

# INFLUENCE OF SOIL MOISTURE ON PHOTOSYNTHESIS, RESPIRATION, AND TRANSPIRATION OF APPLE LEAVES<sup>1</sup>

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(WITH THREE FIGURES)

## Introduction

A deficiency of water under natural and even cultural conditions is probably responsible for the poor growth and death of more plants than diseases, insects, or any other cause. Although it is possible to see with the naked eye how and when a plant responds to low water supply, it is of interest to know the extent to which a drying soil affects metabolic processes before and during the time wilting is visible. It is of interest also to know whether a wilted plant recovers immediately in leaf activity when water has been supplied to the soil, or if normal activity is delayed or never again attained. The results presented in this paper trace the daily effect of a gradually drying soil on apparent photosynthesis, respiration, and transpiration of small apple trees as the soil in which they were growing gradually dried to approximately the wilting percentage, after which it was watered to field capacity.

## Methods

### ENVIRONMENT-CONTROL CHAMBER EXPERIMENTS

In the Horticulture and Forestry Building, Ohio State University, a large insulated chamber (6) seven by eight by eight feet high, inside dimensions, has been constructed for the purpose of controlling light, temperature, and relative humidity while leaf metabolism tests are being made. At the time of these experiments no effort was made to control the amount of carbon dioxide in the air. The air replacing that removed by the pump was drawn from the outside of the building. Carbon dioxide in the air usually averaged about 15 to 17 milligrams per cubic foot, corrected to standard temperature and pressure.

The apparatus used and the procedure followed to determine the carbon dioxide exchange was similar to that previously described by HEINICKE (9) and HEINICKE and HOFFMAN (11) except that a mercury piston air pump<sup>2</sup> was used to draw the air over the leaves. This method measures the amount of carbon dioxide absorbed by the leaf and is therefore a measure of *apparent* photosynthesis and not *actual* photosynthesis. Thus whenever the term

<sup>1</sup> This paper has been published in abstract elsewhere (7).

<sup>2</sup> Thanks are expressed to DR. A. J. HEINICKE, Cornell University, who devised the pump and granted us special permission to use it in our experiments.

photosynthesis is used in this paper it should be considered as meaning apparent photosynthesis.

The Stayman and McIntosh apple trees used in the chamber experiments were two years old and growing in five- and ten-gallon glazed stone crocks. The soil in these containers had a moisture equivalent of 36.4 per cent. and a wilting percentage of 15.2 (determined by analyzing the soil after dwarf sunflowers had grown in it to about 10 inches in height, then allowed to wilt). The trees had been cut back to 8-inch stubs when set in the greenhouse in December, 1938, and one vigorous shoot was allowed to grow from each stub. Six leaves were selected for study on the check tree and six on the test tree, all of which were evenly spaced around the three- to four-foot shoots. Terminal buds did not form on any of the test trees during periods of experimentation.

Daily determinations started at 11:00 A.M. and were run for three hours, immediately after which several respiration determinations were made at times specified later. To make a respiration determination the lights were turned off and an office heating cone, which had been attached to an oscillating fan, was turned on to help maintain with the cooling system a constant temperature level.

The entire bank of lights was usually turned on about 7:45 A.M. each morning. They were turned off between 5:00 and 6:00 P.M. since earlier tests have indicated that small apple trees should receive equal amounts of light each day if a fairly consistent relationship in leaf activity from one day to the next is maintained between two trees.

Transpiration was measured by a method similar to one described previously (10). The system consisted of several Freshman bottles (2 inches in diameter by 4½ inches high, one for each leaf and air-check line) which contained ground pumice stone impregnated with sulphuric acid. The acid efficiently removed water vapor from air flowing through 9-mm. glass tubing at the rate of three to four cubic feet per hour, and did not interfere with the carbon dioxide to be removed later in the absorption towers. After each determination the rubber stoppers, with glass attachments and metal numbers, were removed from the bottles which, in turn, were placed in a drying oven at about 160° C. After 24 hours the bottles were removed and allowed to cool to air temperature, stoppered, and held ready for the next run. These bottles could be used for a month or more until the absorption medium became somewhat weak and it was necessary to impregnate the stones again with sulphuric acid. The common laboratory procedure for preparing these stones was essentially as follows: Place pumice stones about the size of peas in an evaporating dish or casserole and cover with concentrated sulphuric acid. Place on a hot plate and heat until dense white fumes appear, then continue the heating for one-half hour. Allow to cool and drain off all of

the acid. Again heat the pumice until heavy white fumes of sulphur trioxide are given off. At the end of this heating, there should be no excess of sulphuric acid present. Cool in a desiccator and store in stoppered glass containers.

#### GENERAL PROCEDURE

The general procedure employed for the water deficiency experiments was essentially as follows: Determinations of apparent photosynthesis, transpiration and, in some cases, respiration were made from three to five days before the dry period began in order to establish a relationship in leaf activity between the group of leaves to be used as test leaves and those to remain as controls. When a consistent relationship had been established, the test tree ceased to receive water while the check, or control, tree received it daily in order to keep the soil at approximately the field capacity. Daily determinations were continued until the test plant had reached the incipient or permanent wilting stage (as specified later) when the soil was again watered to field capacity and the runs continued for 7 to 10 days. Stomatal observations were made either by removing small sections one centimeter square from neighboring leaves on the shoot and immediately inspecting them under the microscope, or by observing the inverted intact leaf through a mounted microscope.

