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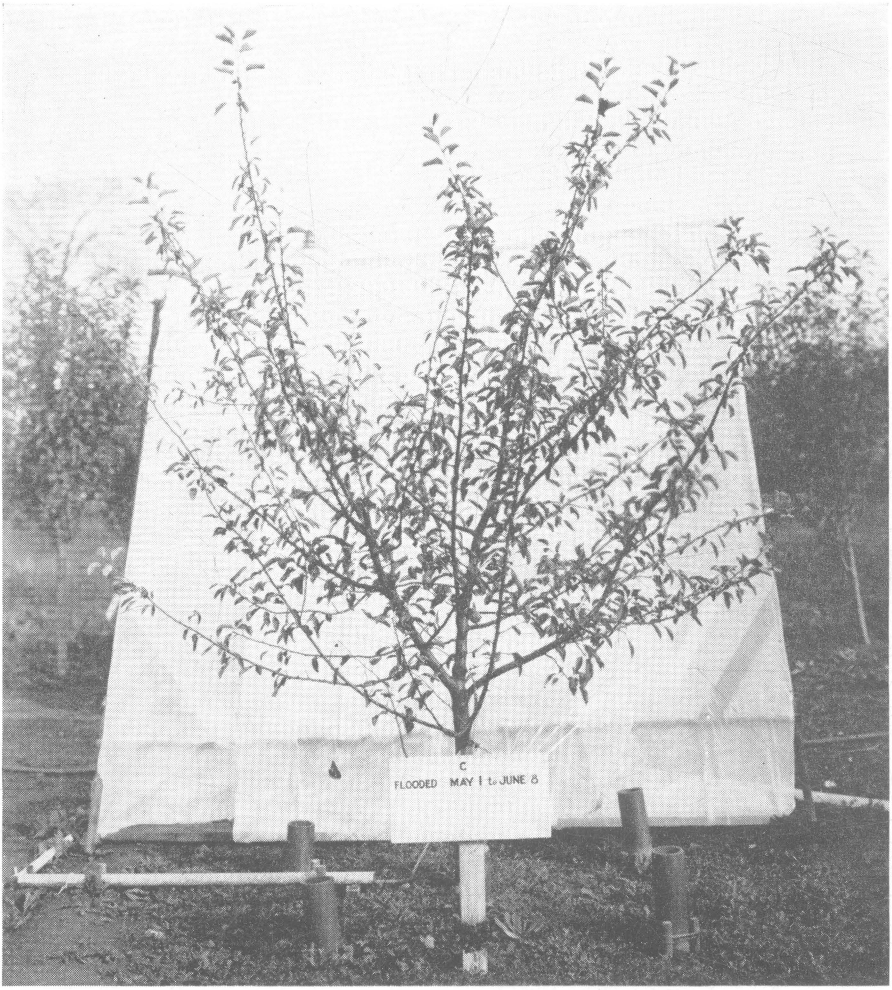
SOME PHYSIOLOGICAL EFFECTS OF EXCESS SOIL MOISTURE ON STAYMAN WINESAP APPLE TREES



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Cover Picture: The Stayman Winesap apple is easily injured by poor soil drainage. This tree was severely retarded by waterlogging the soil for five weeks during bloom and early leaf expansion.

SOME PHYSIOLOGICAL EFFECTS OF EXCESS SOIL MOISTURE ON STAYMAN WINESAP APPLE TREES

SUMMARY

by

Norman F. Childers[1] and David G. White

There are spots in most commercial orchards where soil drainage is not good, particularly following the winter snows and spring rains. Sometimes entire orchards are located on poorly drained land where the soil becomes more or less saturated with water at the critical time of blossoming and leaf expansion. Eventually the water recedes and the soil will appear to be properly drained for the balance of the season. Under conditions of extended waterlogging, the trees may be killed outright, whereas temporary waterlogging in the spring may be repeated for several years before the trees begin to show clear-cut symptoms of poor drainage. Such factors as variety, soil type, length of period of root submersion, and climatic conditions are interrelated in determining how soon the effects of waterlogging become visible.

Under conditions of excess soil moisture, water occupies practically the entire pore space which ordinarily contains about half air and half water. Due to little or no oxygen supply, the roots are unable to carry on this usual rate of respiration. After several days or weeks of waterlogging, the roots lose their capacity to absorb and translocate sufficient water and mineral nutrients to the tree top for proper leaf functioning and good growth. Generally, it is necessary to observe the soil drainage conditions during and immediately after heavy rains in order to properly diagnose symptoms which develop later. Symptoms of excess soil moisture usually begin to appear in early or midsummer and often resemble those caused by nitrogen and/or water deficiency. The yellowish-green leaves may show some marginal and tip burning; they are small and abscise early; shoot growth is weak and ceases elongation early in the season; the bark has a light green or yellowish cast; the overall foliage appears thin both in thickness and number of leaves; blossoming is usually heavy, followed by a light fruit set; and the fruits are small with somewhat high color, dropping early. The trees may linger in a weak condition for several years, or they may be weakened to such an extent that they die at an early age. Weak trees are a liability.

Experiments described in the foresection of this bulletin deal with the effects of submerging the roots of potted young apple trees on their rates of transpiration, apparent photosynthesis, and in some cases,

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apparent respiration. Although some tests were made outside the greenhouse, the studies for the most part were performed under controlled conditions. In several experiments, the determinations were continued after the excess water had been drained from the soil in order to deter-

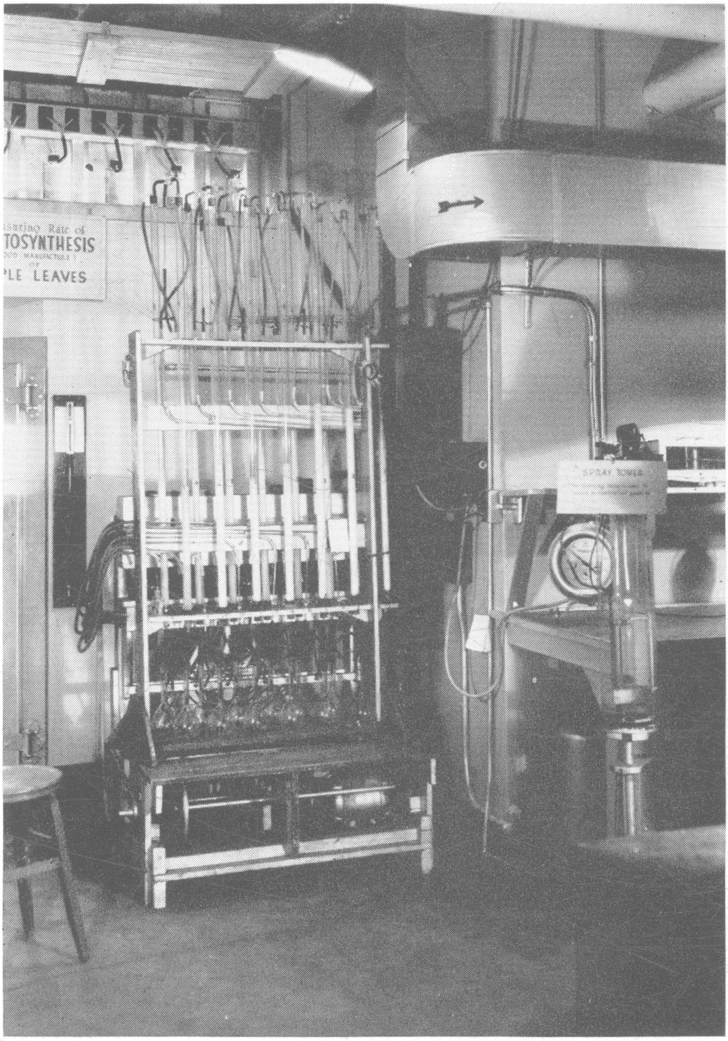


FIGURE 1.—Outside view of controlled-environment chamber used in root submersion studies. Photo shows entrance door at the left, light loft above, Heinicke-Hoffman photosynthesis apparatus in the center, switch boxes and relays to the right, and hot air exhaust from battery of lights at upper right.

mine how soon, if ever, the leaves recover in activity. These experiments reported in part or in detail elsewhere (5, 6, 22) are summarized here and combined with data for orchard trees to give a more complete picture of the effects of poor soil drainage on the Stayman Winesap apple. The Stayman Winesap was selected because it is commercially important in Ohio and also because it appears to be easily damaged by excess soil moisture.

LITERATURE REVIEW

Comparatively few studies have dealt with the effects of submerging the roots of plants on the phsyiology of the leaves. Heinicke (12) studied the effects of submerging the roots of potted McIntosh trees at different seasons of the year. He concluded that apple roots can be submerged from late fall before the ground is frozen to late spring after the ground is thawed without causing apparent injury to the tree. He states, "If the water is drained from the trees before there is any appreciable growth, there seems to be no ill effects from the treatment. On the other hand, if there is any leaf surface present while the roots are still submerged in water, there is likely to be severe damage, provided the trees remain in water for more than two weeks and also provided they are exposed to high temperature or other conditions which cause excessive transpiration". Roots injured by submergence were black in color and had but few rootlets. Leaves were small, light green, and with yellow-browned margins. Injury to leaves of submerged trees was most severe on hot days.

Loustalot (19) demonstrated the influence of waterlogging the roots on apparent photosynthesis and transpiration of young pecan trees. Seedlings were grown in 5-gallon crocks filled with coarse sand and supplied with nutrient solution. Another group of seedlings were grown in crocks in soil. Analyses were made with the Heinicke-Hoffman apparatus (14) similar to that described later. Roots of test trees were submerged with either a nutrient solution or tap water and within five days there was a substantial reduction in apparent photosynthesis. Reductions were greater in afternoons than in mornings. Photosynthesis of leaves of a flooded pecan tree in sand was reduced to a low of 11 percent of its expected rate after 31 days of submergence, whereas apparent photosynthesis of a tree in soil stopped after 20 days of flooding. When excess water was drained, there was a gradual increase in the rate of apparent photosynthesis of both trees and after 12 to 13 days the rates were at their expected pretreatment level. Transpiration rates increased as much as 25 percent above their pretreatment level 4 to 5 days after flooding the trees in sand. Transpiration rates thereafter decreased to about half the expected rates until the excess water was drained when there was a gradual recovery. About 12 days after removing excess water, transpiration rates were again at their expected pretreatment level.

Heinicke, Boynton, and Reuther (13) flooded a mature Northern Spy tree at Ithaca, New York from August 25 to November 14, 1938, and from April 15 to August 11, 1939. Leaf curling, incipient marginal browning of the leaves, and cork development in the fruit tissues were apparent during the 1939 season. Some foliage turned yellow, browned and dropped. Small rootlets were killed and the large roots developed dark colored marks. Flooding caused a reduction in percentage of ash in the dry matter and a reduction in the percentage of boron, potassium, and nitrogen in the leaves. This work showed that the under flooded conditions, deficiencies of nutrients in an apple tree may be accentuated in spite of the fact that the elements are present in the soil. If the soil is waterlogged and the oxygen is unusually low, nutrients are evidently absorbed in much smaller quantities. These conclusions are in accord with those of Hoagland and Broyer (16) who reported that less ash was absorbed from poorly aerated culture solution.

