

GROWTH AND DEVELOPMENT OF THE AVOCADO FRUIT

C. A. Schroeder

Associate Professor Subtropical Horticulture, University of California at Los Angeles.

The avocado fruit exhibits several unusual characteristics both physiological and morphological in nature. One prominent feature is the great quantity of oil which develops in the edible portion, a character comparable in few other fruits except the olive. Another rather unusual aspect is the fact that the fruit will not mature while firmly attached to the tree, hence it must be harvested to soften and to become edible. Physiologically the fruit has been demonstrated to exhibit an unusually high rate of metabolic activity following harvest which is culminated by a marked climacteric rise in respiration prior to softening.

The present report is concerned with some aspects of the developmental morphology of the avocado fruit which offer a partial understanding of its growth and behavior as observed in the laboratory and in the field.

The mature fruit of avocado is a botanical berry comprised of a soft pericarp wall enclosing the single large seed. The rind or skin is formed of an epidermal layer together with a few scattered stone cells as in the thin-skinned varieties or a massive stony layer as found in the thick-skinned varieties. The pericarp or edible portion between the skin and seed consists of a mass of nearly homogenous parenchyma cells which contain the oil. This tissue is permeated by the vascular system which gives rise to the "fibers" of the fruit. The papery seed coats, two in number, surround the starchy embryo.

The avocado fruit develops from the pistil in the center of the flower. At full bloom pollen is transferred from the anthers to the stigmatic surface where the pollen-tube starts to grow downward through stylar tissue to the ovule and egg cell. Fecundation of the egg cell by the pollen-tube nucleus gives rise to the single embryo. Stimulation of cell-division in the ovary wall is initiated at the time of embryo formation and growth of the fruit commences. It can be demonstrated that during early fruit life the process of cell-division is very intense and widespread throughout the tissues. During this period only a moderate but constant increase in size of individual cells is observed. When the fruit has attained approximately half its ultimate size most of the individual cells throughout the tissues will have reached their maximum dimensions. There is very good evidence that in the latter half of the fruit development cell-divisions continue to increase the cell number within the tissues at all stages even as horticultural maturity is approached. The characteristic of cell-division in late fruit life is unique in the avocado in comparison with other fruits such as the apple, peach or cherry in which cell-division activity is restricted primarily to the first three or four weeks immediately following pollination. In these deciduous fruits the latter part of their development results from enlargement of the previously formed cells.

The fact that fruit size increase results primarily from cell-divisions in the avocado may explain in part why the fruit does not soften while still firmly attached to the tree. Only after physical separation of the fruit from the stem will nutrients and water be withheld from the fruit and the process of cell-division cease. In many other species as the cells enlarge and mature the fruit will soften on the tree. The phenomena of continuous cell-division also may partially explain why the avocado fruit exhibits a relatively higher rate of respiration in comparison with other fruits. In young tissues where intense cellular activity occurs such as immature fruits, stem tips and other growing points in the plant, there is usually observed a high rate of respiration. The avocado fruit shows approximately two or three times the respiratory rate as banana, citrus, apple or other common fruits. Thus it might be considered that the greater part of the avocado fruit tissue is actually in a juvenile physiological state throughout its life primarily as the result of the comparatively high rate of cell-division activity which constantly contributes young cells to the tissues. When cell-division activity ceases and physiological maturity of the individual cells is attained then a marked climacteric rise followed by a sudden drop in respiration and subsequent softening of the fruit is observed.

The evidence for some of the above statements can be ascertained by plotting size and number of cells against age or size of fruit. Whereas cell sizes can be determined rather accurately with the aid of the microscope, cell numbers can only be estimated in an empirical manner. A study of such data shows that in horticulturally mature fruits, though of different sizes the cell size is approximately constant, hence one must conclude that differences in fruit size must be attributed primarily to differences in cell number. This is true regardless of the expression of fruit size on a weight or linear size basis.

A study of fruit growth is helpful to understand the response of the fruit to several conditions which may develop in the field. If a number of small fruits are tagged shortly following fruit set and measured at regular intervals throughout the season with a caliper it can be shown that growth of Fuerte, for example, exhibits a sigmoid or S-shaped curve during the season of development (1). Both length and diameter increase rather slowly just after fruit set, but during the warmer months of July to early October both length and diameter increase at a maximum rate. As the fall and cool weather is approached growth in both dimensions is comparatively slower and may stop entirely for periods of time during the winter.

