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CERTAIN WATER RELATIONS OF THE GENUS PRUNUS*

ARTHUR H. HENDRICKSON

This paper is based on a comparative study of stomatal behavior and moisture content of trees of the genus *Prunus* during the rainless summer months in California, where they are grown under conditions of both abundant and scanty soil moisture.

The behavior of stomata in relation to transpiration has been a riddle to physiologists. Lloyd,[15-16] working with *Fouquiera splendens* in Arizona, first stated that the regulatory effect of stomata on transpiration was almost nil. Later he modified this view and showed that transpirational losses followed stomatal opening. Other physiologists thought that, except for the small water loss due to cuticular transpiration, the stomata controlled the transpirational losses. Francis Darwin,[3] Knight,[10-11] and others studied the action of stomata by means of the porometer. This device consisted of a hollow receptacle fastened to the leaf, through which a stream of air was drawn. From the amount of air which could be drawn through a leaf under carefully controlled conditions, these workers drew their conclusions regarding the transpiration of the plant. The value of this method was problematical and Darwin and Pertz[4] stated that "it is not certain that we shall ever be able to deduce the size of stomata from readings of the porometer." Later, however, Darwin[3] showed that the parallelism between transpiration and stomatal aperture held within certain limits with *Hedera helix* and *Prunus*

* Also submitted to the Department of Botany and the Committee on Graduate Study of the Leland Stanford Junior University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Laurocerasus in the moist climate of England. Balls,[1] working with the stomatograph on cotton under tropical conditions in Egypt, found that the stomata in response to light opened quickly to a maximum about 9 A.M. and thereafter closed rapidly. Laidlaw and Knight[12] studied excised stems of various plants by means of the porometer and reported a temporary opening of stomata before permanent closing when wilted. Lloyd[16] did not find this "preliminary opening." Knight[11] later reported that the stomata seemed to continue to open after transpiration fell off. This confirmed some of Lloyd's[16] results.

With regard to the relation of stomatal opening to water content of Gossypium leaves, Lloyd[17] reported that the "opening of stomata is accompanied by a net loss of water by the leaf, more being given off by transpiration than can be obtained to replace it." The same author further reported that the amount of water relative to the dry weight of the leaf decreased until noon or some time thereafter and then increased until 4 A.M. Livingston and Brown[13] reported that the moisture content of leaves of various desert plants in Arizona fell to a minimum during the period 1 P.M. to 5 P.M. and then rose to normal at 7 P.M. They further stated that "non-stomatal retardation of water loss appears to be continuously active until well into the night, its effects becoming mingled with those of stomatal closure at or about sunset. It appears that in the hours just preceding sunrise stomatal retardation seems to be alone manifest." Edith Shreve[18] found with *Parkinsonia microphylla* that the curve of stomatal behavior followed the relative transpiration curve in such a manner that the existence of an interrelation was evident.

Gain[7] showed many years ago that transpiration was affected by the water content of the soil. With regard to the influence of the soil, Edith Shreve[18] reported that the "maxima for relative transpiration . . . . were found to vary directly with the soil moisture." Dole[6] has recently stated that the "amount of available soil water has an important bearing on the rate of transpiration." Gray and Peirce[8] reported that "the factor regulating both food manufacture and stomatal opening is light." Their data tended to show that available soil moisture was also an important factor in stomatal regulation.

One of the most important reports on the action of stomata is that of Loftfield,[14] who worked with a great variety of plants mostly under semi-arid conditions. He reported the maximum of leaf turgor about midnight. He also stated that the stomata of certain plants opened at night in response to moonlight. According to this author, the opening of stomata in nearly all plants was correlated with light when conditions of soil moisture were favorable. When these conditions became unfavorable, the influence of light was decreased and in some cases nullified. He divided the herbaceous plants with which he worked into three general groups according to the behavior of their stomata during the day and night under favorable and unfavorable conditions.

The cereals, in which there was no opening of stomata at night, regardless of the amount of day opening, were placed in the first group. The amount and duration of day opening was dependent upon sunlight, evaporation, temperature, and water content of the leaves. In the second group, of which alfalfa was a member, the stomata normally were open during the day but closed all night. Under unfavorable conditions of soil moisture, however, the stomata of this group showed varying degrees of day closing and night opening. In the third group, which was typical of potatoes and beets, the stomata were normally open all day and all night. If conditions of soil moisture became critical, the stomata tended to remain closed all day and to open at night. Loftfield also worked with the apple, pear, peach, and sweet cherry. He placed these trees in the same general group with alfalfa, showing no midday closure or night opening under favorable conditions. Loftfield found no midday closure of stomata in fruit trees, even when this condition was observed in alfalfa. He attributed this lack of day-time closing to two facts: first, that there was a balance of water on hand in the trunks and branches of the trees, and second, that there was available moisture within reach of their extensive root systems.

Certain aspects of the general problem of behavior of stomata were emphasized by some of these workers. Darwin,[3] Knight,[11] and others pointed out the difficulties involved in connecting stomatal movement and transpiration as determined by the porometer or similar apparatus, Lloyd[15] and Loftfield[14] studied the behavior of stomata of many plants by the absolute alcohol method, and showed the influence of such factors as light, temperature, and soil moisture on stomatal movement.

Livingston,[13] Lloyd,[17] and others showed certain relations between water content and stomatal movement of leaves of certain xerophytic plants, while other workers called attention to the relation of soil moisture to the stomatal movement. In studies on the latter part of the problem the soil moisture conditions were usually not carefully controlled, and the data obtained were[4] not conclusive.

Statement of the Problem

The wilting of plants such as may be observed on any hot day is usually attributed to the fact that more water is lost by transpiration through leaves and other green parts of the plant than is absorbed by the roots and conveyed to the different parts. Thus, wilting is usually most pronounced during the afternoon, although evidence of it may often be seen quite early in the morning. Wilting, then, can be said to be due to a reduction of water content of the tissues of the plant below the amount necessary to maintain turgor in the cells.

Mature orchard trees supplied with ample water by means of irrigation are distinctly different in appearance from unirrigated trees, particularly during the latter part of the growing season. Lack of available moisture is apparent to any one familiar with orchard trees. Previous investigations have shown that stomata are intimately connected with transpiration even though the opening and closing of the stomata did not always seem to be directly correlated with the increase and decrease of transpiration. Various workers have shown that transpiration is regulated to a certain extent by the amount of moisture available in the soil. The behavior of stomata on leaves of fruit trees growing in soil containing available moisture, therefore, should differ from the behavior of stomata on similar trees growing in soil containing little or no available moisture. Series of experiments were carried out to see if such a difference of behavior did exist.

The second point investigated was that of the moisture content of the various tissues of the tree under the conditions previously described. Leaves of trees growing under conditions favorable for transpiration and for the opening of stomata, show a fluctuation in water content. The cohesion theory of the rise of water which is based upon the theory that water in the plant tissues is under tension indicates that the fluctuation occurring in the leaves after transpiration begins should be transmitted back to the trunk and roots fairly rapidly. Investigations were carried out at Davis and at Delhi in 1925 to see if such diurnal fluctuation in the water content of peach trees could be found.

METHODS

The leaves were stripped, killed, fixed, stained with Congo Red, and mounted with balsam according to Lloyd's[15] method. The width of the stomatal openings was measured by means of a micrometer eye-piece. The stomatal dimensions as given in the tables are the average measurement of ten stomata which seemed typical of all the stomata in the sample. In most cases samples were taken every hour. In some of the later experiments samples were taken every two and, in a few cases, every three hours.

The meteorological data included air temperature, relative humidity and notes on cloudiness, wind velocity, and presence of dew. In a few cases atmometer readings were also taken. Soil moisture was determined with a special soil tube. Soil samples were taken each time leaf samples were taken. The soil was sampled to a depth of six feet; the first sample from 0 to 3 feet, and the second from 3 to 6 feet. Each sample weighed about 500 grams. All samples were taken in duplicate or triplicate. The moisture equivalent, wilting coefficient, and hygroscopic coefficient were determined after the method of Briggs and Shantz[2] modified by Veihmeyer, Israelsen, and Conrad.[20] No attempt is made in this paper to discuss the various questions which have been raised regarding the significance or determination of these factors. In this paper, the amount of moisture below the theoretical hygroscopic coefficient was considered as unavailable to the tree. The amount of moisture between the hygroscopic coefficient and the wilting coefficient was considered as being moisture that was secured with difficulty by the tree. In other words, the tree roots were able to reduce the percentage of moisture in the soil below the wilting coefficient, but could not secure from this moisture enough water for the cells to regain turgidity.

Soils.—The soils at Mountain View and at Davis are similar, being classed by the Soil Survey as "Yolo fine sandy loam" and as "Yolo clay loam." The Mountain View soil, however, contained a little more gravel than the Davis soil. The soil at Delhi was classed as an "Oakley and Madera fine sand, undifferentiated," underlaid with a compacted subsoil at a depth of 5 to 6 feet. The moisture equivalent for the Mountain View soil was determined to be 22 per cent. The wilting coefficient and hygroscopic coefficient were 11.9 per cent and 8.05 per cent, respectively. The moisture equivalent of the Delhi soil varied from 5.8 per cent to 13.8 per cent. The wilting coefficient varied from 3.2 per cent to 7.5 per cent, and the hygroscopic coefficient from 2.1 per cent to 5.0 per cent. At Davis the moisture equivalent varied from 12.8 per cent to 29.3 per cent. The wilting coefficients varied from 6.8 per cent to 16.0 per cent, and the hygroscopic point from 4.6 per cent to 10.8 per cent. Because of the sandy nature of the Delhi soil, the relative amount of available moisture was small and lack of moisture was more readily detected by the appearance of the trees than was the case either at Davis or Mountain View.

The water table at Davis was approximately 18 feet below the surface during the time the samples were being taken. If the trees obtained any moisture from this source, it was apparently not sufficient in amount to affect the stomatal behavior. The depth of the water table at Delhi was not determined, but from data from a well near by it was safe to assume that standing water was not encountered closer than 30 feet beneath the surface. From data secured by Veihmeyer* it was found that mature prune trees in a loam soil extract all available soil moisture to a depth of six feet fairly rapidly, and to a depth of twelve feet before the end of the growing season. It seems reasonable to assume that the mature peach trees at Davis behaved in the same way. The presence of a compacted layer of soil about six feet beneath the surface at Delhi makes it probable that moisture below this level did not affect the behavior of the peach trees.

Meteorological Conditions.—Meteorological conditions at Davis and at Delhi are similar, and are typical of the interior valleys of California. The temperature during the day often reaches 100°F. and may go above 100°F. for several days in succession. The maximum temperature is usually between 85°F. and 95°F. The days are usually cloudless although occasionally light clouds persist until 8 or 9 A.M. and sometimes begin to form during the late afternoon. The relative humidity during the hot part of the day often goes as low as 30 per cent. The climate at Mountain View is typical of the central coast region. High fog or clouds often persist until 10 A.M. and the temperature rarely exceeds 85°F. during the hottest part of the day. During certain stages of the so-called "storm movements," the temperature may reach 100°F. and the relative humidity may drop to as low as 30 per cent, although during the greater part of the day it is from 60 to 75 per cent. During the afternoon there is usually a breeze from the San Francisco bay which lowers the temperature and increases the relative humidity. The differences in climatic con-

* Unpublished.

ditions between Mountain View and Delhi are sufficient to bring about marked differences in the fruit industry of the two sections.

The trees used in the experiment at Mountain View were mature Blenheim apricots (*Prunus armeniaca*), approximately twenty years old, and young French prunes (*Prunus domestica*) four years old. At Delhi, Muir peaches (*Prunus persica*) and French prunes were used during their fourth and fifth season in the orchard. At Davis, Muir peaches sixteen years old and French prunes of various ages were used.

Moisture Determinations of Tree Tissues

During a part of the investigation, extensive studies were made on the moisture content of various parts of the tree. Before starting the investigation of the moisture content of the various tissues of the tree, extensive trial determinations were made, using large numbers of samples to determine the degree of reliability of the results obtained when using the methods described below. The samples were taken at three-hour intervals beginning at 6 A.M. Leaves from current growth of the season (shoots) in the upper fully exposed portion of the tree were quickly stripped off, and placed in the tin cans fitted with tight covers. All the leaves on the terminal foot of growth, except the terminal four or five, were used, without stopping to make an accurate count of the number. As the shoots used for stripping were chosen for uniformity in size and length, the number and weight of leaves secured by this method were approximately the same for all samples. Next, the terminal six inches of growth was removed. Buds and remaining leaves were carefully removed. Then the bark was stripped from the xylem, wiped dry with a towel, and wood and bark were placed in separate weighing bottles. In the same manner samples were taken of the basal six inches of growth. Two shoots were used for each sample and the samples were taken in duplicate.

