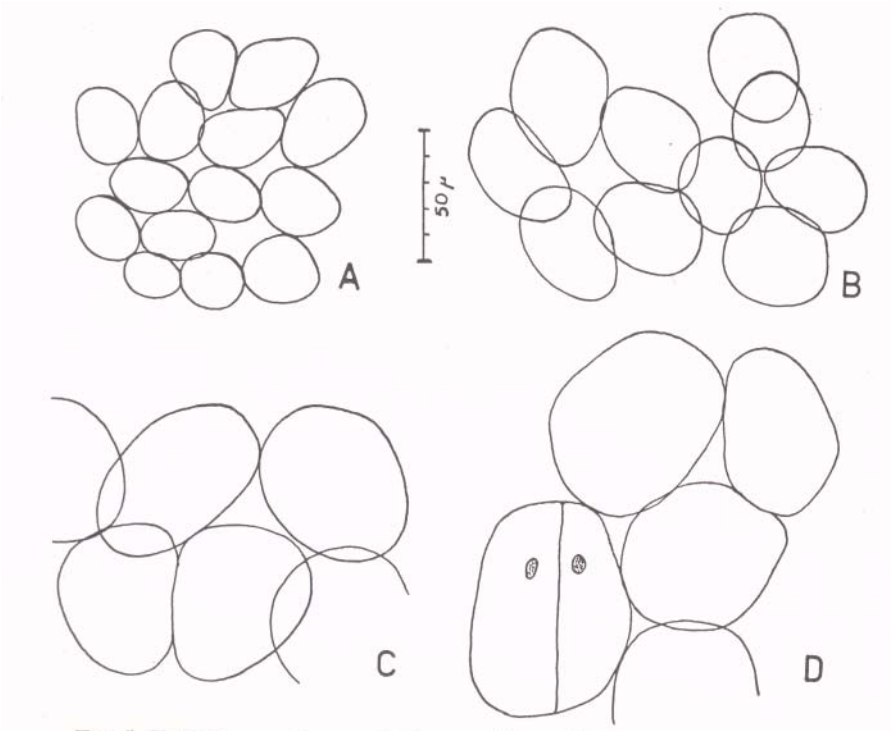

FIG. 5. Typical parenchyma cells from pericarp of avocado fruits of various length size. A: 1.8 mm, B: 32 mm, C: 55 mm, D: 120 mm. Note evidence of recent division in one cell of latter.

The avocado tree differs considerably from the typical deciduous fruit tree in the fact that its period of bloom frequently extends over a very long time, sometimes lasting for six or more months. The time of fruit-set likewise is not sharply marked; thus a period of many weeks may exist between the first and last fruits which set in any given blooming season. Consequently the period of maturity between fruits on a given tree ma}' be highly variable and, likewise, considerable variation in fruit size may be observed on a given tree. The avocado fruit does not soften until removed from the tree and may be

held on the tree for periods up to six months or more following the attainment of acceptable horticultural maturity. Within limits, the longer the fruit remains on the tree the larger it becomes. It is not unusual, however, for fruits of/the same crop on a given tree to differ by twice in length or weight. An analysis of cell size compared to fruit size in mature fruits of various sizes is given in Fig. 4. It will be noted that the mean cell diameter is practically the same for all specimens regardless of size of fruit, provided horticultural maturity has been attained.

SUMMARY

It may be stated in conclusion that the data concerning the development of cell size and cell number in the avocado fruit indicate that increase in fruit growth results from both cell division and increase in cell size during the early period of fruit development, but that cell division is the major factor concerned with increase in fruit size in the latter phase of fruit development. Cell division apparently continues throughout the time the fruit remains on the tree.

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