#### FIELD EXPERIMENTS

The assembly of carbon dioxide absorption towers, electric air pump (instead of mercury piston pump), and wet test meter were located in the greenhouse and connected by glass tubing to individual leaves on two Stayman apple trees. The trees were growing in five-gallon glazed stone crocks outside the greenhouse where they were fully exposed to the sun. Soil surrounding their root systems had a moisture equivalent of 38.4 per cent. and a wilting percentage of 15.55. Leaf cups were attached to six leaves on the test plant and to four leaves on the check while two of the air lines were reserved to determine the amount of carbon dioxide in air before it reached the leaves. Leaves selected on each tree were evenly distributed up and down and around the four- to five-foot shoots. Two four-hour determinations were usually made each day, the first beginning about 7:00 A.M. and the second about 11:30 A.M. Light and temperature readings were recorded at the beginning, middle, and end of each run with a Weston illuminometer and a Fahrenheit dairy thermometer.

### Results

#### ENVIRONMENT-CONTROL CHAMBER

Four experiments were performed in the environment-control chamber. In the first test only apparent photosynthesis determinations were made; in

the second and third experiments apparent photosynthesis, respiration, and transpiration data were recorded; in the fourth only respiration was studied.

EXPERIMENT I (APPARENT PHOTOSYNTHESIS).—The trees used in this experiment were of the McIntosh variety; tree A was the check and tree B the test plant. During each determination the temperature was held at 80° F., and light intensity was constant at an average of about 4000 foot candles for all leaves concerned. Relative humidity was approximately 30 per cent. during the light period. A relationship between the photosynthetic activity of trees A and B was established in the eight-day period from February 14 to February 21. The data in table I show the daily rate of apparent photosynthesis in milligrams of carbon dioxide absorbed per 100 square centimeters of leaf surface per hour, before and after the dry period. The test tree, B, received its last watering the night of February 20, while the check tree, A, received it daily throughout the experiment. The leaf relationship during the standardization period showed that for every 100 milligrams of carbon dioxide assimilated by the check plant the test plant utilized 128.9 milligrams. Thus, the *expected rate* of the test plant was 128.9 per cent. of the check (see foot-note in table I for explanation of figures termed *expected rate and percentage expected rate*). During the first four days of the dry period from February 22 to 25, the test plant showed an average increase in carbon dioxide assimilation of about three per cent. above its rate previous to the treatment. From February 25 until March 3 there was a gradual decrease in the rate of photosynthesis of tree B from 101 to 76 per cent. of the expected rate. At no time during this period did the test tree show signs of wilting, even by late afternoon when the lights were usually turned off. On March 4 there was a sharp reduction in photosynthesis, to 46 per cent. of the expected rate; no wilting was evident, however, until about three hours following the determination when the leaves appeared to be slightly flaccid. The next day, March 5, the test tree was fairly turgid at the start of the run but was wilted at the end of the determination, with the top leaves showing the greatest effect of water deficiency. The entire tree showed signs of wilting on the following morning of March 6 when the lights were turned on. The soil continued drying until March 11 when assimilation had gradually fallen to around 14 per cent. of the expected rate. Stomata on the test tree appeared to be closed continuously during the period of wilting, including the mornings before determinations were started. It is interesting to note that fairly good values for photosynthesis were obtained when the leaves were somewhat wilted and the stomata appeared to be closed. On March 11, about two hours before the determination, water was added to the dry plant and by starting time the tree had almost recovered to complete turgidity. Within another hour the stomata were almost as far open as were those on the check leaves (75 to 100 per cent.).

TABLE I

EFFECT OF SOIL MOISTURE ON THE RATE OF PHOTOSYNTHESIS OF MCINTOSH APPLE LEAVES.  
EXPERIMENT I, TEMPERATURE 80° F.

DATE, 1939	APPARENT VALUES OF PHOTOSYNTHESIS IN CO <sub>2</sub> /100 CM <sup>2</sup> /HR.		EXPECTED RATE OF TEST TREE
	CONTROL	TEST	
	<i>mg.</i>	<i>mg.</i>	<i>%</i>
Feb. 14 .....	31.4	37.7	.....
15 .....	26.8	29.6	.....
16 .....	21.7	30.3	.....
17 .....	23.0	33.0	.....
18 .....	12.9	15.2	.....
19 .....	17.6	26.1	.....
20* .....	15.4	24.4	.....
21 .....	19.7	21.6	.....
Average .....	21.1	27.2	128.9‡
22 .....	11.2	15.0	103.9§
23 .....	15.2	20.1	102.6
24 .....	11.8	16.0	105.1
25 .....	12.5	16.3	101.2
26 .....	18.9	19.1	78.4
27 .....	14.0	11.1	61.4
Mar. 1 .....	7.6	7.5	76.5
2 .....	12.4	12.2	76.3
3 .....	15.7	15.4	76.1
4 .....	8.7	5.0**	44.6
5 .....	20.8	15.4	49.7
6 .....	13.6	5.4	30.8
7 .....	9.1	5.4	46.0
8 .....	15.9	2.3	11.2
9 .....	9.2	2.2	18.5
10 .....	12.4	3.2	13.8
11† .....	10.3	8.8	66.3
12 .....	10.3	8.5	64.0
13 .....	12.2	16.5	104.9
16 .....	10.0	14.9	115.6
17 .....	10.5	13.7	101.2
18 .....	16.0	20.4	98.9
19 .....	11.1	14.9	104.1
20 .....	8.6	10.9	98.3
21 .....	10.5	15.5	114.5
22 .....	15.9	17.9	87.4
23 .....	7.9	8.6	84.5
24 .....	11.9	13.8	90.0
25 .....	12.6	14.2	87.4

\* The test plant last received water on the evening of February 20.