If more careful and accurate continuous fruit measurements are made with special instruments it is observed that growth does not comprise a smooth curve but actually consists of a series of diurnal fluctuations in size, sometimes of considerable magnitude. Measurements to demonstrate these fluctuations can be accomplished by means of two machinists' dial gauges which indicate changes in dimensions of 1/1000 inch (2). One gauge is placed to measure diameter and the other to indicate simultaneously the length fluctuation of a fruit. These gauges are held in place by a C-clamp arrangement. A series of observations made frequently throughout several consecutive days shows that the avocado fruit actually exhibits a series of fluctuations in size each day (Figure 1). Starting in early morning the fruit is turgid and of maximum size for that day. Shrinkage in both diameter and length begins about two hours after sun-up and continues as the temperature rises until late afternoon when the

temperature becomes lower when the fruit begins to increase in size. The fruit continues to expand during the night until the following morning when shrinkage again is detected. Each successive morning the fruit is slightly larger than on the previous morning under ordinary conditions such as exist at Los Angeles when the weather is moderately cool and temperature fluctuations are not great. When wide extremes of temperature are prevalent and the relative humidity may become constantly lowered over a period of several days, there may be observed an actual decrease in fruit growth when measured from day to day. Such marked and extreme climatic conditions may be experienced at certain seasons in such areas as San Dimas where fluctuation in fruit size is extreme (Figure 2). Under these conditions changes of nearly 0.3 inches of fruits about 1.5 inches in diameter have been noted. Such a degree of expansion and contraction of fruit conceivably could result in shearing forces which could easily rupture the fruit tissues and cause the cracking of surface layers with subsequent development of corky layers from subepidermal cells.

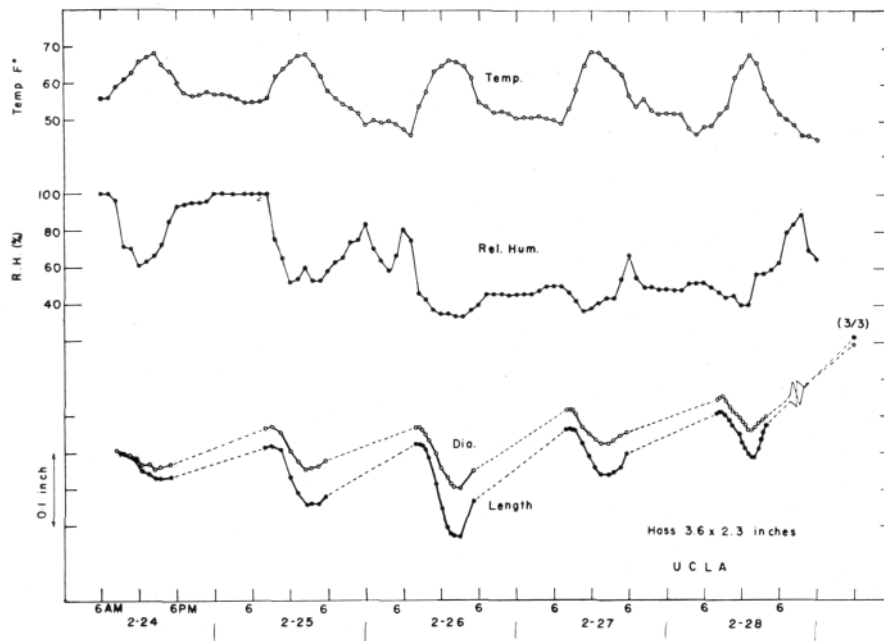


Figure 1. Fluctuation in avocado fruit diameter and length in relation to moderate changes in temperature and relative humidity during a period of five consecutive days.

