GROWTH AND WATER RELATIONS OF THE AVOCADO FRUIT

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(WITH THIRTEEN FIGURES)

Introduction

Some of the heaviest losses of thin skinned avocado fruit are due to end-spots, a name applied by COIT (**1**) to the type of spoilage that affects mature fruits on the tree. In end-spotted fruit the larger end gradually withers and dries and in some cases the cracking may proceed until the seed is exposed. In another type of end-spot called "speckles," small, dark spots occur as dry, depressed areas in the skin. Among the factors involved (**6**) are an overmaturity of the skin in the affected portion of the fruit and a desiccation of the fruit surfaces as a result of an extreme water deficit in the tree.

End-spots may become of greater importance in the near future because of the popularity of thin skinned fruit and the need for additional varieties with maturity dates covering the entire season.

The present paper[1] considers certain phases of the growth and water relations of the avocado fruit. Chemical studies to be reported later furnish data that may aid in gaining an understanding of these physiological diseases. No conclusions are drawn regarding the horticultural application of the results obtained.

Investigation

GROWTH OF FRUITS

From a practical standpoint, growth affects the shape and therefore the marketability of the fruit. From the scientific standpoint, growth governs the distribution of stomata. This distribution in turn is related to water loss and aeration.

In order to arrive at a quantitative measure of the growth of avocado fruits, about twenty-five Northrop fruits of varying sizes were marked on March 23, 1934, with parallel India ink lines (3 mm. apart) made by means of a rubber stamp. One pair of lines was placed near the tip end,[2] another at the location of the largest diameter, and a third near the stem end. All lines were perpendicular to the long (stem to tip) axis.

On May 21, 1934, an average marked fruit was 64 mm. long and 42 mm. wide at its greatest diameter. The average distance apart of the lines near

[1] The writer gratefully acknowledges the interest of Professor W. T. HORNE in these studies and the cooperation of Dr. L. J. KLOTZ in conducting the permeability tests.

[2] In this paper the popular terms "stem" and "tip" ends are used synonymously with the scientific terms "calyx" and "stylar" ends.

the tip end was 4.18 mm., near the region of largest diameter 5.27 mm., and near the stem end 6.22 mm. The region of least growth lies near the tip end, while that of greatest growth occurs between the region of the largest diameter and the stem end. This type of growth differs from that described by HAAS and BLISS (**4**) for date fruits, in which the region of greatest growth occurs at the region of attachment.

STOMATAL DISTRIBUTION

When young fruits of the thin skinned varieties are about 1 inch in length, they show numerous stomata distributed over almost the entire surface. As the fruits develop, the stomata become separated by greater distances toward the stem than toward the tip end, as seen in figure 1.

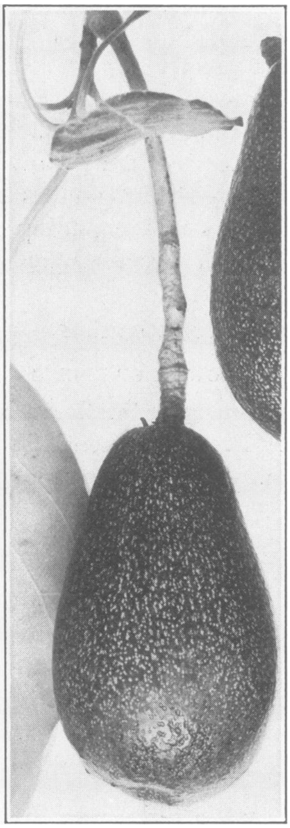


FIG. 1. Mature Fuerte fruit showing distribution of stomata, which are farther apart toward stem end.

Figure 2 *A* shows a cross section of a stoma in the skin of a mature fruit of the Fuerte variety. The guard cells are seen closing the entrance to a