Numerous studies have been conducted on the effects on growth of various degrees of aeration of the roots of many different plants (2, 7, 8, 10, 17), but no attempt will be made here to give a complete review of these studies. Two recent experiments, however, are closely related to the work reported here. DeVilliers (10) grew McIntosh apple seedlings

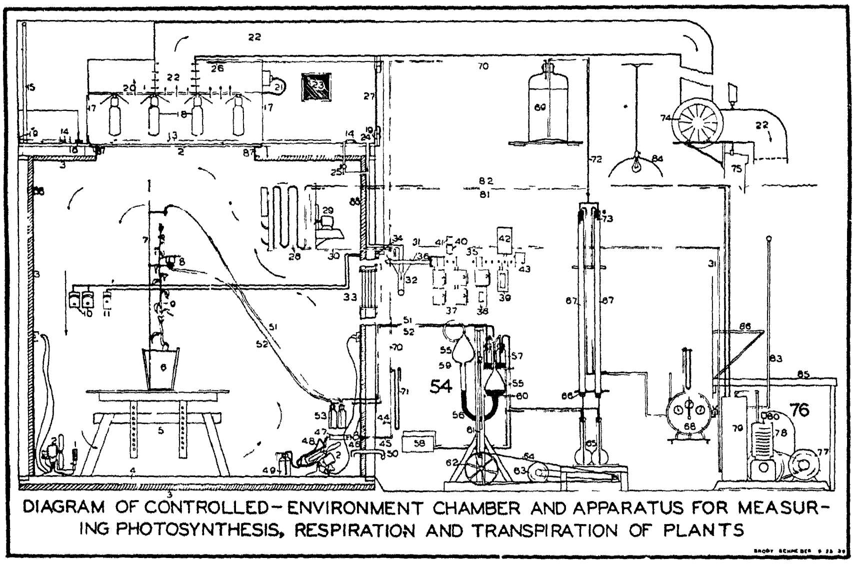


FIGURE 2.—**Diagrom of environment-control chamber (left), and Heinicke-Hoffman photosynthesis apparatus (center right) used to determine the rates of apparent photosynthesis, respiration, and transpiration of potted apple trees (see accompanying key to diagram and Figure 1).**

Key to Figure 2

1. Heating coil
2. 12-inch oscillating fan
3. 2-inch cork insulation
4. Concrete floor
5. Adjustable bench
6. 5-gallon container
7. Leaf-cup support
8. Leaf-cup
9. Stayman Winesap shoot
10. Thermostats
11. Humidistat
12. ½-inch plate glass
13. Water bath
14. Water level baffles
15. Water bath inlet
16. Mercury electrodes
17. Light hood
18. 1000-watt lamps
19. Galvanized iron tank
20. Light support
21. Light cord
22. Warm air exhaust flue
23. Cold air inlet
24. Water bath overflow
25. Water bath drain
26. Expansion bulb for thermostat
27. Light-loft door
28. Expansion coil
29. Expansion coil fan
30. Condensation drain
31. Compressor coil drain
32. General drain
33. Compound window
34. Emergency thermostat
35. 1000-watt lamp, switches
36. Master switch for lamps
37. Fuse boxes
38. Refrigerator control box
39. Exhaust fan control box
40. Refrigerator relay
41. Expansion coil fan relay
42. Automatic master switch
43. Transformer
44. Compressed-air supply
45. Compressed-air for No. 48
46. Solenoid valve
47. Oil trap
48. Glass atomizer
49. Water supply
50. Fresh air to chamber
51. Fresh air line
52. Leaf-cup air lire
53. Transpiration bottle
54. Mercury-piston pump
55. Leveling bulb
56. 1-inch rubber tube
57. Automatic mercury valve
58. Pressure-stabilizing can
59. Oscillating shelf
60. Stationary shelf
61. Connecting rod
62. Crank wheel
63. ½-HP motor
64. Chain drive
65. 500 cc. volumetric flask
66. Jena-glass filter crucible
67. Carbon dioxide absorption tower
68. Wet-test air meter
69. Distilled wash-water
70. Compressed air to No. 69
71. Open-end manometer
72. Wash-water line
73. Wash-water nozzle
74. Warm air exhaust fan
75. Masonry wall
76. 1-HP methyl compressor
77. Compressor motor
78. Compressor block
79. Storage tank
80. High-pressure cut-out
81. Expansion-coil feed
82. Refrigerant return
83. Cold water to compressor
84. 200-watt light
85. Work table
86. Shelf
87. Caulking
88. Aluminum-coated paper
89. Refrigerator door
90. Door in light hood

with roots in various concentrations of oxygen. Low oxygen supply to the roots resulted in reductions of root growth, leaf area, total weight of the plant, and percent of ash. Childs (7) studied the influence of oxygen and carbon dioxide supply to the roots on apparent photosynthesis and transpiration of young McIntosh and Delicious apple trees growing in a sandy loam soil. Growth of the trees was retarded when the soil air was maintained with slightly less than 12 percent oxygen. However, the rates of apparent photosynthesis and transpiration did not decrease until the oxygen was less than 2 percent, below which both processes showed marked decreases. Apparently the concentration of carbon dioxide in the soil air had no measurable effect under the conditions described by Childs.

Methods and Materials

The apple shoots used in these experiments were grown from 2- and 3-year stocks grafted on French Crab roots. The terminal buds had set on all trees by the time the experiments were initiated, with the exception of the shoots used in Experiment VI. The young trees were grown in 5-gallon crocks or slightly larger wooden butter tubs in the greenhouse. A Brookston clay loam topsoil taken from the Ohio State University orchard was used for potting. No attempt was made in these experiments to correlate the soil type with the effects of root submergence. The term "excess water" as used here infers that water constantly

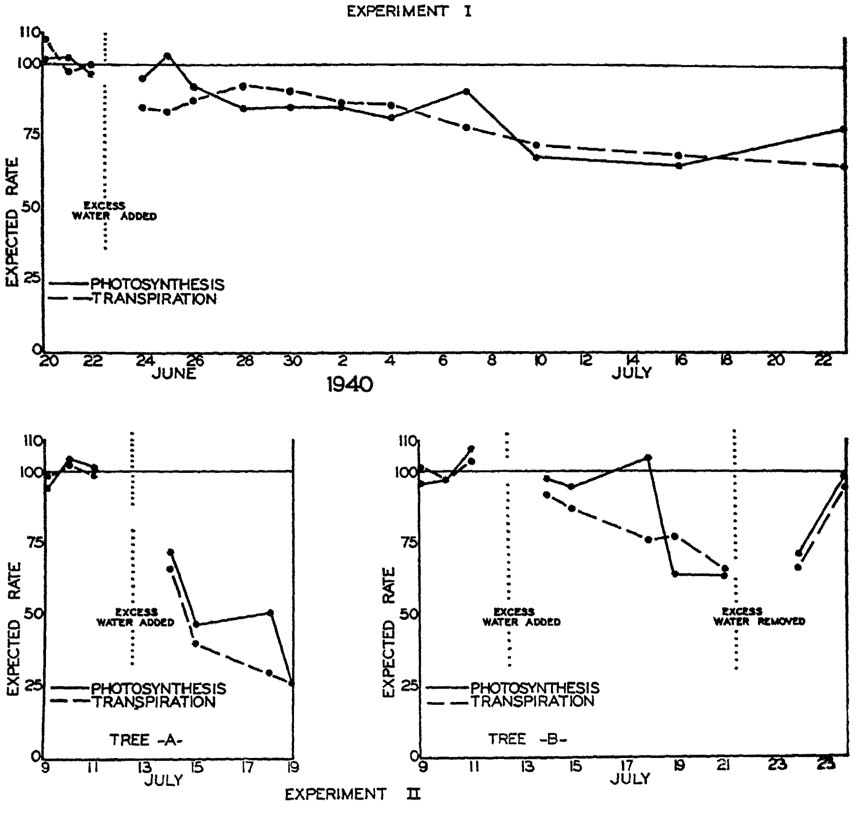


FIGURE 3.—Experiment I was performed in the environment-control chamber; Experiment II was out-of-doors, using leaf cups in both cases. Data are presented as percentage of expected rate before and after excess water was added to the soil. The drop in apparent photosynthesis and transpiration due to root submersion was more rapid out-of-doors than in the the environment-control chamber.

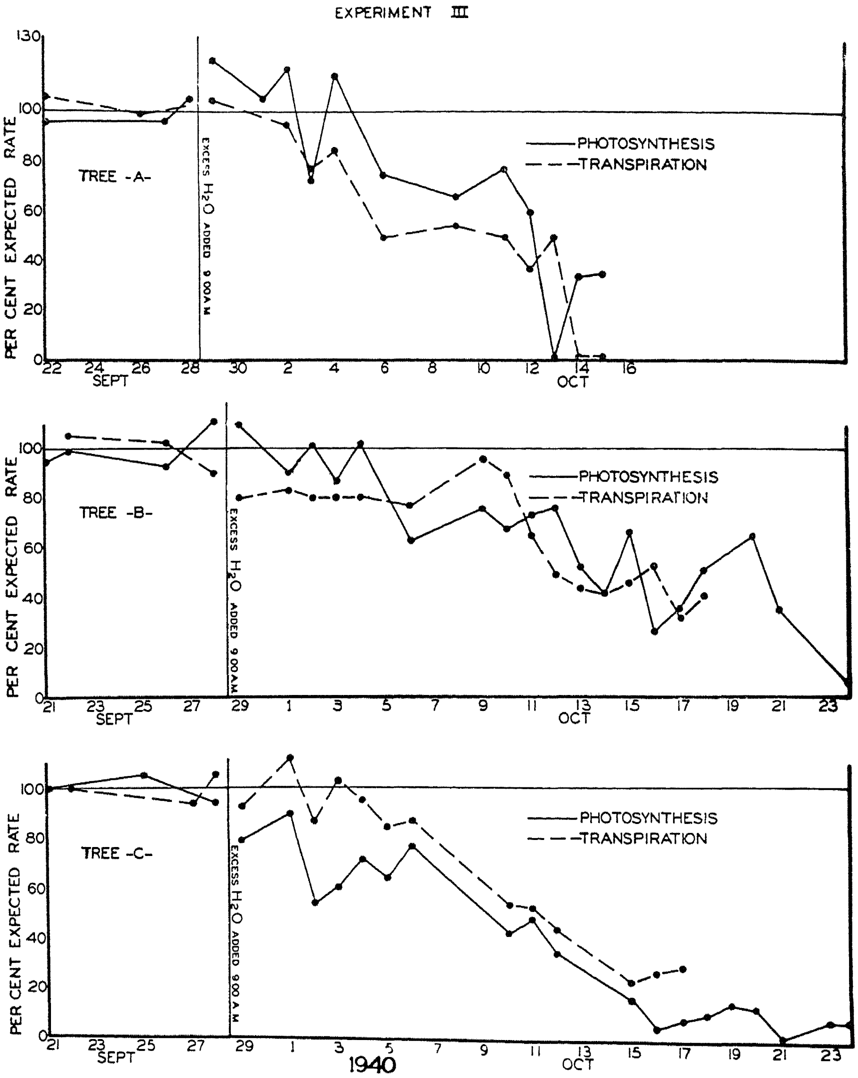


FIGURE 4.—Experiment III, performed out-of-doors during the cool autumn season, using leaf cups. Reductions in transpiration and apparent photosynthesis after root submersion was similar for Trees A, B, and C.

