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Development of Seeded and Seedless Avocado Fruits[1]

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Abstract. **The seed influences rate of growth, size, shape and maturation of avocado fruits. Seeded fruits are 8-10 times larger than seedless ones and contain more and larger cells. The growth pattern of seeded and seedless fruits is similar from June until maturation, when growth rate of seeded fruits decreases. Fruit maturation is characterized by rapid accumulation of oil in the mesocarp, preceded by shriveling of the seed coats, and the discontinuation of the seeds' influence on fruit growth. The role of the seed in the development of avocado fruit is discussed.**

The avocado fruit is unique in several aspects compared with many other horticultural fruits. In most species cell division in the fleshy fruit is limited to a short period near fruit set (15); subsequent growth is by cell enlargement. In contrast, cell division continues in the mesocarp of avocado fruit as long as it is attached to the tree (20). Callus development on the surface of the mature fruit when it is enclosed in a vinyl bag on a tree (21), and grafting of fruit surfaces (22), demonstrate the meristematic character of the avocado fruit. The ripening characteristic of the avocado fruit is also exceptional. In many species, the mature fruit will ripen (become edible) while attached to the tree. In contrast, even mature avocado fruits having high on content and sometimes germinating seeds, will not ripen unless harvested. Healthy fruits remaining on trees stay firm and continue to grow and to accumulate oil for several months after maturation. Fruits of 'Fuerte' have remained on trees for 10 months after attaining horticultural maturity (15 months after fruit set).

The avocado fruit contains a large seed (approximately 20 -60 g in various cultivars) which facilitates observation of morphological changes and collection of tissues for anatomical and chemical examination, even of young fruits. These characteristics and the presence of seedless and seeded fruits on the same tree make the avocado excellent experimental material for studying seed tissues and their role in fruit growth.

Most trees of the cv. Fuerte flower in Israel in March and April, and set fruit in April. A tree produces many flowers (millions), most of which abscise. Fruit set is low (less than

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0.1%). Often 2 or 3 waves of fruit set will occur, on a single tree, probably because of short periods of favorable weather conditions during the long flowering period. The growth of seeded avocado fruit was described (20) and the appearance of seedless fruit in avocado is known (24). This paper describes a third type of fruit, compares the morphology and growth of seedless fruit with those of seeded fruits, and evaluates the role of the seed in avocado fruit development. These data form the morphological background of research describing relationships of endogenous growth substances including: auxins (8), gibberellins (5), cytokinins (3, 7), inhibitors (1, 2) in the growth of avocado fruit tissues.

Materials and Methods

The investigations were carried out over a period of 5 years. Observations, measurements and fruit collections were made in 3 orchards: Bet-Dagan, Kubeba and Kvutsat Schiller.

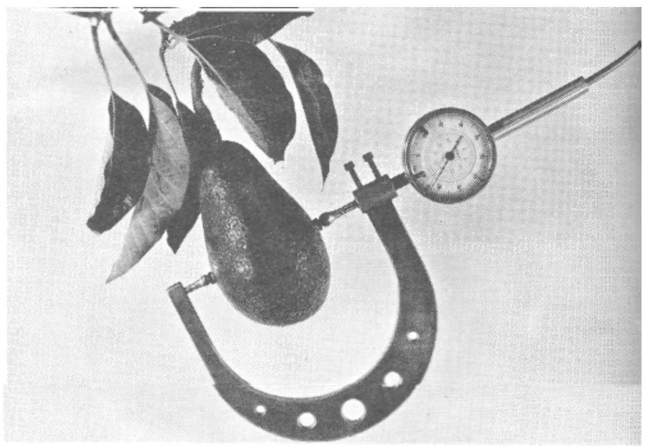

Fig. 1. Measurement of avocado fruit diameter.

Most data are for 'Fuerte', because of its commercial importance in Israel and in California. Comparable data were collected for some other cultivars.

Measurements. Fruit growth was determined on the basis of diam., vol., and wt. Only fruits representing the mode of the population in each tree were examined. At least 10 fruits were harvested at each sampling date. Since the specific wt of avocado fruit changes little during development (10); wt measurements give a good estimation of fruit volume, The growth of the different tissues was determined by weighing each tissue (fresh wt).

