

RELATION BETWEEN ROOT RESPIRATION AND ABSORPTION

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(WITH TEN FIGURES)

Introduction

Various theories have been developed to explain the nature of the absorption of water by roots, embodying what may be called imbibitional, osmotic, and passive forces (MILLER 9). Imbibitional forces have been emphasized and shown to be of great importance by SHULL (15) and others. Although KUNKEL (7) assumed only imbibitional forces to be effective, more recent investigators agree that osmotic forces must also play an important part. But even these forces fail to explain satisfactorily the transference of water across the endodermis into the vascular cylinder. The nature of the Casparian strip seems to indicate that the transfer of water across this region is under the control of the living cells (PRIESTLEY 12, 13, 14). Also the effect of changing environmental conditions led BLACKMAN (1) to believe that vital relations of the cell, involving the transfer of energy, must be concerned in absorption.

Such energy changes would of necessity be manifested at some time in the respiratory processes of the root. There is no direct evidence showing a correlation between the respirational and absorptive activity of the root except that of NEWTON (10, 11), who found that the evolution of carbon dioxide varied with transpiration and with the osmotic concentration of salt solution supplied in the field. The present study was made to determine more accurately the relation between these processes, using plants under strictly controlled conditions.

In order to reduce individual variations as far as possible, seed from a pure strain of corn (Funk's hybrid no. 517, Yellow Dent) was used in all the experiments. The seeds were placed in water for 12 hours, treated with 4 per cent. formalin for 10 minutes, and washed with sterile water. For germination they were placed under sterile conditions in petri dishes containing filter paper moistened with a few cubic centimeters of culture solution. This treatment resulted in normal and vigorous germination. When the radicles had reached a length of 1-2 cm. the seeds were placed on perforated sheets of cork which were floated in large dishes of Knop's solution. The solution was replaced at intervals of three to five days and continuously aerated. The corn plants were kept in the laboratory at full daylight illumination and grown in the cultures one to two weeks until needed.

Experimentation

The first experiments were carried out by means of the apparatus shown in figure 1. When the plants were 10 inches high they were placed in the experimental chamber (A), a 5-inch pyrex test tube with a capacity of

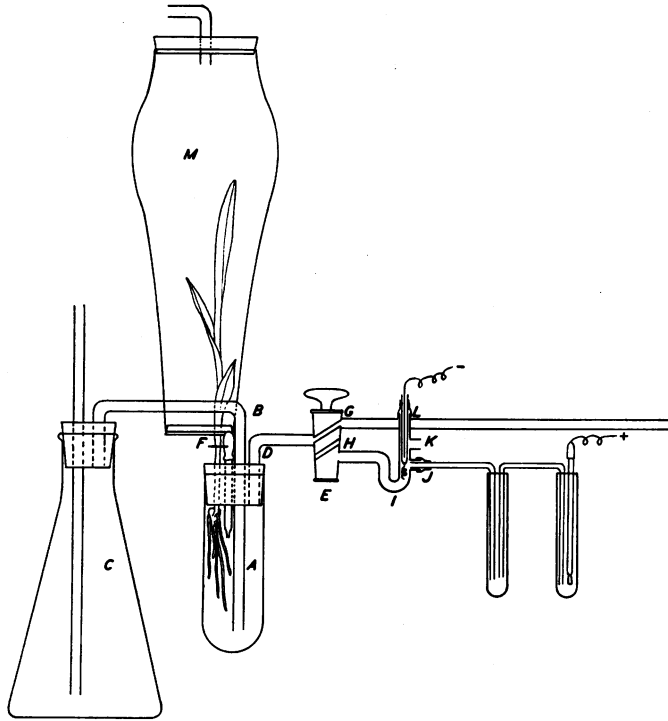


FIG. 1. Diagram of essential parts of apparatus used in determining root respiration by carbon dioxide evolution and water absorption.

90 cc. being used. A rubber stopper was fitted with an inlet tube (B) leading from the flask (C), which in turn was connected with a large bottle of culture solution. An outlet tube (D) led from the test tube to a three-way stopcock (E). A section cut from the stopper permitted the plant to be introduced without undue pressure on the stem. A small pipette (F) with a rubber bulb was also fitted in the stopper for use in stirring the solution before and after each reading.

The opening (G) of the three-way stopcock led to a graduated potometer tube of 1-mm. bore by which was measured the volume absorption during the experimental interval. The second stopcock outlet (H) led to the quinhydrone electrode chamber (I). Two glass tubes were fused into this chamber; J a connection for the KCl bridge, and K a waste outlet.