Samples of trunk bark and trunk wood, and of root bark and root wood were taken with a carpenter's brace and auger bit. For the bark a 1-inch bit was used and for the wood a ¾-inch bit. The wood was taken to a depth of one-half inch. Uniform depth of boring was secured by boring to a file mark on the spiral of the auger. The chips were allowed to fall to a cloth spread on the ground and were then picked up as quickly as possible and placed in weighing bottles. Root samples were taken in the same way, using the part of the tree about eight inches below the surface of the soil just above the point where the main roots started to leave the main cylinder of the tree. This point was chosen for root samples in order to secure bark of approximately uniform thickness. Duplicate samples were not used in the trunk and root determination in order to avoid permanently injuring the trees by boring a large number of holes comparatively close together. The trunk samples were taken in a spiral beginning at the lower branches and ending four to six inches above the surface of the ground. The first samples were taken from the northeast side of the tree. The next samples were taken from the east or southeast and so on. By moving the point from which samples were taken for successive samples in a clockwise direction all samples could be secured from exposed portions of the tree without interference from holes previously bored in the trunk or roots. All samples were dried in a ventilated oven for forty-eight hours at 95°–100°C. The percentage of moisture was calculated on the dry weight of the material.

Samples were taken from both irrigated and non-irrigated trees at Davis and at Delhi during August and September, 1925. Four sets of samples were taken at weekly intervals at each place, the first at Davis on August 6, the first at Delhi on September 11, 1925. Thus, eight different pairs of trees were studied during the season. The experiment was carried on during the latter part of the summer because of the desirability of having the soil moisture on the non-irrigated plots reduced to a minimum so as to afford a marked contrast to the trees in the irrigated plots. All trees had formed terminal buds when the samples were taken. The trees which were adequately supplied with water are hereinafter referred to as "trees in moist soil"; the others, as "trees in dry soil." The moist soil plots were not allowed to reach the wilting coefficient during the experiment. The dry soil plots were allowed to remain at or below the wilting coefficient during the experiment. At other times the treatment given to the dry soil plots was consistent with good orchard practice.

Experiments to Determine the Width of Stomatal Opening

Experiments to determine the behavior of stomata on fruit trees were carried on at Mountain View and at Delhi during the summer of 1924. The leaf samples were taken in the manner previously described. During the early part of the season, there was but little difference in the degree of opening between stomata on the trees in moist soil and those on the trees in dry soil. In many cases the curves showing the amount of opening on the two trees were nearly parallel throughout the day.

On June 3, 1924, stomata on an apricot tree which had been irrigated a few days before behaved in an almost identical manner as with that of the stomata on a similar tree which had not been irrigated. Investigation showed that the soil around the apricot tree which had not been irrigated still contained available moisture, and under the comparatively mild climatic conditions which existed on that day, the stomata were able to open as wide as those on the tree which had been watered. The same results were obtained with peaches at Delhi on June 18, 1924, when soil samples showed that both the irrigated and the non-irrigated trees were still supplied with available moisture.

Still further evidence of this behavior was observed with French prunes and Muir peaches under the hotter and drier climatic conditions at Davis on July 9, 1925. The soil in the irrigated plot upon being sampled was found to contain but a small amount of water more than the non-irrigated plot on the day when the stomata samples were taken. Both soils were above the hygroscopic coefficient. The curves for the stomata from the trees in moist soil and the trees in dry soil show approximately the same characteristics. The results are shown in figures 1 and 2 and the data are given in table 1.

Numerous other trials both at Mountain View and at Davis with prune, apricot, and peach trees gave practically the same results as those just described. There was little or no difference in the stomatal behavior between the trees in the moist soil plots and those in the dry soil plots as long as the moisture content of both plots was above the hygroscopic point. In other words, decisive differences in stomatal behavior between trees in moist soil and those in dry soil were not obtained until after the latter trees had used up the available moisture in the root zone.

As the season advanced, differences in percentage of soil moisture between the plots kept well supplied with water and those which were not irrigated during the period of the experiment increased. These differences were reflected in the widths of the stomatal openings on the leaves of the respective trees. When the soil moisture in the plots with dry soil reached the point where water was not easily available to the tree, the stomata failed to open as wide as those on trees well supplied with moisture. Furthermore, the stomata on the trees in the dry plots often began to close at an earlier hour.

TABLE 1.

BEHAVIOR OF STOMATA ON FRENCH PRUNE AND ON MUIR PEACH TREES AT DAVIS, CALIFORNIA. July 9, 1925.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns French prune				Size of stomata in microns Muir peach			
			Moist soil tree		Dry soil tree		Moist soil tree		Dry soil tree	
			Length	Width	Length	Width	Length	Width	Length	Width
5 a.m.	54	99	15.1	1.4	15.1	1.3	15.5	1.6	15.5	1.6
6 a.m.	57	98	15.5	1.7	15.5	1.6	15.9	1.9	15.5	2.5
7 a.m.	61	89	14.3	2.3	15.9	1.6	15.1	3.3	15.9	2.9
8 a.m.	67	80	15.9	2.7	15.9	2.6	16.8	3.8	16.6	3.8
9 a.m.	73	69	15.9	2.6	15.1	2.7	15.9	4.2	15.5	3.8
10 a.m.	82	52	15.1	2.9	15.1	2.5	16.4	4.1	14.7	3.0
11 a.m.	87	46	16.1	3.1	15.5	2.7	15.5	3.0	15.5	2.6
12 a.m.	88	45	15.1	3.2	15.1	3.2	15.5	2.4	15.9	3.1
1 p.m.	89	41	16.1	2.6	15.5	2.3	15.5	2.2	15.1	1.9
2 p.m.	92	37	16.4	2.5	15.1	2.3	16.4	2.3	15.4	1.8
3 p.m.	94	35	15.1	1.8	15.5	1.6	16.4	2.2	15.1	1.8
4 p.m.	94	35	15.1	1.3	15.1	1.5	16.4	1.8	15.1	1.8
5 p.m.	91	39	15.9	1.7	15.5	1.3	15.5	1.6	15.9	2.2
6 p.m.	83	49	15.5	1.0	15.9	.8	15.5	1.7	14.3	2.0
7 p.m.	73	63	15.5	1.0	15.9	1.0	15.9	1.4	15.5	1.8
8:30 p.m.	65	82	15.1	1.0	15.9	.8	15.9	1.3	14.3	1.1

NOTE:	Per cent
Percentage of moisture in soil around moist soil prune tree, 0–3 feet	—16.1
Percentage of moisture in soil around moist soil prune tree, 3–6 feet	—13.5
Percentage of moisture in soil around dry soil prune tree, 0–3 feet	—14.8
Percentage of moisture in soil around dry soil prune tree, 3–6 feet	—14.3
Percentage of moisture in soil around moist soil peach tree, 0–3 feet	—18.6
Percentage of moisture in soil around moist soil peach tree, 3–6 feet	—18.5
Percentage of moisture in soil around dry soil peach tree, 0–3 feet	—12.8
Percentage of moisture in soil around dry soil peach tree, 3–6 feet	—13.4
Calculated moisture equivalent, prune plot, 0–3 feet	—21.2
Calculated moisture equivalent, prune plot, 3–6 feet	—16.9
Calculated wilting coefficient, prune plot, 0–3 feet	—11.5
Calculated wilting coefficient, prune plot, 3–6 feet	— 9.2
Calculated hygroscopic coefficient, prune plot, 0–3 feet	— 7.8
Calculated hygroscopic coefficient, prune plot, 3–6 feet	— 6.3
Calculated moisture equivalent, peach plots, 0–3 feet	—18.6
Calculared moisture equivalent, peach plots, 3–6 feet	—16.4
Calculated wilting coefficient, peach plots, 0–3 feet	—10.1
Calculated wilting coefficient, peach plots, 3–6 feet	— 8.9
Calculated hygroscopic coefficient, peach plots, 0–3 feet	— 6.8
Calculated hygroscopic coefficient, peach plots, 3–6 feet	— 6.0

Results similar to those described in the preceding paragraph were obtained on many different dates during 1924, both at Delhi and at Mountain View. The curves given show the typical stomatal behavior for French prunes, August 5, 1924, at Mountain View (fig. 3); for Blenheim apricots, August 21, 1924, at Mountain View (fig. 4); and for Muir peaches October 1, 1924, at Delhi (fig. 5). A "high fog" at Mountain View on the morning of August 5 which persisted until about 9 A.M. may help to account for the fact that the stomata on the trees in the dry soil plots opened nearly as wide as those on the watered trees. However, as soon as the sun dispelled the fog, the relative humidity of the air was reduced, transpiration of the leaves probably increased, and the stomata began to close rapidly. The data for the stomatal measurements on French prunes at Mountain View, August 5, 1924, are given in table 2; for Blenheim apricots at

TABLE 2.
BEHAVIOR OF STOMATA ON FRENCH PRUNE TREES AT MOUNTAIN VIEW, CALIFORNIA. August 5, 1924.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns			
			Moist soil tree		Dry soil tree	
			Length	Width	Length	Width
6 a.m.	54	99	13.9	1.6	12.6	1.2
7 a.m.	54	99	15.1	1.5	13.0	1.4
8 a.m.	58	99	14.6	1.9	15.5	1.5
9 a.m.	61	91	15.9	2.2	....	....
10 a.m.	68	81	14.6	2.4	15.5	2.1
11 a.m.	70	77	14.6	1.9	14.6	2.4
12 a.m.	73	75	17.2	3.0	14.1	2.2
1 p.m.	73	73	15.9	2.1	....	....
2 p.m.	75	70	15.5	2.3	....	....
3 p.m.	73	72	16.4	2.2	12.6	1.0
4 p.m.	71	75	16.4	2.1	14.3	1.1
5 p.m.	69	75	15.5	1.6	13.4	0.7
6 p.m.	65	84	14.6	1.9	14.3	0.7
7 p.m.	61	91	15.1	2.6	15.4	0.5
8:30 p.m.	58	98	15.9	1.4	15.9	0.0

NOTE:	Per cent
Percentage of moisture in soil, moist soil tree, 0–3 feet	−19.2
Percentage of moisture in soil, moist soil tree, 3–6 feet	−14.1
Percentage of moisture in soil, dry soil tree, 0–3 feet	−10.1
Calculated moisture equivalent	−22.0
Calculated wilting coefficient	−11.9
Calculated hygroscopic coefficient	−8.05

Mountain View, August 21, 1924, in table 3; and for Muir peaches at Delhi in table 4.* Stomatal measurements from an irrigated French prune at Delhi on the same day are given for purposes of comparison with the stomatal measurements of the peach. The similarity of curves for the peach and the prune when both trees were amply supplied with water is typical of what was found throughout the season. Evidently there is no great difference in the behavior of stomata of these two species.

TABLE 3.

BEHAVIOR OF STOMATA ON BLENHEIM APRICOTS AT MOUNTAIN VIEW, CALIFORNIA. August 21, 1924.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns			
			Moist soil tree		Dry soil tree	
			Length	Width	Length	Width
9 a.m.	62	85	16.4	2.0	17.2	3.0
10 a.m.	65	82	18.1	2.8	17.0	3.0
11 a.m.	69	78	18.5	3.6	17.2	3.2
12 a.m.	70	77	17.3	3.6	17.6	2.5
1 p.m.	72	77	18.9	4.2	17.0	2.5
2 p.m.	71	78	19.7	4.4	17.0	2.3
3 p.m.	71	78	17.2	3.6	18.4	2.0
4 p.m.	70	81	17.2	2.5	18.5	1.9
5 p.m.	68	85	17.2	2.5	17.0	1.9
6 p.m.	64	92	17.6	2.9	18.1	2.0
7 p.m.	61	95	17.6	1.9	17.6	2.4
9 p.m.	57	99	18.4	1.2	18.1	1.6

NOTE:	Per cent
Percentage of moisture in soil, moist soil tree, 0–3 feet	–17.6
Percentage of moisture in soil, dry soil tree, 0–3 feet	–10.3
Calculated moisture equivalent	–22.0
Calculated wilting coefficient	–11.9
Calculated hygroscopic coefficient	–8.05

Twenty-four Hour Observations on Prune and Apricot Trees.—On July 22, 1924, stomata were measured on prune and apricot trees at Mountain View at hourly intervals throughout a twenty-four hour period beginning at 6 A.M. and ending at 5 A.M. the following morning. No extreme climatic conditions were encountered during the time the

* The second three feet of soil in the irrigated plot, because of the existence of a compacted layer about five feet beneath the surface, shows higher moisture equivalents and calculated wilting coefficients and hygroscopic points than the top three feet.

samples were being taken. The temperature ranged from a minimum of 55° F. at 6 A.M. to a maximum of 73° F. at 1 P.M. The relative humidity ranged from 98 per cent during the night down to 68 per cent at 1 P.M. In the morning a "high fog" persisted until about 10 A.M. This condition caused a comparatively wide degree of stomatal opening on the leaves of the trees in both plots. The stomata on the apricots in the moist soil plots reached a maximum width of 3.5 microns at 9 A.M. and the stomata on the trees in the dry soil plots

TABLE 4.