† Test plant watered to field capacity of the soil two hours before determination was made.

‡ Obtained by dividing the average apparent photosynthetic value (27.2) for the test tree by the average value (21.1) for the check tree and multiplying by 100.

§ Obtained by dividing the daily rate of photosynthesis of the test tree (15.0) by the daily rate of photosynthesis of the check plant (11.2), multiplying by 100 and dividing the product by 128.9.

\*\* Test tree showed first signs wilting two hours after run.

Assimilation during this run recovered to 66 per cent. of its expected rate and within 48 hours had returned to its original status.

From March 11 to 15 the test tree was watered daily and then allowed to dry again. During the six-day period which followed March 15, apparent photosynthesis of the test plant averaged 105.4 per cent. of its expected rate; or, in other words, it showed a 5 per cent. increase which corresponded with the average 3 per cent. increase obtained at the beginning of the first dry period from February 22 to 25. Beginning with March 22, however, photosynthetic activity began to decrease at a rate similar to the first test. The experiment was discontinued.

**EXPERIMENT II (APPARENT PHOTOSYNTHESIS, RESPIRATION, AND TRANSPIRATION).**—Stayman Winesap trees were used in this experiment. Temperature in the chamber during each determination was constant at 90° F. and

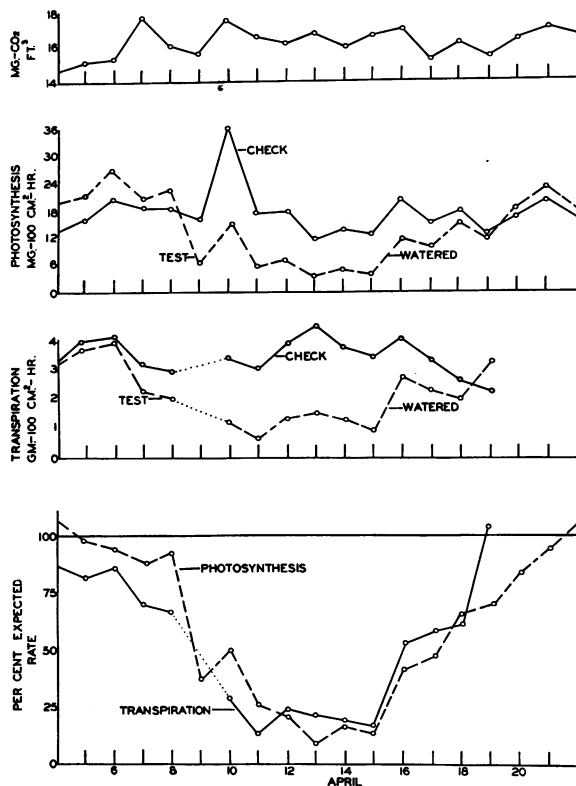


FIG. 1. The influence of a gradually drying soil on apparent photosynthesis and transpiration of apple leaves. The test tree was last given water the evening of April 1. First wilting occurred the afternoon of April 10; soil was watered to field capacity two hours before the determination on April 16 (experiment II).

light averaged approximately 4000 foot candles for the six test and six check leaves. These factors did not vary during the nine-hour day from 8:00 A.M. to 5:00 P.M. At other hours of the day the lights were turned off and the plants remained at room temperature which was about 75° F.

Data for this experiment are presented in table II and graphically shown

TABLE II

INFLUENCE OF SOIL MOISTURE ON PHOTOSYNTHESIS, RESPIRATION, AND TRANSPIRATION OF STAYMAN APPLE LEAVES. EXPERIMENT II, TEMPERATURE 90° F.

DATE, 1939	APPARENT VALUES PER HOUR PER 100 CM <sup>2</sup>						EXPECTED RATE OF TEST TREE*	
	ASSIMILATION CO <sub>2</sub>		TRANSPIRATION H <sub>2</sub> O		RESPIRATION CO <sub>2</sub>		ASSIM.	TRANSP.
	CONTROL	TEST	CONTROL	TEST	CONTROL	TEST		
	<i>mg.</i>	<i>mg.</i>	<i>gm.</i>	<i>gm.</i>	<i>mg.</i>	<i>mg.</i>	%	%
Mar. 27	22.1	26.7	1.9	2.0	.....	.....	.....	.....
28	14.1	20.1	.....	.....	.....	.....	.....	.....
29	12.9	17.1	3.2	3.4	.....	.....	.....	.....
30	22.6	30.7	2.9	3.7	.....	.....	.....	.....
31	19.4	25.9	2.7	3.6	.....	.....	.....	.....
Apr. 1†	17.8	22.8	3.5	3.7	.....	.....	.....	.....
2	16.2	22.1	3.3	3.9	.....	.....	.....	.....
Average	17.9	23.6	2.9	3.4	.....	.....	131.8	117.2
4	13.0	18.2	3.4	3.4	3.6	2.0	106.2	85.3
5	15.7	19.8	3.8	3.6	.....	.....	95.6	80.8
6	20.5	24.8	3.9	3.8	7.0	6.0	91.7	83.1
7	18.4	21.3	3.2	2.4	.....	.....	87.8	64.0
8	18.5	22.0	2.8	2.0	.....	.....	90.2	60.9
9	17.1	5.9	.....	.....	.....	.....	26.2	.....
10	36.4	17.6	3.3	1.0	.....	.....	36.6	25.9
11	18.6	4.2	2.9	0.5	2.6	4.6	17.1	14.7
12	18.6	5.4	3.5	1.0	5.5	6.5	22.0	24.4
13	11.9	1.4	4.2	1.0	.....	.....	8.9	20.3
14	13.8	2.5	3.3	0.6	1.5	3.5	13.7	15.5
15	12.6	2.2	3.2	0.5	4.7	5.2	13.2	13.3
16‡	19.9	11.7	3.8	2.3	3.3	4.0	44.5	51.6
17	14.7	9.5	3.1	1.8	3.8	4.8	49.0	58.0
18	16.5	14.7	2.5	1.6	4.2	5.0	67.6	54.6
19	13.0	12.7	2.4	2.9	2.9	2.9	74.1	103.1
20	14.6	16.6	.....	.....	3.6	3.4	86.3	.....
21	16.7	20.9	.....	.....	2.9	1.5	94.9	.....
22	10.5	14.7	.....	.....	.....	.....	106.2	.....