The electrode used was a platinum wire, one end of which was fused into a glass tube with mercury contact with the potentiometer circuit, and the other end coiled to carry crystals of quinhydrone when inserted into the chamber *I*. Short rubber tube connections attached the bridge and the electrode to the chamber and prevented exposure of the solutions to the air during the time of reading.

The plant was inclosed in the chamber *M*, through which air could be circulated, entering under a constant pressure at the top and escaping at the bottom. Moist or dry air could be directed through the chamber, the former passing through three towers containing water and glass wool and the latter through two towers filled with calcium chloride and equipped with dust traps of cotton wool. The apparatus was placed in a thermostat at 25° C. so that only the chamber *M* was subjected to room temperature. Although the room temperature varied from 20° to 25° C. there was seldom more than 2° of variation during a single experiment. Readings were taken at hourly intervals for from 6 to 15 hours.

The rate of transpiration and hence of absorption could be changed by passing either moist or dry air over the plant, and the accompanying effect on root respiration observed. In the first experiments the plants were placed in rain water which had been aerated for 12 hours previously. The plants were transferred from the culture dishes to the observation tubes 10 hours before readings were begun to minimize any effects due to handling. The volume absorption for any period was read directly from the calibrated potometer tube and the evolution of carbon dioxide computed for the same period from the increase in acidity of the solution, since under aerobic conditions carbonic is the only acid excreted by roots (HAAS 5).

After mixing the culture fluid in *A* by means of the pipette *F*, a 10-cc. sample was displaced slowly through the electrode chamber. During the operation the electrode with its load of quinhydrone was elevated above the waste vent *K*. If the displacement is slow and regular, no mixing results in chamber *A*, since the solution in *C* is at the same temperature and is admitted at the end opposite the outlet. The stopcock *E* and the vent *K* are then closed and the electrode slipped down into the liquid. The quinhydrone crystals float slowly down, saturating the liquid in the electrode chamber and allowing a reading to be made. After each reading the culture around the roots was entirely replaced with fresh solution. This was insured by passing 500 cc. of fresh liquid through the culture tube until acidity determinations showed the constant and original value. All distilled water used was freshly made in a block-tin apparatus. Storage vessels used were of pyrex glass.

The carbon dioxide present may be easily determined from the acidity determination. KENDALL (6) has determined the dissociation constant *K*

of carbonic acid for concentrations up to one atmosphere to be 3.5×10^{-7} ; the amount of carbon dioxide may then be determined from (H^+) , K , and the volume of the solution used.

$$(1) \quad (H^+) = \frac{a}{V}$$

where a is the degree of ionization and V is the number of liters which contain one gram mole of carbon dioxide. If K is the ionization constant, the relationship of these two may be expressed:

$$(2) \quad K = \frac{a^2}{(1-a)V}$$

In these two equations (H^+) and K are known, so the equations may be solved simultaneously and values for a and V determined for a certain pH. From (1) we obtain:

$$(3) \quad V = \frac{a}{(H^+)}$$

Substituting this value for V in (2) we obtain:

$$K = \frac{a^2}{(1-a) \frac{a}{(H^+)}} \text{ or}$$

$$a = \frac{K}{(H^+) + K}$$

Solving for V in (3)

$$(4) \quad V = \frac{K}{(H^+)^2 + K(H^+)}$$

Using KENDALL'S value for K , and the (H^+) corresponding to the observed pH, the molarity of the solution may be found from V in this way:

$$C = \frac{1}{V}$$

where C is the number of gram molecules per liter. The actual weight of carbon dioxide in grams per liter may then be calculated. Since the molecular weight of carbon dioxide is 44, the total weight of carbon dioxide present is $44C$. If n represents the number of cubic centimeters of solution used, the weight of carbon dioxide in n cubic centimeters is:

$$(5) \quad \text{Wt.} = \frac{44Cn}{1000}$$

Since the volume of 1 gram of carbon dioxide at S.T.P. is 509 cc. the volume of gas produced is:

$$(6) \quad \text{Vol.} = \frac{509 \times 44C_n}{1000} \quad (\text{at S.T.P.})$$

Thus it is necessary only to substitute values in equations (4) and (6) to obtain the amount of carbon dioxide.