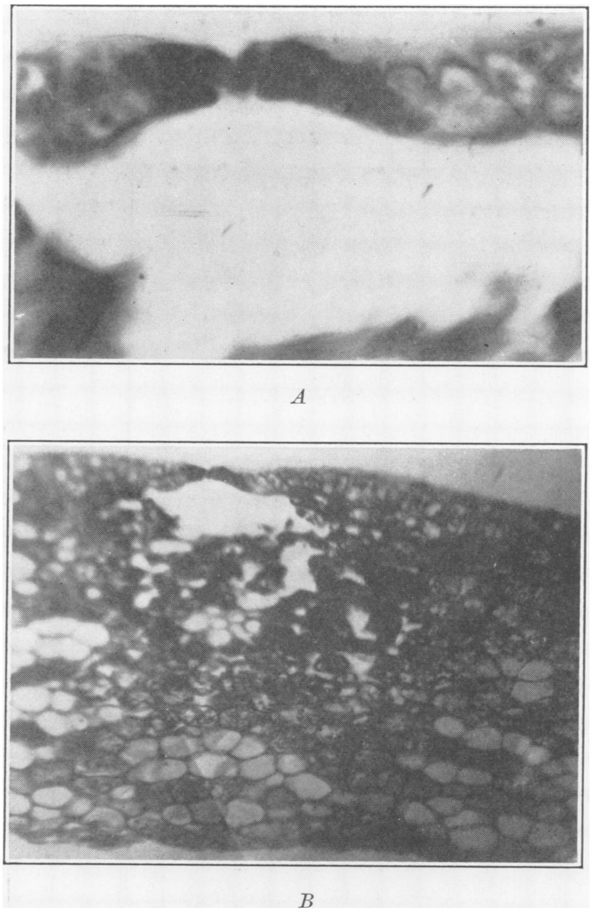
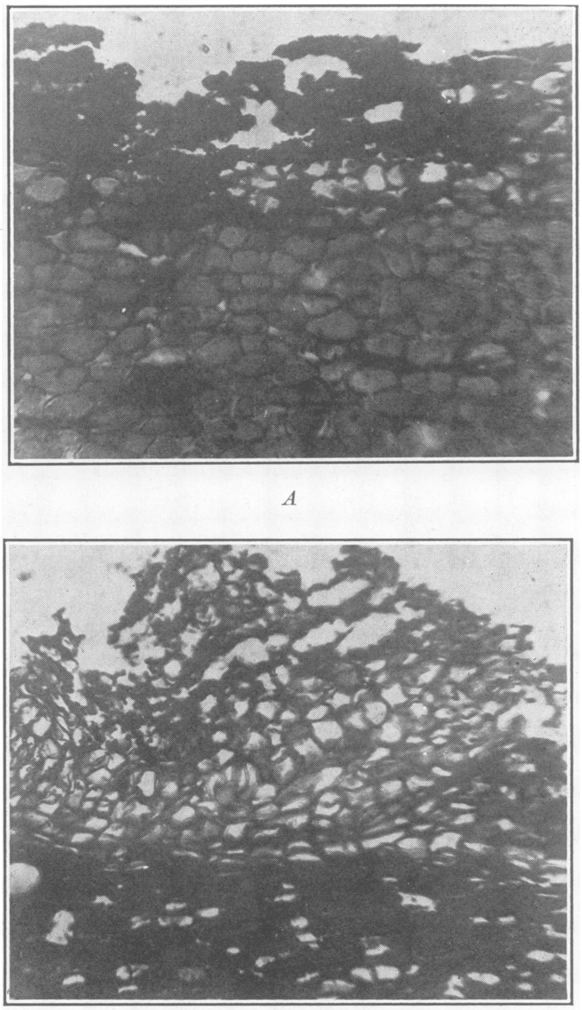


FIG. 2. Cross sections of skin of a mature Fuerte fruit: *A*, guard cells of a stoma in relation to primary stomatal cavity (× 588); *B*, relation of a stoma to primary and secondary smaller cavities and spongy tissue (× 141).

large stomatal cavity. The cuticle of the epidermis is relatively thick. The large stomatal cavity affords an excellent means for aerating the deeper lying tissues and for allowing moisture to escape rapidly from the large surfaces within the cavity.

The stomata gradually function less efficiently as the fruits approach maturity. Microscopic examination of a mature stoma in surface view frequently reveals a browning of the stoma and its eventual death. In some cases the surrounding cells also die. Because of these changes there is less protection against drying out in these areas and the type of end-spots called speckles may result. Secondly, these areas offer agents of decay relatively easy access to the skin and pulp. In Fuerte fruit there is but little, if any, lenticel formation in the region of the stomata, so that mature fruits in a large measure have lost considerable of their previous protection against disease producing agencies.



A

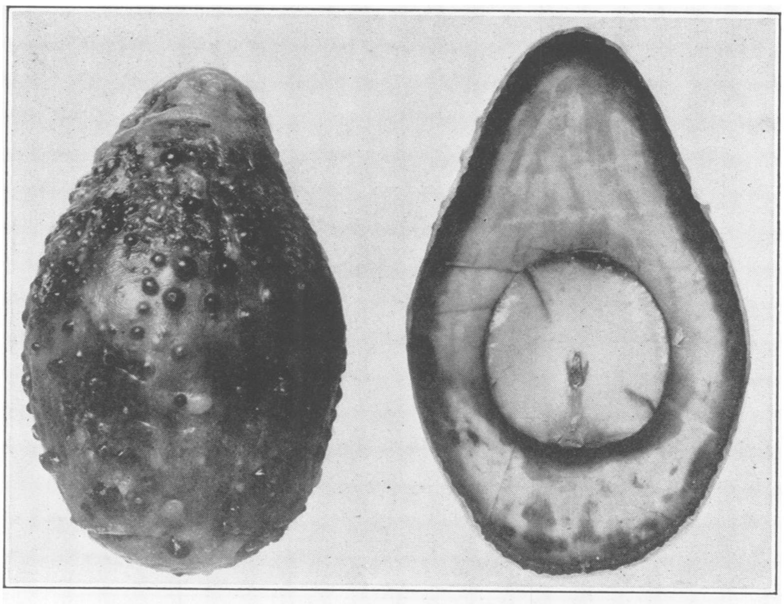
B

FIG. 3. Cross sections of skin of mature fruits of thick skinned varieties (×141): *A*, seedling; *B*, Premier.

Examination of the entire cross section of the skin of a mature Fuerte fruit (fig. 2 *B*), makes clear the relation of the guard cells to the large primary and the smaller, more deeply situated, secondary stomatal cavities. Much of the underlying tissue consists of spongy thin walled cells. The section also gives an idea of the relative thickness of the skin of fruits of thin skinned varieties.