\* See table I for method of calculation.

† Test tree last watered the evening of April 1. (No determination made first day of dry period, April 3.)

‡ Test tree thoroughly watered two hours before test period began.

in figure 1. The relationship between the control tree, C, and the test tree, D, was established in the seven-day period from March 27 until April 2. During this standardization period the test plant was found to have an expected photosynthetic rate of 131.8 per cent. and an expected rate of transpiration of 117.2 per cent. No determinations were made on April 3.

On April 4 the test tree showed an increase of 6 per cent. in photosynthesis. This increased rate of photosynthesis during the early part of the dry period apparently lasted at the most only two days. This shorter period of increased photosynthetic activity, as compared with the four-day period in the previous experiment, was probably due to the 10 degree higher temperature which caused a more rapid drying of the soil and a higher rate of transpiration by the leaves. It is interesting to note that while photosynthesis showed a six per cent. increase on April 4, transpiration showed a 15 per cent. decrease. On the following day, April 5, the percentage expected rate of apparent photosynthesis was about 4 per cent. below its rate previous to the test period; transpiration, however, showed about a 19 per cent. decrease. From April 5 until April 8 photosynthesis of the test tree showed a 19 per cent. decrease and transpiration a 40 per cent. decrease. It is apparent from these data that transpiration showed a marked drop two days before an appreciable reduction in photosynthesis occurred. The test tree showed slight wilting at the tip at the conclusion of the run on April 10. It had recovered, however, within two hours after the lights were turned off in the afternoon. In spite of the slight wilting which occurred at the end of this three-hour run the test plant assimilated carbon dioxide at the fairly good rate of 17.6 milligrams per 100 square centimeters of leaf surface per hour. On April 11 the lights were turned on about three hours before the run began, and at starting time the plant again showed signs of slight wilting at the tip. By termination of this run all leaves were drooping. Carbon dioxide assimilation was 17 per cent. of the expected rate while transpiration was only 15 per cent. of its expected rate. In the period from April 11 to 16 as the plant continued to dry, the photosynthetic activity and transpiration of tree C dropped in each case to about 13 per cent. when the soil in which it was growing had reached a definite wilting percentage.

About two hours before the run was started on April 16 the test tree was thoroughly watered but it did not recover to full turgidity until about three hours after the lights had been turned off in late afternoon. Although the plant was obviously wilted during this run, the rate of photosynthesis and transpiration increased to 44 and 52 per cent., respectively, of their original rate. By April 19 carbon dioxide assimilation of the test plant had increased to about 74 per cent. of its former rate, while transpiration showed a rapid increase to 106 per cent. On the day following this increase in transpiration, photosynthetic activity increased to 86 per cent., and by April 22 showed complete recovery to 106 per cent. of the expected rate. Thus, the time required for this plant to return to about normal transpiration and assimilation after the dry period was four and seven days, respectively.

A three-hour respiration determination was made on several occasions following the above daily tests. Conditions were maintained the same with



the exception that the chamber was darkened. Unfortunately no respiration runs were made before the start of the dry period. On April 4 and 6, however, respiration tests were made on the two sets of leaves when photosynthesis and transpiration had not as yet shown marked reductions. In table II it is apparent that the respiration rate of tree C, the test plant, was lower than that of the check tree, D, for both determinations. By April 11 when the next determination was made, however, respiration of the drying plant had increased above the check and this relationship continued during the dry period, and for four or five days after the water had been added on April 16. It is evident in table II that variations in the rate of respiration were directly opposite to variations in photosynthesis. When the former process showed an increase, the latter showed a decrease as the soil gradually dried; after water was added, the situation was slowly reversed.