Fruit diam was determined by measuring the distant) between 2 metal rings which were glued to a fruit (Fig. 1).The gauge was sensitive to changes of 10 µ.

Mean cell size and cell number in the pericarp was determined from 15µ cross sections along an equatorial radius. The number of cells along the radius and the average cell diameter were determined.

Table 1. Fresh wt (g) of tissues in young 'Fuerte' fruits (Averages of 20-60 fruits, sampling date, April 29th.)

Fruit size	Whole Fruit	Pericarp	Seed		
			Embryo	Seed coat	Endosperm
Small	0.48	0.43	0.003	0.04	0.01
Medium	1.80	1.50	0.13	0.14	0.04
Large	11.33	9.80	0.73	0.62	0.18

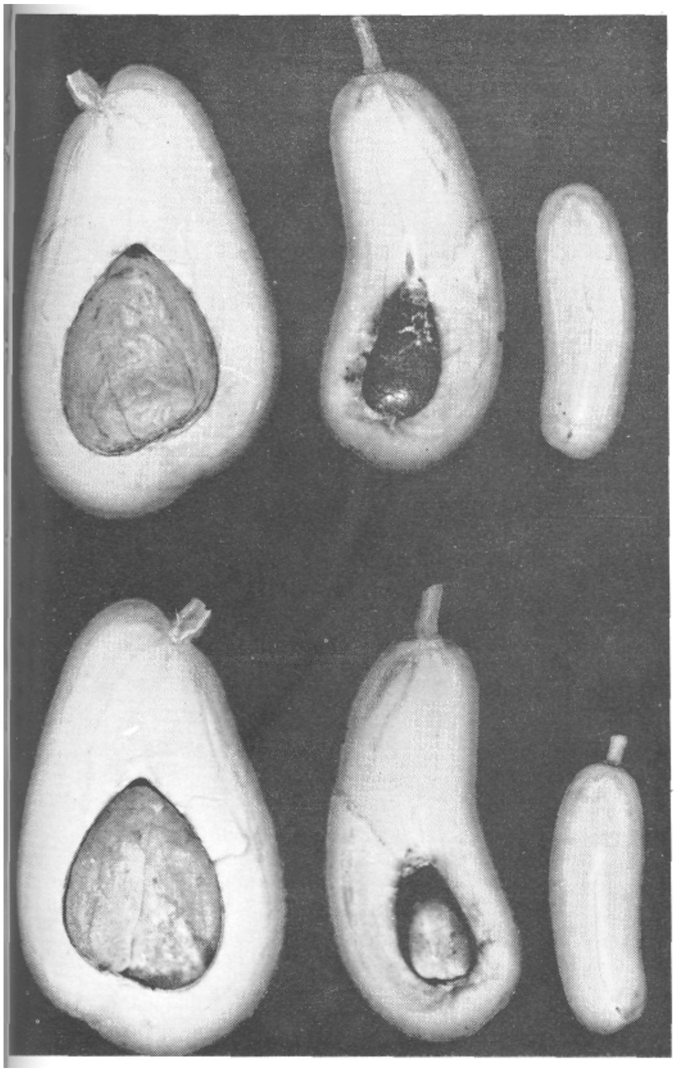

Fig. 2. Three types of avocado fruit. Seeded (left), "intermediate" (middle) and seedless (right); lower row: with embryo; upper row: with embryo removed.

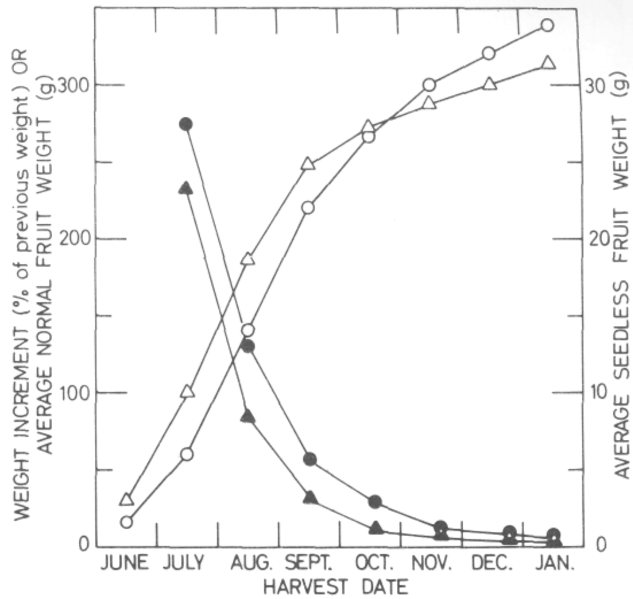

Fig. 3. Growth of seeded and seedless avocado fruit.
△ Seeded – cumulative weight.
▲ Seeded – weight increment.
○ Seedless – cumulative weight.
● Seedless – weight increment.