In fruits of thick skinned varieties the death of the stoma is followed by varying degrees of cork formation, as a result of which lenticels are produced. Figure 3 *A* shows the excessive cork formation in the skin of a fruit of a seedling tree, while figure 3 *B* shows a lenticel in the skin of a fruit of the Premier variety. Such thick skins usually contain groups of stone cells. There is also considerable cork formation in the region below that previously occupied by the stoma. A brief, concise statement by STEVENS (7) describes such transformations of stomata into lenticels.

When the processes of gaseous exchange are greatly reduced, serious injury occurs, as may be seen in figure 4. Detached fruits of the Benik variety were fully coated with a paraffin of low melting point on February 24, 1932, and on March 18, 1932, some of the fruits were photographed. Figure 4 *A* shows the external appearance of the fruit. Figure 4 *B* shows



A *B*

FIG. 4. Effect of complete coverage of mature Benik fruits with low melting-point paraffin. *A*, raised blisters in the paraffin that are filled with a brown liquid; *B*, marked discoloration and decomposition of the pulp.

the fruit cut lengthwise, revealing the internal darkening and decomposition of the pulp tissue.

These artificially induced injuries suggest that the tendency of fruits of certain varieties to darken internally upon advanced maturity may be related to an inadequate gaseous exchange. The probable explanation of what happens is: (1) the fat content increases as maturity is approached, a greater gaseous supply and exchange thus being required; (2) the increasing

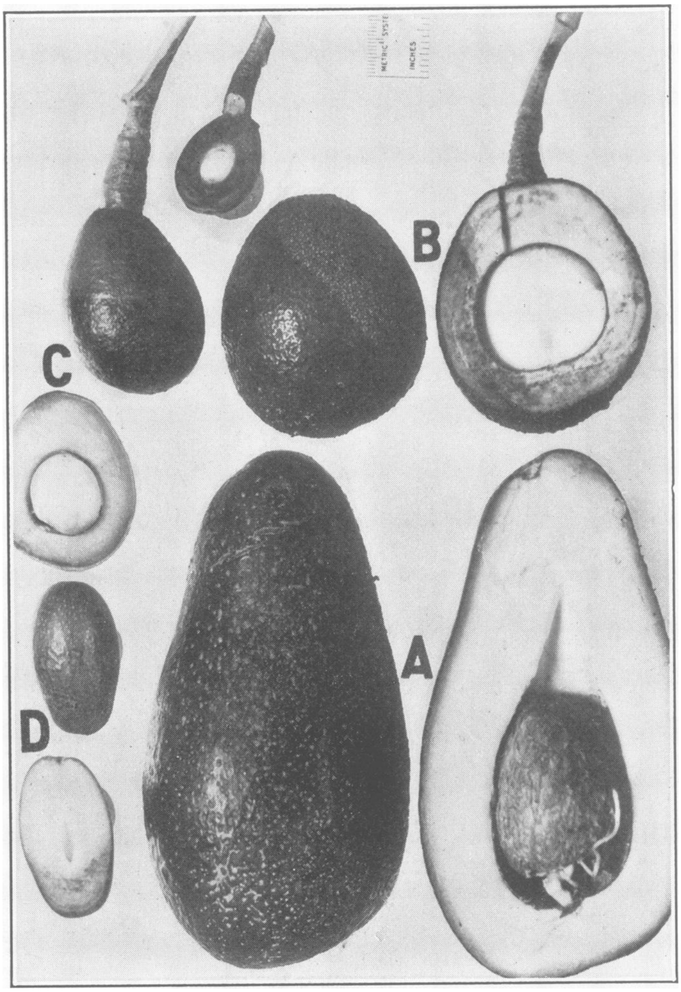


FIG. 5. Effect of immersing Fuerte fruits in distilled water for several days: *A*, mature fruit in which dead tissue surrounds the stomata, giving appearance of speckles. A slight darkening of the pulp occurs near periphery at tip end; *B, C, D*, immature fruits showing discoloration of skin toward tip and darkening of pulp beneath the injured skin.

fat content possibly retards the movement of gases in the tissues; and (3) the fruits of certain thick skinned varieties contain varying amounts of phellogen tissue with different degrees of permeability.

Water relations

Water injury.—The immersion of Fuerte fruits of varying ages in distilled water for several days prevented a sufficiently rapid aeration of the tissues, as shown in figure 5.

The experiment was repeated with about twenty-five fruits of another thin skinned variety (Northrop). Fruits of various sizes were placed in liter beakers containing distilled water. These fruits, which had stems attached, were submerged in water that was frequently changed. At the end of two days no injury was observed, largely because the fruits were viewed from the stem end. After two and one-half days the fruits were taken out of the water, wiped dry, and thoroughly examined. Upon standing an hour or so in the dry condition, portions of the skin began to darken.