**EXPERIMENT III (APPARENT PHOTOSYNTHESIS, RESPIRATION, AND TRANSPIRATION).**—This experiment was carried out under the same procedure and set of conditions as the previous experiment except the temperature was 10° F. higher (100° F.) and the test plant was allowed only to show incipient wilting before water was supplied. Tree E, the control, and tree F, the test, were both of the McIntosh variety. During the standardization period, April 24 to April 28, both trees were watered daily in the evening until the evening of April 28 when only the control tree received water and the test plant was allowed to begin drying. In this experiment, as in the previous two experiments, shortly after the last watering the test plant showed an increase in photosynthetic activity over a two-day period, April 29 and 30, or an average increase of about seven per cent. Transpiration also showed a slight increase on but one day, April 29. According to the data in table III, it is evident again that transpiration shows a decrease before photosynthesis when water becomes limiting. Transpiration dropped slightly on May 30, and photosynthesis showed a slight decrease the next day; the first marked drop in transpiration came on May 3 while the first marked drop in photosynthesis occurred the following day. Toward the end of the determination on May 6 the test plant showed signs of wilting but recovered about two hours after the lights were turned off in the evening. Photosynthesis and transpiration on this day were 44 and 36 per cent., respectively, of their expected rate. Soil in which the test plant was growing was watered to field capacity late in the evening of May 6. The next day photosynthesis had recovered to almost its original status and had completely recovered by May 8. Transpiration showed complete recovery by May 9.

Immediately following each of the above determinations the chamber was darkened and respiration runs were made at the same temperature (100° F.) on four leaves on each of the above test and check plants (see

TABLE III

THE EFFECT OF SOIL MOISTURE ON PHOTOSYNTHESIS, TRANSPIRATION, AND RESPIRATION OF APPLE LEAVES.  
EXPERIMENT III, TEMPERATURE 100° F.

DATE, 1939	APPARENT VALUES PER HOUR PER 100 CM <sup>2</sup>						EXPECTED RATE OF THE TEST TREES*		
	ASSIMILATION CO <sub>2</sub>		TRANSPIRATION H <sub>2</sub> O		RESPIRATION CO <sub>2</sub>		ASSIMILATION %	TRANSPIRATION %	RESPIRATION %
	CONTROL	TEST	CONTROL	TEST	CONTROL	TEST			
Apr. 24	14.6	12.2	2.5	2.7	.....	.....	.....	.....	.....
25	16.9	15.0	2.9	3.2	.....	.....	.....	.....	.....
26	20.6	19.5	3.0	3.2	6.3	4.1	.....	.....	.....
27†	20.6	19.7	3.3	3.6	4.6	3.6	.....	.....	.....
28	17.3	15.5	3.2	3.6	4.5	3.4	.....	.....	.....
Average	18.0	16.4	3.0	3.3	5.1	3.7	91.1	110.0	72.5
29	21.5	20.5	2.9	3.3	.....	.....	104.7	103.4	.....
30	16.2	16.0	3.5	3.8	.....	.....	108.4	98.7	.....
May 1	12.2	10.6	3.4	3.3	6.0	5.9	95.4	88.2	135.6
2	18.2	14.9	4.3	3.9	6.9	6.9	89.9	82.4	137.9
3	19.0	16.5	4.1	2.3	2.8	3.0	95.3	51.0	147.8
4	20.7	9.5	4.2	2.2	2.9	3.2	50.4	47.6	152.2
5	19.7	8.1	4.9	2.0	1.7	2.0	45.1	37.1	162.2
6‡	20.7	8.2	4.6	1.8	2.6	3.0	43.5	35.6	159.1
7	16.2	13.6	3.8	3.8	3.0	2.4	92.2	90.9	110.3
8	15.3	14.7	3.4	3.6	3.0	2.4	105.5	96.3	.....
9	12.5	11.8	3.2	3.7	4.0	2.8	103.6	105.0	96.6
10	18.8	17.4	.....	.....	.....	.....	101.6	.....	.....

\* See table I for method of calculation.

† Test tree last watered evening of April 27.

‡ Test tree watered thoroughly evening of May 6.

experiment IV regarding the remaining four leaf cups which were attached to another drying plant for respiration studies). The data are given in table III and shown graphically in figure 2. It is apparent again that as

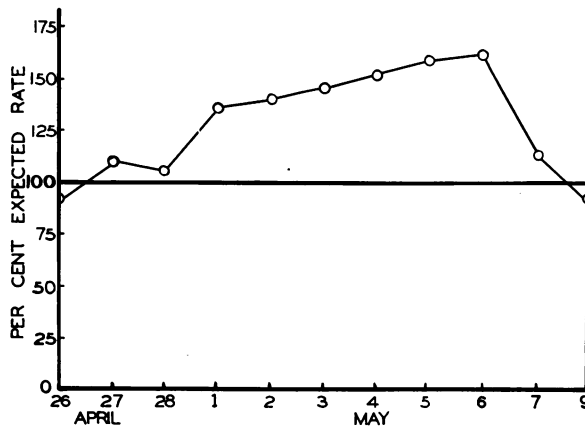


FIG. 2. The influence of soil moisture on respiration of apple leaves. The test tree received the last watering on the evening of April 27. It was watered again the evening of May 6 (experiment III).

water becomes limiting to an apple tree the respiration rate correspondingly increases, but when the plant has been watered again it gradually returns to its original relationship with the check plant. The highest rate of respiration, a 62 per cent. increase, was recorded on May 6 when transpiration and photosynthesis were lowest and the plant showed definite signs of wilting.

EXPERIMENT IV (RESPIRATION).—Data presented in table IV were collected on a McIntosh test tree, G, at the same time respiration determinations were made on tree F in experiment III. Leaf cups were attached to four leaves on test tree, G, while the control tree, E, remained as a reference in both experiments III and IV. The standard relationship between assimilation of the test and control leaves was established between May 4 and 6, and from the evening of May 6 to 9 inclusive the test tree received no additional water. In table IV it is evident that on the first day of the dry period, May 7, tree G showed the beginning of a gradual increase in respiration. On May 8, 9, and 10 there were further increases in respiration to 23, 34, and 30 per cent., respectively. After the test plant had been watered thoroughly the evening of May 10, it returned on May 11 to almost its original relationship in respiration with the reference tree. Thus, it is apparent from these data that when the dry period for an apple tree is short and less severe, respiration of its leaves returns from an increased rate to its normal status more quickly after water again has been supplied.