stood above the soil surface. Check trees were watered daily or once every two days in order to maintain a favorable moisture supply in the soil. The Heinicke-Hoffman apparatus (4, 14) was employed for measuring the rates of transpiration and apparent photosynthesis or respiration. (Fig. 1). Leaf cups were used in all tests except Experiment VI where

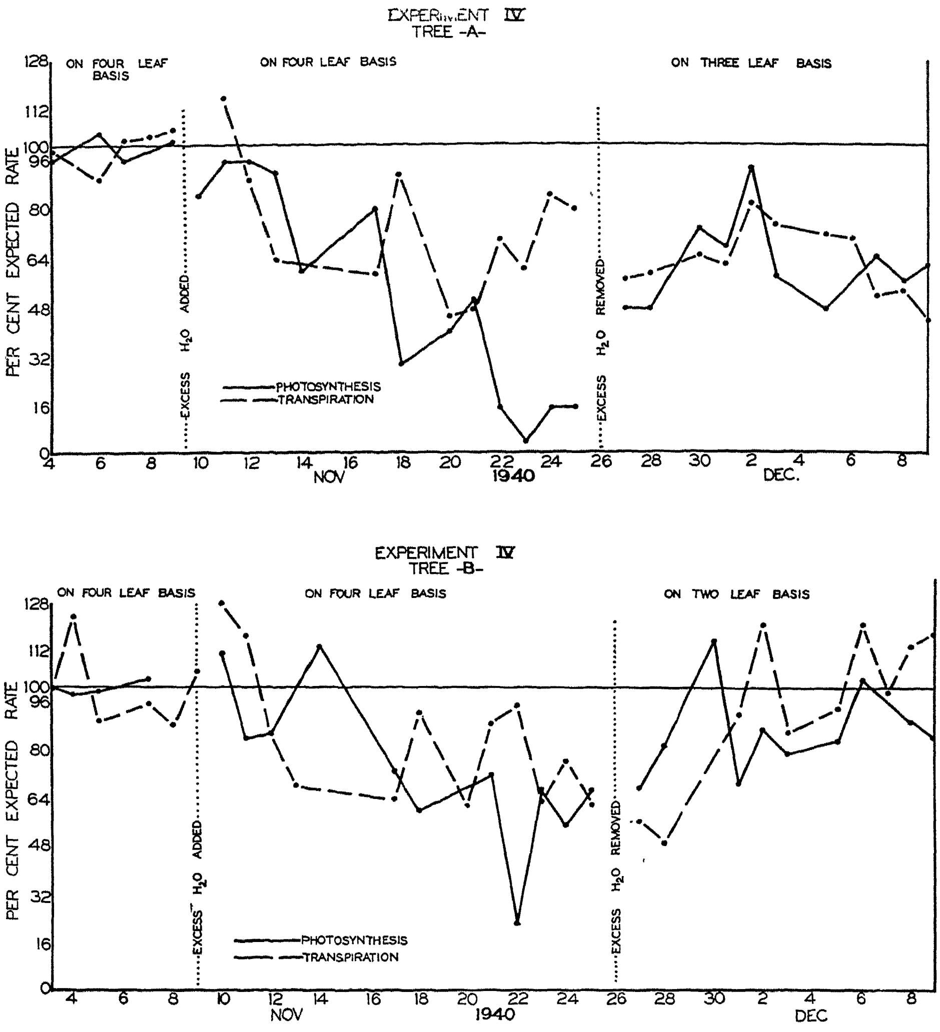


FIGURE 5.—Experiment IV was performed in the environment-control chamber (leaf cups were used). Trees A and B were subjected to excess soil moisture for 18 days, after which water was drained. Leaf activity of Tree A was affected more during and after submersion of the roots than Tree B. See Figure 9 for stomatal behavior of these trees.

Pliofilm hoods were employed over entire shoots. Each determination lasted for a period of 2½ hours.

Four series of experiments were performed in the environment-control chamber (4) (Fig. 2) on a total of ten trees, and two series were performed outside the greenhouse on a total of five trees. Temperature in the chamber was held nearly constant at levels of 80° and 85° F. The vapor pressure was automatically maintained at 16 mm. of mercury, and light averaged between 5000 and 2000 foot candles at the surface of the leaves, depending upon their distance from the battery of lights.

The temperature and relative humidity for the experiments conducted outside the greenhouse were averaged from three measurements at the beginning, middle, and end of each determination. A sling psychometer was used to determine the dew point which was then converted to vapor pressure by use of psychrometic tables (20). Average foot candles of light outside was calculated from the records of a Micromax continuous light recorder connected with a photoelectric cell in the immediate vicinity of the test trees.

Method of Data Caculation. The percentage of expected rate of apparent photosynthesis was calculated as follows: The average milligrams of carbon dioxide absorbed by the proposed test leaves was divided by the average milligrams absorbed by the proposed check leaves. The quotients multiplied by 100 expressed the percentages relationship between test and check leaves before treatment. The average of these percentages found before the treatment began was then considered as 100 percent, or, in other words, this was the rate which the proposed test leaves would be expected to maintain if they were not affected by treatment. Thereafter, the percentage relationships between check and test trees were divided by the average percent relationship of the pretreatment period and multiplied by 100. These products are plotted as percentages of expected rates for each experiment. A typical set of data are presented in Table 1. Apparent respiration and transpiration were calculated in a similar manner.

DISCUSSION OF RESULTS

Apparent Photosynthesis, Respiration, and Transpiration. It is apparent from Figures 3 to 8, inclusive, that submersion of the roots in water caused reductions in apparent photosynthesis and transpiration within 2 to 29 days, usually within 2 to 7 days after submersion. In some cases, the rates of transpiration and apparent photosynthesis became so small with continuous root submersion that they could not be measured with the apparatus employed. When excess water was drained from the soil after a period of submersion, transpiration and apparent photosynthesis of the leaves of some trees recovered to approximately their pretreatment rates within a period of about a week, whereas other trees showed little or no recovery. The ability of a tree to recover after waterlogging treatment is no doubt dependent upon the initial vigor and character of growth, the length of the submersion period, as well as upon the climatic conditions to which the tree is subjected during the submersion period. Certainly, temperature is an important factor influencing injury to a tree by root submersion. With other climatic conditions favorable, the higher the temperature, the quicker and the more severe the damage to the tree.

In these tests, it was not possible to show a correlation between stomatal activity during the day and the reduced rate of photosynthesis due to root submersion. Where the effect of root submersion on upper young leaves and middle mature leaves of apple shoots was studied (Fig. 6), there was some indication that the apparent photosynthesis of the upper leaves was affected somewhat more than that of the middle leaves; transpiration of the upper and middle leaves seemed to be affected to about the same degree.

In a study of the effects of root submersion on apparent respiration and transpiration of apple leaves in the dark, it was evident that root submersion caused an increase in apparent respiration and a decrease in transpiration (Fig. 7). This increase in carbon dioxide emitted by the leaves as a result of root submersion helps to explain to some extent the reduced rate of apparent photosynthesis of the same leaves in light. When the temperature of these leaves was measured with thermocouples, there appeared to be no difference in the temperature of leaves of trees which were submerged and those which were watered in the usual manner.

By comparing the graphs in Figure 8, it is evident that the rate of leaf development near the tip of a shoot is affected somewhat sooner than the apparent rate of photosynthesis of these same leaves. The condition of the check and test plants at the end of this experiment is shown in Figure 9.

Tree Symptoms of Excess Soil Moisture. Basal leaves of submerged plants showed the effects of excess soil moisture first. These leaves turned yellow or brown and abscised. In some cases, light green areas developed between the leaf veins, and the foliage wilted and drooped at the distal ends of the petioles. In case of the three trees subjected to the outside cool autumn temperatures, as presented in Figure 4, there was a greater development of the anthocyanin pigments in the leaves of the submerged trees. With other trees placed outside the greenhouse in July, marginal leaf burning occurred within 8 days after submerging, apparently because of the high temperatures. The data for these trees is shown in Figure 3. The leaf blades in this experiment curled upward at the margins on the upper leaves, but the leaves did not droop. The symptoms of leaf injury which appeared were similar to those described by Heinicke, Boynton, and Reuther (13) for a flooded orchard tree.

TABLE 1.—The Average Rates of Apparent Photosynthesis and Transpiration of Potted Stayman Winesap Shoots in an Environment-control Chamber. Roots of the Test Tree Were Submerged on June 23, 1940.

Experiment I

Date	Apparent Photosynthesis				Transpiration			
1940	Carbon dioxide absorbed per 100 sq. cm. per hour		Daily relation of test to check	Percentage of average expected rate	Water transpired per 100 sq. cm. per hour		Daily relation of test to check	Percentage of average expected rate
	test	check	$\frac{A}{B} \times 100$	$\frac{C}{112^*} \times 100$	test	check	$\frac{E}{F} \times 100$	$\frac{G}{106^*} \times 100$
	A	B	C	D	E	F	G	H
	mgr.	mgr.	percent	percent	gm.	gm.	percent	percent
Average			(112*)				(106*)	
June 23	Roots of test tree A submerged							
June 24	22.48	21.16	106	95	2.63	3.05	86	81
25	24.50	21.25	115	103	2.59	3.09	84	79
26	27.09	26.35	103	92	2.98	3.24	92	87
28	24.57	26.19	94	84	2.84	2.98	95	90
30	19.33	20.20	96	86	2.87	3.06	94	89
July 2	16.11	17.00	95	85	3.00	3.36	89	84
4	18.63	20.40	91	81	2.38	2.68	89	84
7	17 29	17.17	101	90	2.67	3.28	81	76
10	15.45	20.25	76	68	2.72	3.62	75	71
16	10.37	14.26	73	65	2.11	3.02	70	66
23	14.87	16.59	90	80	2.17	3.24	67	63

*Average expected rate before beginning treatment.