BEHAVIOR OF STOMATA ON MUIR PEACHES AND FRENCH PRUNES AT DELHI, CALIFORNIA. October 1, 1924.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns					
			Moist soil peach tree		Dry soil peach tree		Moist soil prune tree	
			Length	Width	Length	Width	Length	Width
7 a.m.	55	94	14.3	1.7	15.1	2.1	14.2	3.6
8 a.m.	65	91	15.1	2.5	15.3	2.1	13.0	3.8
9 a.m.	71	78	14.2	2.5	15.3	2.3	12.1	3.8
10 a.m.	74	70	14.2	3.6	15.1	1.9	15.1	4.2
11 a.m.	76	67	14.2	3.3	15.3	2.0	14.2	4.5
12 a.m.	79	60	14.3	3.4	16.1	1.9	14.2	4.2
1 p.m.	82	57	14.3	3.3	16.3	1.9	....	....
2 p.m.	82	55	15.9	2.9	16.3	1.7	15.5	3.2
3 p.m.	82	51	14.3	2.9	15.1	1.5	17.2	1.7
4 p.m.	84	45	15.5	2.3	15.4	1.5	15.5	2.2
5 p.m.	81	48	15.9	1.9	15.9	1.4	15.5	2.0
6 p.m.	75	56	16.4	1.6	14.7	1.2	15.1	1.8
7 p.m.	73	61	16.8	0.9	16.8	1.1	15.5	1.6

NOTE: Per cent

Percentage of soil moisture, moist soil tree, 0–3 feet — 6.9
Percentage of soil moisture, moist soil tree, 3–6 feet —12.9
Percentage of soil moisture, dry soil tree, 0–3 feet — 1.2
Percentage of soil moisture, dry soil tree, 3–6 feet — 2.0
Calculated moisture equivalent, moist soil tree, 0–3 feet — 6.9
Calculated moisture equivalent, moist soil tree, 3–6 feet —13.3
Calculated moisture equivalent, dry soil tree — 6.5
Calculated wilting coefficient, moist soil tree, 0–3 feet — 3.8
Calculated wilting coefficient, moist soil tree, 3–6 feet — 7.2
Calculated wilting coefficient, dry soil tree — 3.5
Calculated hygroscopic point, moist soil tree, 0–3 feet — 2.5
Calculated hygroscopic point, moist soil tree, 3–6 feet — 4.9
Calculated hygroscopic point, dry soil tree — 2.4

reached a maximum width of 3.2 microns at the same hour. Thereafter, throughout the day the stomata on the moist plot trees showed a markedly wider degree of opening than the trees in the dry soil plots. The greatest closure in both cases occurred at 11 P.M., after which hour the stomata on both trees began to open.

The stomata of the prune trees in the moist soil plots attained a maximum width of 3.2 microns at 10 A.M. and then slowly began to close. On the trees in the dry soil plot; the maximum opening which was not reached until 2 P.M., was only 2.2 microns. The greatest average closure of stomata on trees in both plots was reached at 9 P.M., after which the stomata began to open slowly as in the case of the apricot trees. With both the apricots and the prunes, there seemed to be a tendency for the stomata to open slightly at 5 P.M. or 6 P.M. before finally closing to the minimum a few hours later. The data were so similar to those of a second twenty-four hour period on September 11 that only the latter are given in this paper.

On September 11, 1924, the stomata on Blenheim apricot and French prune trees were again studied throughout a twenty-four hour period. The stomata of the trees in dry soil did not open so wide as those on the tree in moist soil and began to close earlier in the day. This difference, which was particularly marked in the case of the French prune, may have been due to the rather severe climatic conditions which prevailed. A maximum temperature of 91° F. was reached at 1 P.M., while the relative humidity was 21 per cent at the same hour. The stomata showed the greatest closure between 8 P.M. and 10 P.M. Although there was bright moonlight until 4:30 A.M., this condition did not seem to have any effect on the opening of the stomata, which opened in much the same way as on July 22. The results are shown graphically on figures 6 and 7. The data for all four trees are given in table 5.

Behavior of Stomata on Different Parts of the Tree.—An experiment was carried out on September 15, 1925, at Davis to determine whether any difference existed in the behavior of stomata on different parts of the trees on moist soil and on dry soil. Five-year-old Robe de Sergeant prunes (*Prunus domestica*) which had made an average new growth of four feet were used. Samples were taken from the terminal leaf, from the tenth leaf below the terminal, from the twentieth leaf below the terminal, and from leaves produced on fruit-spurs low down on the main branches of the tree. The results are shown graphically in figure 8. The stomata from the tree in dry soil did not show much variation in their behavior. They all opened to approx-

TABLE 5.

BEHAVIOR OF STOMATA ON BLENHEIM APRICOT AND FRENCH PRUNE TREES AT MOUNTAIN VIEW, CALIFORNIA. September 11, 1924.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns							
			Moist soil apricot tree		Dry soil apricot tree		Moist soil prune tree		Dry soil prune tree	
			Length	Width	Length	Width	Length	Width	Length	Width
6 a.m.	46	100	13.9	3.0	14.3	2.4	14.3	1.6	13.9	0.7
7 a.m.	47	94	16.8	3.2	15.9	2.2	15.5	1.5	13.9	1.1
8 a.m.	62	77	16.4	3.5	16.4	2.7	15.1	2.1	15.5	1.5
9 a.m.	72	63	17.2	3.8	16.8	3.1	15.5	2.5	16.4	1.7
10 a.m.	81	47	15.1	3.9	19.0	3.6	15.1	4.3	15.1	1.7
11 a.m.	87	34	15.9	4.0	17.2	3.0	15.5	4.4	14.6	1.3
12 a.m.	93	22	15.5	3.9	16.4	3.4	13.9	3.8	14.6	1.1
1 p.m.	95	21	16.8	3.4	14.6	2.9	16.4	2.6	13.9	0.8
2 p.m.	94	21	16.4	2.8	16.4	2.9	13.9	3.0	13.9	1.0
3 p.m.	93	21	17.6	2.5	19.0	2.5	15.1	2.6	13.9	1.5
4 p.m.	91	28	15.5	2.7	16.4	2.2	14.3	2.0	15.1	1.6
5 p.m.	89	27	15 1	2.8	16.8	2.0	14.3	2.1	14.6	1.0
6 p.m.	74	75	18.5	2.4	15.5	1.9	15.5	1.8	13.0	1.3
7 p.m.	69	84	18.1	1.8	15.9	2.0	15.1	1.7	14.6	1.0
8 p.m.	65	85	18.1	2.6	17.2	2.2	14.3	1.6	14.6	0.2
9 p.m.	61	89	16.8	0.5	16.8	1.6	15.5	0.7	16.4	0.2
10 p.m.	58	92	15.9	0.7	16.4	1.0	15.5	0.9	14.6	0.4
11 p.m.	56	92	16.4	1.0	15.5	1.7	14.3	1.0	15.1	0.4
12 p.m.	54	92	16.4	1.4	16.4	1.8	15.5	0.6	....	....
1 a.m.	51	94	18.5	2.1	18.5	2.2	15.1	1.4	15.5	0.4
2 a.m.	50	95	16.8	2.1	16.8	2.3	15.5	1.5	14.6	0.7
3 a.m.	50	95	18.1	2.5	16.4	2.1	14.6	1.3	14.6	0.8
4 a.m.	48	96	17.6	2.3	15.5	2.1	15.1	1.5	15.1	0.6
5 a.m.	49	99	16.8	2.5	16.1	2.1	14.6	1.7	15.5	0.6

NOTE:	Per cent
Percentage of moisture in soil, moist soil apricot tree, 0–3 feet	−15.0
Percentage of moisture in soil, dry soil apricot tree, 0–3 feet	− 9.9
Percentage of moisture in soil, moist soil prune tree, 0–3 feet	−14.9
Percentage of moisture in soil, moist soil prune tree, 3–6 feet	−10.5
Percentage of moisture in soil, dry soil prune tree, 0–3 feet	− 9.9
Calculated moisture equivalent	−22.0
Calculated wilting coefficient	−11.9
Calculated hygroscopic coefficient	−8.05

imately the same width (about 1 micron). The leaves from the branch on the tree in moist soil showed marked differences in amount of stomatal opening. The first and tenth leaves showed a stomatal opening of slightly more than 2 microns before they started to close. The stomata on the twentieth leaf opened to 3 microns and those on the spur leaf to 3.8 microns, before closing.

It is interesting to note how closely these results agree with those obtained by the author[9] in 1920, which showed that the terminal leaves on current season's shoots transpired less rapidly than the spur leaves further down on the main branches of the tree. The data are given in table 6.

Effect of Shade on Stomatal Behavior.—The effect of continuous shade on stomata was shown by an experiment carried on at Davis, July 28, 1925. Three Elberta peach trees were used. One tree in moist soil and one tree in dry soil under open orchard conditions, and in addition one tree growing in well moistened soil under the shade of a muslin tent, which was erected soon after growth started in the spring, were used. The shaded tree was covered with a tent stretched on a framework of sufficient size to allow normal growth of the tree. The cloth extended down on the sides of the tent to within three feet of the ground leaving an open space on all sides, which allowed free circulation of air. Before being enclosed in the tent, the shaded tree had been given the usual orchard treatment. The air temperature in the tent and in the shade of the tree in the open were practically the same throughout the day. The evaporation rate, which was determined with porous cup atmometers, within the tent was approximately two-thirds of that in the direct sunlight during the period from 8 A.M. July 28 to 8 A.M. July 29.

Leaves on the shaded tree were much larger but thinner than leaves on the trees growing in the open. The stomata of the leaves on the shaded tree as shown in figure 9 opened much later than did those on the trees outside of the tent. They opened wider than the stomata on the tree in dry soil outside of the tent, but not so wide as those on the unshaded tree in moist soil. After 1 P.M. the width of the stomatal opening on the leaves of the shaded tree and of the irrigated tree remained about the same. The stomata on the dry tree began to close earlier than either the irrigated or the shaded tree. Essentially similar results were obtained a week earlier when the percentage of soil moisture around both the irrigated and the shaded tree was much lower than in the case for which the curves are given (fig. 9). The data are given in table 7.

TABLE 6.

BEHAVIOR OF STOMATA ON ROBE DE SERGEANT PRUNE TREES AT DAVIS, CALIFORNIA.
September 15, 1925.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns							
			Terminal leaf				Tenth leaf			
			Moist soil tree		Dry soil tree		Moist soil tree		Dry soil tree	
			Length	Width	Length	Width	Length	Width	Length	Width
6 a.m.......	52	97	15.5	0.4	15.5	0.6	15.9	0.8	15.5	0.5
8 a.m.......	64	91	15.1	2.4	15.5	1.3	15.5	1.5	15.9	0.8
10 a.m.....	74	65	15.1	2.1	15.9	0.8	15.9	2.1	16.4	1.1
12 a.m.....	81	52	15.1	1.6	15.5	0.9	15.5	1.9	15.9	1.1
2 p.m.......	84	46	15.5	1.4	15.5	1.0	15.9	1.5	15.9	0.8
4 p.m.......	82	47	15.9	1.0	15.9	0.8	15.9	1.3	15.9	1.0
6 p.m.......	78	55	15.5	0.5	15.9	0.4	15.5	0.4	16.4	0.9
			Twentieth leaf				Spur leaf			
6 a.m.......	52	97	15.5	1.3	15.9	0.8	15.5	0.7	15.5	0.4
8 a.m.......	64	91	15.9	3.0	15.5	1.1	16.8	3.2	15.9	0.5
10 a.m.....	74	65	15.5	2.2	15.5	1.0	15.9	3.8	15.9	0.8
12 a.m....	81	52	15.9	1.4	15.9	0.7	15.1	3.4	15.9	1.0
2 p.m.......	84	46	15.5	1.5	15.9	0.8	15.5	1.9	15.9	0.6
4 p.m.......	82	47	15.5	2.1	15.5	0.6	15.5	2.3	15.5	0.4
6 p.m.......	78	55	15.1	1.4	15.9	0.8	15.1	1.6	16.4	0.5

NOTE:	Per cent
Percentage of soil moisture, moist soil tree, 0–3 feet..	–15.5
Percentage of soil moisture, moist soil tree, 3–6 feet..	–17.6
Percentage of soil moisture, dry soil tree, 0–3 feet..	– 8.1
Percentage of soil moisture, dry soil tree, 3–6 feet..	– 8.9
Calculated moisture equivalent, 0–3 feet..	–20.0
Calculated moisture equivalent, 3–6 feet..	–25.2
Calculated wilting coefficient, 0–3 feet..	–10.8
Calculated wilting coefficient, 3–6 feet..	–13.7
Calculated hygroscopic coefficient, 0–3 feet..	– 7.3
Calculated hygroscopic coefficient, 3–6 feet..	– 9.3

TABLE 7.

BEHAVIOR OF STOMATA ON ELBERTA PEACH TREES AT DAVIS, CALIFORNIA.
July 28, 1925.