TABLE IV

EFFECT OF SOIL MOISTURE ON RESPIRATION OF MCINTOSH APPLE LEAVES.  
EXPERIMENT IV

DATE, 1939	APPARENT VALUES FOR RESPIRATION IN CO <sub>2</sub> / 100 CM <sup>2</sup> /HR.		EXPECTED RATE OF THE TEST TREES*
	TEST	CHECK	
	<i>mg.</i>	<i>mg.</i>	<i>%</i>
May 4 .....	2.9	4.5	.....
5† .....	1.7	2.7	.....
6 .....	2.6	4.2	.....
Average .....	2.4	3.8	158.3
7 .....	3.0	5.7	120.0
8 .....	2.2	4.3	123.4
9 .....	4.0	8.5	134.2
10‡ .....	1.7	3.5	130.0
11 .....	2.2	3.7	106.3

\* See table I for method of calculation.

† Test tree received last watering evening of May 5.

‡ Test tree watered to field capacity evening of May 10.

FIELD EXPERIMENTS<sup>3</sup>

During the summer of 1938 three experiments were carried out in a manner similar to those in the control chamber with the exception that the trees were placed outside the greenhouse where they were exposed to environmental conditions typical of central Ohio. The data are presented in figure 3 for one experiment which we considered, in general, almost identical with results obtained in the other two tests. Before it was evident that small variations in soil moisture had definite effects on leaf metabolism (as has been pointed out in the chamber experiments), it was decided to water the control plants in these tests only at intervals of 2 to 4 days when the soil appeared dry on the surface. The interval of watering obviously depended upon whether days were cloudy or sunny. This probably accounts for the fact that the relationship in photosynthesis between the two trees held practically constant for about three days after the dry period began (July 12) when the control tree also did not receive water for two days. Daily records show that water was applied to the control tree the mornings of July 12, 14, and the late afternoon of July 15 during the early part of the test period. From the afternoon of July 14 to the morning of July 18 the drying plant showed a definite relative increase (as much as 70 per cent., July 15) in carbon dioxide assimilation, which is similar to the behavior of drying plants in the chamber experiments. Beginning with the morning of July 19 there

<sup>3</sup> The authors appreciate the assistance of Mr. VERNON PATTERSON, senior in pomology, in performing the routine chemical analyses of the solutions.

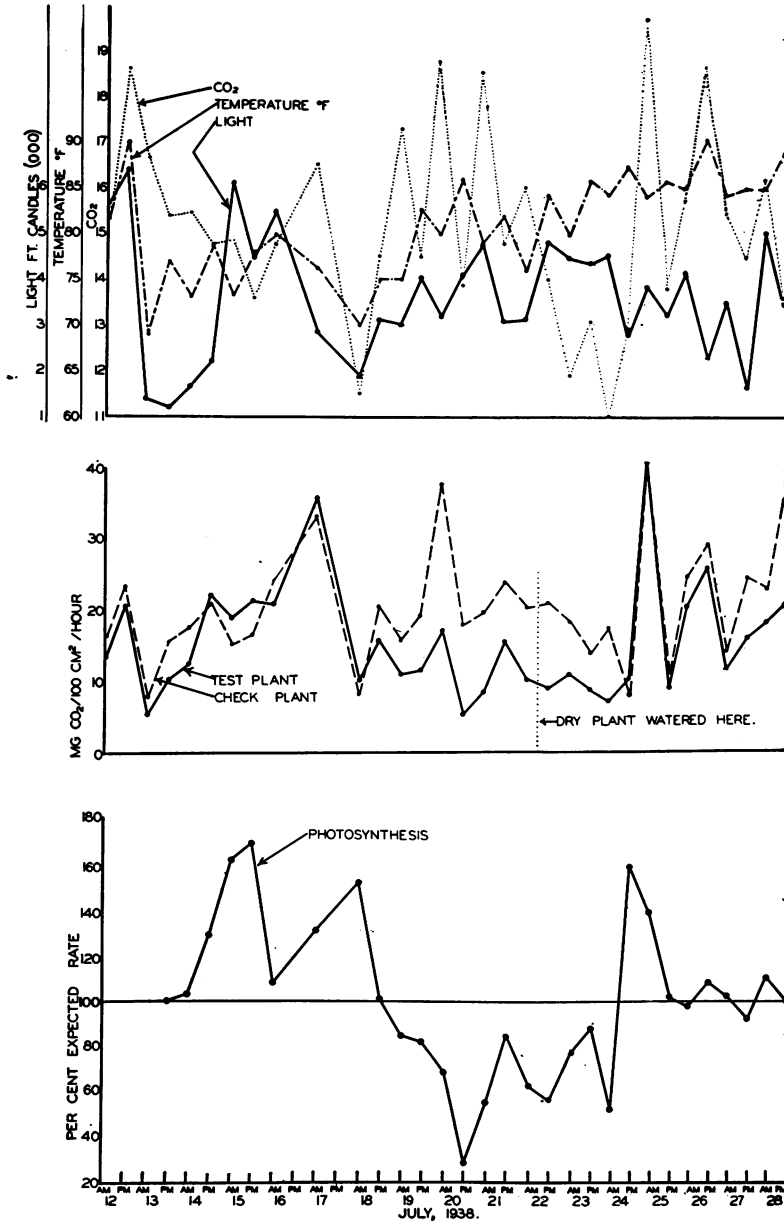


FIG. 3. The influence of soil moisture on apparent photosynthesis of apple leaves under central Ohio weather conditions in July. The test plant received water on July 12 and again on July 22 at 10:50 A.M. In the lower part of the figure the relationship in photosynthesis between the test and check trees on July 12 and 13 was taken as a standard for comparison of leaf activity on the remaining days.