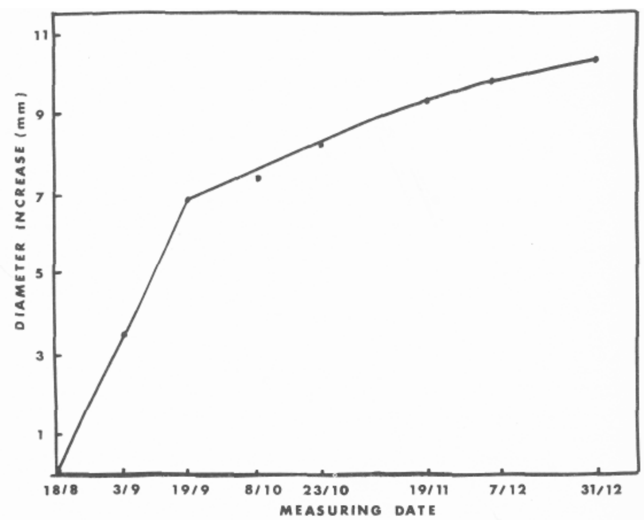

Fig. 4. Increase (cumulative) in 'Fuerte' avocado fruit diameter from August onwards, during and after maturation.

Results and Discussion

In 'Fuerte', 3 main types of fruit were recognized according to shape, namely: seeded, seedless and "intermediate" fruits (Fig. 2).

When growth of 'Fuerte' fruits is expressed as cumulative fresh wt or volume, the growth curve is sigmoid (Fig. 3), confirming the results of Schroeder (20) and Valmayor (25). The growth patterns of seeded and seedless fruit are similar from June onward, except during September when the seeded fruits approached maturity, their growth rate

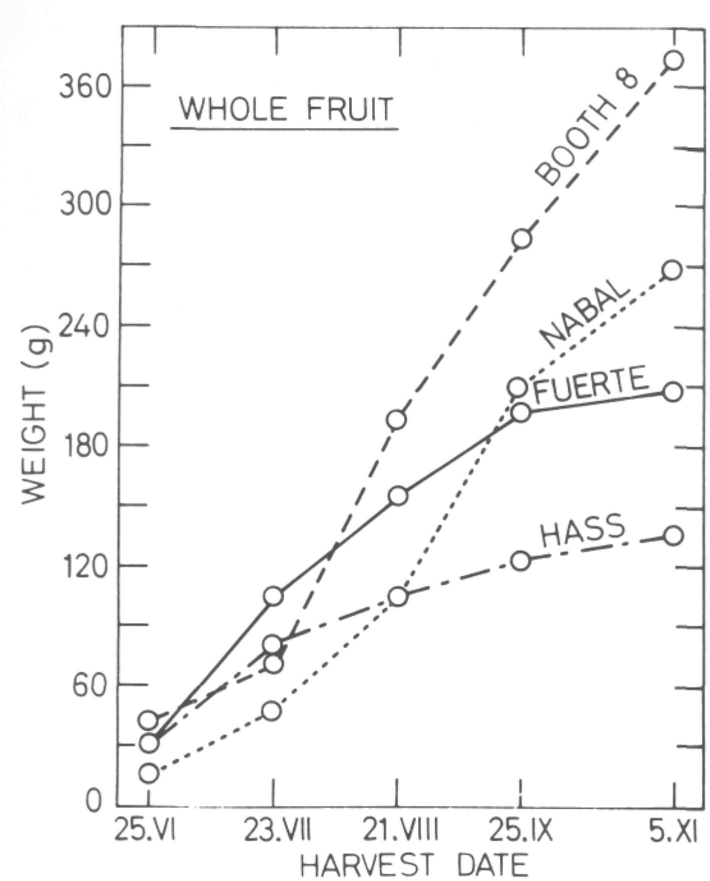

Fig. 5. Growth of the whole fruit of different avocado cultivars.