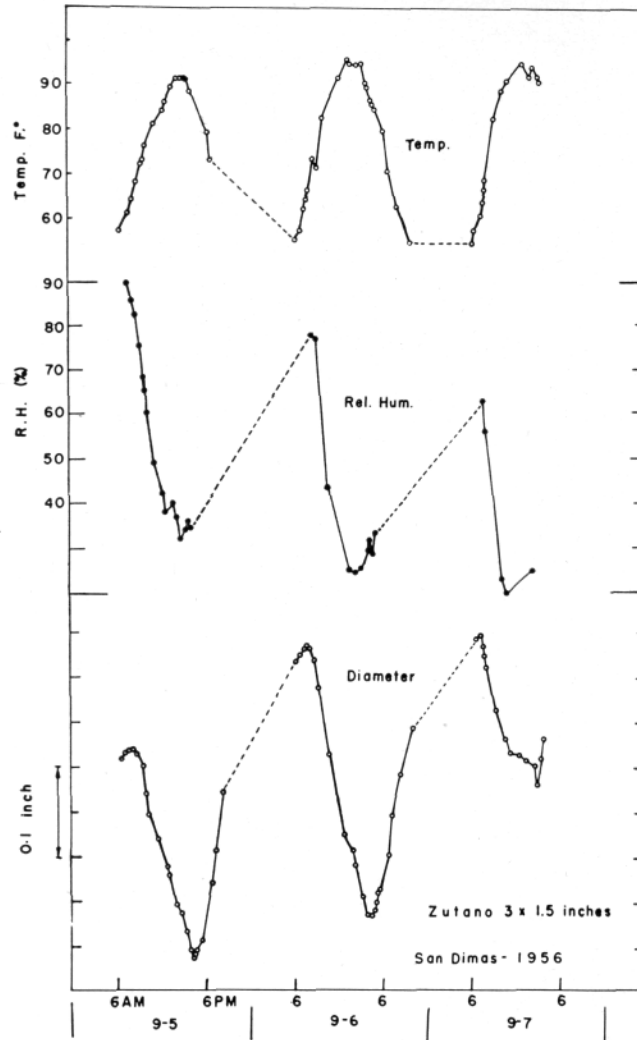


Figure 2. Diameter fluctuation in avocado fruit in relation to a wide range of temperature and relative humidity during a period of three days.

The relationship between relative humidity and fruit shrinkage is vividly demonstrated on warm days. If the daily fruit growth curve is followed it is observed to drop abruptly upon the increase in temperature. This downward trend can be altered by wetting the tree with a water spray, and raising the relative humidity in the immediate vicinity at mid-day when fruit shrinkage is normally most rapid. The response is a sudden leveling of the fruit growth curve followed by an actual increase in fruit size. Fruits on nearby trees not wetted at noon will continue to decrease in size until late afternoon. This response suggests the intimate relationship between transpiration or water loss by the leaf and moisture within the fruit. Moisture will be withdrawn from the fruit by transpiration of nearby leaves when conditions of high transpiration exist.

Although shrinkage of fruit on the tree results primarily from the withdrawal of water by adjacent leaves there is a substantial loss of moisture directly from the fruit itself which accounts for a portion of the contraction. This is demonstrated by measurements made on a detached fruit kept in the laboratory under which conditions a shrinkage of 0.1 inch was associated with a moisture loss of approximately 5 per cent in a Hass fruit (Figure

3). Other measurements made on Fuerte fruits suggest comparable losses of moisture or weight as the fruit shrinks. It can be visualized from this response that near mid-day or early afternoon fruit size is at a minimum and that fruit weight may be 5 per cent less than it was earlier in the day, a factor which may prove of some practical importance.