was a gradual decrease in photosynthesis as the plant continued drying. During this period the weather was generally cool and often cloudy which afforded ideal conditions for a very gradual drying of the plant, thus avoiding any sudden scorching of the leaf tissues. The leaves on the test tree showed no signs of wilting until late afternoon of July 19 when slight wilting on the lower leaves occurred; this again stresses the fact that there may be a marked reduction in photosynthesis by apple leaves before wilting is visible to the eye. On the morning of July 20 the test tree had recovered, but by mid-afternoon two lower leaves were scorched at the tip and margins and the lower leaves, in general, were badly wilted. Again, early in the morning of July 21, the plant had shown noticeable recovery overnight, but by late afternoon several more leaves were scorched and the entire plant was very definitely wilted. At 10:50 A.M., July 22 the dry plant was thoroughly watered but did not recover until late afternoon. The morning of July 23 it appeared to be fully turgid, and according to figure 3 had recovered in photosynthesis in about three days. It then was allowed to begin drying again when the experiment was discontinued.

#### Discussion

The data in experiments I, II, and III obtained in the environment-control chamber and the data obtained in the field (fig. 3) have shown a consistent increase in photosynthesis when the moisture in a relatively heavy type of soil fell below its field capacity. In an earlier report by HEINICKE and CHILDERS (11) similar results were noted and it was suggested that "the optimum soil moisture for photosynthesis of apple trees may be below the field capacity of the soil, or certainly, below a degree of saturation which persists for a day or so after watering." This would seem reasonable to expect in view of the numerous reports (2, 15, 21) which stress the importance of good soil aeration as it influences root and top growth. From the standpoint of moisture content of the leaves, BRILLIANT (4) has shown that photosynthesis is at its maximum when leaf moisture was reduced 5 to 15 per cent. in *Hedera helix* and *Impatiens parviflora*. It may also be noted in experiment II (90° F.) that transpiration showed a decrease of 15 per cent. at a time when there was a 6 per cent. increase in photosynthesis. It is probable that if transpiration tests had been made at the lower temperature of 80° F. (experiment I) when the period of increase in photosynthesis extended over a four-day period, the above relationship between photosynthesis and transpiration would have been more pronounced.

It has been stated by MILLER (18) that water plays both a direct and indirect rôle in photosynthesis: directly, by entering into chemical combination with carbon dioxide to form carbohydrates; and indirectly, by governing the opening of the stomata which, in turn, governs the intake of carbon

dioxide. In case of moderate water shortage to apple leaves, however, MAGNESS (17) states that there is so much water present in the leaf, even at time of stomatal closing, that it seems doubtful if a deficiency of water is a direct factor in reduced photosynthesis. In our experiments it has been difficult to establish a definite relationship between photosynthesis and stomatal opening at the time water becomes limiting; in several observations made by the junior author at Ithaca, N. Y., it appeared that there was a drop in carbon dioxide assimilation about the same time, or shortly after closing of the stomata was evident, due to water shortage. It does seem fairly clear, however, that under moderate weather conditions, there may be a 5 to 15 per cent. reduction in transpiration before stomata begin to show the effects of low water supply and before photosynthesis begins to show a definite decline (experiment II). MAGNESS (17) also found that moisture supply in the apple leaf may be reduced to an appreciable extent before stomata begin closing, "in some tests being approximately 5 to 7 per cent. higher at the time of stomatal opening than at the time of stomatal closing." He further states that under orchard conditions the early closing of stomata has proved to be about the best indication of the beginning of water shortage. Stomata, in most cases, were more sensitive to water deficiency than was the growth rate of the fruit.

With the type of soil used here (moisture equivalent of 38.4 per cent.; wilting coefficient of 15.55 per cent.) it is clear that there may be marked reductions in photosynthesis and transpiration and an increase in respiration before wilting in the apple is apparent. The length of time before wilting that these reductions may take place is dependent obviously upon the evaporating power of the air (experiments I (80°), II (90°), and III (100° F.)) and the mass of soil about the roots as well as the soil structure. The results presented here are in accord with those of LEWIS, WORK, and ALDRICH (16) who report in the case of heavy soils at Medford, Oregon, that fruit and tree growth were reduced significantly before soil about the majority of the roots of pear trees reached the wilting point. They state that fruit growth was reduced whenever soil moisture content fell below 70 per cent. of the available capacity. In case of the lighter soils (wilting coefficient of 8 to 10 per cent.) in California, however, HENDRICKSON and VEIHMEYER (12) have pointed out that fruit and tree growth were not reduced if the soil moisture remained about one per cent. or more above the wilting coefficient. HOWLETT (13) also states that with the Wooster Silt Loam (wilting coefficient of 7.5 to 8.0 per cent.) he was unable to detect any significant reduction in rate of fruit growth in the apple as long as the moisture was above the wilting coefficient.