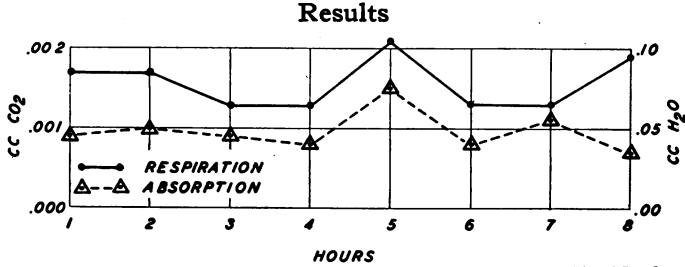


FIG. 2. Absorption of rain water and evolution of carbon dioxide by corn roots (plant 2). Leaves exposed to room conditions.

The results of the first two experiments are shown in table I. Readings were begun at 9 A. M. and the plant tops were exposed to room atmosphere, so that environmental conditions varied throughout the day. Plant 1 showed an unmistakable correlation between absorption and carbon diox-

TABLE I

ABSORPTION OF RAIN WATER AND EVOLUTION OF CARBON DIOXIDE BY CORN ROOTS; LEAVES EXPOSED TO ROOM CONDITIONS

HOURS	PLANT 1		PLANT 2	
	ABSORPTION PER HOUR	CO ₂ EVOLVED PER HOUR	ABSORPTION PER HOUR	CO ₂ EVOLVED PER HOUR
	<i>cc.</i>	<i>cc.</i>	<i>cc.</i>	<i>cc.</i>
1	0.050	0.0017	0.040	0.0017
2	0.050	0.0012	0.050	0.0017
3	0.030	0.0012	0.045	0.0013
4	0.020	0.0007	0.040	0.0013
5	0.035	0.0022	0.075	0.0021
6	0.050	0.0022	0.040	0.0013
7	0.070	0.0007	0.055	0.0013
8	0.050	0.0004	0.035	0.0019

ide evolution, although discrepancies appear, particularly toward the end of the experimental period. The results for plant 2 are somewhat more consistent and have been graphed in figure 2. It is evident that this plant showed a remarkably close correlation between respiration and absorption rates, and that there was no departure from this except at the final period

of observation. Variable factors evidently influenced respiration and absorption in a similar direction and to a similar degree. Thus the high rate of absorption at the fifth hour is closely paralleled by the rate of respiration, and both rates fell at the sixth hour to lower values. These high rates of absorption and respiration at the fifth hour correspond to the time of maximum illumination in the laboratory.

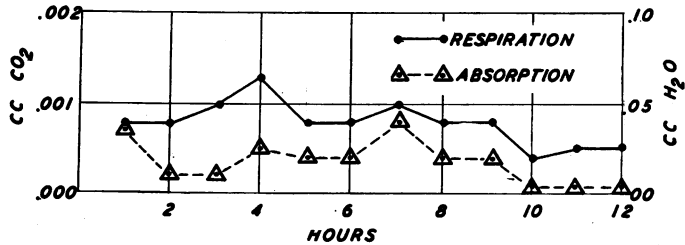


FIG. 3. Absorption of rain water and evolution of carbon dioxide by corn roots (plant 4). Leaves exposed to dry conditions for the initial eight hours.

In table II are shown the results of four experiments carried out similarly to the two previous ones, except that the tops of the plants were inclosed in dark chambers in which the humidity conditions were controlled as indicated. All plants exhibited an essentially similar relation between absorption and respiration. Plant 3 showed considerable variability but a distinct correlation between the two processes. The results for plant 4 are shown in the graph of figure 3. During the initial period of 8 hours the plant was subjected to dry air. During the 12 hours of this experiment the respiration and absorption curves show a close correlation. A high rate of absorption occurred when the plant was first exposed to dry air, but the values quickly fell to a lower level, perhaps indicating the effect of stomatal adjustment. This high initial transpiration rate is not reflected in the rate of carbon dioxide evolution. The change from dry to moist air resulted in a depression of both absorption and respiration rates, a movement which appeared after one hour and required two to reach the minimal level.

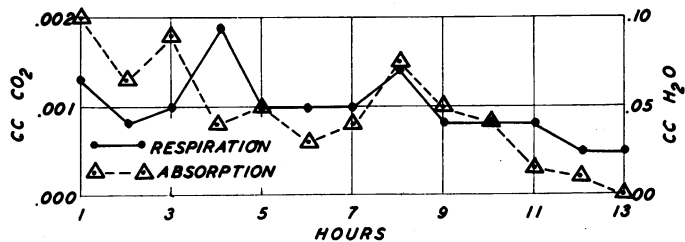


FIG. 4. Absorption of rain water and evolution of carbon dioxide by corn roots (plant 5). Leaves exposed to dry conditions for the initial eight hours.