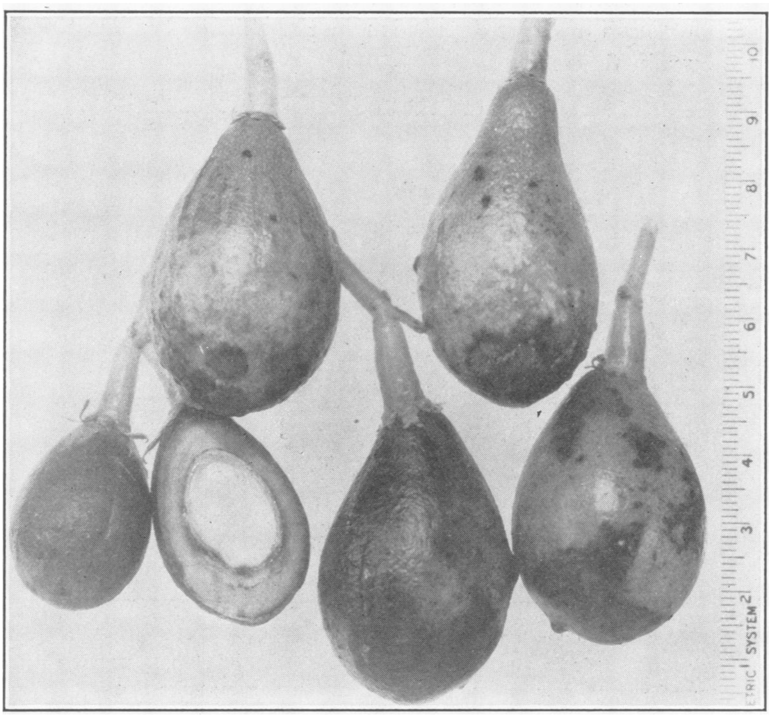


Fig. 6. Discoloration of skin of young, immature Northrop fruits (about 2.5 cm. diameter × 4 cm. long) by immersion in distilled water for 2 to 3 days. Photograph made one hour after fruits were dry.

Other experiments were conducted at room temperature to ascertain the period required for such damage to occur. After immersion for 8 hours, only one of the fourteen fruits showed injury after being dry four days, after 32 hours' immersion, five out of the eleven fruits showed injury after being dry 63 hours, after immersion for 48 hours every one of the eight large fruits showed injury after being dry 48 hours, and after immersion for three days each of eleven fruits showed injury after being dry 24 hours. In the long-necked fruits in the lot immersed for the longest period, severe checking[3] and darkening occurred on the neck portion.

Figure 6 shows the almost complete brown discoloration of the skin of the small Northrop fruits. After remaining in a dry condition overnight the discolored skin turned from brown to black and marked the location of sunken or depressed areas. The underlying pulp tissue was also darkened to varying depths. Frequently the stomata were included in small, sunken areas of dead skin, giving them the appearance of speckles.

The characteristic injury (called carpellary water injury) was evident at the extreme tip end where the fusion tissue of the ovary was weak. This fusion tissue forms a slight depression in the skin of the fruit at the tip end, as shown in figure 7.

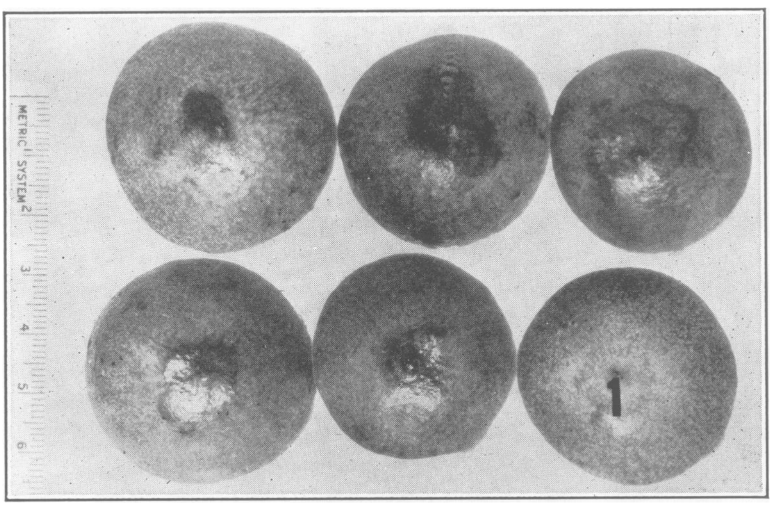


FIG. 7. Effect of immersion of half-grown (about 4 cm. diameter × 5 to 6. cm. long) Northrop fruits in distilled water for 2 to 3 days. Death of skin to varying depths into the pulp occurred at and surrounding the weak fusion tissue at the tip end. Photograph made one hour after fruits were dry. Apparent cavity where weak fusion tissue occurred is indicated by the "1" on control fruit in photograph.

[3] The term "checking" is used to designate small, visible, and also microscopic splits or ruptures in the skin of the fruit (HAAS and BLISS, 4).

Similar results were produced in fruits of various sizes still attached to the tree in the field by immersing them for periods of one to three days in jars of distilled water suspended from the branches. In this experiment considerable spotting of fruits resulted. The water apparently can penetrate the weak fusion tissue of the carpellary structure rather rapidly and then diffuse laterally after absorbing or pushing aside the bubble of air from the depression at the tip end. In penetrating at this point the water kills the tissue, the by-products of which are then free to kill or injure the adjacent tissue.

These results indicate the type of injury that may occur when fruit is continuously bathed with distilled water. After standing overnight the discolored skin and pulp of the artificially injured fruit becomes nearly black and a sinking of the tissue occurs in the injured areas as the affected tissues dry out.