It is generally considered uncertain that stomata are tightly closed even though they appear so under the microscope; it is interesting, however, to

note that on several occasions in these experiments we have obtained fairly high rates of photosynthesis when the stomata appeared to be completely closed. In his work with corn, SAYRE (19) has pointed out from considerable experience in the field where the "ultrapak" microscope was employed that "there is no close relation between stomata and photosynthesis in corn and that maximum photosynthesis can go on in the absence of open stomata." BERNBECK (1) also found that stomatal opening and photosynthesis operate independently under conditions of moderate water deficiency.

The time required for a wilted plant to recover to normal leaf activity after it has been watered is correlated, as one would expect, with the severity and length of the drought period [experiments II and III, and in the field (fig. 3)]. In experiment II, when the test plant was allowed to remain wilted for several days before watering, transpiration returned to approximately normal within 4 days while respiration and photosynthesis did not show complete recovery until the sixth and seventh day. In experiment III, where the plant was allowed to wilt only a single day, photosynthesis, transpiration, and respiration recovered within a day or two after the watering. Test plants in the field (fig. 3) were allowed to remain wilted for about two days and until several of the lower leaves on the shoots showed scorching and abscission before they were supplied with water. The time required for photosynthesis to recover was about two days. It should be pointed out that these reductions in leaf activity which persisted after water was supplied to the wilted plants, occurred even though the plants regained full turgidity within a few hours after watering. ILJIN (14) who worked with *Bidens tripartita* and *Phlomis pungens* also found that photosynthesis did not recover as soon as the wilted plants regained full turgidity but continued to show reductions of 29 per cent. 16 hours after recovery of turgor.

It is the opinion of YUNCKER (22) and others that when water supply to plants is reduced, the rate of respiration is likewise reduced; this does not seem to be the case in results presented here. In every case where respiration determinations were made on drying plants there was a relatively greater amount of carbon dioxide evolved from the drying leaves until the plant was watered, after which respiration gradually recovered to its normal relationship with the control tree. This is in line with the work of SMITH (20) who removed water from the leaves of snowdrop, stem tip of *Tropaeolum*, and young stems of *Asparagus* by means of a vacuum desiccator and showed that there was an increase in respiration proportional to the amount of water lost until 30 per cent. of the water had been removed. Respiration remained about the same when water was further diminished 50 to 60 per cent. From the data in tables II, III, and IV it is evident, also, that respiration of apple leaves assumed a more or less level status after the first two- or three-day climb, then dropped back upon addition of water.



In figures 1 and 3 it is evident that when data from the field are expressed in terms of percentage, the trend in photosynthesis is not so smoothly plotted as for data obtained in the environment-control chamber. For example, in figure 3, one would logically expect a greater reduction in assimilation of the drying plant on July 21 than on the previous day, July 20, because the soil, if anything, would be drier on the second day. The reverse, however, was true: there was a 66 per cent. reduction in photosynthesis on July 20 and only a 16 per cent. reduction on July 21. This and other unexpected variations in the photosynthetic relationship between the control and the test trees in the field might be explained by the wide variations in light, temperature, and other uncontrollable factors.

### Summary

1. Determinations of apparent photosynthesis, transpiration and, in some cases, respiration were made on small apple trees while the soil in which they were growing gradually dried to the wilting percentage, after which it was watered to field capacity. The reference trees were watered at regular intervals. Experiments were performed both in the field and in a large insulated chamber where light was held constant at an average of about 4000 foot candles for all leaves concerned, humidity at about 30 per cent., and temperature at levels of 80°, 90° or 100° Fahrenheit.

2. The data show that an increase in apparent photosynthesis was associated with a slight decrease in soil moisture below the field capacity of the dark, fairly heavy soil employed in these experiments. Under temperature conditions of 100° F. this period of increase in photosynthesis was shorter (1 to 2 days) than when the temperature was 80° F. (2 to 4 days); this was probably due to the more rapid drying of the soil and the greater transpiration rate at the higher temperature.

3. At a temperature of 80° F. the first reduction in apparent photosynthesis occurred the fifth day after the last watering; at temperatures of 90° and 100° F. the first reduction in assimilation occurred on the third day. Ordinarily, under conditions of a gradually drying soil, there was a reduction in the rate of transpiration for at least one day before there was a reduction in photosynthesis. If evaporation conditions were low, this reduction in transpiration sometimes extended over a longer period of time before photosynthesis showed a definite decrease.

4. Before wilting was evident, there were marked reductions in apparent photosynthesis and transpiration, and an increase in respiration; in one case there was a 55 per cent. reduction in photosynthesis, a 65 per cent. reduction in transpiration, and a 62 per cent. increase in respiration. Stomata at this time appeared to be completely closed.

5. On several occasions fairly high rates of photosynthesis were obtained when the stomata appeared to be closed.

6. When the plants showed definite wilting, and the soil moisture was approximately at the wilting percentage, there was an 87 per cent. reduction in both photosynthesis and transpiration. It was not uncommon for wilted apple leaves to absorb from one to ten or more milligrams of carbon dioxide per 100 square centimeters of leaf surface per hour.

7. When water was applied to the soil in which wilted apple trees were growing, the leaves usually attained turgidity within three to five hours, depending upon their degree of wilting. They did not, however, recover to their original relationship with the controls in photosynthesis and respiration before two to seven days after the watering. Transpiration usually recovered about the same time as photosynthesis or slightly earlier.

8. The general trend of photosynthesis for the test plants was approximately the same in the field as in the environment-control chamber.

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