TABLE II
 ABSORPTION OF RAIN WATER AND EVOLUTION OF CARBON DIOXIDE BY CORN ROOTS; TOPS INCLOSED IN DARK CHAMBERS WITH MOIST OR DRY (*) AIR CIRCULATION

HOURS	PLANT 3		PLANT 4		PLANT 5		PLANT 6	
	ABSORPTION PER HOUR	CO ₂ EVOLVED PER HOUR	ABSORPTION PER HOUR	CO ₂ EVOLVED PER HOUR	ABSORPTION PER HOUR	CO ₂ EVOLVED PER HOUR	ABSORPTION PER HOUR	CO ₂ EVOLVED PER HOUR
1	cc. 0.010	cc. 0.0067	cc. 0.035*	cc. 0.0008	cc. 0.100*	cc. 0.0013	cc. 0.025	cc. 0.0011
2	0.010	0.0110	0.010*	0.0008	0.065*	0.0008	0.040	0.0007
3	0.015	0.0139	0.010*	0.0010	0.090*	0.0010	0.043	0.0008
4	0.015	0.0139	0.025*	0.0013	0.040*	0.0019	0.040*	0.0006
5	0.060*	0.0132	0.020*	0.0008	0.050*	0.0010	0.075*	0.0008
6	0.040*	0.0132	0.020*	0.0008	0.030*	0.0010	0.075*	0.0007
7	0.065*	0.0160	0.040*	0.0010	0.040*	0.0010	0.040*	0.0005
8	0.070*	0.0160	0.020*	0.0008	0.075*	0.0014	0.040*	0.0005
9	0.055*	0.0160	0.020	0.0008	0.050	0.0008		
10	0.075*	0.0132	0.005	0.0004	0.040	0.0008		
11	0.075*	0.0193	0.005	0.0005	0.015	0.0008		
12			0.005	0.0005	0.010	0.0005		
13				0.0005	0.000	0.0005		

The graphs of the results obtained for plant 5 are shown in figure 4. The conditions of this experiment were identical with those of the preceding. Here again, although the curves of water absorption and of respiration are variable, they show a good correlation throughout the course of the experiment. During the initial dry period the high rate of absorption of the first hour fell through a variable course to one-third the original value, and then rose. The transfer to moist air was followed, as in the preceding experiment, by a rate of absorption which gradually fell to a minimum. The rate of evolution of carbon dioxide followed the general course of that of absorption, fluctuating during the initial period and gradually falling to a minimum during the exposure to moist air. Similarly, after the initial hour, the two processes recorded for plant 6 showed a close correlation. Since the results obtained from plants 3 and 6 are similar to those of 4 and 5, they have not been graphed.

Because the respiratory values obtained in these experiments seemed low, it was thought that buffer substances were present in the rain water, preventing a hydrogen ion concentration corresponding to the total amount of carbonic acid present. Freshly distilled and aerated water was therefore used in place of rain water. No toxic effects could be detected even over periods much longer than the duration of the experiments. The higher values obtained seemed to confirm the assumption just mentioned. Thus the values obtained in rain and distilled water cannot be compared, but only the correlation between root respiration and absorption in the two media.

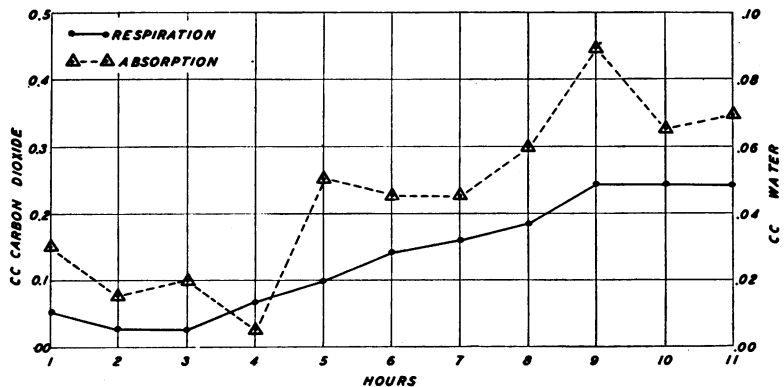


FIG. 5. Absorption of distilled water and evolution of carbon dioxide by corn roots (plant 7). Leaves exposed to moist air for the first four hours.

The results obtained when distilled water was used are shown in table III for plant 7 which was kept in a saturated atmosphere for the first four hours of the experimental period. The curves in figure 5 show a good

correlation between the rates of respiration and absorption. Both rates remained at low levels during the initial four-hour moist period and rose to maximum values at the ninth hour. In this unbuffered solution the values obtained probably more nearly represent the respiratory activity of the root system than do those for the plants observed in rain water. It is significant that in both rain and distilled water there is a good correlation between the respiratory and the absorptive activities of the root system.