Fruit on trees may become dry at the tip end, shrink, and crack, thus exposing the deeper tissue of the pulp to further drying and to other destructive agencies. Premature coloration and drying out of the weak fusion tissue of Northrop fruits at various stages of their development have been

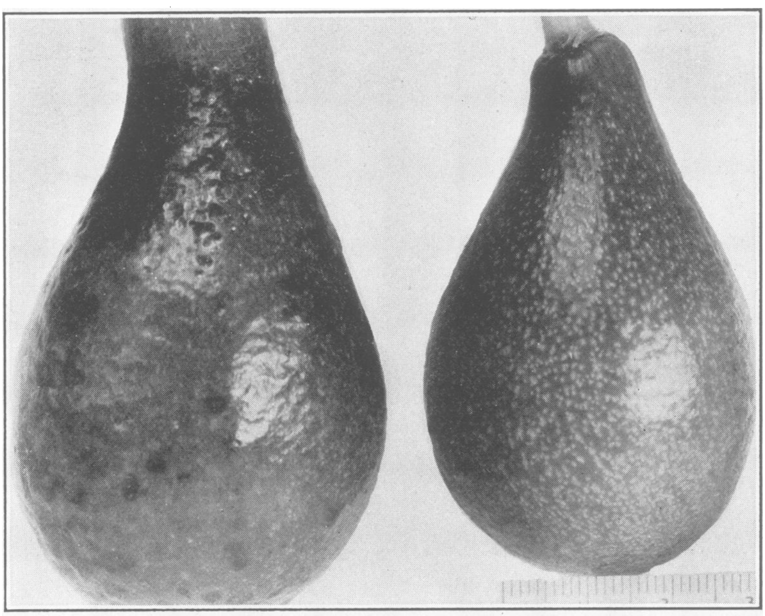
FIG. 8. Mature fruit of Blake variety affected with end-spot as a result of severe water deficit in the tree.

produced by withholding water for too long a time from the soil. Water applied to the soil after wilting appeared did not prevent the abscission of many young fruits. After several weeks the effects became more apparent on the more advanced fruit (about 4 cm. diameter × 7 cm. long). In addition to showing premature coloring, many of these fruits also showed some drying out and shrinkage.

The weak fusion tissue, in addition to absorbing water rapidly, also dries out readily when trees are under considerable stress for water. Fruits of the Northrop variety that were prematurely fully colored or even partially colored, showed, when under a water stress, a sunken, darkened area about this carpellary region (fig. 8).

Some of the more mature, but still fully green, Northrop fruits (about 4.5 cm. diameter × 8.5 cm. long) after being immersed nearly 3 days in distilled water and then wiped dry were photographed within an hour after being removed from the water. Figure 9 *A* shows such a water-injured fruit, together with a control fruit.

Dark areas in the skin and underlying pulp were scattered over much of the fruit. The dark region on the neck and that near the weak fusion tissue



A *B*

FIG. 9. *A*, water injury of a fully green, immature Northrop fruit (about 4.5 cm. diameter × 8.5 cm. long) produced by immersing fruit for nearly 3 days in distilled water; *B*, control fruit not immersed. Note checking of skin in neck portion of affected fruit.

were badly checked. As a result of these checks the dark areas soon lost water and began to sink. These checks are in some respects comparable with those studied and produced by HAAS and BLISS (**4**) by immersing date fruits in water. Overnight the water-injured fruit illustrated in figure 9 showed such increased injury that it was again photographed after 20 hours (fig. 10).

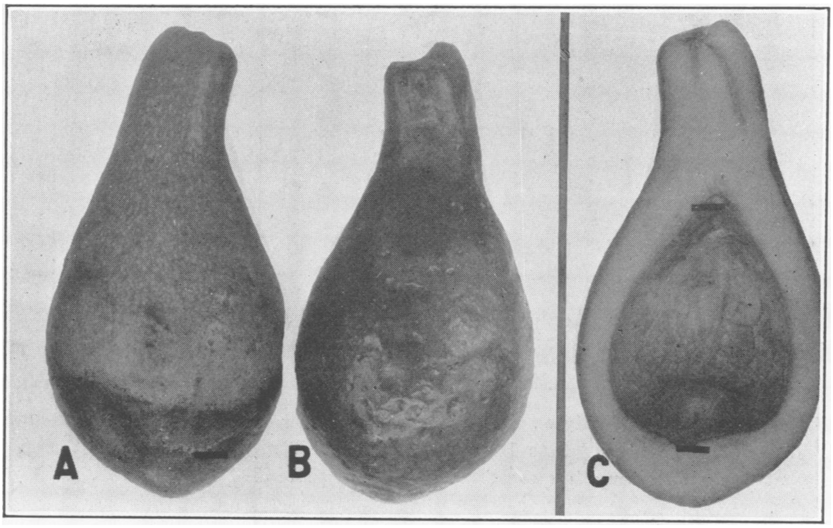


FIG. 10. Increasing effect of time on water injury in fruits shown in figure 9. Photograph was made about 20 hours after fruits were dry. *A* and *B* show exterior of the halves and advance of dark, sunken areas. Distance from mark in *A* to living skin indicates advance of injury during 20 hours. Checking of skin is shown on the neck in *B*. Two lines in *C* point toward water-soaked appearing pulpy tissue.

Water injury may be produced artificially in fruits of thick skinned varieties such as Tiger (fig. 11), as well as in fruits of thin skinned varieties such as Fuerte, Puebla, Blake, and Northrop.