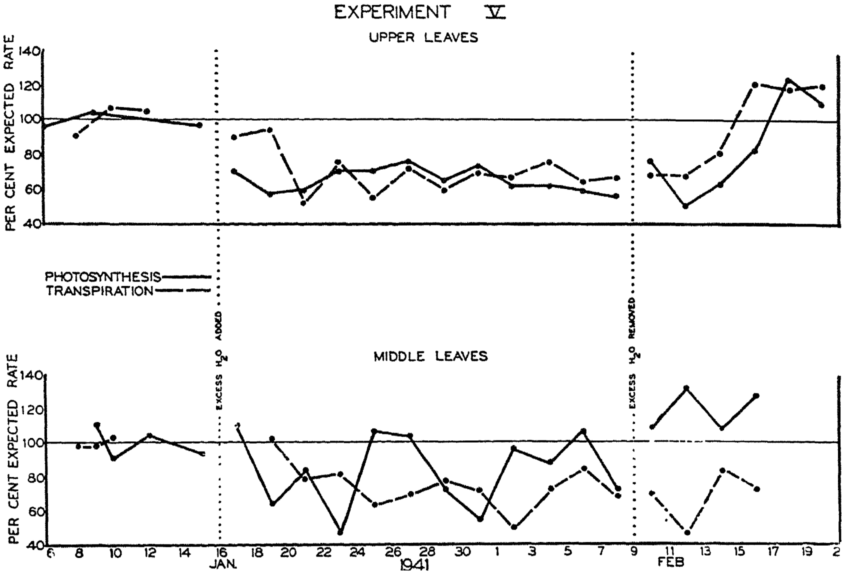


FIGURE 6.—Effect of root submersion on transpiration and apparent photosynthesis of young upper and middle mature set of leaves on 1-year tree in Experiment V (leaf cups were used; see Figure 2).

Root Growth. Root growth of apple seedlings planted in glass-sided boxes was studied both for trees with roots submerged and those to which water was added regularly but not in excess. Results are based on the linear growth of over 300 visible roots appearing against the glass sides. Submersion of the roots under these conditions inhibited the formation of new roots, but did not cause an immediate reduction in the linear growth of roots already present. These results are in agreement with those of Boynton (3) who concluded that a higher level of oxygen may be necessary for the production of new rootlets than for the maintenance of existing roots. Apple rootlets under normal conditions in studies reported here grew from 2 to 4 mm. a day and occasionally 1 cm.: they lived only about one week (Fig. 10). After 18 days of submersion, all visible roots against the glass sides were dead. The free water was drained from the soil and within eight days after drainage, new root tips were evident close to the soil surface, and within two weeks, new root tips were apparent at all soil depths.

Root Respiration Studies. In connection with root submersion studies, it was deemed of interest to know how the respiration rate of roots responded to root submersion or to treatments resembling submersion. For this study, Stayman Winesap apple trees were grown in 5-gallon glazed stone crocks, as shown in Figure 11. Pea-size quartz gravel was used for a rooting medium and a full nutrient solution (16) was pumped to the root system once a day until the tests began. At this time, the top of the crock was sealed with layers of cheesecloth, quarter-inch galvanized cloth, and grafting wax. By the system shown in Figure 12, it was possible to pump the nutrient solution into the crocks and to force the air out of the crocks and into a trap bottle from which small air samples were withdrawn for analyses with a Haldane gas analysis apparatus (11). As the nutrient solution drained back into the bottle, the air was returned to the gravel medium. Thus, the air could be stagnated by being used repeatedly by the root system for several days. Such a situation might resemble poor soil drainage and poor aeration under field conditions. With this equipment, it was possible also to submerge the roots for given periods of time in the nutrient solution, thus giving some idea of how the root system reacted before and after root submergence.

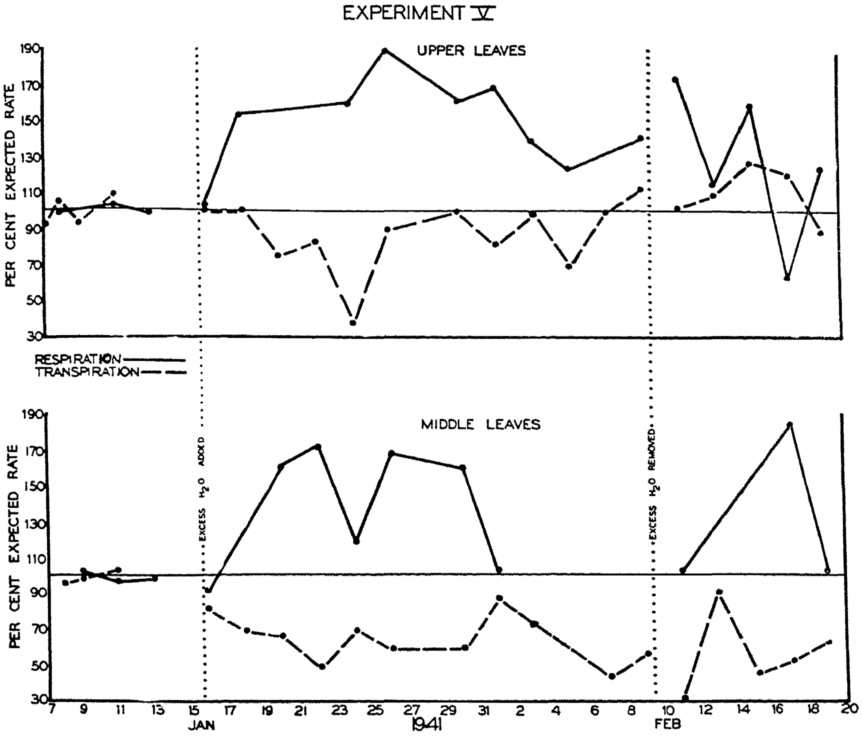
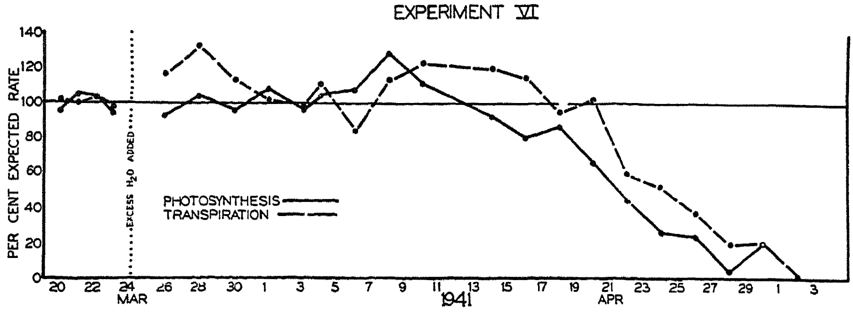


FIGURE 7.—Transpiration and apparent respiration of upper and middle set of leaves of a submerged and check tree for which data are given in Figure 6, Experiment V. Note increase in apparent respiration and decrease in transpiration after root submersion.



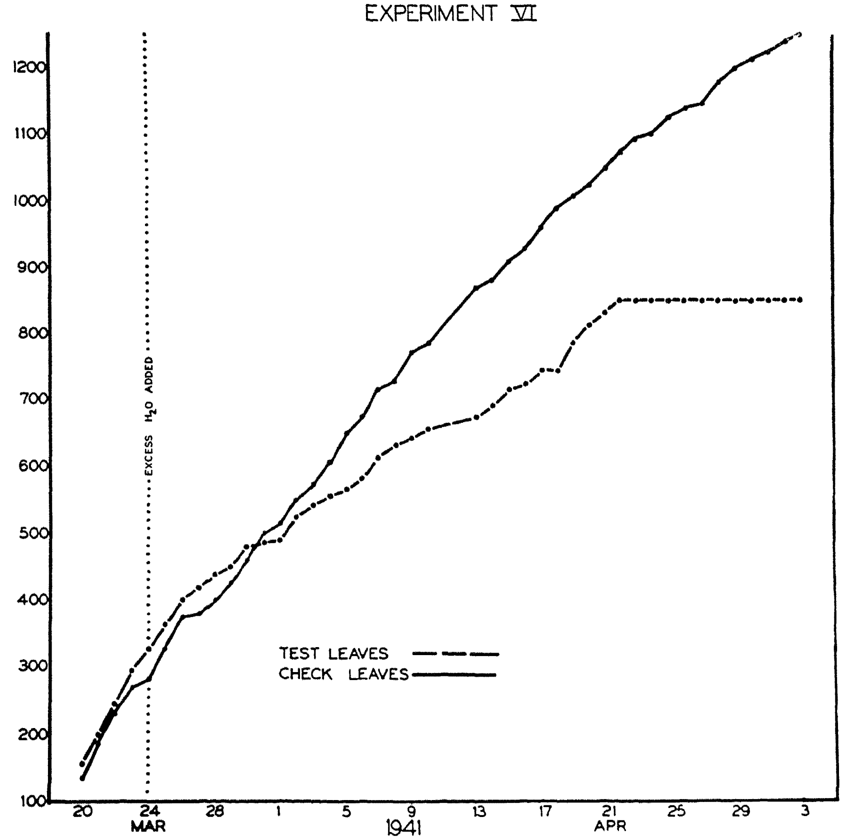


FIGURE 8.—(Upper chart) Transpiration, apparent photosynthesis, and (lower chart) increase in leaf area of young leaves on apple shoots in Experiment VI. Pliofilm hoods were used. Root submersion checked the rate of increase in leaf area of young shoot leaves before a reduction occurred in apparent photosynthesis and transpiration. See Figure 10 for condition of trees at end of experiment.

Figure 12, A and B, show typical tests where the same air was supplied to the root system over a period of about a week, after which fresh air was added, and the procedure repeated. In Test A, root respiration was not noticeably affected until after four or five days, whereas in Test B, root respiration was affected within two days.

Figure 12C shows the reaction of the root system when it was submerged for a period of four days from December 8 to 12, 1941. When the water was drained from the crock and fresh air admitted, the rate of root respiration almost doubled as in Test A, but as the same air was used over and over again, the rate of respiration gradually dropped.

Figure 12D is typical of several similar tests which showed that if apple roots were supplied the same air day after day, they have the capacity to reduce the oxygen supply to about 1 or 2 percent and increase the carbon dioxide content to between 8 and 10 percent, after which the trees begin to show the same symptoms associated with waterlogging.

It will be noted that the rate of respiration of the root system is not adversely affected when the air surrounding it is allowed to stagnate over a period of about a week. The capacity of the root system to carry on normal respiration, however, is eventually retarded considerably due apparently to a low oxygen supply. The buildup of carbon dioxide around the root system also may have a detrimental effect on the apparent respiration rate and account in part for the reduced rate in stagnated air.

EFFECT OF GROUND WATER TABLE ON ORCHARD TREES

Methods and Materials

The Stayman Winesap trees used in this study were growing on French Crab roots, and had been interplanted in the Ohio State University orchard in the autumn of 1936 with Jonathan, Golden Delicious, and Rome Beauty. Planting distance was 10 feet in the row and 20 feet between rows. The soil was Brookston clay loam with a hardpan at a depth of about 30 inches. The moisture equivalent of the soil varied as follows: Between 21.0 and 23.7 percent at 0 to 10 inches, 21.8 to 24.8 at 10 to 20 inches, and 25.1 to 28.3 at the 20- to 30-inch depth. Four-inch tile had been laid in areas which were poorly drained. The trees were growing in sod and were fertilized with a nitrogenous fertilizer in the springs of 1938 and 1939. The trees received dormant and foliage sprays regularly until this experiment was started, after which the foliage sprays were applied only when necessary to control scab and red mite. Leaves used in the photosynthesis and transpiration studies were protected by bags during spray application.