For following the respirational activity, the micro-Winkler method of measuring dissolved oxygen was employed either alone or with the electro-metric method of carbon dioxide estimation. As used by many workers, this modification of the original Winkler method requires a sample of but 10 cc. To obtain greater accuracy the sodium thiosulphate solution was used in a concentration of N/160 instead of the usual N/40, and was added from a micro-burette. A Thompson and Miller apparatus as described by ZIMMERMAN (16) was found best suited to the work. The sample for analysis was withdrawn, with proper precautions against agitation and exposure to the air, through the potometer tube into the apparatus. The reagents were added immediately from the attached burette tubes and titration promptly carried out.

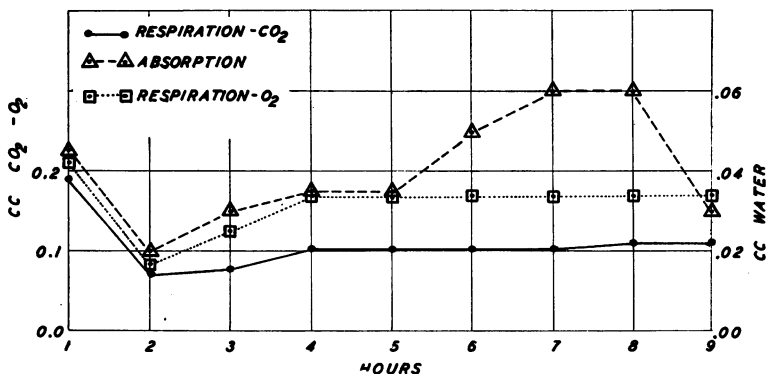


FIG. 6. Absorption of distilled water and root respiration as measured by carbon dioxide evolution and oxygen consumption (plant 8). Leaves exposed to moist conditions for the initial two hours.

The respiration of plant 8 was measured by the oxygen consumption and the carbon dioxide evolution while the root system was immersed in aerated distilled water. The results are given in table III and the curves shown in figure 6. The plant was exposed to moist air for two hours and to dry for the remainder of the experimental period. The curves show a general correlation, the discrepancy being the high rates of the sixth to eighth hours. From the initial high reading all curves fell to minimum values during the second hour, and, except for the high values just men-

tioned, rose to a moderate level for the remainder of the experiment. The curves of carbon dioxide evolution and of oxygen consumption parallel each other throughout the course of the experiment. It is evident that the rate of root respiration measured by either of the two methods gives curves which differ only in level.

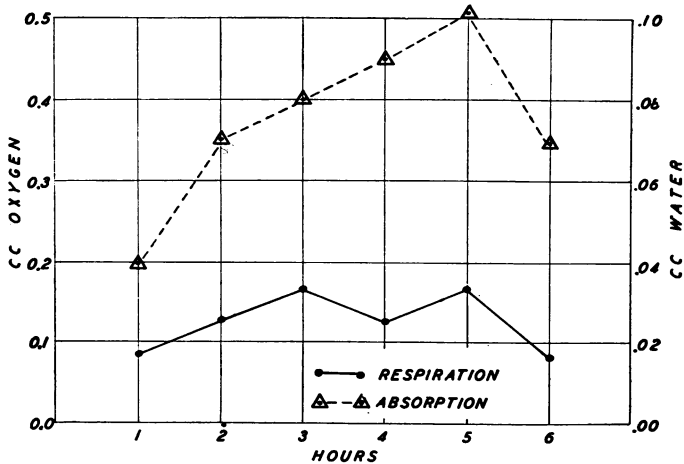


Fig. 7. Absorption of distilled water and of oxygen by corn roots (plant 9). Leaves exposed to dry conditions during the entire experiment.

The root respiration of plant 9 was followed by means of the micro-Winkler method while kept in aerated distilled water. The results are given in table III and the curves shown in figure 7. Oxygen and water absorption show a general correlation. During the initial three hours both

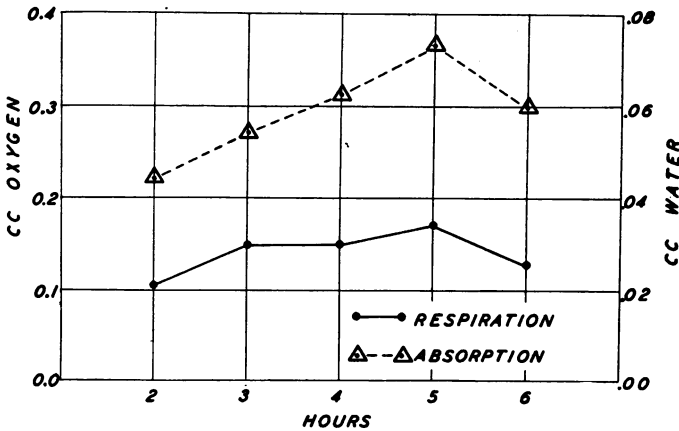


Fig. 8. General course of root respiration and absorption in distilled water (averages of plants 8 and 9).