Time	Temperature °F.	Relative humidity per cent	Size of stomata in microns					
			Moist soil tree		Dry soil tree		Shaded tree	
			Length	Width	Length	Width	Length	Width
5 a.m.	51	99	15.5	1.8	15.5	1.7	15.9	0.9
6 a.m.	52	99	16.9	1.9	15.9	1.8	15.5	1.0
7 a.m.	58	99	15.9	2.0	14.6	2.0	14.6	1.2
8 a.m.	63	92	15.9	2.0	15.5	1.9	15.1	1.6
9 a.m.	67	85	15.1	1.8	15.5	1.6	15.9	1.5
10 a.m.	76	69	15.5	2.2	15.5	1.6	15.5	1.8
11 a.m.	83	58	16.4	2.5	15.9	1.6	14.6	2.1
12 a.m.	87	46	15.9	2.0	16.1	1.3	15.5	1.9
1 p.m.	90	40	15.5	1.9	15.1	1.1	15.1	2.0
2 p.m.	94	36	15.5	1.7	15.1	1.0	15.9	1.7
3 p.m.	95	34	15.5	1.4	15.5	0.8	15.9	1.5
4 p.m.	96	35	15.9	1.3	15.5	0.8	15.9	1.4
5 p.m.	94	36	16.1	1.3	15.9	0.9	15.1	1.2
6 p.m.	93	40	15.1	1.1	16.4	0.7	14.6	0.9
7 p.m.	85	44	15.5	1.0	15.5	0.7	15.5	0.7
8 p.m.	75	52	15.5	0.9	....	....	16.1	0.4

NOTE:	Per cent
Percentage of soil moisture, moist soil tree, 0–3 feet	25.6
Percentage of soil moisture, moist soil tree, 3–6 feet	27.4
Percentage of soil moisture, dry soil tree, 0–3 feet	9.7
Percentage of soil moisture, dry soil tree, 3–6 feet	15.7
Percentage of soil moisture, shaded tree, 0–3 feet	24.5
Percentage of soil moisture, shaded tree, 3–6 feet	31.0
Calculated moisture equivalent, moist soil and shaded tree, 0–3 feet	22.4
Calculated moisture equivalent, moist soil and shaded tree, 3–6 feet	29.4
Calculated moisture equivalent, dry soil tree, 0–3 feet	29.5
Calculated moisture equivalent, dry soil tree, 3–6 feet	25.2
Calculated wilting coefficient, moist and shaded tree, 0–3 feet	12.2
Calculated wilting coefficient, moist and shaded tree, 3–6 feet	15.9
Calculated wilting coefficient, dry soil tree, 0–3 feet	16.0
Calculated wilting coefficient, dry soil tree, 3–6 feet	13.7
Calculated hygroscopic coefficient, moist and shaded tree, 0–3 feet	8.3
Calculated hygroscopic coefficient, moist and shaded tree, 3–6 feet	10.8
Calculated hygroscopic coefficient, dry soil tree, 0–3 feet	10.6
Calculated hygroscopic coefficient, dry soil tree, 3–6 feet	9.3

Experiments on the Determination of Moisture Content of Various Parts of the Tree in Relation to Stomatal Movement

The data showing the moisture content of the leaves, twigs, trunk, and roots of the trees studied are shown in figures 10 to 18. Because of the difficulties of showing the data concerning the stomatal movement, temperature, and relative humidity on the same charts with the

TABLE 8.

Moisture Content in Percentage of Dry Weight of Leaves, Twigs, Trunk, and Roots of Trees in Moist and in Dry Soil at Davis.
September 4, 1925.

Time	Leaves		Terminal twig bark		Terminal twig wood		Basal twig bark	
	Moist soil	Dry soil	Moist soil	Dry soil	Moist soil	Dry soil	Moist soil	Dry soil
6 a.m.	164.8	151.3	162.8	147.8	118.9	103.4	142.0	129.3
9 a.m.	149.5	141.5	153.3	125.3	107.6	80.9	138.5	116.1
12 m.	146.1	132.6	146.4	123.0	107.3	84.5	129.4	110.9
3 p.m.	142.4	135.3	139.4	121.1	90.6	85.5	135.3	105.8
6 p.m.	143.0	133.9	149.0	131.3	101.2	92.7	135.7	110.0

Time	Basal twig wood		Trunk bark		Trunk wood		Root bark		Root wood	
	Moist soil	Dry soil	Moist soil	Dry soil	Moist soil	Dry soil	Moist soil	Dry soil	Moist soil	Dry soil
6 a.m.	72.0	63.2	85.2	67.4	65.3	54.0	126.9	100.0	74.1	63.1
9 a.m.	61.2	58.3	69.9	68.0	52.2	49.2	116.2	84.1	63.7	53.4
12 m.	56.7	57.6	72.7	64.5	53.8	48.1	111.5	90.3	71.7	54.1
3 p.m.	57.0	56.4	69.4	65.5	50.9	48.7	106.0	86.9	62.6	58.7
6 p.m.	65.9	60.3	86.1	66.9	56.2	50.2	113.8	96.5	65.1	55.5

percentage of moisture in the various tissues, these data are shown in figure 19. Data for the determination made on September 4, 1925, at Davis, which are typical of all the results obtained, are given in table 8. The data for the other seven weeks of the experiment are on file in the office of the Pomology Division of the University of California. A summary of the soil moisture conditions at Davis and at Delhi is given in table 9.

Percentages of moisture calculated on the dry weight of the material are plotted against time. The curves in the upper part of

TABLE 9—SUMMARY OF SOIL MOISTURE CONDITIONS EXPRESSED AS PERCENTAGE OF DRY WEIGHT OF TREES AT DAVIS AND DELHI FROM WHICH WATER DEFICIT DATA WERE OBTAINED.

Date	Location	Tree in moist soil								Tree in dry soil							
		First three feet				Second three feet				First three feet				Second three feet			
		Per cent moisture	Moisture equivalent	Wilting coefficient	Hygroscopic coefficient	Per cent moisture	Moisture equivalent	Wilting coefficient	Hygroscopic coefficient	Per cent moisture	Moisture equivalent	Wilting coefficient	Hygroscopic coefficient	Per cent moisture	Moisture equivalent	Wilting coefficient	Hygroscopic coefficient
8-6-25	Davis	14.5	16.7	9.1	6.2	11.8	14.5	7.8	5.3	9.7	18.6	10.1	6.8	9.5	16.4	8.9	6.0
8-13-25	Davis	13.7	15.2	8.3	5.6	10.5	12.6	6.8	4.6	9.8	18.6	10.1	6.8	10.4	16.4	8.9	6.0
8-25-25	Davis	14.8	18.8	10.2	6.9	8.5	16.2	8.8	5.9	9.3	18.6	10.1	6.8	10.1	16.4	8.9	6.0
9-4-25	Davis	17.9	18.8	10.2	6.9	15.1	16.2	8.8	5.9	8.6	18.6	10.1	6.8	7.1	16.4	8.9	6.0
9-11-25	Delhi*	13.6	5.8	3.2	2.1	21.5	13.8	7.5	5.0	1.7	6.5	3.5	2.4	2.6	6.5	3.5	2.4
9-18-25	Delhi*	6.5	5.8	3.2	2.1	15.2	13.8	7.5	5.0	1.3	6.5	3.5	2.4	1.7	6.5	3.5	2.4
9-25-25	Delhi*	9.4	5.8	3.2	2.1	17.4	13.8	7.5	5.0	1.5	6.5	3.5	2.4	2.5	6.5	3.5	2.4
10-2-25	Delhi*	3.0	5.8	3.2	2.1	14.0	13.8	7.5	5.0	1.5	6.5	3.5	2.4	2.9	6.5	3.5	2.4

* Abnormally high moisture content of soil at Delhi was due to a break in irrigating pipe line and impervious layer of soil which did not permit water to drain away to lower levels.

the chart are for the results obtained at Davis; in the lower, at Delhi. In each case the results from the tree on moist soil are shown on the left and the tree in dry soil on the right. The dates show the time of taking the samples.

Various irregularities in the curves occurred. Some of these were due to errors of sampling, inevitable with the type of material used. A few of the irregularities were due to other causes. Thus, some samples of leaves late in the season showed an abnormally high percentage of moisture at 6 A.M. This particular fact can undoubtedly be attributed to the dew which could not be removed from the leaves satisfactorily. On September 11 at Delhi, cloudy weather persisted until about 8:30 A.M. As a result, the leaves and terminal twigs of both trees in moist soil and trees in dry soil did not show a decrease in moisture content until after 9 A.M. On August 25 at Davis it was necessary to use some rather small roots for the determination of moisture in the root bark. As a consequence the curve for the root bark of the tree in moist soil rose until 12 o'clock instead of falling as was usually the case.

The similarity of the curves, particularly for the leaves and twigs, was apparent. There was a decrease in moisture content for the various tissues from 6 A.M. to 9 A.M. or from 6 A.M. to 12 noon, and there was an increase in moisture content from 3 P.M. to 6 P.M. The significance of these differences was tested by Student's Method[19] and, if it is assumed that this method is applicable to this case, the differences are significant. In a few cases where the significance of the differences between 6 A.M. and 9 A.M. was indicated by rather short odds, when the differences for the same tissues were calculated from 6 A.M. to 12 noon much greater odds were obtained.

Discussion of Results Obtained in the Determination of Moisture Content of Various Tree Tissues

The curves showing the behavior of the stomata on the trees in moist soil and in dry soil during the season of 1925, as shown in figure 19, are essentially similar to, and show the same characteristics which were shown in, the detailed studies on stomatal movement in 1924. Generally speaking, the stomata showed a rather uniform behavior. They began to close as a rule between 9 A.M. and 12 noon. The stomata on the trees in dry soil consistently showed less opening than did those on the trees in moist soil. These curves are given in a separate figure because they could not be satisfactorily grouped on the charts showing the moisture content of the various tree tissues studied.

A complete summary of the soil moisture conditions for the top three feet and the second three feet of soil are given in table 9. The moisture equivalents, wilting coefficients, and hygroscopic coefficients expressed as percentage on a dry weight basis are given for purposes of comparison. The trees used in the experiment were growing in similar types of soil, but were handled in such a way as to give extreme conditions of soil moisture.

As may be seen from the table, the trees in moist soil were abundantly supplied with moisture, while those in dry soil usually had little or no available moisture to draw upon. The decisive results obtained may have been due to the fact that there was such a marked difference in soil moisture content between the plots in the experiment.

One of the most striking features of the moisture curves, as shown in the accompanying figures, was their similarity. In general, there was a decrease in moisture content of all parts studied between 6 A.M. and 9 A.M., and an increase in moisture content between 3 P.M. and 6 P.M. These results were similar to those obtained by Livingston and Brown,[13] who found that the minimum water content of certain desert plants occurred between 1 P.M. and 5 P.M. and then rose to a maximum at 7 P.M. One exception to this rule occurred on September 11 at Delhi, when the leaves, bark, and wood of the terminal ends of twigs failed to show a decrease until after 9 o'clock. This exception can probably be explained by the fact that the weather remained cloudy until after 8:30 A.M. The fall and rise of the water content of all the measured portions seemed to be associated with, or at least occurred at practically the same time as the opening and closing of the stomata.

The succulent portions of the tree, i.e., the leaves, and the terminal and basal portions of the twigs, showed a marked progressive decrease in water content during the early part of the season, which meant that these portions were increasing in dry matter. This decrease in water content of the leaves and twigs was slight after the middle of September. Trees in moist soil both at Davis and at Delhi showed a relatively greater decrease in water content from week to week than did the trees in dry soil. The trunks and roots did not show such a marked decrease in water content from week to week as the season advanced, although the decrease was fairly noticeable during the first few weeks of the experiment.

The leaves and terminal twigs of the trees in moist soil showed a consistently higher water content than these parts from the trees in dry soil. The same condition seemed to hold true for certain series of samples from the older tissues of the trees. At Delhi the wood and bark of trunks and root of trees growing in moist soil contained more water than the wood and bark of trees growing in dry soil. This difference seemed remarkable when the method of sampling was considered. With the older portions of the tree, a considerable part of each sample consisted of old and probably inactive tissue. This old tissue increased the relative amount of dry matter and may have tended to mask the results. It is also interesting to note that with the wood of the basal part of the twig, there was no great difference between the trees grown in moist soil and those grown in dry soil.

The comparatively high moisture content of the root bark on the trees in moist soil can probably be accounted for by the fact that these trees were irrigated two or three days before the sample was taken. The outer layers of bark may have absorbed and held sufficient water to account for this difference. Also, there was practically no loss by evaporation from the surface of the bark. The difference in water content between the trunk bark and the root bark may also be explained in the same way.

In general, the trunk and root samples, particularly in the case of the bark, showed greater irregularity than did the samples of leaves and twigs. This irregularity may have been due to the fact that old outer bark does not slough off evenly. There was no satisfactory method of judging the thickness of bark at the point chosen for taking samples. Furthermore, the wood samples sometimes showed evidence of brown tissue, the presence of which could not be foretold before making the boring. These factors which could not be guarded against probably contributed to the irregularity in the results obtained.

The bark of the terminal and basal portions of the twigs contained a larger percentage of moisture than the wood of these parts, except for the succulent terminals early in the season. This fact might suggest the relatively more rapid increase of dry matter in the xylem than in the phloem. Essentially the same condition was observed in the bark and wood of the older portions of the tree, but the lower moisture content of the wood in this case may have been due to depth of boring, as mentioned in a preceding paragraph.

Succulent portions of the trees during the latter part of the season seemed to resist loss of water beyond a certain point. Thus, the leaves on the trees in moist soil at Delhi, during the last three weeks of the experiment reached approximately a common minimum during the middle of the day. The same thing occurred in the case of the terminal twig portions of the trees at Delhi in both the moist and the dry soils.