During the first four years in the orchard, the trees were trained to the modified-leader system by college classes in pruning. The five trees under study, referred to as A, B, C, D, and E, were of about the same size, varying from the larger to the smaller in approximately the following order: A, E, B, D, and C. They were selected as near to one another as posible in order to facilitate the leaf activity measurements

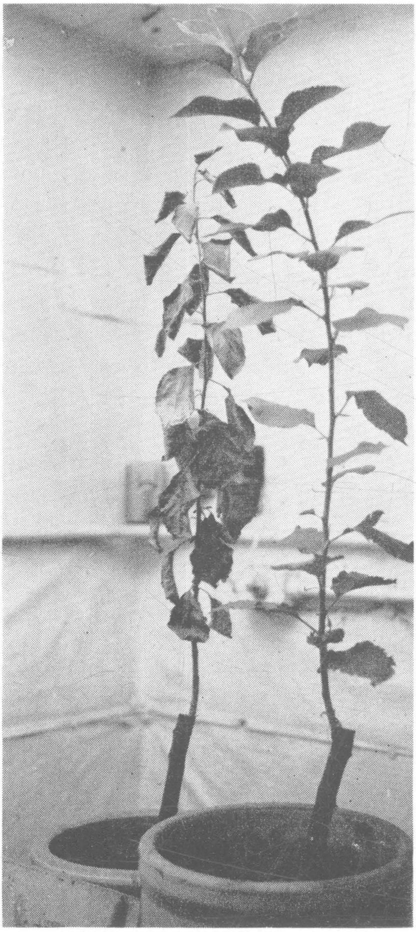


FIGURE 9.—Roots of test tree on the left were submerged in water for 45 days in the environment-control chamber; Check tree on right was watered every second day. Both trees were of equal vigor at the outset. See figure 8 for comparison of transpiration, apparent photosynthesis, and increase in leaf area of young leaves.

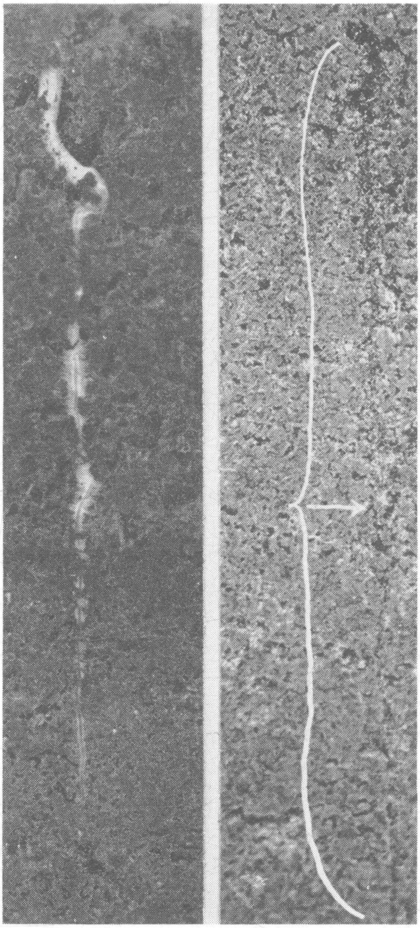


FIGURE 10.—Under favorable soil conditions, apple rootlets against glass-sided boxes (left) grew from 2 to 4 mm. a day, occasionally 1 cm., and died after about a week (note empty channel at right). Submersion inhibited formation of new rootlets but did not cause immediate reduction in growth of rootlets already present.

from a centrally-located Heinicke-Hoffman apparatus (Fig. 13). Flowering was sparse in the spring of 1941 when the test was initiated.

The treatments established on May 1, 1941, were as follows:

Tree A—Water table maintained 10 *inches* below soil surface during growing seasons of 1941, 1942, and 1943.

Tree B—Check (located next to and used as a check for Tree A).

Tree C—Flooded for 5 weeks from May 1 to June 8, 1941.

Tree D—Check (located next to and used as a check for Trees C and E).

Tree E—Water table maintained 20 *inches* below soil surface during growing seasons of 1941, 1942, and 1943.

In order to maintain the desired ground-water-table conditions, the root system of each tree, including the checks, was encased with No. 20 gauge galvanized sheet metal in a 10-foot square to a depth of 30 inches (Fig. 13). An impervious gray hardpan, about 6 to 10 inches thick, was located at 30 inches depth and served more or less as the bottom for the rooting compartments. Interlocking sleeve joints at the corners of each rooting compartment and a coat of asphalt paint were used to seal the joints and to help preserve the sheet metal.

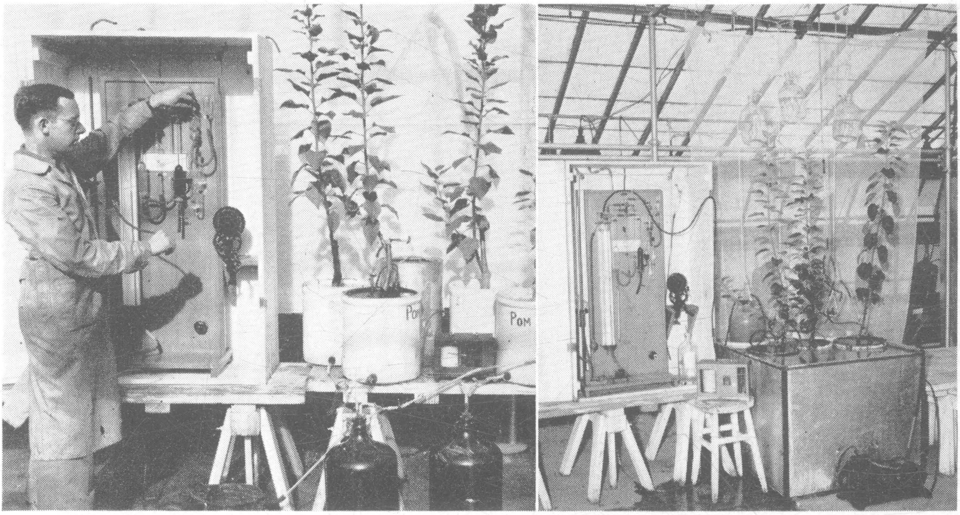


FIGURE 11.—Equipment used for root respiration studies. (Left) Stone crock at left center is sealed with grafting wax in preparation for collecting air around apple roots and analyzing with Haldane gas analyses apparatus on left. (Right) Essentially same equipment with improvement of a temperature-control bath (running tap water varied only about 1°F day and night). The drooping leaves on right tree is due to stagnated air around the roots and reduced root respiration.

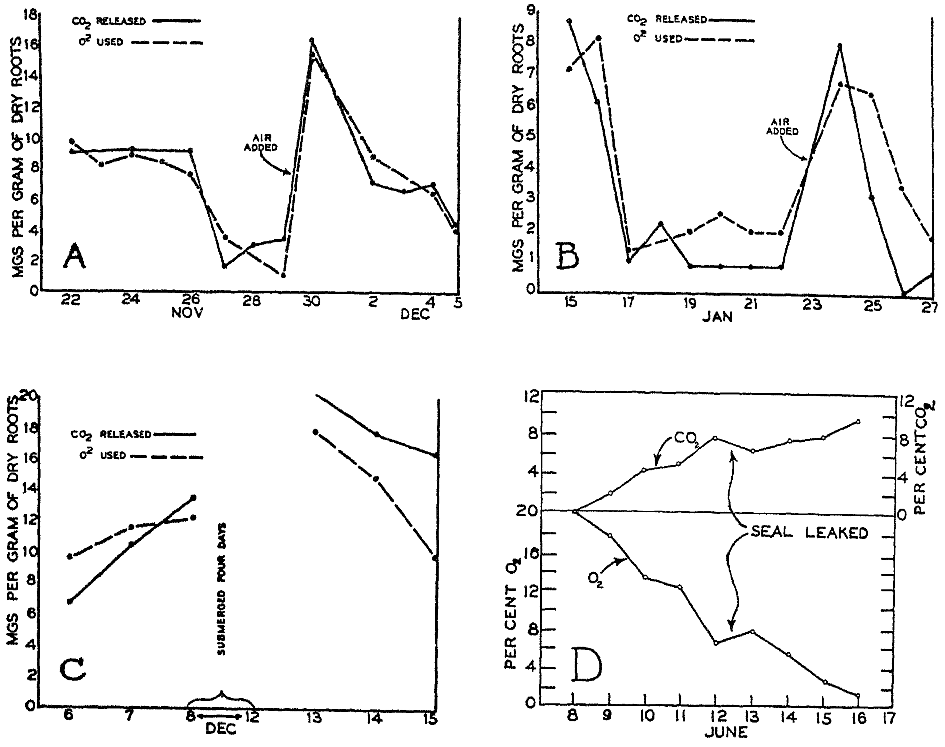


FIGURE 12.—The respiration of apple roots. In tests A and B the same air was supplied to the roots for first few days; note reduction in respiration until fresh air was admitted. In test C the roots were submerged for 4 days. In test D the daily rate of decrease in O_2 and increase in CO_2 in the air volume about the root system is shown.

The water table was maintained at the 10-inch and 20-inch levels by feeding water into five vertical 4-inch tiles which were sunk to a depth of 30 inches in each compartment. The water table in each set of tiles was maintained by an automatic watering system consisting of 50-gallon barrels and pieces of garden hose, as shown in Figures 15 and 16. The airtight 50-gallon steel drums each had a water outlet at the base and an air inlet at the top. When the water table in the tile dropped below the specified level, air entered the upper hose and permitted water to flow from the drum through the lower hose until the water level in the tile rose to the point where no further air could enter the drum. The height of the water table in the tiles did not fluctuate more than one-half inch. Periodic tube samplings of the soil indicated that the soil water table within each compartment was close to that maintained in the vertical tiles. Two or three 50-gallon drums filled twice