decreased (Fig. 3). The change in rate of growth was even more pronounced when fruit diameter was measured by a sensitive gauge (Fig. 4). Late maturing cultivars such as 'Booth 8' (Fig. 5) and seedless Fuerte' fruits (Fig. 3) were still growing rapidly at this time, indicating that the sharp decrease in growth rate of seeded Fuerte' fruit was inherent and did not depend on the decreasing temperatures at the end of summer.

Seeded fruits, pericarp. The edible portion of avocado fruit includes the thick mesocarp and endocarp which consists of 2 or 3 layers of small cells. The mesocarp cells are parenchyma, uniform in shape and size, and reach a diameter of 55-60 *n,* as observed by Schroeder (20), by Valmayor (25), and as shown in Table 2. Cell division occurs as long as the fruit is attached to the tree. It is rapid in young fruits and slower in mature ones (20). Cell number and cell size were measured directly. The rates of cell division and cell enlargement are more rapid in young fruits than in older ones (Table 2). Cummings and Schroeder described the vascular system in avocado fruits (6). By following the distribution of a dye (eosin blue 1%) applied through the pedicel to intact or harvested fruits, it was found that almost all the vascular bundles in the pericarp join together to enter the seed coat (Fig. 6), where they separate and form a branched net of bundles (Fig. 7).

Table 2. Cell number and diameter in ‘Fuerte’ mesocarp; measured along a radius in the middle of a fruit, average of 15 fruits.

Sampling date		April 29	May 10	July 8	Sept. 26
Seeded fruit	No. of cells	103	134	292	313
	Cell diameter (µ)	28.5	34	50	55
Seedless fruit	No. of cells		113	131	
	Cell diameter (µ)		32	36	

Seed tissues. The seeds were separated into embryo, endosperm and seed coat.

Embryo. When the embryo is first seen it is small and narrow, and grows rapidly during the first month, becoming the heaviest component of the seed at the end of this period (Table 1).