In the laboratory an experiment was carried on with mature thick skinned fruits of the Spinks variety. Figure 12 shows the more violent type of water injury comparable to that which HAAS and BLISS (**4**) have designated as "tearing." The exposure to distilled water produced minute checks. When the fruit was allowed to dry the skin was drawn more tightly about the pulp and with further shrinkage was severely torn.

Attention thus far has been called to the artificial production of water injury in avocado fruits. The same type of water injury has been found under natural conditions in the field. On August 24, 1935, after an extended period of foggy mornings, nearly 2 inches of rain fell at the Citrus

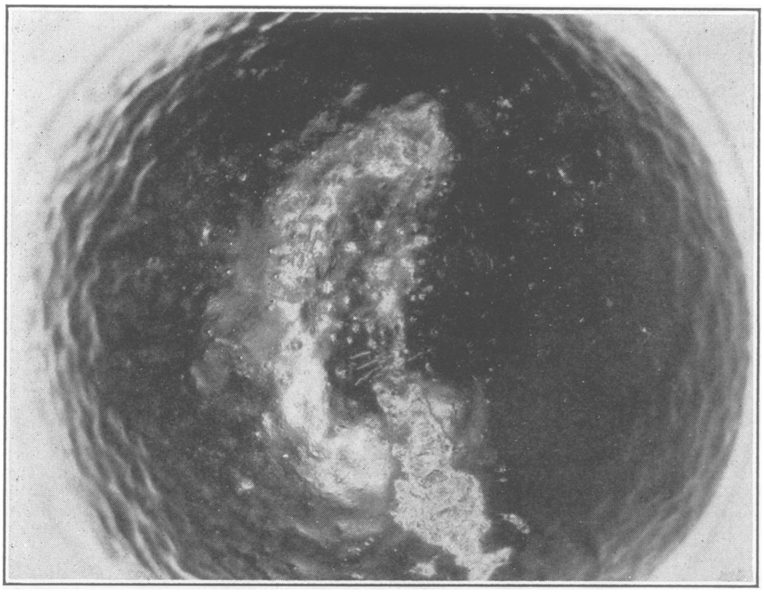


FIG. 11. Checking of skin at tip end of mature Tiger fruit produced by immersing in distilled water from April 9 to 16, 1934 (fruit was attached to a tree in the field). Subsequent drying of skin after the fruit was detached tended to increase visibility of the checks.

Experiment Station. Light sprinkles of rain occurred on August 26 and on several other previous days. On August 29, 1935, many fruits were found on trees at the Citrus Experiment Station that showed injury as a result of checking. Figure 13 shows affected fruits that were photographed under water after rubbing talcum powder into the checks in order to improve their visibility.

These results are of interest because FRAZIER (2) has stated, regarding the cracking of tomato fruits, that the most consistent effect obtained was the cracking after the applications of water to the fruits or to the soil.

Thick skinned fruits on trees grown in soil kept very wet over a prolonged period because of heavy rains may abscise in large numbers. It is possible that such abscission follows a reduced oxygen content of the soil solution which has injured some of the younger roots.

PERMEABILITY OF SKIN.—The relative permeability of stem and tip halves of fruits was investigated by the methods employed by HAAS and KLOTZ (5) in determining the permeability gradients in citrus fruits.

Two lots each consisting of five mature Puebla fruits (somewhat changed from green to mahogany purple color, but firm) were collected November 1,

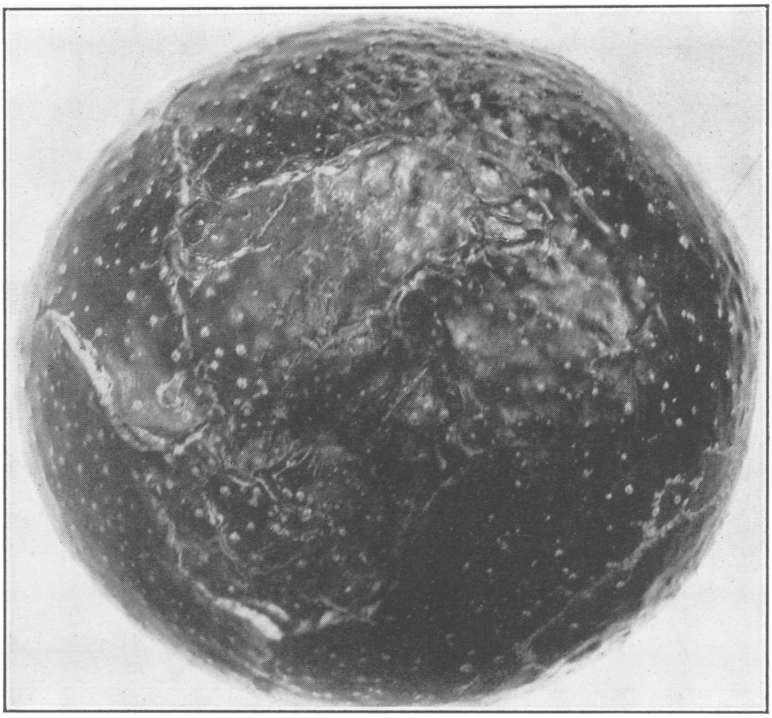


FIG. 12. Tearing type of water injury in fruit of Spinks variety produced artificially in the laboratory by immersing tip half of mature fruit in distilled water at room temperature from March 30 to April 6, 1934. Minute checks gradually enlarged until the tearing of the skin resulted. Drying of slightly torn skin exaggerates torn condition.