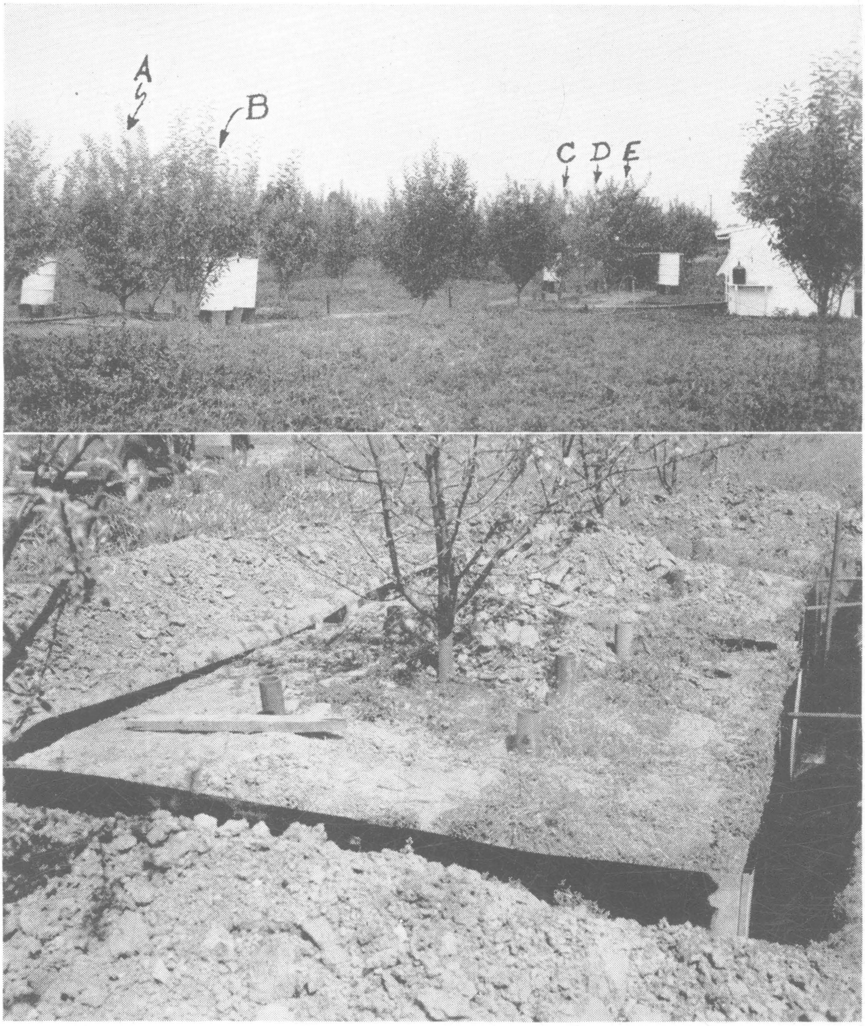


FIGURE 13.—(Above) General location of the five Stayman Winesap trees used for photosynthesis-transpiration studies in the field. Tree B is partially hidden by a Rome Beauty tree in the foreground. The shed at the right housed the Heinicke-Hoffman photosynthesis apparatus. Glass tube air-sampling lines were encased in iron pipe for protection and distributed to each test tree.

(Below) The root system of each test tree was confined in a 10-foot square area by water-tight sheet metal painted with water asphalt emulsion. The sheet metal was sunk to a depth of 30 inches to a hard-pan layer.

every 21 hours were generally required to maintain a desired water table. The source of water was from an overhead irrigation system carrying water under continuous high pressure.

The rates of apparent photosynthesis and transpiration were determined with a Heinicke-Hoffman apparatus similar to that used in the foregoing greenhouse and environment-control experiments. Six representative leaves well exposed to light on the eastern half of each tree were chosen for study. They were located about midway on the current season terminal shoots at a distance of about 5 feet above ground. The determinations usually were started at 8:30 a.m. on good days and included only one test tree and one check tree on any one day. The test leaves were enclosed in cellophane bags (14) about 3½ by 5 inches in size (Fig. 15). A glass "Y" tube and copper lead tube were taped on the shoot so that the "Y" tube was suspended in the bag just beneath the leaf blade. Glass tubing was then connected with the short copper tube to a quart fruit jar at the base of the tree where air samples from

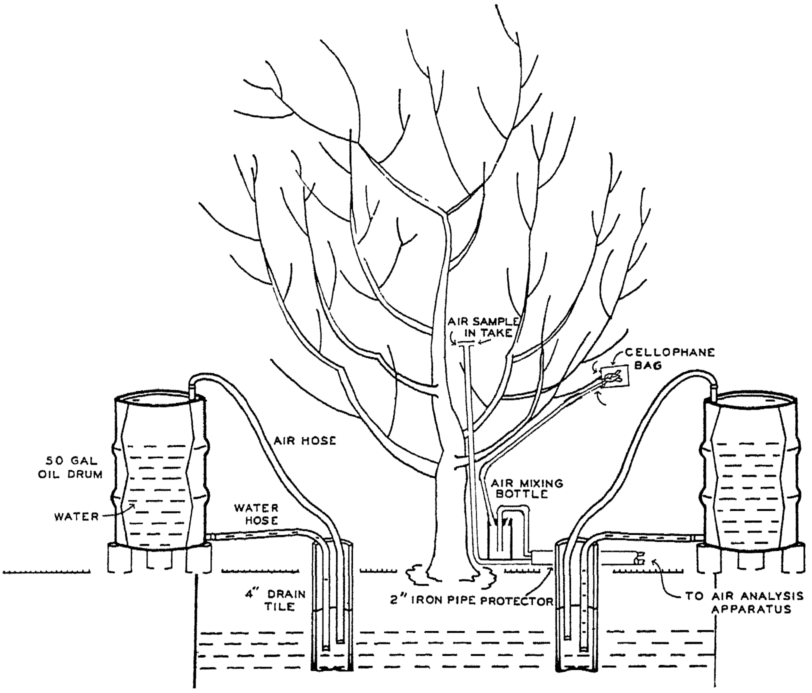


FIGURE 14.—Diagrammatic sketch of the air sampling equipment and the automatic watering system used to maintain a constant table within each rooting compartment.

all six leaves on a tree were mixed (Fig. 14). A single glass tube outlet from the quart jar led to the gas analysis apparatus in the central shed. Just before entering the shed, the air from the six leaves of each tree passed through a single quart jar and was distributed through 6 glass tubes attached to 6 transpiration bottles and 6 absorption towers. Thus, each analysis from a check or test tree had 6 replicates from which an average figure was computed. With this system of analysis, it was possible to detect readily a mechanical error in any one of the 6 towers. The average figure for each tree was based only on figures which were in close agreement.

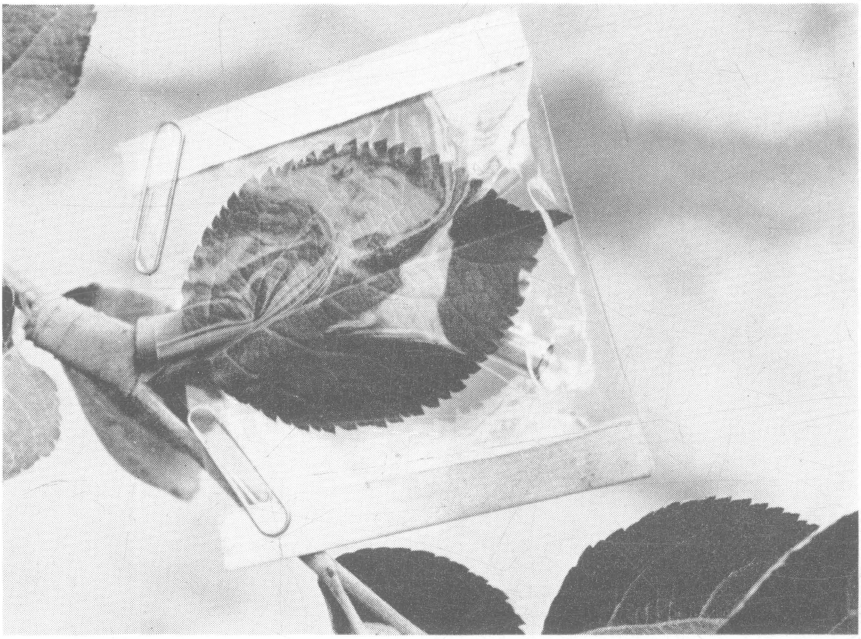


FIGURE 15.—Cellophane envelopes with paper clips (after Heinicke and Hoffman 14) were used for enclosing test leaves and collecting air samples from the orchard trees. Air entered near the leaf petiole and was sucked around the leaf into the "Y" glass tube located under the leaf.

Apparent photosynthesis of the orchard leaves was expressed in milligrams of carbon dioxide absorbed per square decimeter of leaf surface per hour. Transpiration was expressed as grams of water transpired per square decimeter of leaf surface per hour. The relative condition of the sky as to sunshine and clouds was recorded together with the average temperature during each $2\frac{1}{2}$-hour determination.

DISCUSSION OF RESULTS

Apparent Photosynthesis and Transpiration. The foliage was beginning to appear on May 1, 1941, when the treatments were started. Determinations of apparent photosynthesis and transpiration, however, were not initiated until June 28 when the leaves were fully expanded. The first determinations were made with Tree A (10-inch water table) and with Tree B (check). Differences in leaf activity between the two trees were small throughout the summer and, if anything, were slightly higher for test Tree A (Fig. 16). There was a slight decline in the rates of apparent photosynthesis and transpiration during late summer with a slight increase in apparent photosynthesis for both trees during the cool autumn days.

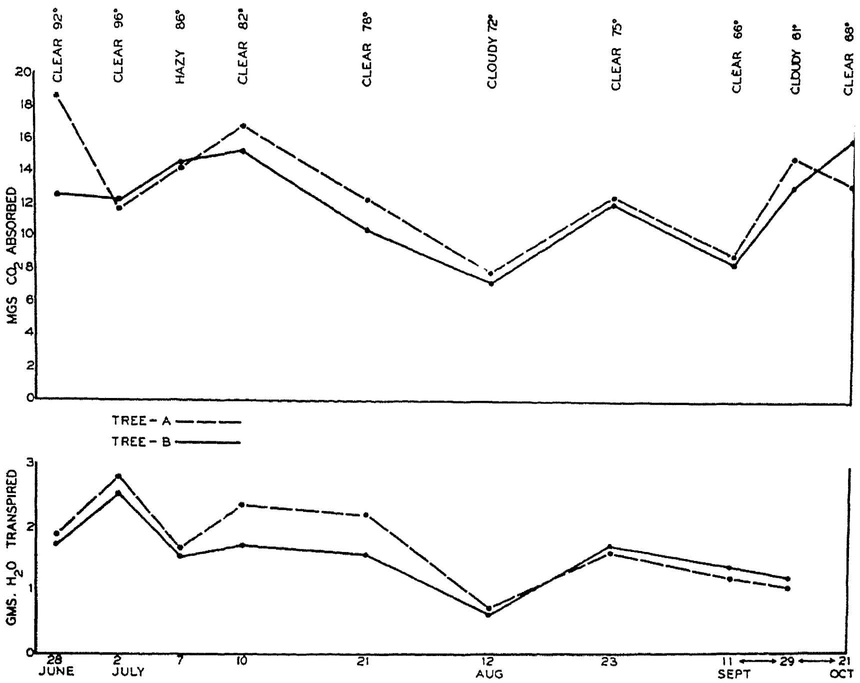


FIGURE 16.—Apparent photosynthesis and transpiration of Trees A (10-inch water table) and B (check) during the summer of 1941. There were no consistent differences in leaf activities between the two trees.

Periodic determinations of apparent photosynthesis and transpiration of orchard Tree C (flooded May 1 to June 8) were begun on June 30, together with determinations of check Tree D. By this time, the foliage of Tree C was obviously small and curled at the margins as a result of the flooding treatment. The data for these trees for the 1941 season are given in Figure 17. Rates of apparent photosynthesis and transpiration of Tree C were markedly less throughout the season than those for check Tree D; they were also the lowest of all trees under study. Tree C was in poor condition in late July, 1941.

Determinations of the rates of apparent photosynthesis and transpiration of Tree E (water table at 20 inches) were begun on July 1, 1941, and were compared with simultaneous determinations for check Tree D.