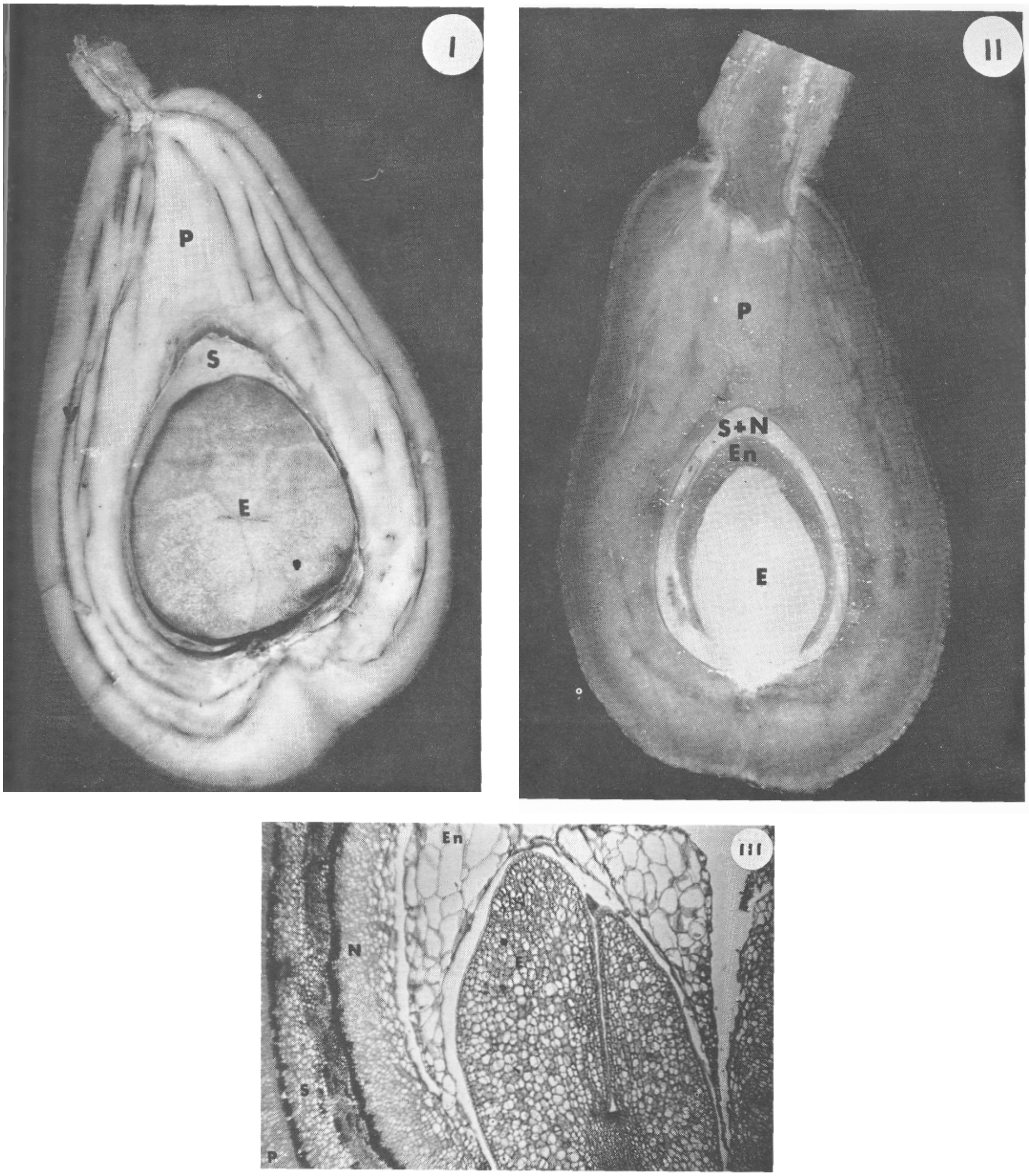

Fig. 6. Avocado fruit tissues. E-Embryo, S-Seed coat, En-Endosperm, N-Nucellus, V-Vascular system. I – Mature fruit; II – Young fruit (1 ½ months old); III – Fruitlet (2 weeks after set).

The embryo in ‘Fuerte’ develops from time of fruit set until September when complete shriveling of the seed coats cuts off the nutrient supply (Fig. 8). The fruit embryo axis weighs only 0.1 — 0.2 g in a mature 'Fuerte' Most of the embryo consists of the 2 cotyledons.

Endosperm. In the early stages of fruit development a gelatinous endosperm envelops the embryo. During fruit development, the embryo grows toward the distal end of the seed cavity pushing the endosperm toward the proximal end of the seed cavity. The endosperm completely disappears approximately 3 months after fruit set in 'Fuerte'. The endosperm wt is about 0.25 g in 'Hass' and about 0.35 in 'Fuerte', 'Nabal' and 'Booth 8'.

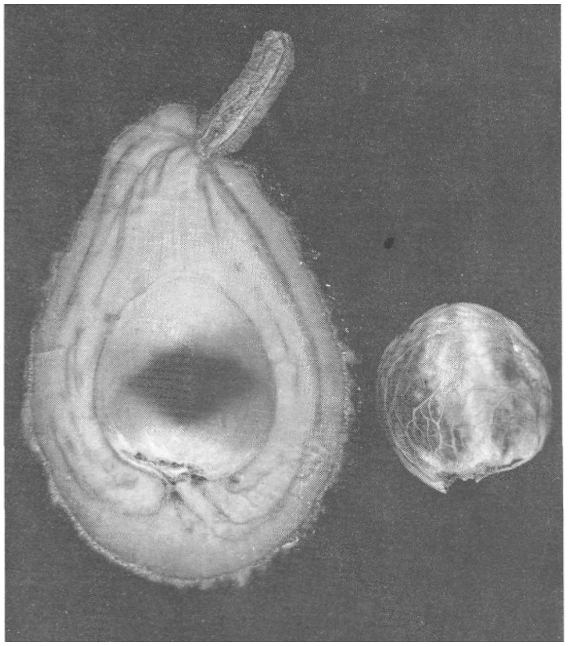

Fig. 7. Vascular system in the pericarp (left) and in the seed coat (right) of mature avocado. The seed coat (right) was removed from the seed cavity.