1932, at Riverside, California. For the permeability tests it was necessary to secure equal surface areas on both halves of the fruit. Equal lengths of ½-inch adhesive tape were placed on the stem half of one lot and on the tip half of the second lot. In both cases the entire fruit was momentarily immersed in paraffin of low melting point. The tape was then removed and the fruits immersed in 700 cc. of tap water for 53 hours.

The data in table I show that the permeability of the skin of the tip halves is greater than that of correspondingly equal areas of skin of the stem halves.

A greater number of stomata occur at the tip than at the stem end (fig. 1). In fruits of the thick skinned varieties the corky lenticels may be much larger than the stomata which they have replaced and may be so close to one another as to show a coalescence.

Since stomata and lenticels are supposed to function chiefly in gaseous exchange and at the same time to permit a loss of water, the greater number

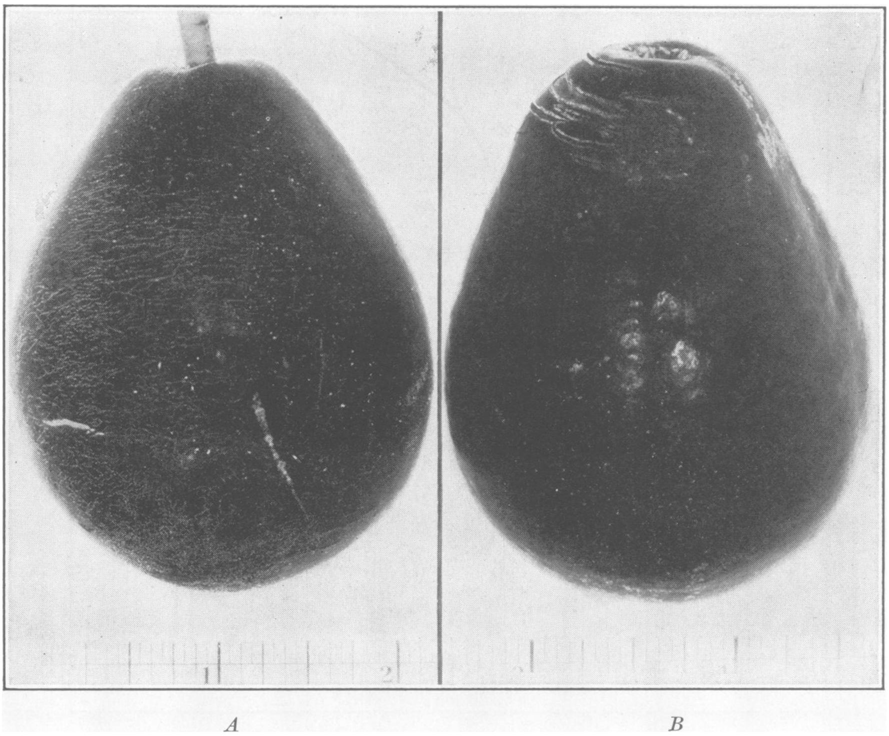


FIG. 13. Water injury of thin skinned varieties of fruits as it occurs in the field after periods of heavy fogs or rains during certain stages in maturation of the fruit: *A*, fruit of Mexican seedling tree; *B*, fruit of Mexicola variety.

at the tip end would permit a more rapid exudation of substances that catalyze the reaction involved in the reduction of $KMnO_4$. As has been shown, the permeability of the skin of Puebla fruit is greatest in the tip half, whereas that of citrus fruit (**5**) is greatest in the stem half.

TABLE I

TIME (MINUTES AND SECONDS) REQUIRED TO MATCH 25 CC. $KMnO_4$ STANDARD

PORTION OF FRUIT	STANDARD (3 DROPS $KMnO_4$ PER 50 CC. TAP WATER)		STANDARD (1 DROP $KMnO_4$ PER 50 CC. TAP WATER)
	min. and sec.	*min. and sec.*	*min. and sec.*
Stem half (3 sq. in. not paraffined)	5:50	5:35	1:55
Stem half (3 sq. in. not paraffined)	1:50	1:45	0:30

RATE OF WATER LOSS.—Lots of three to thirteen mature fruits (depending on the fruit size) were obtained at Riverside on September 12, 1931. The rate of water loss was determined at room temperature in two ways: (1) by cutting the fruits into portions and placing the cut surface on glass plates coated with boric acid powder, and (2) by paraffining the stem or the tip half of the fruit.

After certain periods the water loss was calculated as a percentage of the original fresh weight. The results in table II show that regardless of the method used, the water loss is consistently greater in the tip than in the stem half, and that it is intermediate in the middle portion of the fruit.