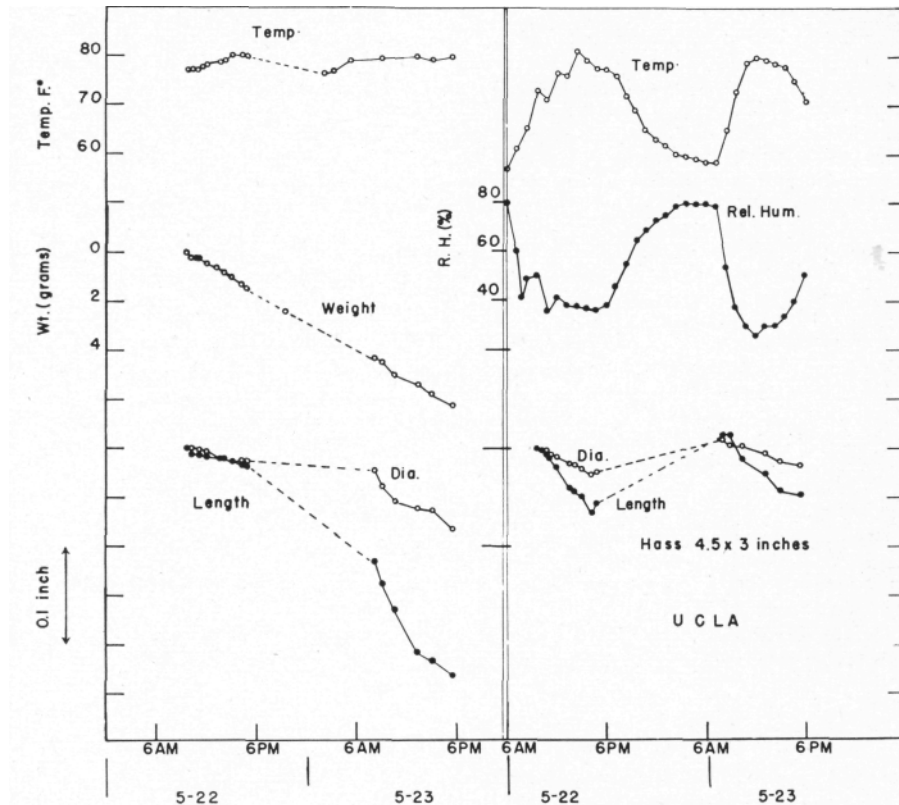


Figure 3. Fluctuation in size and weight of detached avocado fruit (left) and in size of attached fruit (right).

Several aspects of the behavior of the avocado fruit during development indicate the potentialities of the tissues to maintain a state of active cell-division even as maturity and full size is approached. One can observe the response when a nearby mature fruit still attached to the tree is enveloped in a vinyl-film plastic bag which allows a free exchange of gases but prevents moisture loss. A fruit placed under these conditions for a period of three or four weeks will develop on its surface a mass of tissue resembling to the casual observer a white mold or fungus. This surface growth actually is the result of massive cellular proliferation of the subepidermal tissue. This gives rise to a great number of cells from a cambial-like layer comparable to the cork cambium which develops as a response to wounding in other vegetative plant parts. If such a surface proliferation is exposed to the air, it quickly becomes brown and desiccated and develops into a typical corky structure very similar to the condition noted on the fruits of many varieties of avocado. Normally only a limited surface proliferation is produced in those fruits which tend to become corky but under constantly high relative humidity this proliferation tendency is greatly accentuated.

Another avenue of research which has offered some degree of understanding

concerning the behavior in growth and development of avocado fruit has been the utilization of tissue culture techniques. It is possible by this method to isolate portions of fruit tissue and to maintain it or cause it to grow for varying periods of time in a vial or test tube. Tissue pieces are removed from the fruit under aseptic conditions and transferred to vials containing appropriate nutrient solutions in agar. Such solutions include inorganic salts, sugar as a source of energy and growth promoting substances such as indole-acetic acid. Under these conditions pieces of fruit can be induced to undergo extensive cellular proliferation and growth such that they may increase several fold in weight and size over a period of six to eight weeks and may be maintained alive and in a growing condition for periods up to a year or more though the original piece was taken from a fruit which was nearly mature at the time of cutting. The application of this technique to the study of the avocado fruit appears possible because the tissues can easily be induced to undergo cell-division, a property lacking or not easily demonstrated in many other common fruits. After the tissue pieces have been isolated and are growing in vitro one can now investigate the effect of environmental factors such as temperature, light, moisture and nutrient supply on the behavior and growth of the tissue mass. One might study the effect of light quality or intensity on color development, or the effect of nutrients on oil formation, or possibly the effect of temperature on cell-division or enlargement, hence growth in general. Investigations of this kind are under way at present.

In summary it can be stated that the avocado fruit exhibits several unusual characteristics of morphology and physiology compared with other fruits.

Seasonal growth consists of a sigmoid or S-shaped curve which when observed very carefully is found to be comprised of daily fluctuations of contractions during the day and enlargement during the night. Sometimes under extremes of weather conditions this daily fluctuation may be of considerable magnitude.

Fruit growth throughout the season is determined to a considerable extent by cell-division activity at nearly all stages of development. Evidence of cell-divisions in mature fruits is easily demonstrated.

The pericarp parenchyma of mature fruit can easily be stimulated to undergo cell-division either in vivo when enclosed in a plastic film or in vitro when sections of fruit tissue are grown in vials on nutrient agar media.

The property of potential cell-division in the tissues at all stages of development explains in part some of the physiological behavior of the fruit observed in the laboratory and in the field.

LITERATURE CITED

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2. Schroeder, C. A., and P. A. Wieland. Diurnal fluctuation in size in various parts of the avocado tree and fruit. Proc. Amer. Soc. Hort. Sci. 68: 253-258. 1956.