It was evident that more water could not have been removed from these tissues under the given climatic and soil moisture conditions. In other words, the twigs had reached a certain stage of maturity where they resisted loss of moisture below a certain point. Inasmuch as this stage of maturity was reached at approximately the same time for the trees both in the well irrigated soil and in the dry soil, it seems evident that the data presented in this paper have an important bearing on a number of questions regarding the relation between irrigation and the hardening or maturing of the wood and buds of peach trees. It also seems evident from these results that the single factor of high soil-moisture content is insufficient to account for various types of so-called "winter injury," where these troubles occur, particularly if the injury seems to be influenced by the immaturity of the new growth of the tree.

The results presented in this paper indicate a relationship between stomatal movement and water content of various tissues of peach trees in California, and further, show that this relationship is markedly influenced by whether moisture is available in the soil or not. The general opening of stomata during the early morning hours is rapidly followed by a decrease in the water content of the bark and wood of the tree. The leaves and succulent twigs show a relatively great loss early in the day, and this fluctuation is rapidly propagated back to the roots. It may be detected in the root tissues as early as 9 A.M. Later in the day when the stomata begin to close, there is an increase in moisture content in all parts of the trees. The loss which takes place during the morning and early afternoon is rapidly replenished between 3 P.M. and 6 P.M.

While no data were secured during the progress of this particular experiment upon the actual measuring of transpiration, some were obtained on this phase of the question in 1920 while using many of the same trees included in the 1924 and 1925 experiments. A study of the original notes obtained in 1920 indicates that under similar conditions of climate and soil moisture, the curves for stomatal opening and for transpiration are parallel. Edith Shreve[18] has shown that a similar relation holds for leaves of *Parkinsonia microphylla*. Transpiration, however, in practically every case began to decrease somewhat before the average time for the beginning of stomatal closure. Thus, the present data in connection with those published in 1920 indicate a relationship between stomatal movement, transpiration and moisture content of the various tissues of peach trees.

The rapid loss of moisture which accompanies stomatal opening may help to explain why stomata, in many cases, begin to close before the light has reached its greatest intensity. Under conditions favorable for maintaining turgidity such as occur during the night, the stomata are sensitive to the action of light and probably are controlled chiefly by it. Thus, with the coming of daylight, the stomata open rapidly. Next, water loss occurs until such time as the guard cells or surrounding epidermal cells begin to lose their turgidity. When the cells adjacent to the stomata or the guard cells, themselves, are no longer turgid, closure of the stomata begins even if light conditions are favorable for them to remain open. Thus it seems that light is important in bringing about the opening of stomata when the leaves are turgid, but when the cells around the stomata have lost sufficient water to cause them to lose their turgidity and the guard cells themselves have lost a small amount of moisture, a factor opposing the influence of light is introduced which is sufficient to cause the stomata to begin to close.

The sensitive response to changes in stomatal opening or closing as shown by corresponding fluctuation in the water content of the tree tissues seems to furnish additional evidence in support of the cohesion theory[5] of the rise of water in trees. If the water in the conducting tissues of the plant is continuous, as claimed by the supporters of this theory, the effects of any water loss from the cells surrounding the stomatal cavity should be quickly noticeable in the adjoining cells and, furthermore, should be rapidly propagated down to the roots. Data from well watered trees and from trees in dry soil secured for eight successive weeks during the summer of 1925 show that diurnal fluctuations in water content of the leaves of peach trees are propagated down to the roots with remarkable speed.

Summary

1. The stomata of peach, prune, and apricot trees reached their maximum degree of opening between 9 A.M. and 12 o'clock noon, after which they began to close. The greatest closure of stomata in prune and apricot trees was observed between 8 P.M. and 11 P.M.

2. Peach, prune, and apricot trees growing under conditions of little or no available soil moisture showed a smaller maximum stomatal opening than trees growing in soil containing a supply of available moisture.

3. Leaves at the apex of vigorous current season's shoots of prune trees growing in moist soil, showed less stomatal opening than older leaves farther back on the branch. On the prune trees which were suffering for water, all leaves on various parts of the tree showed approximately the same small degree of opening.

4. Stomata on shaded peach trees in moist soil did not reach the maximum degree of opening until several hours after those of trees in moist soil under open orchard conditions.

5. The decrease in moisture content which occurs in the leaves of peach trees, under California conditions, shortly after 6 A.M. is propagated backward rapidly and may be detected in all parts of the tree as early as 9 A.M. This loss of moisture is partly replenished between 3 P.M. and 6 P.M.

6. Decrease in moisture content of various tissues of peach trees was observed in many cases before the stomata had reached their maximum opening. Replacement of this loss began in the afternoon while the stomata were still open and while climatic conditions were still favorable for transpiration.

ACKNOWLEDGMENTS

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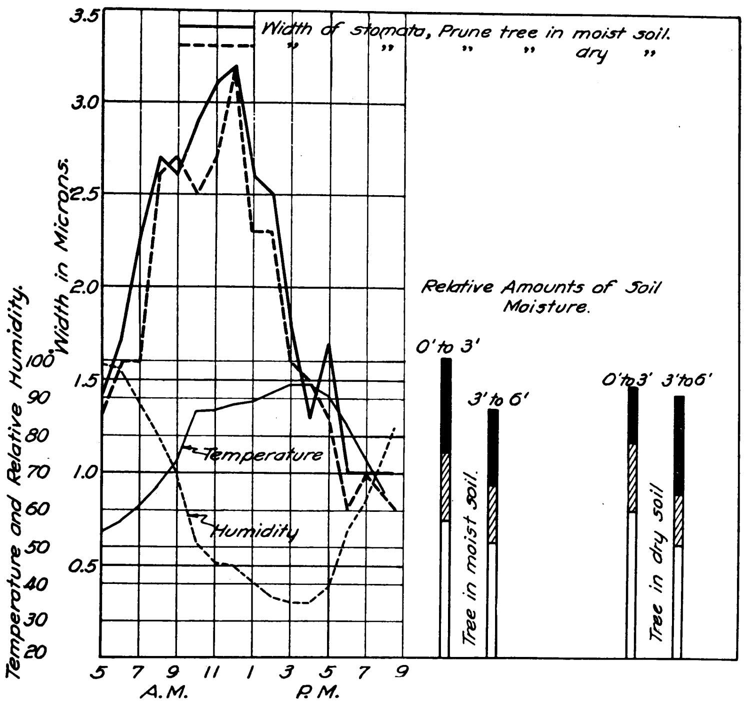

Fig. 1. Width of stomatal opening on prune trees in moist soil and in dry soil at Davis, California, July 9, 1925. Temperature and relative humidity are shown by light lines in lower left-hand corner. Relative amount of soil moisture above the wilting coefficient is shown by solid black column; relative amount of soil moisture below hygroscopic coefficient is shown by the unshaded portion.

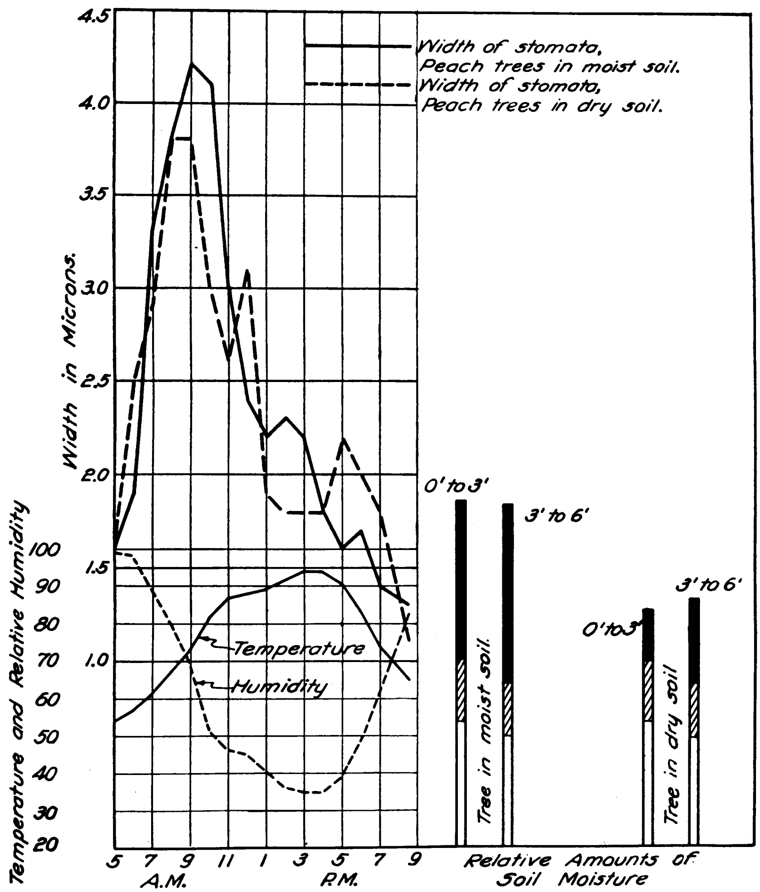

Fig. 2. Width of stomatal opening on peach trees in moist soil and in dry soil at Davis, California, July 9, 1925. Temperature and relative humidity are shown by light lines in lower left-hand corner. Relative amount of soil moisture above the wilting coefficient is shown by solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

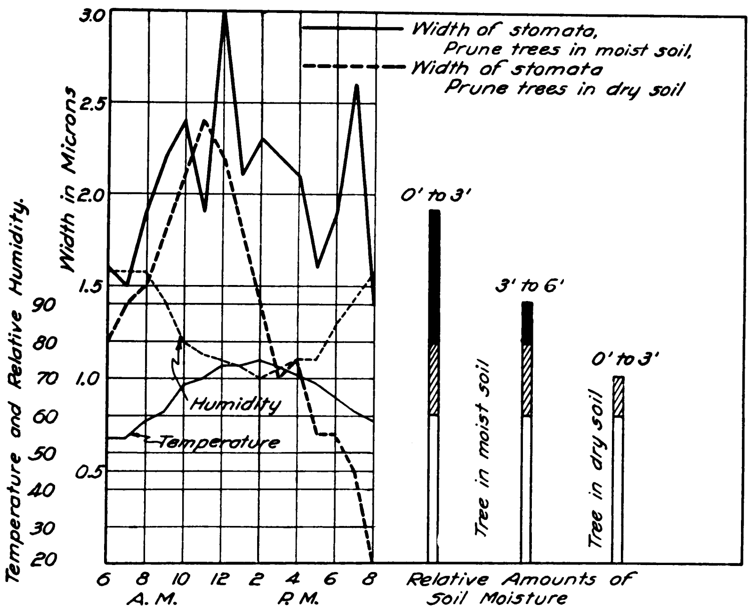

Fig. 3. Width of stomatal opening on prune trees in moist soil and in dry soil at Mountain View, California, August 5, 1924. Temperature and relative humidity are shown by light lines in the lower left-hand corner. Relative amount of soil moisture above wilting coefficient is shown by solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

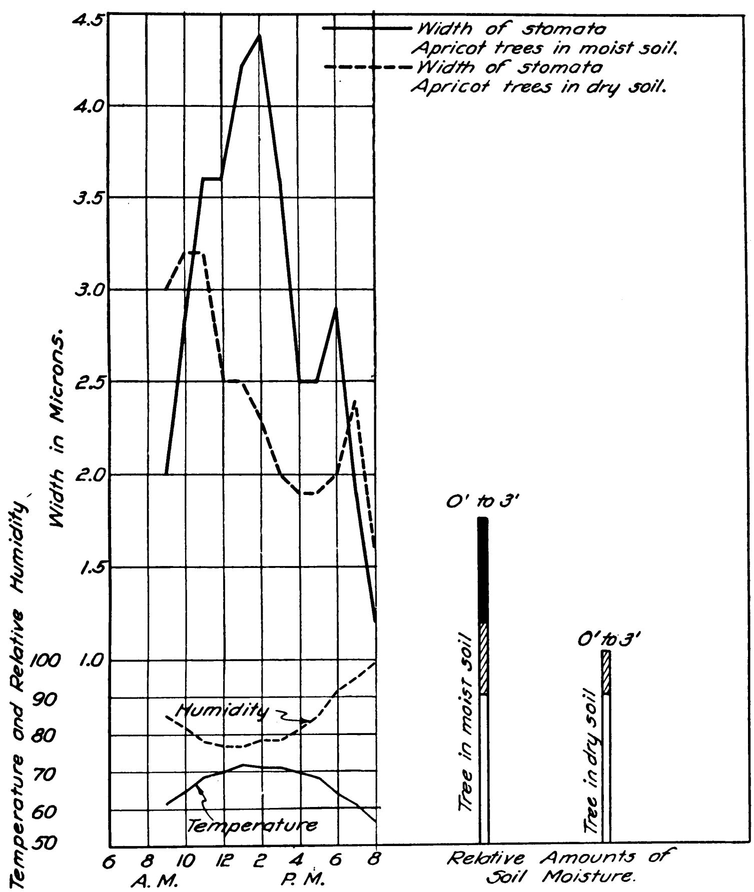

Fig. 4. Witdh of stomatal opening on apricot trees in moist soil and in dry soil at Mountain View, California, August 21, 1924. Temperature and relative humidity are shown in lower left corner. Relative amount of soil moisture above the wilting coefficient is shown by solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