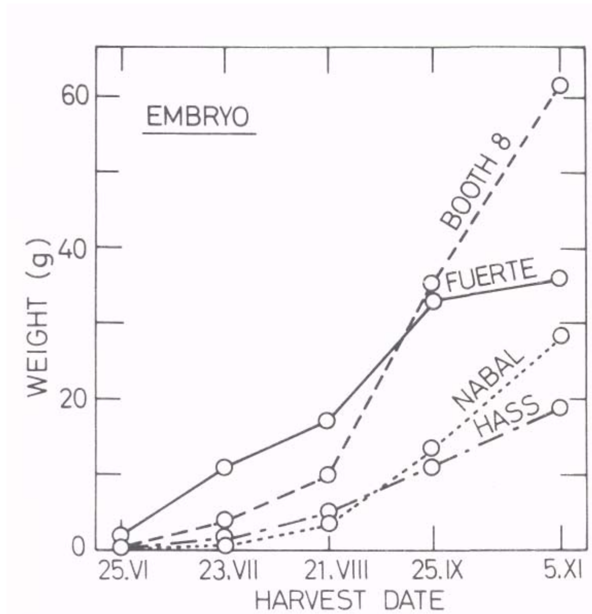

Fig. 8. Growth of the embryo of different avocado cultivars.

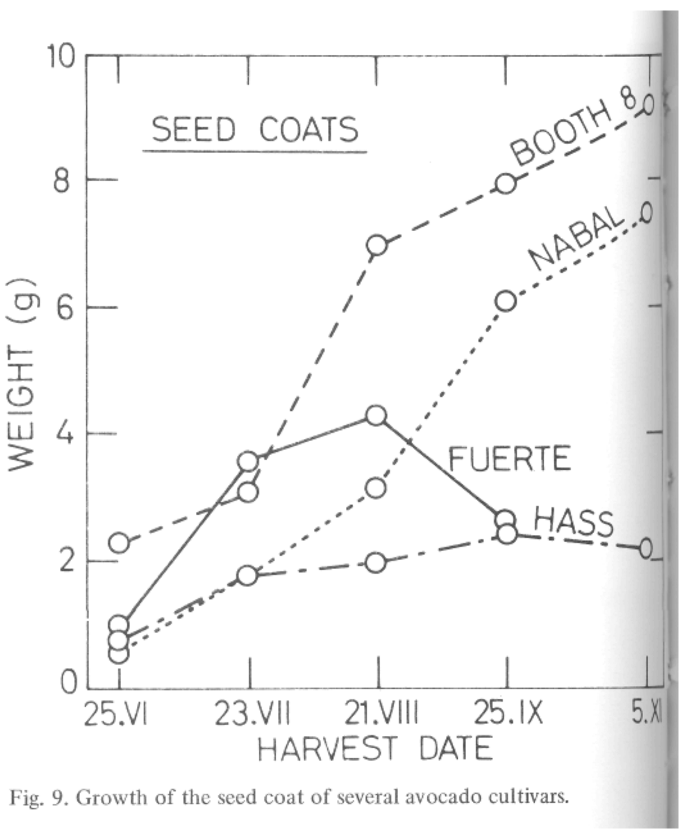

Fig. 9. Growth of the seed coat of several avocado cultivars.

Seed coat. In immature fruit the developing seed coat is white, thick and fleshy. At that time it includes the nucellus. Its thickness in 'Fuerte' can be up to 2 mm, and its maximal wt is 3.5 - 4.0 g. In other cultivars like 'Ettinger' or 'Booth 8', it is even thicker and heavier (Fig. 9).

About 3 weeks after set, the seed coat is the heaviest component of the seed (Table 1).

The seed coat reaches maximum wt in 'Fuerte' in August, and at different dates in other cultivars which differ in time of maturity. It begins to shrivel and darken until completely dry. The vascular system in the seed coat also dries and is incapable of transferring materials as evaluated by the dye technique mentioned above.

Thereafter, there can be no rapid interchange of materials between the embryo and the pericarp and the influence of the embryo on fruit growth stops completely. At this stage the embryo is often free in the seed cavity, indicating horticultural maturity of the fruit.