rates increased, a movement which continued through the following two hours only for the absorption of water. Both curves rose to maxima at the fifth hour and fell to lower values at the sixth. These variations may have been due to changes in the rate of air flow over the tops, or to periodic fluctuations in the plant itself.

The average values from plants 8 and 9, showing the absorption of distilled water and of oxygen, are given in table III and the curves of the values are shown in figure 8. The first hour, during which the plants were not adjusted to the experimental condition, has not been included. The correlation between the two processes is evident.

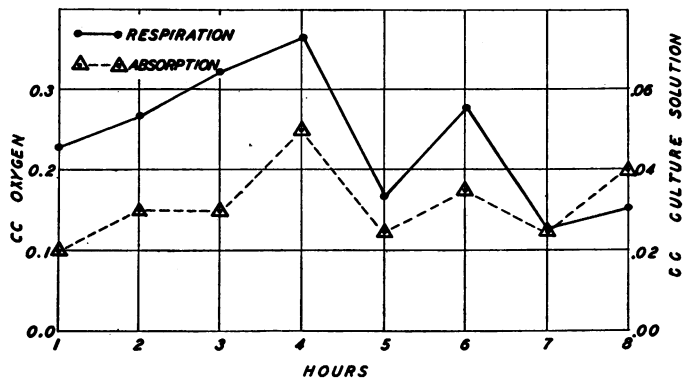


FIG. 9. Absorption of culture solution and oxygen consumption by corn roots (plant 11). Leaves surrounded by moist air for the initial hour.

Since the rain water and distilled water used in the experiments might be thought to produce abnormal root behavior, further work was carried out using culture solutions similar to those in which the plants had been grown. It is obvious that buffer action does not interfere with the determination of oxygen, and that the micro-Winkler method can be used with equal accuracy for observations in distilled water, rain water, or mineral nutrient solutions. Experiments 10, 11, and 12 were carried out in Knop's solution identical in composition with that in which the plants had been grown. The results are given in table IV. The curves of the values obtained for plant 11 are shown in figure 9 as typical of the set. It will be seen that a close correlation between respiration and absorption was shown, the two processes paralleling each other throughout the course of the experiment. From the initial low values obtained under conditions of moist air, the maximum rates of both respiration and absorption were reached at the fourth hour, after which the two processes varied simultaneously and similarly. The results obtained for plants 10 and 12 are similar to those for plant 11. The effects of moist and dry air are not so obvious as in earlier experiments.

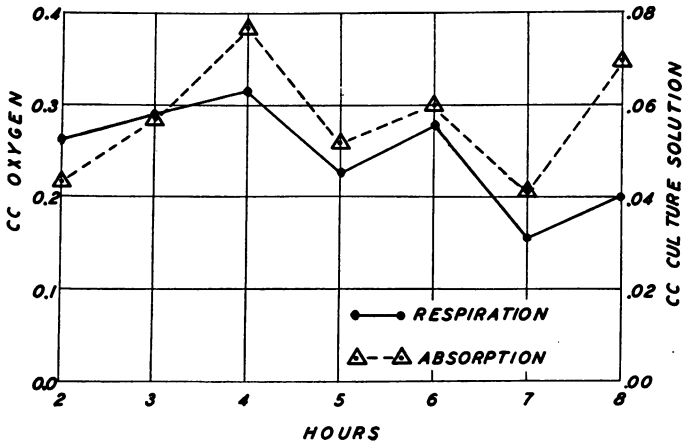


FIG. 10. General course of root respiration and absorption in culture solution. Averages of plants 10, 11, 12.

The averages for the absorption of water from the culture solution and for the consumption of oxygen are given in table IV and the curves of these values are shown in figure 10. At the first reading in experiment 12 the plant apparently had not become adjusted to the experimental conditions and hence this value is not shown in figure 10. It will be seen that the correlation between the absorption of liquid and of oxygen is close, the processes varying in parallel throughout the period.