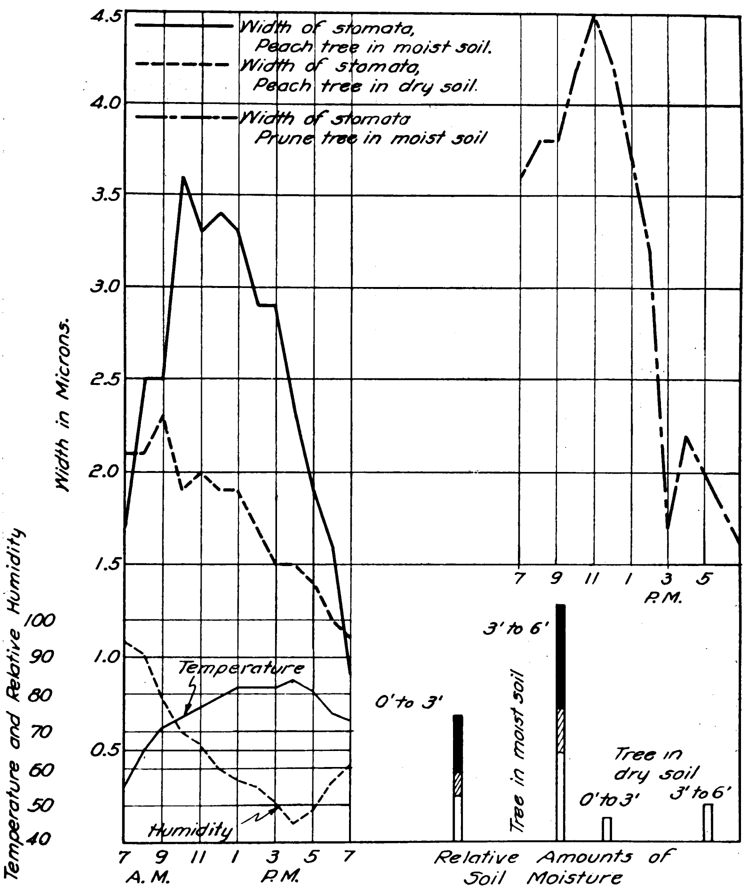

Fig. 5. Width of stomatal opening on peach and prune trees in moist soil and peach tree in dry soil at Delhi, October 1, 1924. Temperature and relative humidity are shown in lower left corner. Relative amount of soil moisture above wilting coefficient is shown by solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

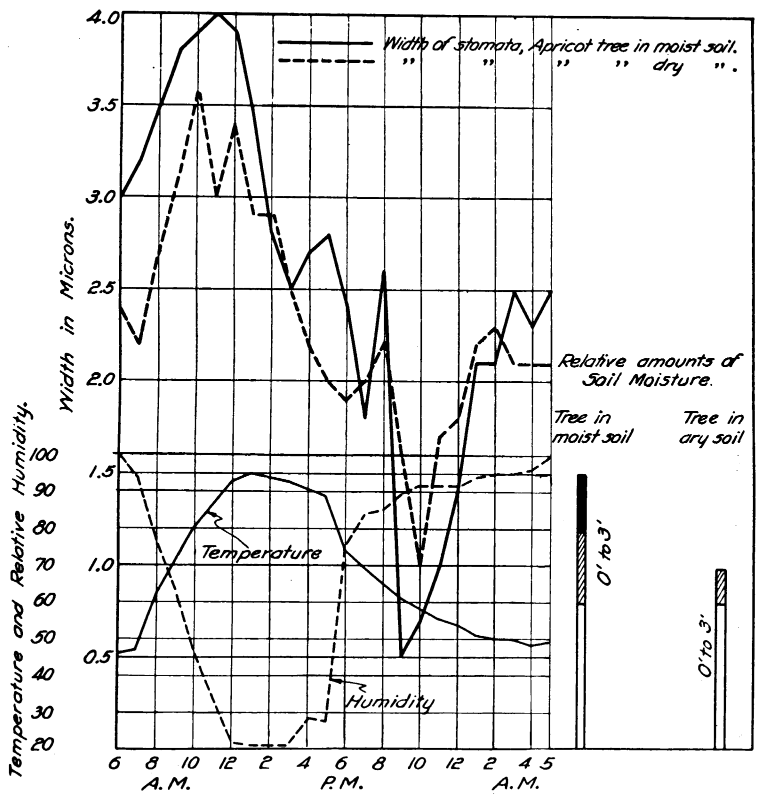

Fig. 6. Width of stomatal opening on apricot trees in moist soil and in dry soil at Mountain View, September 11, 1924. Temperature and relative humidity are shown in lower left corner. Relative amount of soil moisture above the wilting coefficient is shown by the solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

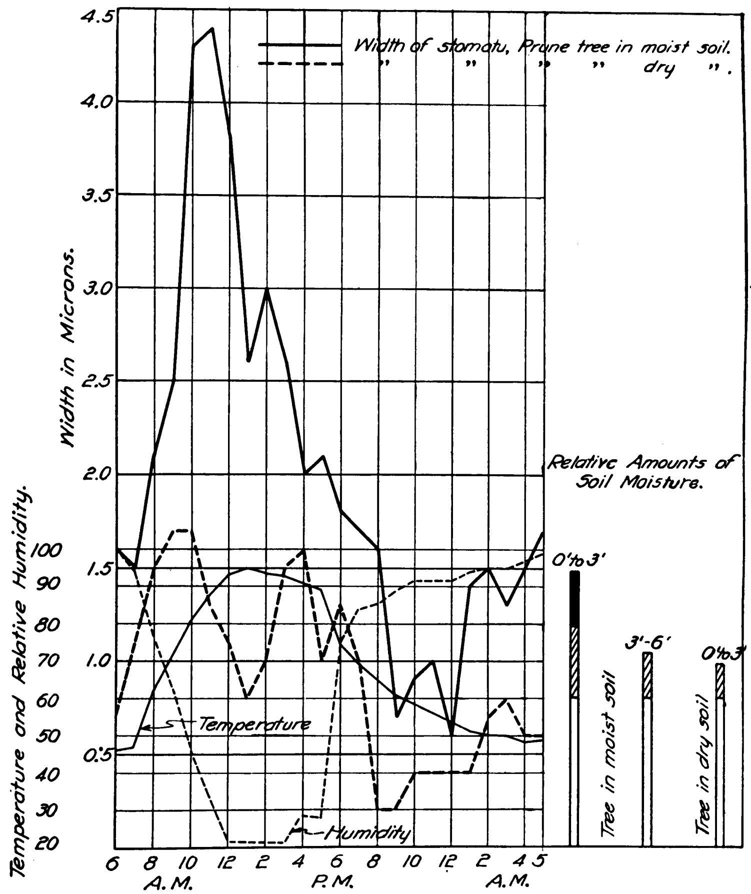

Fig. 7. Width of stomatal opening on prune trees in moist soil and in dry soil at Mountain View, California, September 11, 1924. Temperature and relative humidity are shown by the light lines in the lower left corner. Relative amount of soil moisture above the wilting coefficient is shown by the solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

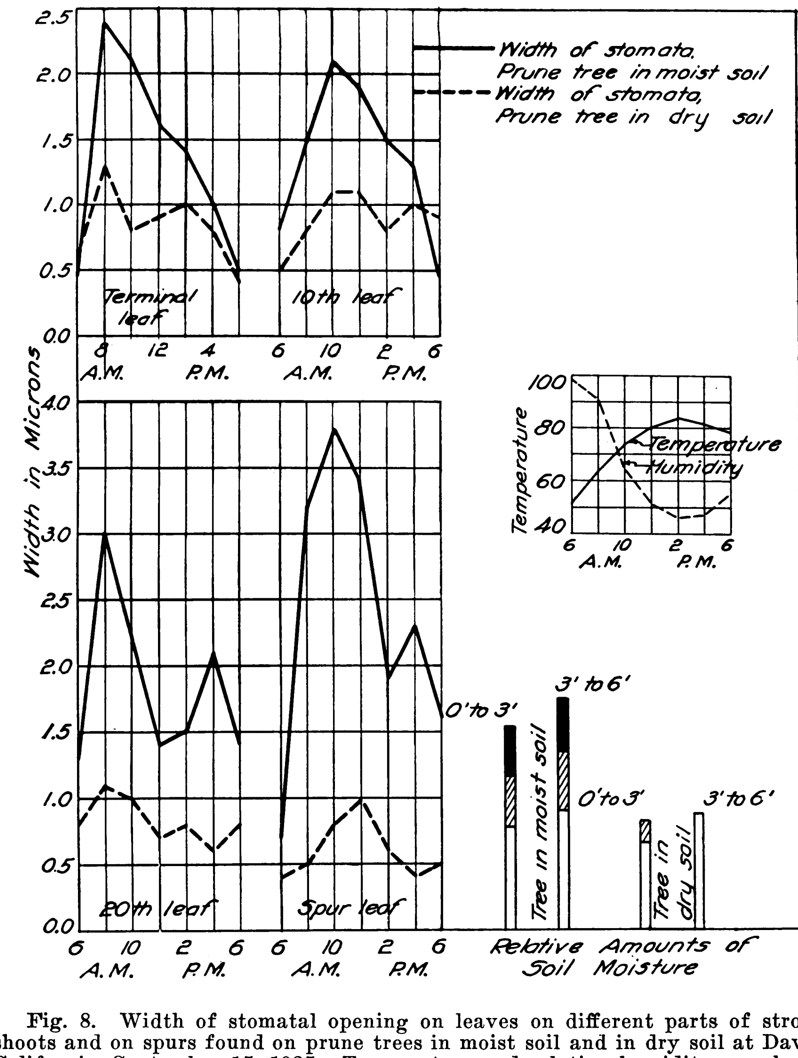

Fig. 8. Width of stomatal opening on leaves on different parts of strong shoots and on spurs found on prune trees in moist soil and in dry soil at Davis, California, September 15, 1925. Temperature and relative humidity are shown at the right. Relative amount of soil moisture above the wilting coefficient is shown by the solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

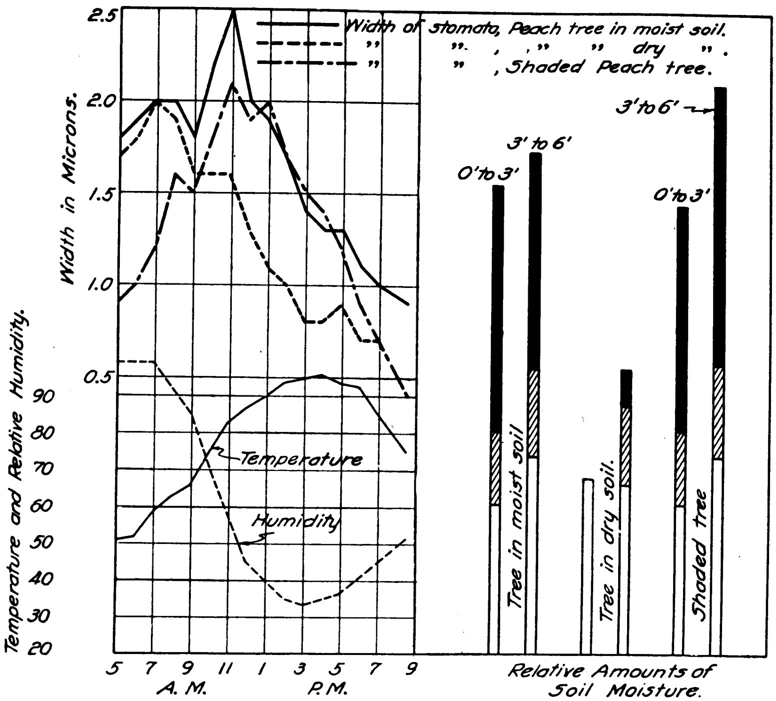

Fig. 9. Width of stomatal opening on shaded peach tree in moist soil and unshaded peach trees in moist soil and in dry soil at Davis, California, July 28, 1925. Temperature and relative humidity are shown in the lower left-hand corner. Relative amount of soil moisture above the wilting coefficient is shown by the solid black column; relative amount of soil moisture below the hygroscopic coefficient is shown by the unshaded portion.