TABLE II

WATER LOSS THROUGH VARIOUS PORTIONS OF SKIN OF AVOCADO FRUITS

VARIETY	PORTION OF FRUITS	WATER LOSS AS PERCENTAGE OF ORIGINAL FRESH WEIGHT		
		28 HOURS	68 HOURS	95 HOURS
	Fruits cut into halves			
		%	%	%
Mexicola	Stem halves	5.66	....	17.52
	Tip halves	6.83	....	21.25
Mexicola	Stem halves	6.13	....	17.83
	Tip halves	6.79	....	21.70
Blake	Stem halves	6.47	....	18.95
	Tip leaves	7.75	....	23.25
Blake	Stem halves	6.80	....	20.40
	Tip halves	8.20	....	23.55
Blake	Stem halves	....	14.00	19.53
	Tip halves	....	16.15	22.56
Blake	Stem-end thirds	....	16.26	22.49
	Middle thirds	....	17.94	24.80
	Tip-end thirds	....	18.87	26.42
One-half of fruit	paraffined	69 hours	235 hours	452 hours
Blake	Stem halves	4.51	12.44	27.72
	Tip halves	5.33	14.87	34.12
Fuerte	Stem halves	2.52	7.13	14.90
	Tip halves	4.58	12.05	24.29
One-half of fruit	paraffined	48 hours	237 hours	432 hours
Benik	Stem halves	3.84	13.89	26.08
	Tip halves	4.36	15.65	29.25
Puebla seedling	Stem halves	3.04	10.73	19.08
	Tip halves	3.89	14.65	25.71
One-half of fruit	paraffined	53 hours	292 hours	502 hours
Benik	Stem halves	3.66	14.26	22.34
	Tip halves	4.04	16.09	25.12

The effect of fruit size on the rate of water loss from fruits kept at room temperature was next studied. Immature avocado fruits were obtained at Riverside on April 14, 1930, and their original water content was determined by drying similar samples at 80° C. in a well ventilated oven. The original fresh weight per fruit (table III) gives some idea of the fruit size.

As shown in table III, the smaller fruit (younger) of a given variety lost water more rapidly than the larger (older) fruit of the same variety, although both lots of fruit contained the same percentage of water in the original fresh weight. This difference in water loss from fruits that depends on the fruit size or age may be due to several causes, two of which are: (1) there are fewer stomata per unit area of skin as the fruit increases in size (fig. 1); (2) the larger fruits have less surface exposed per unit volume, a condition shown by HAAS (3) to be a factor in water loss from young citrus fruits.

TABLE III

EFFECT OF FRUIT SIZE ON RATE OF WATER LOSS

VARIETY	NUMBER OF FRUITS	ORIGINAL FRESH WEIGHT PER FRUIT	ORIGINAL WATER CONTENT	LOSS OF ORIGINAL FRESH WEIGHT	
				48 HOURS	91 HOURS
		gm.	%	%	%
Blake	29*	0.5641	84.77	46.58	73.30
	20	1.2153	84.82	40.34	68.03
Caliente	38*	0.3196	84.84	60.27	79.93
	21	0.8125	84.74	47.61	73.40
Mexicola	29*	0.4537	86.27	48.79	77.46
	8	2.5785	86.32	30.95	57.15
Tiger	39*	0.3755	86.09	51.69	78.95
	17	1.6012	86.19	38.64	67.65

* Smallest fruits of the two lots.

Summary

1. The growth of young Northrop fruits was found to be greatest in the stem end and progressively less toward the tip end.

2. The region of greatest growth in a fruit may be found by observing the distribution of stomata. In young fruits the stomata are rather uniformly distributed, but as growth proceeds, the greater growth toward the stem end separates the stomata more than in other regions of the skin.

3. Stomata in the skin of mature fruits afford a rapid means of gaseous

exchange and transpiration; however, under certain conditions they also afford a rapid means of wide-spread fungus distribution within the tissues of the skin and pulp. In thick skinned varieties the death of a stoma is usually followed by the formation of lenticels, but in the thin skinned varieties such as Fuerte there is little lenticel formation.

4. Reduction in the gaseous exchange results in serious damage to the quality of the fruits.

5. Immersion of fruits of the Fuerte variety in distilled water injured the tissue in the skin of the mature fruit in the region of the stomata, and especially injured the skin tissue at the tip end. The pulp underlying the damaged skin is variously injured, depending on the length of the period of immersion.

6. Immersion of nearly mature Northrop avocado fruits in distilled water for three days produced: (1) checking in the neck portion at the stem end; (2) carpellary water injury at the tip end, where slight checking also may occur; and (3) injury or death of tissue in the region of the stomata. The more immature the fruits the more rapid the injury, with the exception of checking in the neck portion which occurred primarily in the more mature fruits with the prolonged immersion. These injuries were produced both in the laboratory and in the field while the fruits were still attached to the tree. Similar injuries can occur to fruits under natural conditions in the field.

7. Carpellary water injury was produced in fruits in the field by withholding water for too prolonged a period while the fruits were young. Abscission of some of the small fruits occurs while some of the large ones dry out in the region of the weak fusion tissue of the ovary. The lack, as well as an excess, of water in this region of the fruit brings about somewhat similar effects. Such injury is usually followed later by checking, drying, shrinking, and decay.

8. Checks located only at the tip end were produced in thick skinned, mature fruits of the Tiger variety when immersed for seven days in distilled water while the fruits were still attached to the tree. Tearing of the skin of a nearly mature fruit of the Spinks variety resulted when the tip half of the fruit was immersed for seven days in distilled water in the laboratory.

9. The permeability of the skin of the tip halves of Puebla fruits is greater than that of correspondingly equal areas of skin of the stem halves.

10. The rate of water loss from the tip halves of fruits exceeds that of the stem halves.

11. Small fruits lose water more rapidly than larger (older) ones of the same variety.

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