Discussion

The thermodynamic conception of an organism is less prominent in the work of the plant physiologist than in that of workers in the field of animal physiology. Respiration, as an indication of physiological activity, may be taken as a measure of work done, even when the exact nature of this work is not evident. The thermodynamic relations of plant activities have received too little attention. Comparatively few detailed studies of the energy relations of any plant activity have been reported. Thus while we know how to evaluate respiration in terms of energy, we do not possess such knowledge concerning the use of this energy in the plant. For instance, in the fundamentally important water relations of plants many workers have hesitated to assign any endothermic physiological relation. Since the work of DUTROCHET, the osmotic mechanism is a widely accepted explanation of water absorption and transport, in spite of the fact that many of the concentration gradients along the paths do not agree in direction with that of the movement of water.

Following the work of SACHS, imbibitional forces have been accepted by

TABLE IV
 ABSORPTION OF CULTURE SOLUTION AND OF OXYGEN BY CORN ROOTS; TOPS INCLOSED IN DARK CHAMBERS WITH MOIST
 OR DRY (*) AIR CIRCULATION

HOURS	PLANT 10		PLANT 11		PLANT 12		AVERAGE	
	ABSORPTION PER HOUR	O ₂ CONSUMP- TION PER HOUR	ABSORPTION PER HOUR	O ₂ CONSUMP- TION PER HOUR	ABSORPTION PER HOUR	O ₂ CONSUMP- TION PER HOUR	ABSORPTION PER HOUR	O ₂ CONSUMP- TION PER HOUR
1	cc. 0.020	cc. 0.215	cc. 0.020	cc. 0.229	cc. 0.050	cc. 0.449	cc. 0.030	cc. 0.298
2	0.050*	0.355	0.030*	0.269	0.050	0.169	0.043	0.264
3	0.090*	0.373	0.030*	0.322	0.050	0.178	0.057	0.291
4	0.110*	0.338	0.050*	0.364	0.070*	0.237	0.077	0.313
5	0.060*	0.279	0.025*	0.169	0.070*	0.237	0.052	0.228
6	0.075*	0.322	0.035*	0.279	0.070*	0.237	0.060	0.279
7	0.060*	0.245	0.025*	0.127	0.040*	0.102	0.042	0.158
8	0.120*	0.322	0.040*	0.152	0.050*	0.127	0.070	0.200

many workers as an explanation of water absorption. KUNKEL (7) believed these forces to be the main ones concerned in the intake of water by roots, and that osmotic forces play no part. SHULL (15) assigned an important rôle to imbibitional forces, but did not exclude the osmotic. According to either of these conceptions, the energy for the absorption of water would be the absorbed radiant energy necessary for vaporization and for photosynthesis in the aerial parts of the plant. Both the imbibitional and the osmotic explanations of water absorption and transport fail to explain satisfactorily exudation pressure and also the fact that an oxygen supply is necessary for normal root activity. Similarly guttation is explained with difficulty on this basis. In order to explain the transport of water under these conditions various hypotheses have been suggested. PRIESTLEY and NORTH (14) believed the endodermis to be the functional absorbing surface of the root; they assign to it the rôle of a semipermeable membrane, separating the intercellular cortical fluids from those of the xylem vessels. PFEFFER formulated a hypothesis based on differences in the osmotic pressure of the plasma membrane in different parts of the cell to explain the movement of water from a solution of high concentration to a low one. Although he later abandoned this as being unlikely, LEPESCHKIN (8) used it to explain the exudation of water by sporangiophores and by hydathodes.

More recently workers coming from the field of animal to general physiology have considered that osmotic work must be done. The actual mechanism involved is not yet clear. A secretory action may take place in the endodermis or in other tissues; but since the mechanism of glandular activity is still imperfectly understood, such a hypothesis is not very clarifying. Similarly electro-endosmosis is a possible explanation, but until more facts substantiating this have been found such an assumption is of little value.

It is apparent that irrespective of any mechanism involved, osmotic work must be done. Any system of cells along the line of water absorption and transport must maintain a gradient of increasing osmotic pressure from root hair to leaves. This will be seen to be true whether the osmotic or the imbibitional mechanism be assumed, since in any active cell there will be an equilibrium between the forces of the colloids present in the cell walls and the osmotic activities of the solutes of the cell sap. Since the actual concentration gradient observed does not conform to this requirement, and since positive exudation pressures are not thus explicable, these theories are incomplete.

If work is accomplished, the necessary energy must be furnished directly or indirectly by respiration processes and can be detected and estimated by them. The present study was undertaken with this in view.