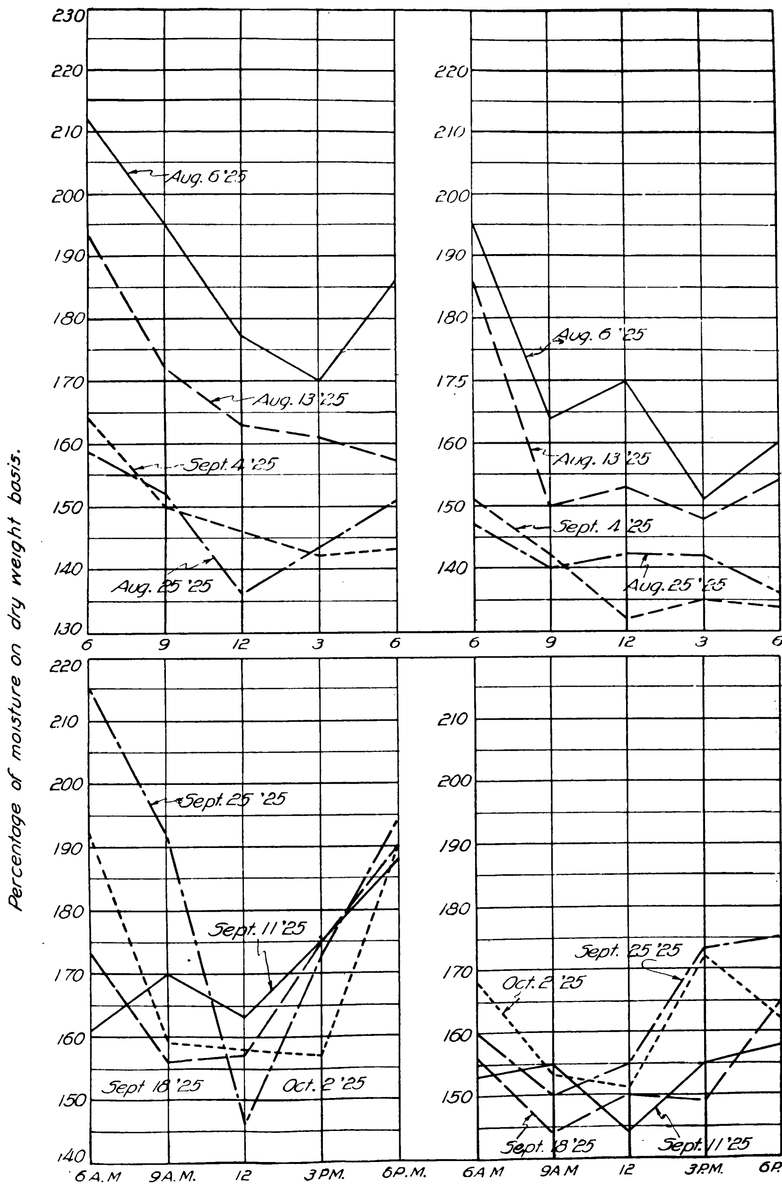

Fig. 10. Curves showing fluctuation in water content of peach leaves. Results from trees in moist soil shown on the left; from trees in dry soil, at the right. The upper curves show results obtained at Davis; the lower, at Delhi.

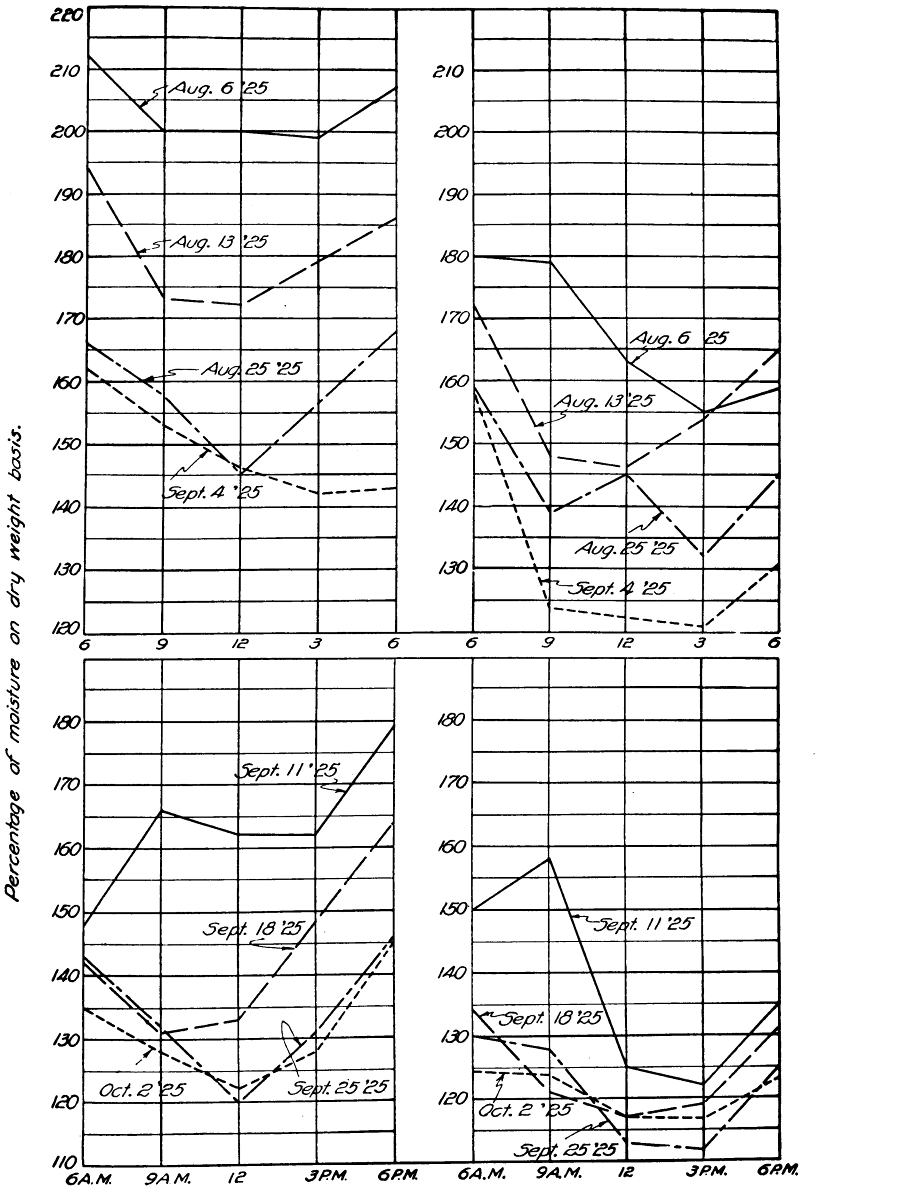

Fig. 11. Curves showing fluctuation in water content of bark from terminal six inches of current season's shoots on peach trees. Results from trees in moist soil are shown on the left; from trees in dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

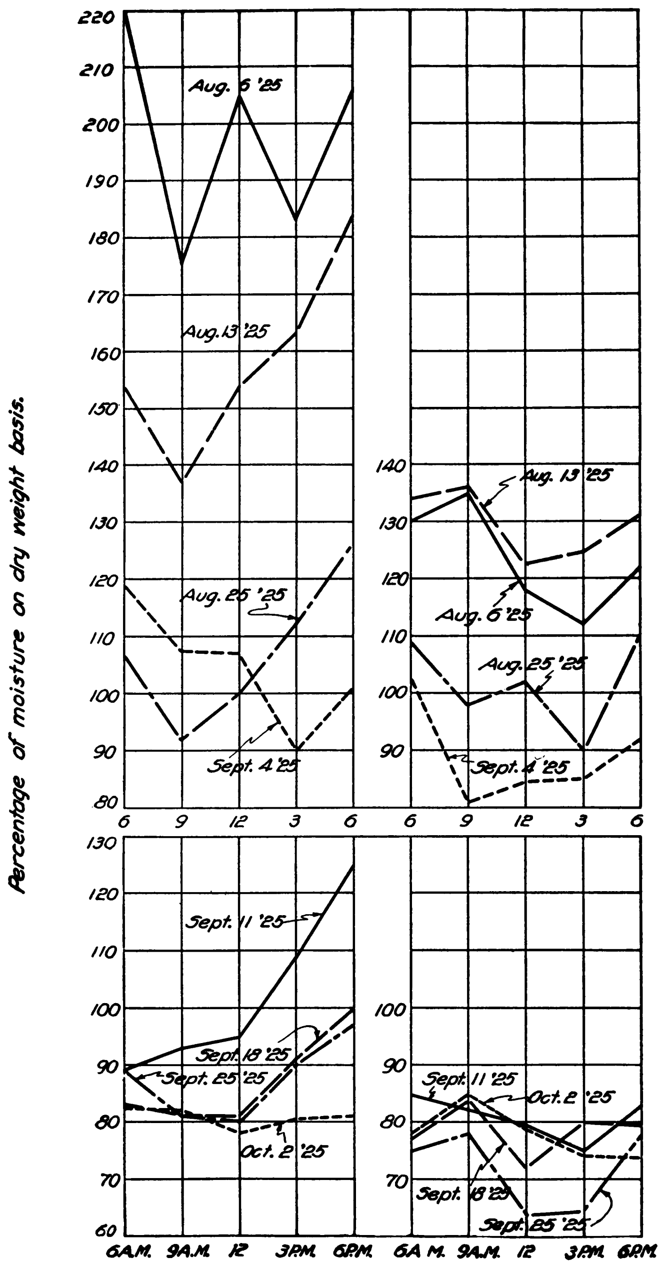

Fig. 12. Curves showing the fluctuation in water content of wood from the terminal six inches of current season's shoots on peach trees. Results from trees in moist soil are shown on the left; from trees in dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

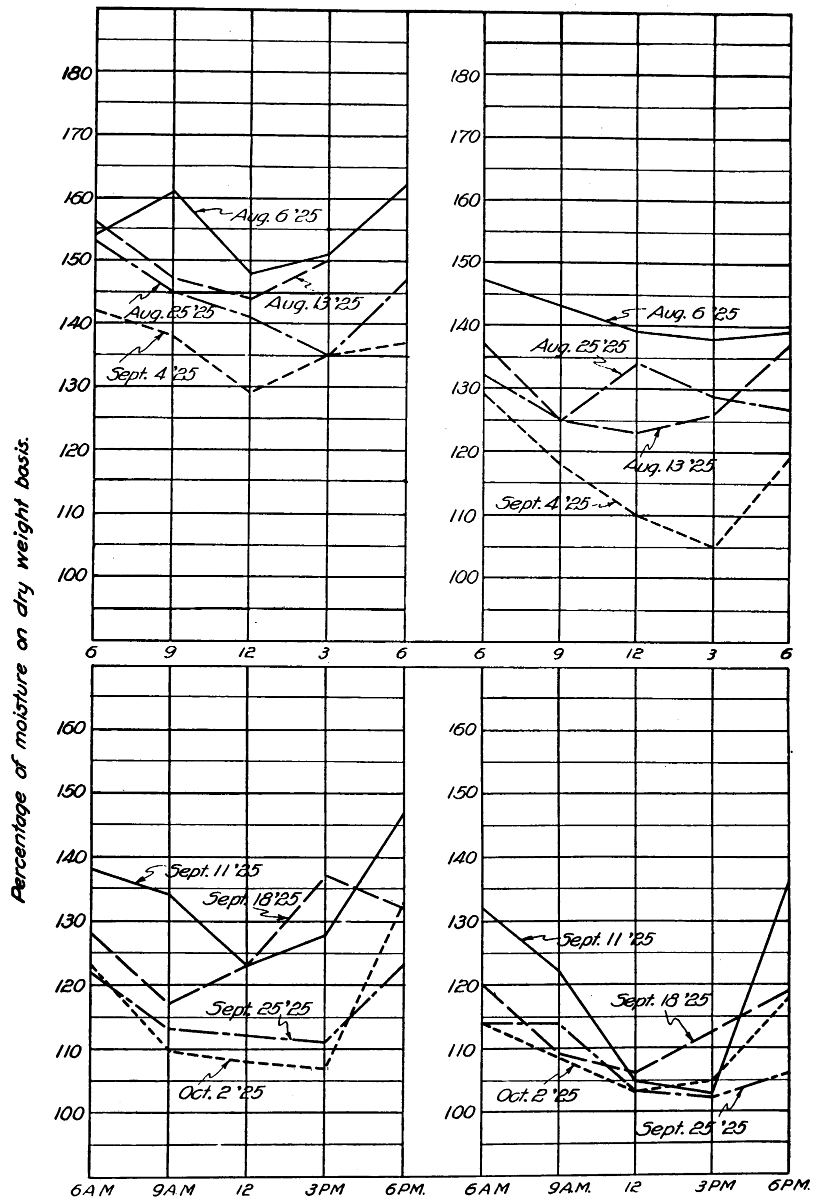

Fig. 13. Curves showing the fluctuation in water content of bark from the basal six inches of current season's shoots of peach trees. Results from trees in moist soil are shown on the left; from trees in dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

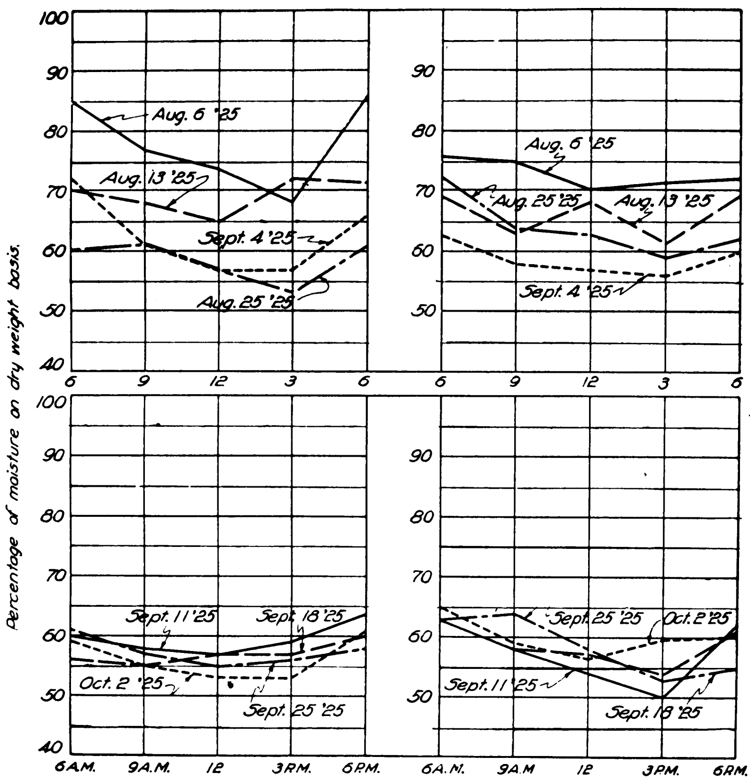

Fig. 14. Curves showing the fluctuation in the water content of wood from the basal six inches of current season's shoots on peach trees. Results from trees in moist soil are shown on the left; from trees in dry soil, on the right. The upper curves show results at Davis; the lower, at Delhi.