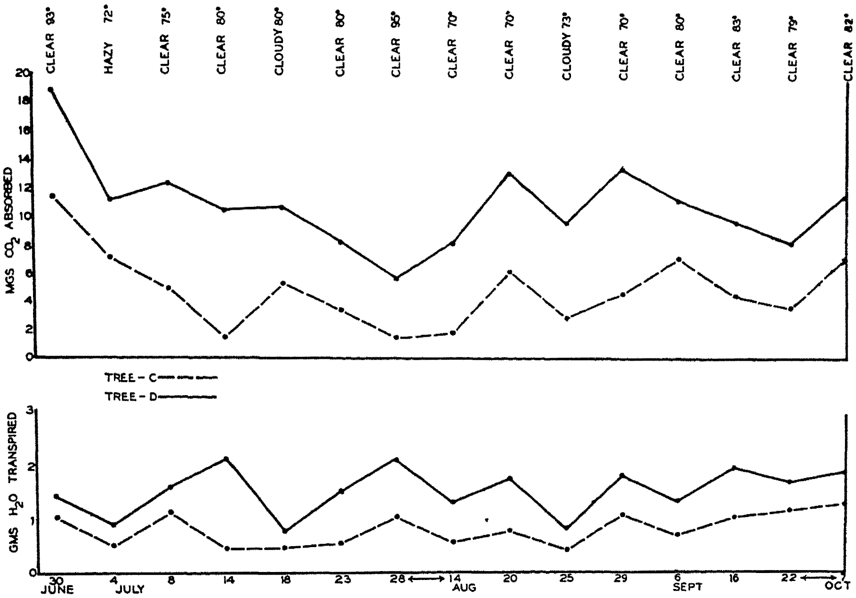


FIGURE 17.—Apparent photosynthesis and transpiration of Trees C (flooded) and D (check) during the summer of 1941. Note relatively low leaf activity of flooded Tree C throughout the summer.

The results presented in Figure 18 show no consistent differences in the photosynthetic activity of the two trees, although check Tree D appeared to have showed greater fluctuations throughout the season. On September 23, the rate of apparent photosynthesis of check Tree D was unusually low for no apparent reason. With two minor exceptions, check Tree E appeared to have a somewhat higher rate of transpiration throughout the season than check Tree D.

DRY WEIGHTS OF FOLIAGE FROM TREES

The relative sizes of the trees in the autumn of 1941 were indicated by the weights of their foliage. The oven dry weights of leaves stripped from each tree on November 14 were as follows: Tree A (10-inch water table), 1900 grams; Tree B (check), 1080 grams; Tree C (flooded May 1 to June 8), 370 grams; Tree D (check), 681 grams; and Tree E (20-inch water table), 1290 grams. The rank of the trees on the basis of their total leaf areas on September 23 were in this same order.

The leaves of Tree C were obviously smaller and fewer than those on other trees in the test. Tip leaves were frequently curled inward and seemed to be of tougher character than the leaves on other trees. Many of the leaves on Tree C turned yellowish in July, developed some reddish discolorations, and abscised early. Foliage of Trees A, B, D, and E appeared similar to that of other Stayman Winesap trees in the orchard throughout the season.

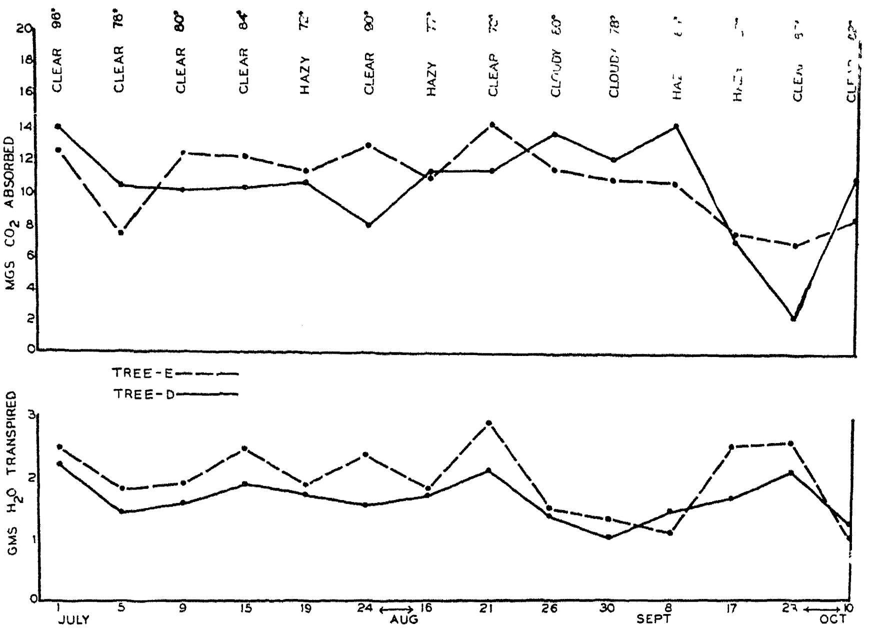


FIGURE 18.—Apparent photosynthesis and transpiration of Trees D (check) and E (20-inch water table) during the summer of 1941. Photosynthetic activity of Tree E did not differ consistently from that of check Tree D. Transpiration of Tree E, with two exceptions, was slightly lower than that of Tree D.

Flowering. Flowering on all trees was sparse during the spring of 1941; no records were kept. Less than a dozen fruits developed on any one tree. Three fruits on Tree A (10-inch water table) had water core. Fruits on Tree C (flooded May 1 to June 8, 1941) were small and unusually highly colored; they matured and dropped early. Tree E (20-inch water table) had no fruit. No winter injury was noticed on any of the trees during the 1941-42 winter in spite of the late and succulent growth of Tree A. The trees were not pruned.

During the spring of 1942, the flower clusters and average number of flowers per cluster were counted on May 5 and are presented in Table 2. Tree C developed an exceptionally large number of flowers. Tree A also had a large number of flowers, but this tree was relatively a much larger tree at this time than Tree C. Flowering of Tree E (20-inch water table) in 1942 was intermediate between Trees B and D (check).

TABLE 2.—The Effects of Excess Soil Moisture During the 1941 Season on the Flowering of Orchard Trees, May 5, 1942.

Tree	Treatment in 1941	Total flower clusters	Average flowers per cluster†	Total flowers
		No.	No.	No.
A	10-inch water table	530	3.82	2028
B	Check	70	4.75	333
C	Flooded May 1 to June 8	899	3.88	3483
D	Check	126	4.70	594
E	20-inch water table	69	5.45	376

† Derived from counting 50 random clusters.

Apparent Photosynthesis During 1942.[2] Measurements of apparent photosynthesis were initiated on June 23, 1942, using the same procedure as followed the previous year. The treatments, likewise, were maintained during the 1942 season, except that Tree C was not flooded. Transpiration data were not obtained in 1942. Apparent photosynthesis of Tree A with one exception was higher during the season than that of check Tree B. Apparent photosynthesis of Tree C, on the unit-area basis, was, for the most part, higher than that of its check Tree D. The photosynthetic level of Tree C was higher than in 1941 and could be considered approximately normal or about 12 milligrams of carbon dioxide absorbed per 100 square centimeters of leaf surface per hour (15). The apparent photosynthesis of Tree E was not consistently different than that of Tree D. The average rate of apparent photosynthesis on a unit-area basis during the 1942 season for each tree may be ranked in decreasing order as follows: A, B, E, C, and D. Thus, the high water tables for Trees A and E did not seem to adversely affect apparent photosynthesis the second season of treatment.

During 1942 there were no visible differences in character of foliage of trees under study, except that the leaves of Tree C (flooded May 1 to June 8, 1941) were obviously smaller in size and fewer in number. It was readily apparent, however, that the vigor of Tree C had improved

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[2] The authors appreciate the assistance of Harry W. Ford, student assistant, in obtaining photosynthesis and growth data for the 1942 season.

over its 1941 condition, but it was still a weak tree. The usual seasonal foliage changes in color and dropping occurred simultaneously with all trees.

Fire Blight Infection. During June, 1942, it was evident that fire blight was more pronounced on some trees than on others. One June 30, the number of shoots affected from fire blight and their total length was measured for each tree; the data are given in Table 3. Trees A and E with the highest water supply to the roots and most succulent growth showed the largest amount of fire blight; the weakened Tree C showed the least.

TABLE 3.—Relationship Between Incidence of Fire Blight and Soil Moisture Treatments of Stayman Winesap Trees, June 30, 1942.

Tree and treatment	Number of shoots affected	Total length affected
		inches
A (10-inch water table)	27	267
B (check)	5	28
C (flooded May 1 to June 8, 1941)	6	21
D (check)	5	29
E (20-inch water table)	10	166

Fruit Set and Fruit Harvested. Table 4 gives the fruit set for each tree on June 6, the fruit picked on September 22, and the average fresh weight of the harvested fruits in 1942. While Tree C (flooded May 1 to June 8, 1941) had by far the greatest number of blossoms, it set the smallest percentage of fruit, which also were the smallest in size at maturity. Tree A (10-inch water table) showed heavy blosoming followed by a fair set and maturity of crop. Check Trees B and D and

TABLE 4.—Flowering and Fruiting of Stayman Winesap Trees Under Different Soil Moisture Treatments, 1942.

Tree and Treatment	Blossoms April 27	Set on June 6		Mature fruit September 22		
		Number	Percent of blossoms	Number	Percent of blossoms	Average fresh weight in cms
A (10-inch water table)	2028	118	5.8	77	3.8	184.1
B (check)	333	54	16.2	31	9.3	183.7
C (flooded May 1 to June 8, 1941)	3483	62	1.8	8	0.2	106.8
D (check)	594	95	16.0	55	9.3	166.4
E (20-inch water table)	376	64	17.0	43	11.4	200.7

test Tree E (20-inch water table) were more or less similar in their flowering and fruiting responses. However, Tree E showed the largest percentage of flowers maturing fruit; also, the individual size of the fruit was the largest.

The 1943 Season. No pruning was performed during the 1942-43 winter. During the spring and summer of 1943, war conditions made it impossible to obtain skilled personnel to make reliable measurements. It was posible, however, to maintain Tree A with a 10-inch water table and Tree E with a 20-inch water table throughout the growing season. All trees passed through the winter of 1943-44 without pruning and without signs of winter injury.

Experiment Concluded in 1944. In June, 1944, after determining the amount of blossoming and fruit set, the trees were removed and final data obtained on their physical differences.

The number of blossoms on May 1 and the number of young fruits developing on June 6 are given in Table 5. Tree A (10-inch water table) showed relatively heavy blossoming followed by a moderate set of 4.7 percent, Tree C (flooded May 1 to June 8, 1941) showed moderate blossoming in 1944, but only 2 percent of the flowers set fruit. Tree E (20-inch water table) had a moderate number of blossoms followed by an unusually heavy set of 16.9 percent. Check Tree B had the smallest number of blossoms, but an appreciable set of 10 percent on June 6, while the reverse occurred with check Tree D in which there were a large number of blossoms followed by 4.3 percent set.

TABLE 5.—Flowering and Fruiting of Stayman Winesap Test Trees During the 1944 Season.