The shriveling of the seed coat is related to fruit maturity, i.e., the seed coat dries up early in earlier maturing cultivars (not shown) and later in late maturing cultivars like 'Nabal' and 'Booth 8' (Fig. 9).

The shriveling of the seed coat in 'Fuerte' precedes the decrease of fruit growth rate in September (Figs. 2, 3, 4). This seems to be due to the cessation of the influence of the seed on fruit growth. When for some reason the seed coat shrivels early but after mid-July, "intermediate" fruits develop. In both cases maturation of the fruit takes place, as characterized by rapid accumulation of oil in the mesocarp.

Seed coat and fruit abscission. No exact information about avocado fruit abscission is available; however, preliminary observations with 'Fuerte' show at least 3 waves of abscission. The first occurs during the first 10 days after set, the second during the next month, and the third in July. In the first wave some damage to the seed was generally observed, often to the seed coat. Shriveled and brown seed coat was frequently found in fruit abscising in the subsequent waves. When damage was caused to the fruit by removing a piece of tissue with a cork borer (6 mm diameter) at the end of July, the fruit abscised only if the seed coat had been damaged. In September, even severe damage to the fruit, such as removing half of it, did not cause abscission.

"Intermediate" shape fruits. Fruits with shape different from that of seeded or seedless ones were found from July onwards on 'Ettinger', 'Fuerte' and 'Hass' trees. Such fruits were always narrower (Fig. 2). When these fruits were opened, an embryo smaller than usual or even a degenerated embryo was found, and their seed coats were always shriveled and brown. It appears that changes which occur in September during normal fruit maturation, also occurred in the "intermediate" fruits but about a month earlier. The oil content of "intermediate" fruits was much higher than in seeded ones, (12-14% compared to 6-7% in the latter).

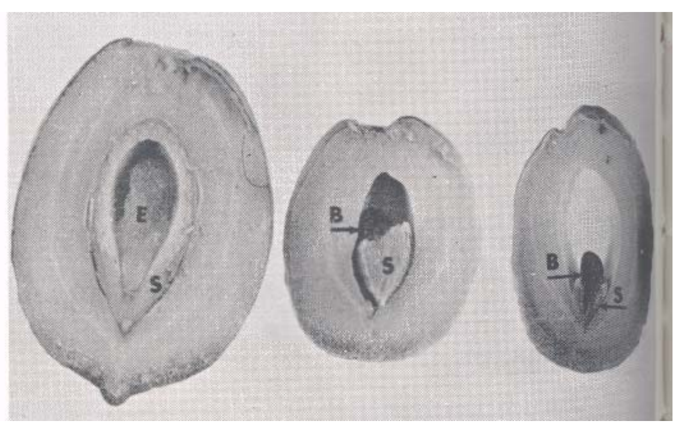

Fig. 10. Seeded (left) and seedless (middle and right avocado fruit, 3 weeks after set. E – Embryo, S – Seed coat, (apparently including the nucellus), B – Degenerated black part of the seed coat.

Seedless fruits. Seedless fruits were found in large numbers on 'Ettinger' and 'Fuerte' trees. The number of seedless fruits found in a particular orchard or geographical region varies widely in different years. In some years few seedless fruits were found, and in others almost all fruits on many trees were seedless. Our observations showed that in each year many seedless fruits are set, but they normally abscise during the first wave of fruit abscission. However, under certain (unidentified) environmental conditions many seedless fruits do not abscise, Therefore, variations of climactic conditions in different years and regions during fruit set may result in different numbers of seedless fruits.

Except when they are very young, seedless fruits differ in their appearance from seeded fruits, they are smaller (Fig. 2, 3) generally shorter, and always much narrower than seeded fruit (Fig. 2). It is impossible to distinguish seedlessness until about 2 weeks after set. Later the distal end is conical in seeded fruits and rounded or flattened in seedless ones (Fig. 10).

When seedless fruits were cut longitudinally, a small body was observed at the distal end of the seed cavity (Fig. 10) Anatomical examinations showed (Gottreich unpublished) that it was partially degenerated seed coat, the black upper part being its shrunken, and apparently, dead part (Fig. 12).