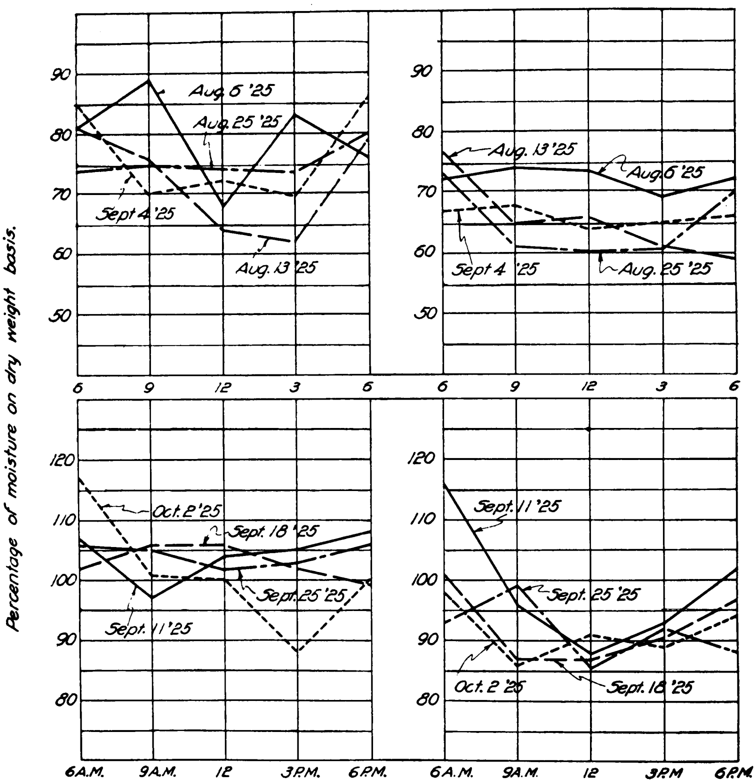

Fig. 15. Curves showing the fluctuation in water content of bark from the trunk of peach trees. Results from trees in moist soil are shown on the left; from dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

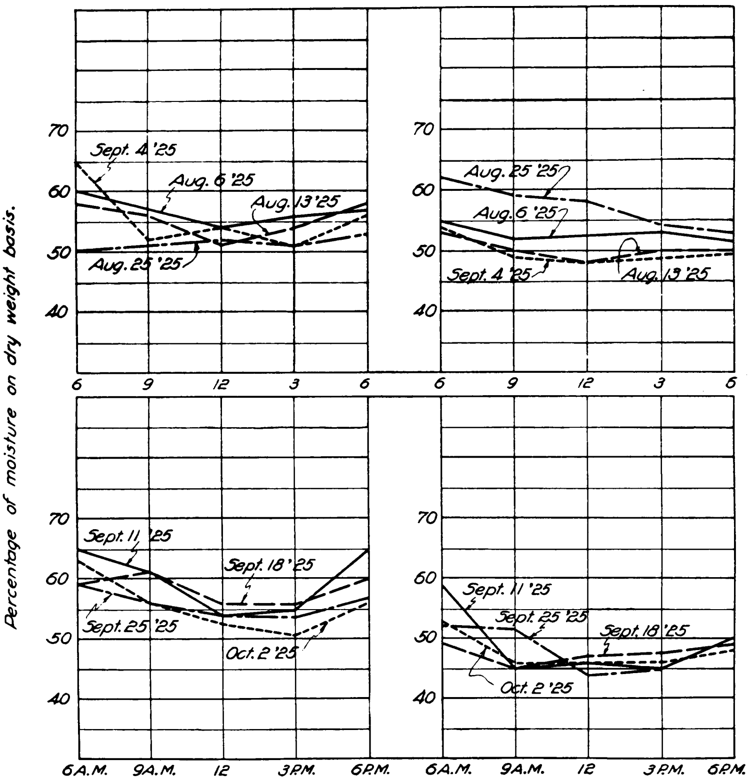

Fig. 16. Curves showing the fluctuation in water content of wood from the trunk of peach trees. Results from trees in moist soil are shown on the left; from trees in dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

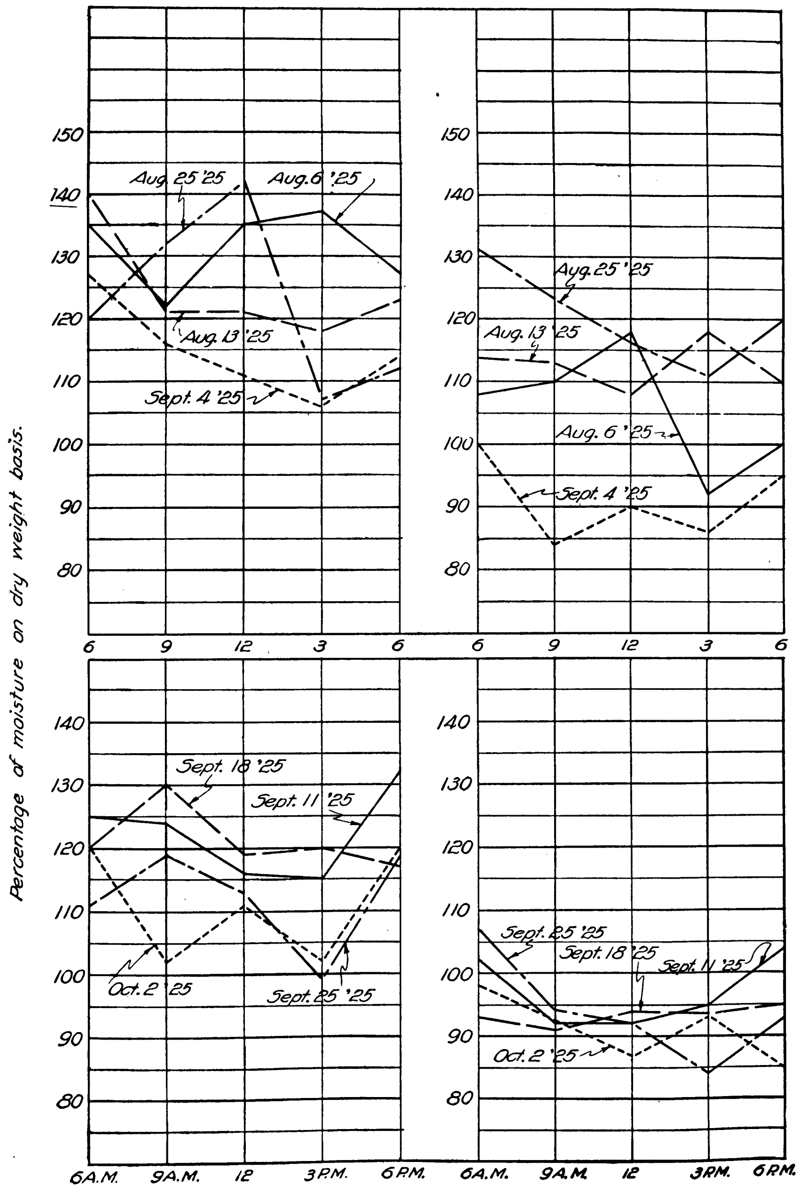

Fig. 17. Curves showing the fluctuation in water content of bark from the roots of peach trees. Results from trees in moist soil are shown on the left; from trees in dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

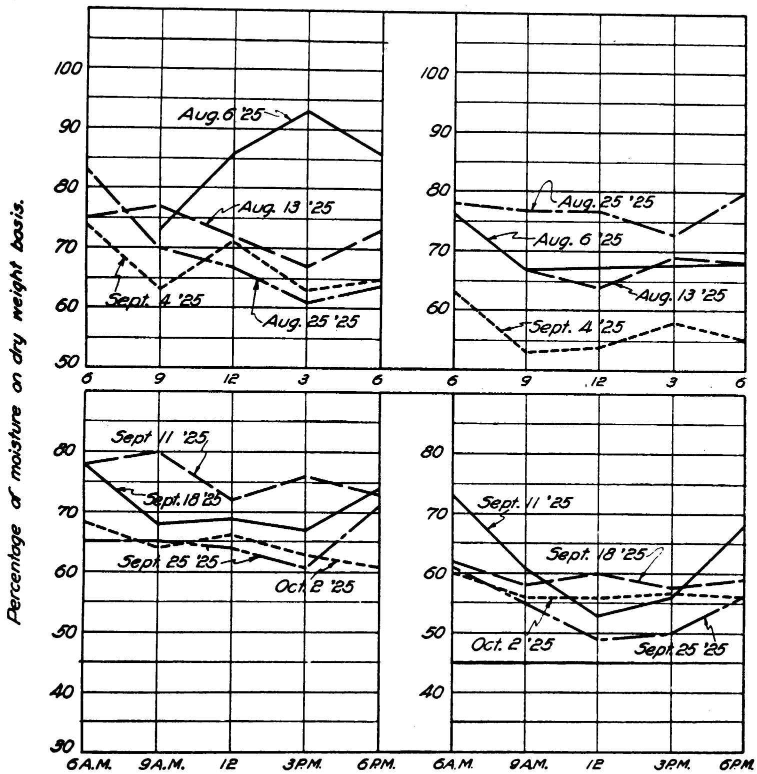

Fig. 18. Curves showing the fluctuation in water content of wood from the roots of peach trees. Results from trees in moist soil are shown on the left; from dry soil, on the right. The upper curves show results obtained at Davis; the lower, at Delhi.

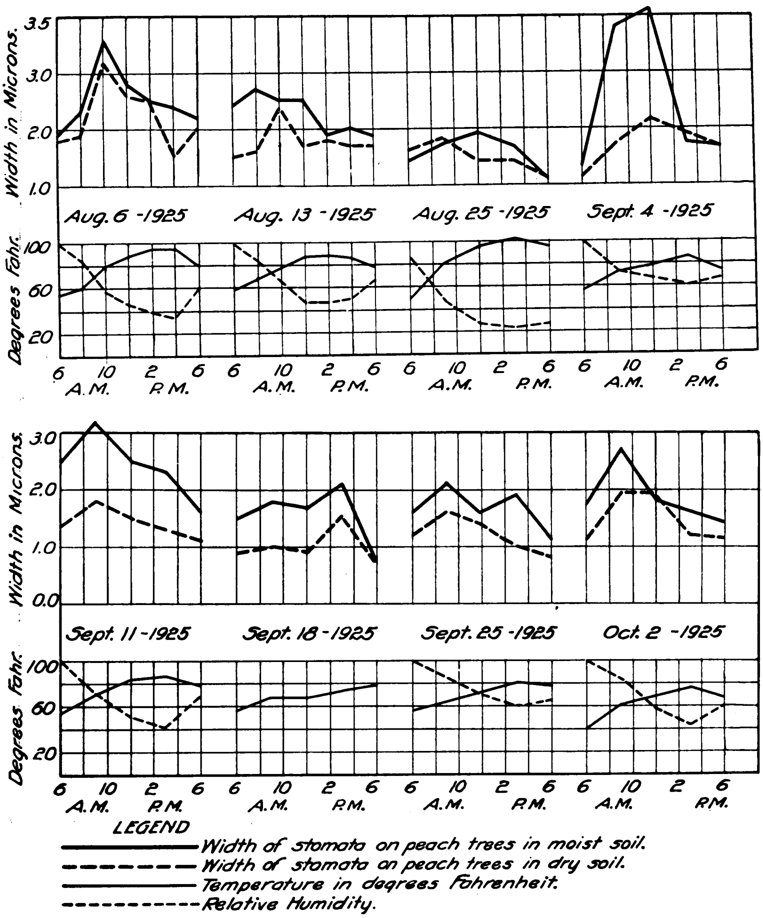

Fig. 19. Curves showing the behavior of stomata on peach leaves at Davis and at Delhi, during August and September, 1925. The leaf samples from which the stomatal measurements were made, were taken on the same day the samples of wood and bark were secured.