Tree and Treatment	Blossoms May 1	Fruit set on June 6	
		[illegible] Number	Percent of blossoms
	No.	No.	percent
A (10-inch water table)	5624	264	4.7
B (check)	549	55	10.0
C (flooded May 1 to June 8, 1941)	888	18	2.0
D (check)	4486	194	4.3
E (20-inch water table)	1403	237	16.9

The experimental trees were entirely stripped of their leaves between June 7 and 11. Fresh weights were obtained and 100 random leaves from each tree were laid aside for leaf area determinations. The remaining leaves were dried in a large, ventilated, steam-heated oven until constant in weight. The total area of each 100-leaf sample was measured with an area photometer (built by American Instrument Company), after which the dry weight of each sample was determined. The leaf area per unit dry weight was multiplied by the total dry weight of leaves in order to obtain the total leaf area on each tree. The results are presented in Table 6, and show that Tree A possessed the greatest total leaf area, check Tree B was next, followed in order by Trees E, D. and C.

TABLE 6.—The Total Area and Weight of Leaves from Stayman Winesap Test Trees in June, 1944.

Tree and Treatment	Total fresh weight	Total dry weight	Dry weight of 100 leaves	Area of 100 leaves	Total leaf area
	gm.	gm.	gm.	(sq. cm.)	(sq. meters)
A (10-inch water table)	10,601	5,200	13.13	1,857	73.54
B (check)	8,399	3,990	11.38	1,964	68.86
C (flooded May 1 to June 8, 1941)	5,380	1,985	14.03	2,022	28.61
D (check)	7,877	3,010	12.07	1,563	38.98
E (20-inch water table)	9,194	4,095	11.56	1,665	58.98

Four soil samples were taken within each tree compartment in June, 1944 to a depth of 30 inches, using a King soil tube. The borings were divided into the following depths: 0 to 10 inches, 10 to 20 inches, and 20 to 30 inches. Duplicate samples were taken from the composites for

TABLE 7.—The Moisture Equivalent at Different Depths of Brookston Clay Loam Soil Sampled in June, 1944.

Tree and treatment	Moisture equivalent		
	0 to 10 inches	10 to 20 inches	20 to 30 inches
	percent	percent	percent
A (10-inch water table)	21.0	21.8	25.1
B (check)	23.6	23.2	26.8
C (flooded May 1 to June 8, 1941)	22.6	24.0	27.1
D (check)	23.3	24.8	28.3
E (20-inch water table)	23.7	24.6	27.5

moisture-equivalent determinations. The results in Table 7 show no consistent differences in moisture equivalent between treatments. In general, however, the moisture equivalents and, thus, the fineness of the soil increased slightly with depth of soil sample.

The distribution of roots within each compartment was mapped by digging a trench 30 inches deep by 18 inches wide, and extending it from the tree trunk diagonally to the sheet metal wall. One side of the trench was sheared smooth and crossmarked at intervals of 10 inches with a string. Roots were exposed along the walls by pricking the soil with an ice pick. The location and size of each root within a 10-inch square was marked on a sheet of paper of the same size. Root sizes were recorded within the following ranges: (1) Less than 1 mm. in diameter, (2) 1 to 5 mm., (3) 5 to 10 mm., and (4) larger than 10 mm. Roots of each tree, regardless of treatment, were well distributed over the profile. The high water tables for Trees A and E apparently did not affect the root distribution nor the size of the roots. Tree C (flooded May 1 to June 8, 1941) in comparison had a relatively scanty root system.

After the tops of the trees had been removed and the root distribution studies completed, the entire root system of each tree was removed. The roots were separated as larger or smaller than 5 mm. in diameter and oven dried. The results in Table 8 show that Tree A had the greatest dry weight of roots, followed in order by Trees B, E, D, and C. It is also interesting to note that Trees A and E with the high water tables had considerably more small roots (less than 5 mm. in diameter) than the other three trees.

Discussion. The effects of submerging the roots of a 5-year Stayman Winesap tree from May 1 to June 8, 1941, closely resembled the effects obtained with similarly treated potted trees, as discussed in the foresection of this paper. The small amount of growth and the low rates of apparent photosynthesis and transpiration were probably caused by reduced root respiration as a result of the waterlogging treatment. Although the experiment does not indicate what the effects of flooding might be at some other time of year, there can be no doubt of the severe injury and retardation which followed submersion of the roots during blossiming and early leaf development. The large number of blossoms that appeared in the spring of 1942, one year after treatment, indicated a disruption in the translocation system of the tree which resembled that caused by bark ringing of an apple tree trunk. It is probable that the translocation of carbohydrates and other materials was inhibited to such an extent by root submersion that they accumulated in the aboveground portion of the tree and were at least partly responsible for the excessive flower-bud differentiation. On the other hand, nutrient elements, particularly nitrogen, were probably not available in sufficient quantities at the time of fruit set in 1942 and thus, only a small percentage of

TABLE 8.—The Dry Weights of Large and Small Roots of Orchard Test Trees, July, 1944.

Tree and treatment	Dry weight of roots		
	Small**	Large††	Total
	gm.	gm.	gm.
A (10-inch water table)	4,017	8,800	12,817
B (check)	3,065	9,225	12,290
C (flooded May 1 to June 8, 1941)	1,561	2,725	4,286
D (check)	2,726	6,233	8,959
E (20-inch water table)	4,373	7,757	12,030

** Less than two centimeters in diameter.

†† Larger than two centimeters in diameter.

the blossoms developed into fruits. Also, the scanty root system of the flooded tree undoubtedly lacked the capacity to supply adequate water for fruit enlargement in addition to other growth requirements. In general, the behavior of the flooded Tree C was typical of many commercial orchard trees subjected to poor soil drainage conditions.

The vigorous response of Tree A and Tree E to the high water tables of 10 and 20 inches, respectively, was somewhat surprising. Both trees were unquestionably stimulated by such treatment; there were no signs of retardation of growth at any time. Several reasons may be suggested as to why the trees were not injured over the 3-year period of treatment. First, the water supplied to these trees in rather large and continuous quantities may have contained considerable dissolved oxygen, inasmuch as it was supplied by a high-pressure irrigation pump. The situation in general was probably comparable with conditions in an apple orchard in England observed by Rogers (16). He noted that sturdy trees had developed with most of their roots submerged much of the time in clear running water of a nearby creek and concluded that the required amount of oxygen apparently was dissolved in the fresh water. However, this explanation does not hold for Tree C which was flooded from May 1 to June 8, 1941.

Another possible explanation for the above situation is that the roots above the water table functioned under the rather ideal conditions of sub-irrigation. Thus, the roots never lacked a supply of water and were continually able to supply unlimited quantities to the tops, resulting in vigorous vegetative growth. With such provisions, the foliage performed well and supposedly supplied adequate synthesized food materials to the roots submerged below the water table which, at least, obtained sufficient oxygen in the water to perform a satisfactory rate of respiration. The situation seems analagous to that observed by the junior author (White) in his father's orchard. There was a low area in which the water stood within one foot of the soil surface. Apple trees planted at the usual depth failed to survive more than one or two seasons in this area. On the other hand, trees were vigorous and productive when planted in the same area on large mounds of soil 1½ to 2 feet above the general soil level. In later years, there was occasion to remove some of the established trees and it was presumed that they would be shallow-rooted, but this was not the case. Roots of these trees were found to penetrate to a depth of 3 to 4 feet or below the usual water table. Thus, these trees, as in the experiment discussed above, were evidently functioning largely with the root system in the upper soil horizon and, in addition, were supplied with a plentiful supply of moisture from the lower roots.

In this connection, it may be of interest to note, also, a suggested practice for planting a cherry or peach tree in backyard gardens where drainage conditions may not be particularly favorable (1). Both of these fruits are known to be easily damaged by excess soil moisture. The suggestion is that the soil be mounded 1½ to 2 feet and about 15 feet across at the base where the tree will be planted. Trees so-planted often succeed and fruit well where other trees planted on neighboring sites without such soil preparation may fail completely.

From results reported in this paper, it appears that *complete* submergence of the root system of a fruit tree for several days or weeks is a most important factor governing tree injury.

SUMMARY

1. Laboratory and greenhouse experiments were conducted to determine the effects of root submersion on apparent photosynthesis, respiration, and transpiration of the leaves of potted Stayman Winesap apple trees. In some cases, respiration of the roots was determined.

2. Transpiration and apparent photosynthesis of potted apple trees were reduced within 2 to 29 days, usually within 2 to 7 days, after the roots were submerged. In some cases, transpiration and apparent photosynthesis were stopped with continued root submersion.

3. Leaf temperature and stomatal behavior could not be correlated with the low leaf activity resulting from root submersion.

4. Apparent respiration of the leaves was increased within about two days after submersion of the roots. When water was drained from the soil, the rate of respiration returned to near pre-treatment level.

5. Leaves from submerged trees contained less water and less ash per unit of leaf surface than leaves from check trees.

6. Root respiration studies were conducted on young apple trees growing in the greenhouse in stone crocks containing pea-sized gravel and supplied with nutrient solution. The crocks were made airtight and the root systems forced to reutilize the same air for several days, thus resembling poor soil drainage and poor aeration under field conditions. After 1 to 4 days under these conditions, root respiration began to show a decrease which continued for several days until the oxygen of the surrounding air was reduced to 1 to 2 percent and the carbon dioxide increased to between 8 and 10 percent. Trees under these conditions developed leaf and shoot characteristics similar to those with roots submerged in water for several days.

7. Development of new roots and the formation of root hairs were inhibited by submersion of the root system.

8. When roots of a 5-year Stayman Winesap tree were submerged in the orchard from May 1 to June 8, 1941, there were marked reductions in apparent photosynthesis and transpiration for the balance of the growing season. Flowering was exceptionally heavy in the spring of 1942, but fruit set was light. Apparent photosynthesis per unit leaf area of this tree (C) was relatively higher in 1942 than in 1941. Rate of development of leaves, shoots, and roots on this tree were greatly retarded during the 3-year test period.

9. Tree symptoms caused by root submersion under controlled or field conditoins were as follows: Yellowish-green small leaves with marginal and tip burning, dropping early; weak shoot growth, ceasing elongation early in the season; light green to yellowish bark; foliage thin and limited; and heavy blossoming followed by a light set with fruits dropping early.

10. The maintenance of water tables in the orchard at 10 and 20 inches below the soil surface for three growing seasons had no detrimental effect on apparent photosynthesis and transpiration of Stayman Winesap trees. Flowering and fruiting were moderate to heavy and growth was vigorous. Root studies in 1944 showed good root distribution and development to a depth of 30 inches. It was concluded that roots above the water tables functioned under more or less ideal sub-irrigation conditions. Roots below the water table evidently received adequate food

materials from the tops and sufficient oxygen dissolved in the continually changing water to carry on adequate respiration and growth.

11. The data indicate that submergence of the entire root system of an apple tree for several days to a few weeks, particularly during blossoming and leaf expansion, may prove extremely harmful, whereas submergence of only the lower portion of the root system may not be detrimental. Results of the orchard experiment may account in part for the fact that fruit trees may survive and produce satisfactorily in poorly drained areas, provided they are planted on mounds.

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