In seeded fruits the seed fills the whole seed cavity (Fig. 11) Seed coat and nucellus layers develop from maternal tissue, Therefore, their presence does not indicate that fertilization took place, as does the presence of an endosperm or an embryo,

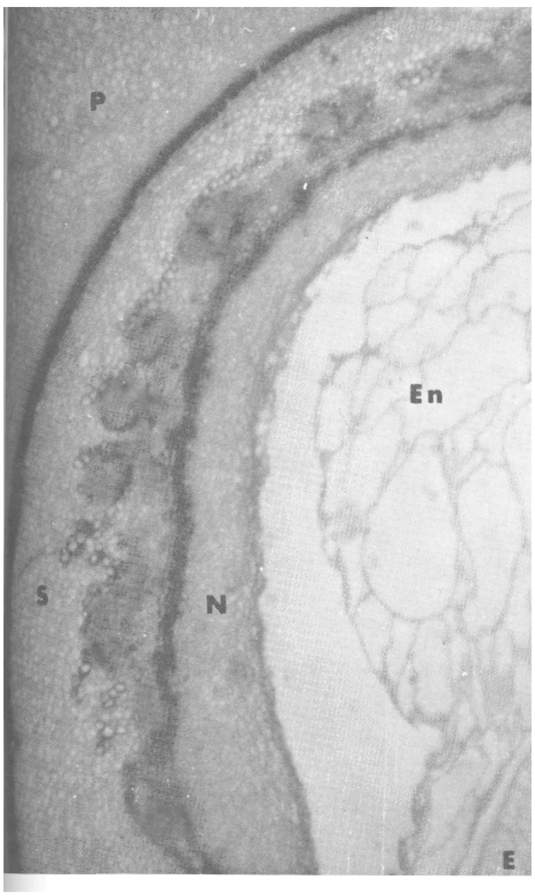

Fig. 11. Tissues of seeded fruitlet. The seed fills the seed cavity. Symbols as in Figs. 6 and 10.

Fig. 12. Section, through seed cavity or seedless fruitlet, showing a partially degenerated seed coat. Symbols as in Figs. 6 and 10.

Pericarp sections were examined in order to determine the reasons for the difference in size between seeded and seedless fruits. Three weeks after fruit set (May 10, in Table 2), the differences between the 2 types of fruits were small (Table 2). it is assumed that in earlier stages of development (for which we do not have data for seedless fruits), little or no difference existed. Later on, cell number and size increased faster in seeded fruits. During a period of 2 months (May 10 to July 8), cell number increased 2.2 times and cell size (calculated as a sphere increased 3.2 times in seeded fruit, and only 1.2 and 1.4 time respectively, in seedless fruit. Thus, the difference in fruit size results from differences in both cell number and cell size.

The role of the seed in fruit development. Fleshy fruits can divided into 2 main groups according to the importance of the seeds in their development: (a) fruits in which seeds are vital for normal growth and development; (b) fruits in which normal development does not depend on the presence of seeds.

There is evidence today to show that fruits act as sinks for nutrients. The sink's strength, relative to the foliage differs between fruits of different species. For example, apricot and peach which belong to group (a) according to the above mentioned classification, compete better with new foliage (11) as do some oranges (13) which belong to group (b).

Seedless avocado fruits are always smaller than seeded ones (Fig. *2,* 3), even without competition of the latter. Such is also the situation in many other fruits (9, 14, 16, 17, 18). Furthermore, after the natural disconnection of the avocado seed from the pericarp, the rate of fruit growth decreases considerably (Fig. 3).

The avocado seed seems to be a strong sink organ in the fruit evidenced by its effect on fruit growth as well as by its large size and high dry matter content. Furthermore, the vascular system (Fig. 6) directs movement of nutrients mainly toward the seed. Preferential movement of nutrients toward places on the plant treated with growth regulators is known (12, 23). High levels of endogenous growth substances in the seeds probably have similar effect and make the fruit a sink. Indeed, the avocado seed tissues contain much higher levels of auxins, gibberellins and cytokinins than the pericarp (3, 5, 7, 8), and based on indirect evidence, it was suggested that the seed tissues can synthesize growth substances (4, 5). Substituted various effects of seeds (like fruit set, prevention of abscission) by growth regulators, and the need for repeated treatments of seedless fruits of several species to achieve growth similar to that of seeded ones, support the idea that the seeds influence on the development of the fleshy pericarp, is via growth substances.

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