The results obtained from a simultaneous measurement of water absorption and root respiration, as measured by the evolution of carbon dioxide

computed from the changes of pH in rain water, show a close correlation between the two processes. Even in the two experiments where the plants were exposed to light this relation was evident. When transpiration was increased by changing the air over the tops from a high to a low humidity, the rate of absorption increased and was accompanied or closely followed by a rise in the rate of carbon dioxide evolution.

When the evolution of carbon dioxide was followed in aerated distilled water a correlation similar to that observed in rain water appeared. In general this correlation was somewhat more perfect than that observed in rain water.

It is to be noted that, assuming the most intimate relation between root respiration and the absorption of water, a perfect correspondence between the rates would not be expected in experiments such as those here reported. This arises from the fact that some of the respiratory carbon dioxide is carried up in the transpiration stream and hence is not evolved (CERIGHELLI 2, 3, 4). This may be considered as the explanation for the low rate of respiration accompanying high absorption at such points as the third hour of figure 4; and also for the failure, in cases like that shown in figure 6, of the respirational curve to follow the rise of absorption. Since the curves of carbon dioxide evolution and of oxygen consumption are parallel, any lack of agreement between the former phenomenon and the absorption of water is without significance in these experiments. This study gives no evidence of the transport of carbon dioxide or of any effects upon the evolution of the substance due to the photosynthetic activity of the leaves.

Computations from the results of experiments 1-6, in which the root systems were observed in rain water, show great variability and an average of 0.08 cc. (S.T.P.) carbon dioxide evolved per cubic centimeter of water absorbed. A similar average for plants observed with the root systems in distilled water is 2.6 cc. This difference is doubtless due to the buffering substances present in rain water and the latter value is to be regarded as the more accurate.

The consumption of oxygen offers a more reliable measurement of respirational activity, and in experiment 8 the absorption of 1 cc. of water required 3.9 cc. of oxygen and evolved 2.6 cc. of carbon dioxide, giving a respiratory quotient of 0.67. The average consumption of oxygen per cubic centimeter of water absorbed from distilled water is 2.4 cc. If we accept the value of 5.047 small calories per cubic centimeter of carbon dioxide, we have in experiment 8 an expenditure of approximately 13.1 calories per cubic centimeter absorption. If the consumption of oxygen be considered a more accurate measure of work, the result is approximately 19.7 calories.

Similar computations for plants observed with the root systems in Knop's solution give an oxygen consumption of 4.7 cc. per cubic centimeter

absorption. The average consumption of oxygen per volume absorption in distilled water is but 52 per cent. of that in Knop's solution. Computed on the basis of the average values obtained in distilled water, the oxygen consumption of the root systems in Knop's solution is 193 per cent. Comparing the calorific values per cubic centimeter absorption, we have 13 calories for distilled water and 23.7 for Knop's solution. Since the osmotic pressure of the Knop's solution used was 1.75 atmospheres, it appears that the energy required for the absorption of distilled water is equivalent to that expended against an osmotic pressure of $\frac{23.7 - 13}{1.75 \times 13}$, or 2.12 atmospheres.

In view of the fact that the resistance to flow through capillary tubes is a linear function of the rate, it might be expected that the energy requirement would vary directly with the rate of absorption. Computations show that the reverse relation holds in the present study, doubtless because the basal rate for the tissues comprises an increasing proportion of the whole, since at the lower absorption rates the time interval is increased.

It is to be noted that the respiration as here recorded was not anaerobic or modified by deficient aeration. This is obvious from the fact that the fluid around the roots was replaced at hourly intervals with aerated medium, and that the amount of dissolved oxygen contained in this was 1.4 cc. The observed absorption was never more than 0.5 cc. and usually was much less than this amount.

For corn seedlings in liquid cultures the correlation between the volume absorption and the respiration of the root indicates the expenditure of energy by these organs in the process of absorption. Further and more exact determinations of the energy values with plants under strictly controlled conditions should throw much light on the nature of the mechanism involved.

Summary

1. A method was developed for obtaining simultaneous measurements of root respiration and volume absorption of the roots.
2. The evolution of carbon dioxide was measured by change in the pH of the medium in the absence of buffers, and the absorption of oxygen was measured by the micro-Winkler method.
3. A correlation between the evolution of carbon dioxide, the absorption of oxygen, and the volume absorption of the root system of corn seedlings is shown to occur in rain water, distilled water, and in Knop's solution.
4. The energy as calculated from the respiratory exchange is 93 per cent. greater in Knop's solution with an osmotic pressure of 1.75 atmospheres than in water.
5. The absorption of water by corn roots is accompanied by the expenditure of energy.

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AUSTIN, TEXAS

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